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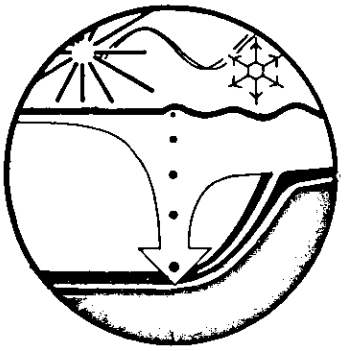
"SEDIMENTATION IM EUROPÄISCHEN NORDMEER"



Nr. 17

The influence of zooplankton on sedimentation in the Norwegian Sea

NOJI, T.

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The influence of zooplankton on sedimentation in the Norwegian Sea

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This is dedicated to my parents and Carola.

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1. Introduction

Sedimentation in the pelagial has become a topic of intense interest in the last decade (e.g. Bishop *et al.* 1980, Smetacek 1980, Honjo 1982, Deuser 1986). Studies have indisputably documented the spatiotemporal variability in vertical flux (e.g. Deuser *et al.* 1981, Lampitt 1985, Bishop *et al.* 1986, Honjo *et al.* 1988, Wakeham and Canuel 1988). Variability has primarily been explained through physico-biological models, e.g. "new vs. regenerated production" (Dugdale and Goering 1967, Eppley and Peterson 1979), and grazing of phytoplankton stocks. However, it is now evident that sedimentation is the result of a complex network of interactive biological responses to the changing physical environment. Simple models cannot satisfactorily explain the quantitative and qualitative character of sedimenting particles (Bodungen 1989).

One of the least understood influences on sedimentation is the stock of metazooplankton. Until recently the major roles of zooplankton with respect to vertical flux of particles have been considered to be grazing and fecal pellet production. Indeed, grazing can decisively hinder the accumulation and bulk sedimentation of phytoplankton stocks. In contrast, the production of fast-sinking fecal pellets can enhance local sedimentation. However, the properties of the vehicles of transport have now been recognized as being vital for the characterization of vertical flux; morphology, composition and size of these vehicles affect their sedimentation through the water column. The stock of metazooplankton can strongly influence sedimentation via their regulation of these large particles. This may occur via the production of aggregates including fecal material (e.g. Pilskaln and Honjo 1987, Bodungen 1986) and zooplanktonic corporal parts (e.g. Honjo *et al.* 1988) or the modification of existing large fast-sinking particles through processes such as disaggregation (Karl *et al.* 1988, Suess 1988, Lampitt *et al.* in press).

The aim of this study is twofold - to identify the metazooplankton-regulated processes which influence sedimentation and to assess the influence of metazooplankton stocks on sedimentation on the Vøring Plateau in the Norwegian Sea. The first endeavor is approached largely with the aid of experimental findings. The central theme of most experimentation was the production and destruction of aggregates, especially fecal pellets. The second is based on the application of these findings and reports in the literature to field data collected during expeditions on the Vøring Plateau and recorded continuously with sediment traps over a period of nearly three years. Seasonal patterns in pelagic biology and sedimentation are described. Further, variations in these patterns are specifically discussed in terms of the distribution of zooplankton stocks and their specific means of influence on vertical flux.

The study was conducted within the Sonderforschungsbereich (special research project) 313 - "Sedimentation in the European Nordic Seas" at the University of Kiel, Federal Republic of Germany. The author was a member of the subproject "Flux of Particles from the Pelagial".

2. Material and Methods

Material and methods employed during this study are described here in three parts: Investigation area and expeditions (section 2.1), Field investigations (section 2.2) and Experimental studies (section 2.3).

2.1. Investigation area and expeditions

This investigation was conducted from November 1985 to February 1989 on and within the vicinity of Vøring Plateau (67° 44'N, 05° 55'E) in the eastern Norwegian Sea (Figs. 1 and 2).

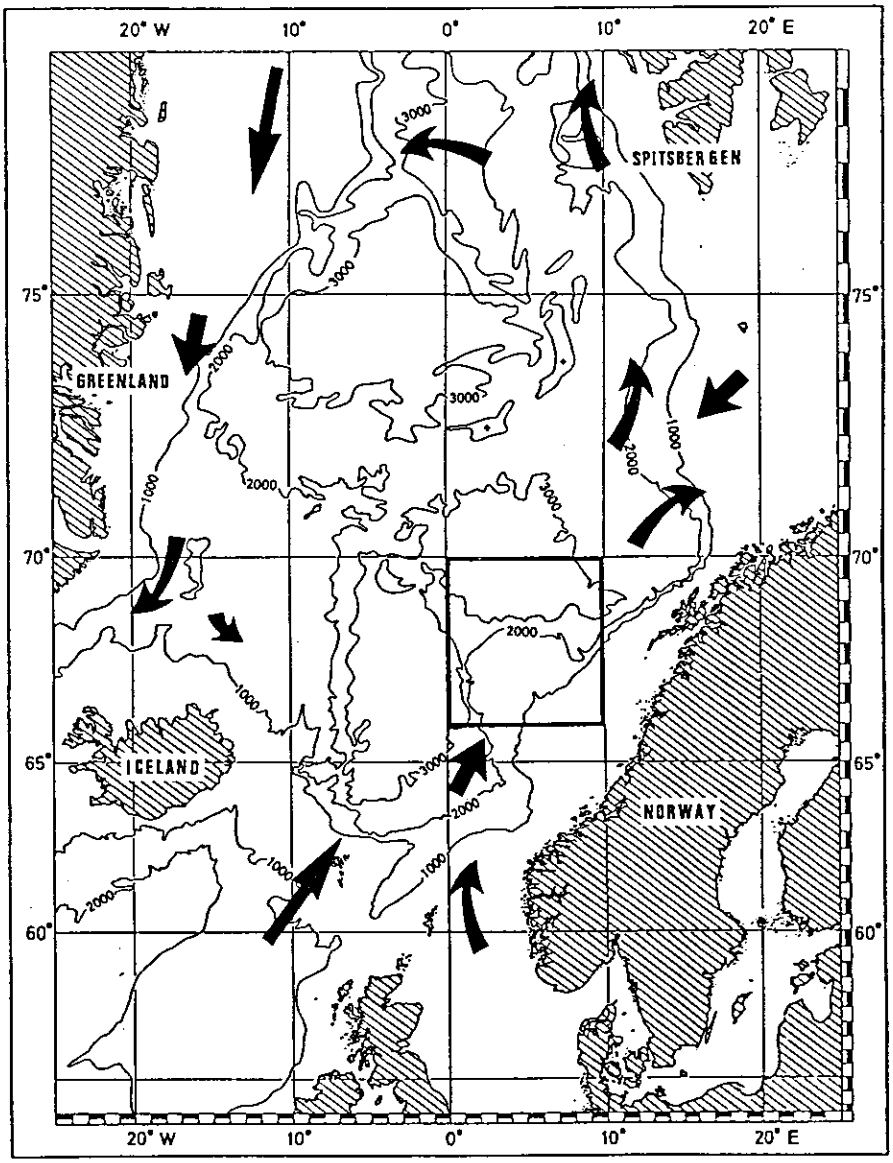


Figure 1. Location of investigation area, the Vøring Plateau (in box) in the Norwegian Sea. Major surface currents are indicated by arrows. (map courtesy of J. Rumohr)

Field data and samples for later analysis were collected with three German research vessels (R.S. "Poseidon", R.S. "Meteor" and R.S. "Valdivia") at different seasons (Fig. 3) during the following 8 expeditions:

POS 128/1 (7 - 23 May 1986)
POS 128/2 (25 May - 8 June 1986)*
MET 2/1 (19 June - 2 July 1986)*
POS 137 (3 - 20 February 1987)*
VAL 61 (25 July - 23 August 1987)
POS 142/2 (1 - 12 November 1987)*
MET 7/3 (24 July - 14 August 1988)
MET 7/4 (17 August - 3 September 1988)*.

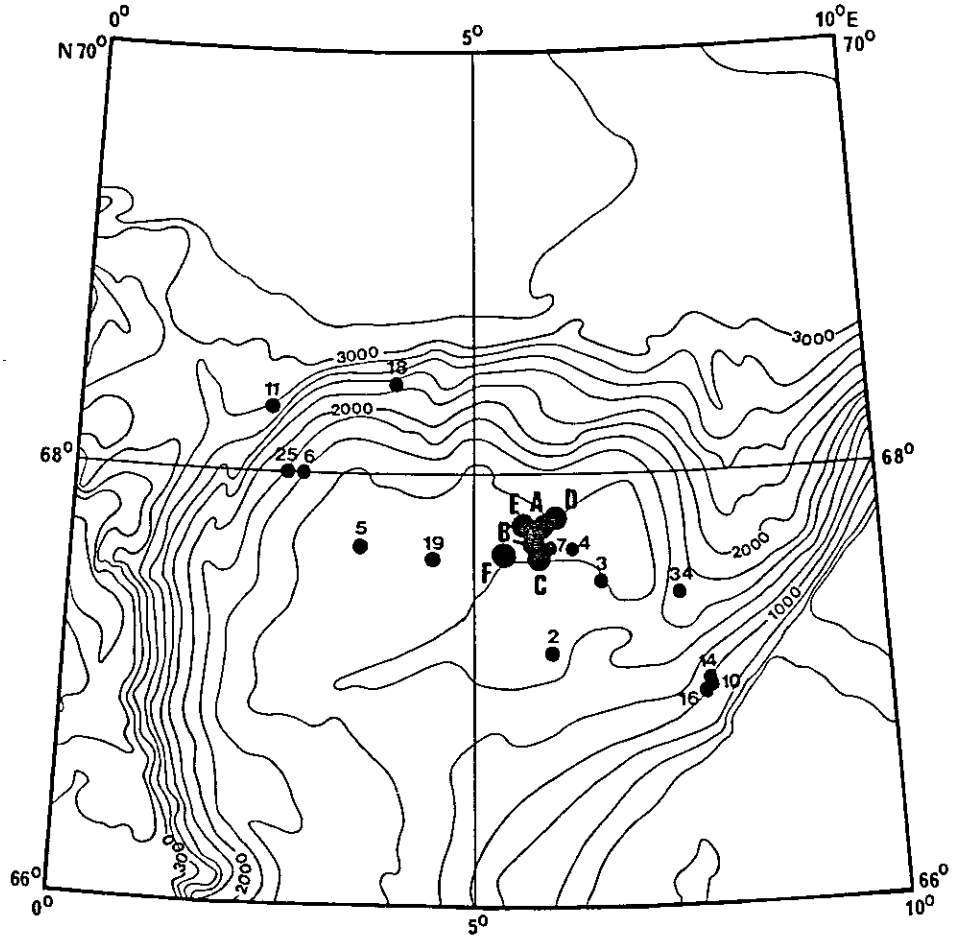


Figure 2. Vøring Plateau in the Norwegian Sea. Stations at which metazooplankton were collected are indicated; A=stations 63 and 166; B=stations 65, 92, 478 and 1191; C=stations 175 and 186; D=stations 489, 1155, 1157, 1158, and 1159; E=stations 86, 459, 477 and 531; F=stations 469, 474 and 475; 2=sta.168, 3=sta.247, 4=sta.259, 5=sta.268, 6=sta.276, 7=sta.282, 10=sta.69, 11=sta.82, 14=sta.96, 16=sta.176, 18=sta.187, 19=sta.4, 25=sta.1196, 33=sta.534. (see Appendix 1 for details concerning stations)

* Personal participation

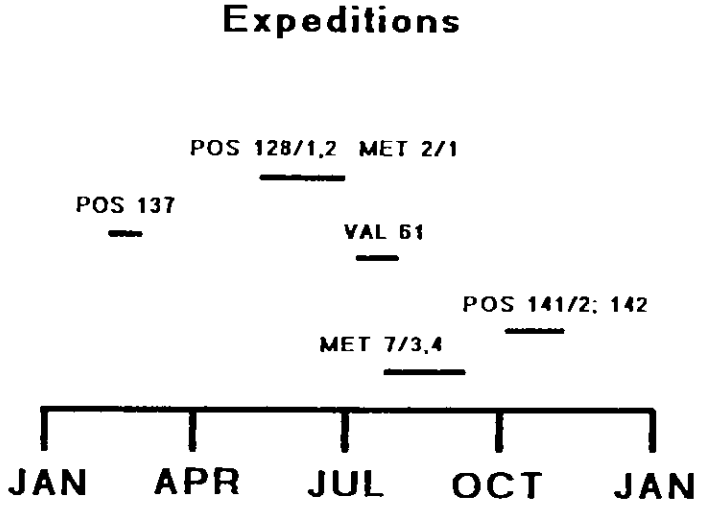


Figure 3. Seasonal distribution of expeditions on the Vøring Plateau during this investigation.

2.2. Field investigations

Material and methods for collecting field data are divided into six sections: (1) *Hydrography and nutrients*, (2) *Suspended particles* (not including phytoplankton and zooplankton), (3) *Phytoplankton and primary production*, (4) *Metazooplankton and fecal pellets* and (5) *Sedimentation*. Sampling was for the entire water column or to a depth well below the euphotic zone (usually 200 m) for all expeditions. Only data on hydrography and metazooplankton were collected during VAL 61.

With the exceptions of primary production measurements (conducted by B. von Bodungen), microscopy of sediment trap material (conducted by U. Bathmann) and microscopy of metazooplankton (conducted by the author), the data were jointly collected by the planktologists of the subproject A1, "Flux of Particles from the Pelagial", of the SFB 313.

Hydrography and nutrients

Hydrographical profiles were recorded continuously with depth. Nutrients were measured from hydrocast samples obtained using 10 or 12-l Niskin bottles from up to 15 discrete depths.

The following parameters were analyzed:

- -temperature (°C) and salinity (10^{-3} S) using a CTD-probe (Meerestechnik, Trappenkamp, F.R.G)
- -nitrite, nitrate, ammonium, phosphate and silicate according to Graßhoff (1976).

Suspended particles

Water for analyses on suspended particulate matter was collected as for nutrients and filtered using precombusted and preweighed (except for chlorophyll *a* analyses) Whatmann GF/F glass fibre filters.

The following parameters were measured:

- -seston (Lenz 1971)
- -carbonate (difference in weight after acidification of material on filters over fuming hydrochloric acid and subsequent washing with destilled water)
- -particulate organic carbon (POC) and particulate organic nitrogen (PON) measured with a Perkin-Elmer 240 C CHN analyzer
- -chlorophyll *a* (chl. *a*; modified after Jeffrey and Humphrey 1975).

Phytoplankton and primary production

Water was collected as for nutrient analyses. Subsamples for microscopy (using a Zeiss inverted microscope) of phytoplankton were preserved with buffered (with borax) formaldehyde to an end concentration of 0.4 %.

The following parameters were analyzed:

- -phytoplankton composition (Utermöhl 1931, 1958) and phytoplankton carbon content (modified after Edler 1979)
- -primary production at simulated *in situ* light intensities (described in Peinert *et al.* 1987) for the 100, 50, 30, 20, 10, 5, 1 and 0.1 % light depths.

Metazooplankton and fecal pellets

Metazooplankton was collected in vertical hauls using a multiple opening and closing "multinet" (Hydrobios, Kiel, F.R.G.; opening of 0.25 m^2) fitted with 64 or 200-µm mesh sized nets. 50 and 300-µm mesh sized conical Apstein nets (opening diameter of 17 cm) were occasionally employed. (See Appendix 1 for date, time, site, depth and net-type for metazooplankton sampling.) Hauling speeds of 0.5 $m \cdot s^{-1}$ were used for 64-µm and 50-µm mesh sized nets and 0.7 $m \cdot s^{-1}$ for 200 and 300-µm mesh sized nets. Collected material was immediately preserved with borax-buffered formaldehyde (4 % end concentration) and stored in bottles for later microscopical analysis. Identification and counting with a dissecting microscope (Wild-M5 or Wild-M8) were conducted according to the recommendations of Cassie (1979). Genus, species, length, and for copepods, sex and developmental stage were recorded; identification only to the family level was made for some less common forms.

30-l Niskin bottles were used to regularly collect water for concentrating (with 20-µm mesh sized sieves) fecal pellets during POS 128/2 and MET 2/1; during other expeditions vertical hauls using a 20-µm mesh sized conical Apstein net (opening diameter of 17 cm) were conducted to collect pellets for selected depth strata.

The following parameters were analyzed:

- -metazooplankton carbon content of individual plankters (applying conversion factors and allometric equations from the literature (see Appendix 2 for summary of conversions) as well as from carbon analyses using a CHN analyzer (Perkin-Elmer 240 C))
- -fecal pellet carbon content (Bathmann *et al.* 1987).

In addition, selected fecal pellets were regularly dehydrated for scanning electron microscopy (SEM; Cambridge-S150) using an alcohol dilution series according to Bathmann and Liebezeit (1986) or critical point drying. A Balzer-SCD 004 sputterer was employed for coating pellets with gold-palladium.

Sedimentation

Sedimenting particles were collected using moored and free-drifting funnel-shaped Kiel sediment traps with collecting areas of 0.41, 0.13 and 0.03 m^2 (see Zeitzschel *et al.* 1978 for details of trap design). Moored deployments on the central Vøring Plateau (67° 44'N, 05° 55'E; 1250 m water column depth) consisted of traps in up to four depths. These moorings were deployed for periods of five days to about one year and fitted with 1 to 21 collecting cups; collecting interval was approx. 2 to 4 weeks for a deployment of one year. Drifting arrays deployed for one to

two days were usually within 50 nautical miles of the moored deployment and included one or two traps at different depths. See Appendix 3 for a summary of deployments, collection times and depths.

The *in situ* preservative was 1 ml mercury chloride (saturated solution; 70 g $HgCl_2$/l) per collecting cup or 0.5 ml chloroform per cup (see Appendix 3). Upon recovery, sedimented material was stored at approx. 4°C until removal of larger metazooplankton (> approx. 2 mm) with a tweezer. Collected material was separated into aliquots in the laboratory.

For samples preserved with chloroform, analyzed pigments were measured as chlorophyll *a* - equivalents (chl. *a* - equiv. = chl. *a* + pheopigments), since chloroform promotes the breakdown of chl. *a* to pheopigment (Hendrikson 1975). Otherwise aliquots were analyzed for the same parameters as for suspended particles.

2.3. Experimental studies

Experiments involving zooplankton grazing, fecal pellet identification and production and aggregate formation and degradation were conducted during expeditions (Shipboard experiments - section 2.3.1) as well as in the laboratory in Kiel and in Tromsø and Bergen, Norway (Land-based laboratory experiments - section 2.3.2).

2.3.1. Shipboard experiments

Experimentation during expeditions is presented in three categories: (1) ***Zooplankton feeding behavior and fecal material identification***, (2) ***Copepod grazing potential*** and (3) ***Copepod-pteropod interactions.***

Zooplankton feeding behavior and fecal material identification

Numerous incubations were conducted to observe the feeding behavior of selected zooplankters and to collect and identify their fecal products. Zooplankton was collected using a multinet (with 200-µm mesh) or a large conical net (113 cm in diameter; 500-µm mesh) fitted with closed cod-ends. Collections were immediately placed at *in situ* temperatures; animals were generally used for experimentation within one day of capture. Care was taken to avoid injury to the animals during selection by pipetting. Incubations using filtered seawater were conducted for one to several days in darkness at ambient temperatures either in 0.5-l or 1.0-l plastic jars or in specially designed plexiglass fecal pellet collectors of 3 or 6 l in volume (Fig. 4).

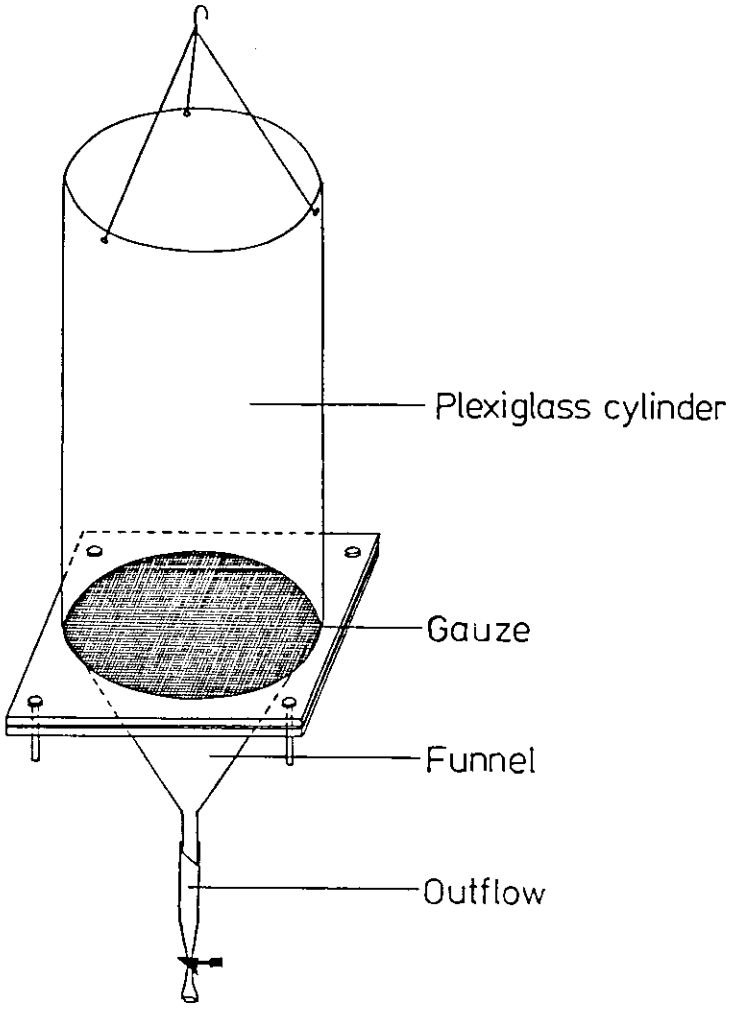


Figure 4. Fecal pellet collector. Volume of collectors used in this study was 6 l. A removable PVC plate with gauze permits rapid changes of mesh size.

Animals were briefly (less than 3 minutes) exposed to light every 6 to 10 h to note behavior, e.g. swimming activity or distribution. In most cases zooplankton was offered a supplemental food source of plankton from illuminated 1000-l tanks containing natural seawater or enrichments (using a 20-µm sieve) of natural phytoplankton. Fecal material was collected from fecal pellet collectors by opening the stop. From plastic jars fecal material was collected by gentle pipetting. Material was preserved with borax-buffered formaldehyde (end concentration 4 %). A summary of these incubations is presented in Table 1.

Table 1. Experiments on zooplankton feeding behavior and fecal material identification

[1]Zooplankton (ind. per incubation)	Incubation volume (l)	Date	Expedition
Calanus finmarchicus (20-25)	3	1 June 86	POS 128/2
		4 June 86	POS 128/2
[2]*C. finmarchicus* (approx. 10)	1	1 Nov. 87	POS 142/2
		6 Nov. 87	POS 142/2
Calanus hyperboreus (25)	6	31 May 86	POS 128/2
Euchaeta norvegica (6) + *C. finmarchicus* (27)	6	4 June 86	POS 128/2
[3]*E. norvegica* (4) + [2]*C. finmarchicus* (20)	1	1 Nov. 87	POS 142/2
[3]*E. norvegica* (6-7) + [2]*C. finmarchicus* (30)	1	1 Nov. 87	POS 142/2
		6 Nov. 87	POS 142/2
[3]*E. norvegica* (3) + [2]*C. finmarchicus* (40)	1	1 Nov. 87	POS 142/2
mixed copepods (approx. 50) > 500 µm	6	24 June 86	MET 2/1
		27 June 86	MET 2/1
[3]mixed copepods (8) + [2]*C. finmarchicus* (25)	1	1 Nov. 87	POS 142/2
euphausiids-*Thysanoessa* sp.(2-3)	0.5	1 Nov. 87	POS 142/2
		6 Nov. 87	POS 142/2
[4]ostracods-*Conchoecia obtusata* (6) + [2]*C. finmarchicus* (10)	0.5	6 Nov. 87	POS 142/2

[1]Adult female copepods from surface waters unless otherwise noted
[2]Overwintering C5 copepodites from depths below 500 m
[3]Copepods (C5-6) from depths below 250 m; all or mostly carnivores
[4]From depths below 500 m

Copepod grazing potential

In order to study the grazing potential of copepods in winter, incubations with surface and deep-water copepods were conducted during the expedition POS 137 on 19 - 20 February 1987. Zooplankton was collected using an Apstein net (opening diameter of 17 cm) with 300-µm mesh. The seawater medium was supplemented with natural phytoplankton obtained from illuminated tanks. Phytoplankton concentration (cells and chl. *a* per liter) before and after incubation as well as fecal pellets produced were determined. Conducted chiefly by U. Bathmann of the Sonderforschungsbereich 313, details of this experiment are described in Bathmann *et al.* (in press).

Copepod-pteropod interactions

During the expedition MET 7/4 in August 1988 two experiments addressing the feeding of the dominant surface copepod *Calanus finmarchicus* and the pteropod *Limacina retroversa* were conducted. The purpose of these experiments was to study aggregate formation by feeding pteropods and the effect of copepods on this process and to compare the ability of the two species to feed on small particles (< 2 µm in diameter). In addition, sinking velocities of aggregates and *Calanus finmarchicus* fecal pellets were measured.

Zooplankton was collected from surface waters using a 500-µm mesh-sized conical net (opening diameter of 113 cm) fitted with a removable 3-l cod-end. After collection zooplankton was immediately sorted in a temperature-regulated room at *in situ* temperature and held separately in 5-l aquariums. Behavior was regularly noted. Aggregates were gently siphoned from the floor of the aquariums and preserved with borax-buffered formaldehyde (end concentration of 0.4%) for microscopy.

Aggregate formation

In order to study the formation of aggregates by *Limacina retroversa* (> 1.0 mm in length) and the effect of *Calanus finmarchicus* (CV copepodites) on aggregate formation, 24-h incubations using 1.2-l bottles on a grazing wheel (1 - 2 r.p.m.) were conducted. In phytoplankton-enriched natural seawater (2.94 µg Chl. *a* per liter) parallel incubations of 5 individuals of *L. retroversa*, 10 *L. retroversa*, 5 *L. retroversa* + 5 *C. finmarchicus* and controls without animals were conducted at 4 ± 1°C. At the termination of the experiment material was fixed with borax-buffered formaldehyde to an end concentration of 0.4 %. Using a Wild M-8 dissecting microscope, aggregates > 400 µm in diameter were counted for entire samples.

Feeding on small particles

The aim of this experiment was to compare the clearance rates of *L. retroversa* with those of *C. finmarchicus* on particles < 2 µm in diameter. Natural seawater was filtered with 2-µm membrane filters. Prior to incubation two samples for microscopy and three for Chl.*a* analyses were taken from the medium. Incubations (same procedure as for *aggregate formation study* above) with 5 *C. finmarchicus*, 10 *C. finmarchicus*, 5 *L. retroversa*, 10 *L. retroversa* or without animals were conducted in parallel at 4 ± 1°C. After 22 h 250-ml subsamples for microscopy of particles (1 - 2 µm in diameter) were collected and preserved with borax-buffered formaldehyde (end concentration of 0.4 %); 890 ml were filtered for chl. *a* analyses. Shipboard experimentation was conducted with U. Bathmann. The author microscoped samples.

Sedimentation velocities

The sinking velocities of 10 newly produced, unpreserved aggregates formed by *Limacina retroversa* (> 1.0 mm in length) in aquariums as well as 15 newly produced fecal pellets from *Calanus finmarchicus* were measured within a 5-l beaker with a diameter and height of 15 and 30 cm, respectively. The seawater medium in the aquariums and in the beaker was the same; salinity and temperature gradients within the beaker were presumably avoided. Sinking velocities were measured over distances of 20 cm (starting 5 cm below the surface) or for a maximum period of 5 minutes.

2.3.2. Land-based laboratory investigations

Three major series of land-based laboratory experiments were conducted: (1) *Production and aging of fecal pellets* from July to August 1987 in Tromsø, Norway, (2) *Coprophagy studies* from October 1987 to February 1988 in Kiel and (3) *Coprorhexy studies* in June 1988 in Bergen, Norway.

Production and aging of fecal pellets

From 1 July to 16 August 1987 experiments on copepod fecal pellets were conducted in Tromsø, Norway at the Institute for Biology and Geology (now the Norwegian College of Fishery Science) at the University of Tromsø in Norway (Fig. 5). The purpose of these experiments was to study fecal pellet production in relation to food supply and degradation of fecal pellets in relation to age.

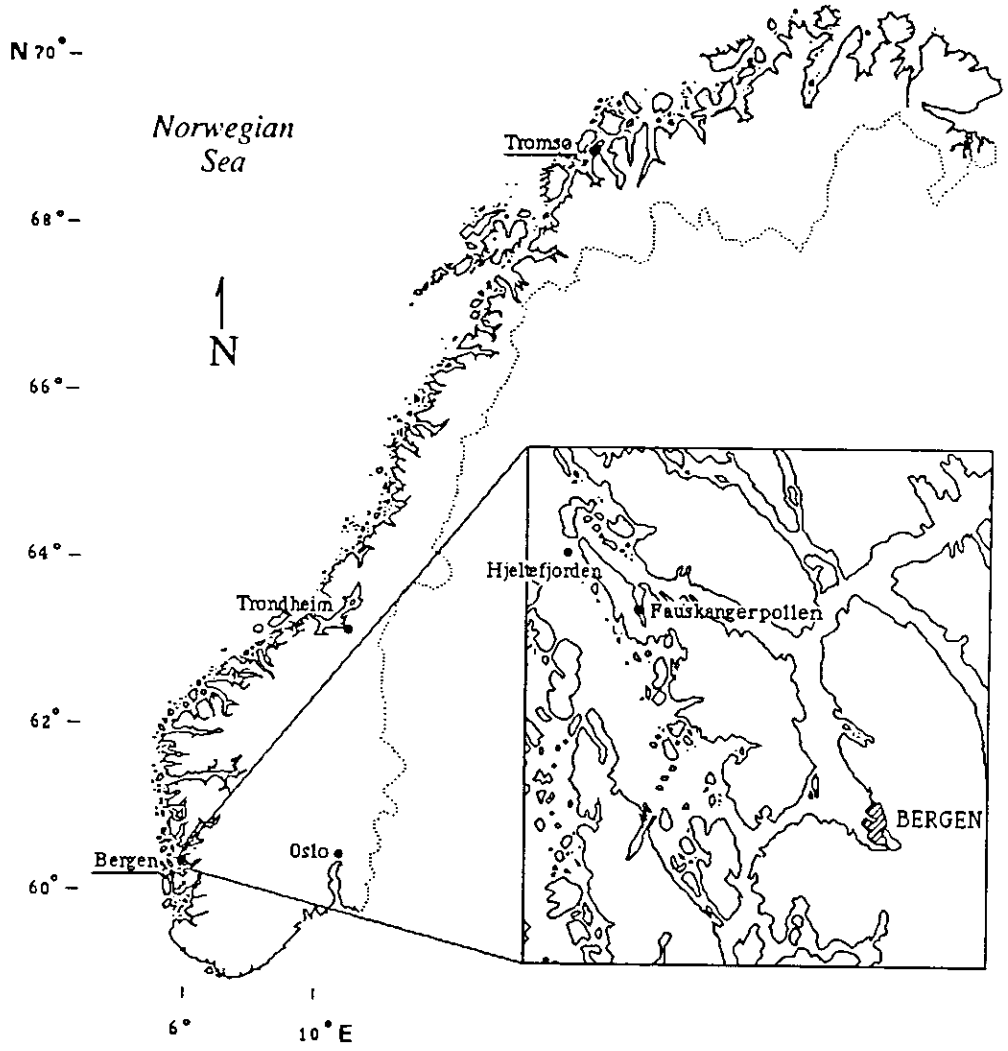


Figure 5. Map of Norway showing the location of Tromsø and Bergen (with adjacent fjord area) where fecal pellet production and coprorhexy studies were conducted. (from Noji *et al.* submitted)

Using the research vessels "Hyas" and "Ottar" of the University of Tromsø, zooplankton was collected from Balsfjord (maximum depth of 195 m) with WP2 nets (200 and 500-µm mesh; opening diameter of 64 cm). Zooplankton was placed in large (35 - 50 l) aerated tanks in temperature-regulated rooms (*in situ* temperatures of 1 ± 0.5°C). Animals were fed daily with natural phytoplankton, and water in the tanks was renewed every two days.

Fecal pellet production studies

Copepods for experimentation were placed in filtered seawater (using Whatmann GF/F glass fibre filters) for at least 3 h to allow gut clearance. Adult female *Calanus finmarchicus* copepods were then sorted and 36 to 100 individuals per bottle were placed in 1.2-l glass bottles filled with natural seawater containing phytoplankton which had been concentrated from natural seawater using a 20-µm sieve. 3 to 7 parallel incubations were conducted per series. Two bottles filled only with phytoplankton served as controls. In two cases 30 *Calanus hyperboreus* adult females and 16 euphausiid (*Thysanoessa* sp.) juveniles (2 - 3 cm in body length; approx. one year old) were incubated. Bottles were incubated in the dark at *in situ* temperatures of 1 ± 0.5°C for 24 h on a grazing wheel (1 - 2 r.p.m.). At the end of incubation fecal pellets were pipetted into filtered seawater. Pipetting was repeated until pellets were free of detritus. The pellets in filtered seawater were split volumetrically into aliquots and filtered onto preweighed, precombusted GF/C filters for chl. *a*, POC and PON analyses. Sinking velocities of selected fecal pellets from some experiments were measured, as described above. Details of experiments are summarized below (Table 2).

Table 2. Experiments on fecal pellet production in relation to food concentration

Date	Copepod species	Chl.a (µg/l)	Number of bottles
8 July	*C. finmarchicus*	1.11	3
	"	2.41	3
11 July	*C. finmarchicus*	1.32	7
	"	3.18	7
15 July	*C. finmarchicus*	0.99	7
	"	2.46	7
17 July	*C. finmarchicus*	1.56	7
	"	4.21	7
21 July	*C. finmarchicus*	1.31	6
	"	3.22	6
	C. hyperboreus	1.31	1
	T. sp.	3.22	1

Aging of fecal pellets

Fecal pellets (< 24-h old) from tanks containing almost exclusively adult females and copepodites of *Calanus finmarchicus* were collected and placed in filtered seawater. Pellets were collected and rinsed as described above. Pellets in filtered seawater were split volumetrically into 5 aliquots. From one aliquot selected fecal pellets were collected to determine sinking velocities as described above; the rest of the aliquot was split for POC, PON, chl. *a* and microscopical analyses. The remaining four aliquots were placed in glass dishes, covered with aluminum foil and placed in the dark at 1 ± 0.5°C to be split for the same analyses after a predetermined period of time.

This experiment was conducted three times. Sampling intervals were 2, 3 and 5 days.

Coprophagy study

From October 1987 to February 1988 experiments (reported in Lampitt *et al.* in press) designed to address the effectiveness of coprophagy were conducted with R. Lampitt, at that time guest scientist at the SFB 313. Incubation experiments with *Centropages hamatus* copepods and fecal pellets were analyzed microscopically and by a ^{14}C-tracer technique. ^{14}C-distribution in four fractions - fecal pellets, non-fecal detritus, dissolved matter and copepod bodies - was measured by scintillation counting. For two series of incubations the dissolved inorganic and dissolved organic carbon (DIC and DOC) fractions were also measured.

Zooplankton collection and handling

Zooplankton was collected using Apstein nets with 200-µm mesh and an opening of 17 cm. Animals were held in 5-l glass beakers at ambient temperatures (10 ± 1°C) and fed daily with a culture of the diatom *Skeletonema costatum*. Water was renewed about every two days. Zooplankton was checked vigorously for contamination by parasites. Individuals were selected by gentle pipetting for incubations.

^{14}C-labelling of fecal pellets

500 ml of the diatom culture were incubated with 2 or 10 mCi ^{14}C-sodium bicarbonate for 38 to 48 h. Cells were then repeatedly washed using a 20-µm sieve and suspended in 500 ml seawater; activity of the washed culture was 0.2 to 1.4 x 10^6 CPM/ml*. The labelled cells were added to a 4-l

* "counts per minute" per ml

beaker filled with seawater and adult copepods dominated by *C. hamatus*. The beaker was placed in the dark at 10 ± 1°C. After 14 h fecal pellets were siphoned from the bottom of the beaker and rinsed by pipetting into filtered seawater. The last step was conducted 5 times. Clean pellets were stored at 2°C until the initiation of incubation experiments two days later.

Coprophagy incubations

Adult female *Centropages hamatus* copepods were placed in filtered seawater for at least 2 h to allow gut clearance. 10 to 25 individuals were pipetted into 300-ml bottles. Bottles without copepods served as controls. Labelled fecal pellets were again washed as described above and a known number (20 - 300) of fecal pellets were then added to each bottle. Bottles were incubated as described above in *Fecal pellet production studies* at 10 ± 1°C in a dim 12 hour light/dark cycle (Fig. 6).

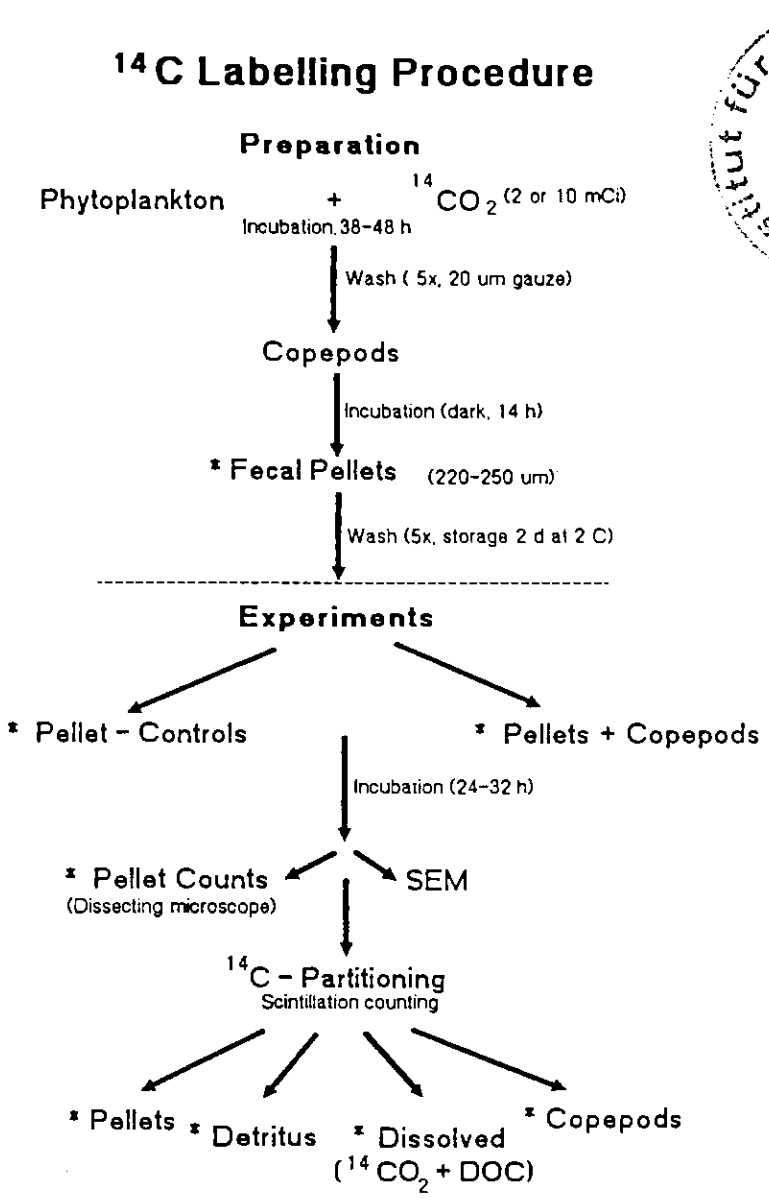


Figure 6. Procedure for labelling of fecal pellets with ^{14}C and for incubation experiments. "*" indicates that particles are radioactively labelled.

After about 28 h bottles were removed. Intact fecal pellets were counted under the dissecting microscope and pipetted into 25-ml scintillation vials. (In one series of incubations fecal pellets were fragmented by homogenization with glass beads and then added.) Vials were gravimetrically filled to 5 ml with seawater and frozen at -20°C. Copepods were placed in filtered seawater for 2 h to allow gut clearance, removed and frozen in 25-ml scintillation vials. The seawater medium used for incubation was filtered (0.45-µm membrane filter); 5 ml of the filtrate were frozen in a 6.5-ml scintillation vial. Water used for gut clearance was then filtered with the same filter, which was frozen in a 6.5-ml scintillation vial. The filtrate fraction is defined here as dissolved matter, and material retained on the filter as the detrital fraction. Frozen material was later defrosted and 19.5 and 6.0 ml scintillation cocktail ("Lumagel SB") were added to the 25 and 6.5-ml scintillation vials, respectively. Scintillation counting was performed using a Beckmann LS100C and a Packard Minaxi Tri-Carb 4000.

In two incubations series, DIC was measured by acidification of a 10-ml sample and extraction of gaseous $^{14}CO_2$ by 400 µl ethanol amine.

For incubations using unlabelled fecal pellets, *C. hamatus* and pellets were collected and prepared as described above. Phytoplankton used for fecal pellet production, however, was not labelled with ^{14}C.

Scanning electron microscopy of fecal pellets was regularly conducted.

Coprorhexy study

From 10 to 19 June 1988 incubation experiments designed to study the fragmentation of fecal material (coprorhexy) were conducted in Herdla (30 km northwest of Bergen), Norway (reported in Noji *et al.* submitted) during the workshop, "The role of zooplankton grazing and defecation in pelagic carbon and nitrogen cycles", sponsored by PROMARE (Norwegian Program for Marine Arctic Ecology). F. Norrbin (Norwegian College of Fishery Science in Tromsø) and K. Estep (Institute of Marine Research in Bergen) aided in sorting of zooplankton and image-analysis, respectively. I. Martinussen (Department of Microbiology and Plant Physiology at the University of Bergen) conducted analyses for protease activity.

Zooplankton collection and handling

Copepods for experimentation were collected from surface waters of two nearly adjacent fjords (60° 30'N, 05° 00'E), Fauskangerpollen (maximum depth 190 m) and Hjeltefjorden (maximum depth 280 m), about 30 km northwest of Bergen (Fig. 5) using WP-2 nets (opening diameter of 64 cm; mesh sizes of 200 and 500 µm). Nets were fitted with 10-l cod-ends containing removable plastic bags designed to minimize injury to animals. Subsamples of the two size fractions were transferred separately to 5-l glass jars and placed in water baths at ambient surface temperature (approx. 12°C). The zooplankters were fed daily with a mixture of natural and cultured (*Chroomonas* sp. and *Chaetoceros* spp.) phytoplankton. Cultures were provided by J. Nejstgaard. Fecal pellets were collected daily for experimentation. Fresh fecal pellets were collected twice for measurements of aerobic and anaerobic bacterial protease activity.

Coprorhexy experiments

Prior to each experiment zooplankton was sorted and placed in filtered seawater (using GF/F glass fibre filters) for at least 3 h to allow gut clearance. Fecal pellets (< 24-h old) were carefully cleaned through repeated pipetting into filtered seawater. Following gut clearance copepods were pipetted into 300-ml polyethylene bottles filled with filtered seawater. The clean fecal pellets in filtered seawater were split volumetrically and aliquots added to the bottles. Bubble-free bottles were allowed to float for 21 h (early afternoon to late morning) in a shaded area at a pier. The gentle wave action presumably held particles in suspension. At the end of incubation the contents of these bottles were preserved with borax-buffered formaldehyde (end concentration of 0.4 %). Subsamples (50

ml) for image-analysis were permitted to settle in Utermöhl chambers for exactly 1 h. Comparisons of results from subsamples settling for 48 h revealed no substantial differences for the size ranges measured in this study.

Three series of experiments were conducted. Each consisted of incubation bottles containing (a) a selected species of copepod with fecal pellets (referred to as coprorhexy incubations), (b) only the copepod species, (c) only pellets or (d) only the seawater medium. For experiments with *Acartia clausii* and *Pseudocalanus elongatus*, pellets of 180 - 250 and for *Calanus finmarchicus* 500 - 650 µm in length were used. The concentration of fecal pellets introduced to bottles was about 600, 1800 and 20 per liter for the *Acartia clausii*, *Pseudocalanus elongatus* and *Calanus finmarchicus* series of incubations, respectively. The first two concentrations agree well with surface concentrations of 500 to over 2000 per liter for similarly sized fecal pellets in spring in Kiel Bight (Smetacek 1980). The concentration for *C. finmarchicus* fecal pellets is similar to concentrations for this species (10 per liter) recorded at the surface in the Norwegian Sea in late spring (Bathmann *et al.* 1987). The numbers of copepods per bottle were 10, 10 and 2 for *A. clausii*, *P. elongatus* and *C. finmarchicus*, respectively. Only adult female copepods were selected. With the exception of incubations of only seawater and *P. elongatus* with fecal pellets, all bottles were conducted in parallel.

Analysis

Total numbers, length, breadth, surface area and spherical volume of particles were automatically determined using a Zeus image-analysis system (A/S Pixelwerks) (Fig. 7).

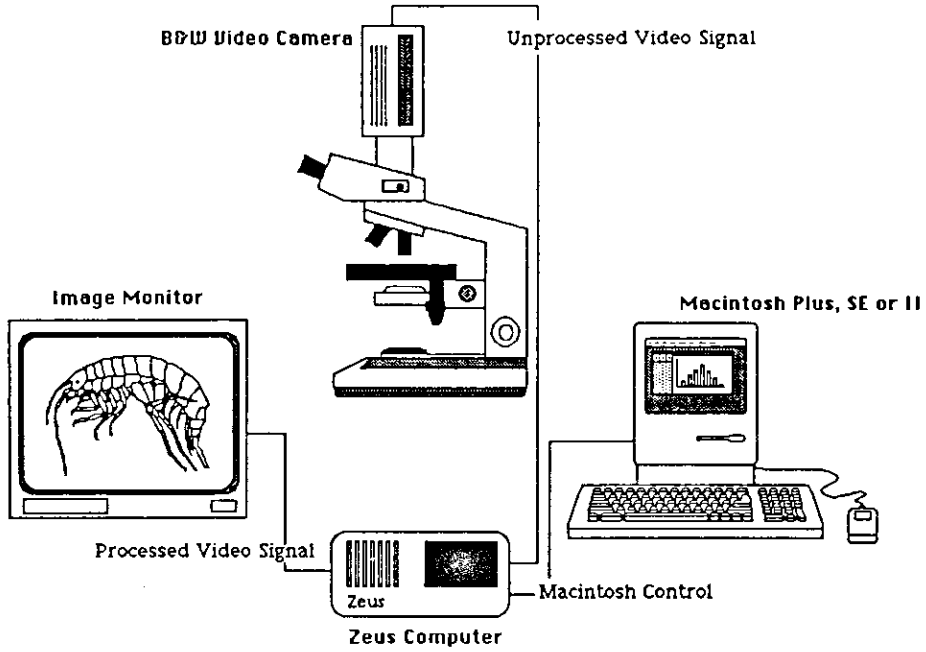


Figure 7. Image-analysis system consisting of a Zeus computer, a Macintosh SE computer, a Dage-MTI 67 M camera with light sensitive Passecon camera tube and Mitsubishi C3479 color monitor. The video camera was attached to a Zeiss Axioplan microscope with brightfield, darkfield, fluorescence and Nomarski optics.

The system uses the following equations for quantifying surface area and volume of objects:

$$\text{Surface area} = 4(\text{circular diameter})^2 \text{ and}$$

$$\text{Volume} = 3\pi^{1/2}(\text{object area})^{3/2}.$$

Large and small particle size fractions for each sample were analyzed. For incubations involving pellets of 180 - 250 µm in length, size ranges (equal to maximum linear dimension of object) of 2 - 40 and 41 - 250 µm were analyzed. Size ranges of 2 - 40 and 41 - 650 µm were analyzed for incubations with pellets of 500 -650 µm in length. Particles < 2 µm in length were not measured. An analysis of any size range was considered complete when a minimum of 300 particles or 15 fields of vision had been counted. Data from the two size ranges of any one sample and from parallel incubations were collated and treated as one data set.

To permit the direct comparison of controls (involving only fecal pellets or only copepods) with coprorhexy incubations (pellets and copepods incubated together), theoretical data sets (referred to as Control-*Acartia*, -*Pseudocalanus* and -*Calanus*, depending on the genus involved) were constructed. Each of these theoretical counterparts was composed of the combined results of the two controls (fecal pellet control + copepod control) for that genus. Note that small particles (which persist despite filtration) associated with the seawater medium used for incubations are represented twice in these theoretical data sets, as these small particles are included in each of the control types! This must be considered when interpreting results.

3. Results

Results are presented in two sections according to the nature of the work: **Field investigations** (section 3.1) and **Experimental studies** (section 3.2).

3.1. Field investigations

This section is divided into three parts: **Hydrography, nutrients and suspended particles** (section 3.1.1), **Metazooplankton** (section 3.1.2) and **Sedimentation** (section 3.1.3).

3.1.1. Hydrography, nutrients and suspended particles

The aim of this section is to identify the major bodies of water encountered during expeditions on the Vøring Plateau in the Norwegian Sea and to briefly describe phytoplankton growth regimes and the distribution of pelagic biomass. For this purpose typical vertical profiles for temperature (T°C), salinity (10^{-3} S) and concentrations of nitrate (NO_3), chlorophyll *a* (chl. *a*) and particulate organic carbon (POC) in the water column are presented. If available, data on phytoplankton composition and primary production are also provided.

Late winter

Salinities greater than 35 x 10^{-3} S and temperatures between 3 and 6°C were recorded above a depth of 400 to 500 m on the Vøring Plateau in late winter 1987. In underlying water values from 34.8 to 35.0 x 10^{-3} and 0 to 2°C (Fig. 8) were measured. Due to technical problems during data collection, a temperature above 0°C was recorded at a depth of 1000 m. It is assumed that temperatures in deep-water layers were in reality below -1°C (Johannessen 1986). Thus hydrography was characterized by Atlantic Water (AW) in the upper 400 to 500 m, below which was a layer of Arctic Intermediate Water (AIW). The former is characterized by salinities greater than 35 x 10^{-3} S; the latter is formed by cooling of AW and mixing with Norwegian Sea Deep Water (NSDW), which is defined by salinities slightly lower than 35 x 10^{-3} S and temperatures below -1 °C (Johannessen 1986). NSDW was below AIW. Nitrate concentrations in the upper 150 m were about 12 µM and in deeper water approached 16 µM, which indicates little uptake of nutrients at the surface. With concentrations of less than 0.1 µg per liter, chl. *a* concentrations were very low. Primary production was measured to be 15 mg C per m^2 per day (n = 1). Chl. *a* integrated from 0 to 100 m was 4.88 mg per m^2. Maximum concentrations of POC of about 100 µg per liter at the

surface decreased to between 40 and 60 µg per liter by a depth of 50 m, below which concentrations remained low. The integrated value of 6.65 g POC per m^2 was calculated from 0 to 100 m. Concentrations of chl. *a* and carbon biomass were the lowest recorded during the entire investigation.

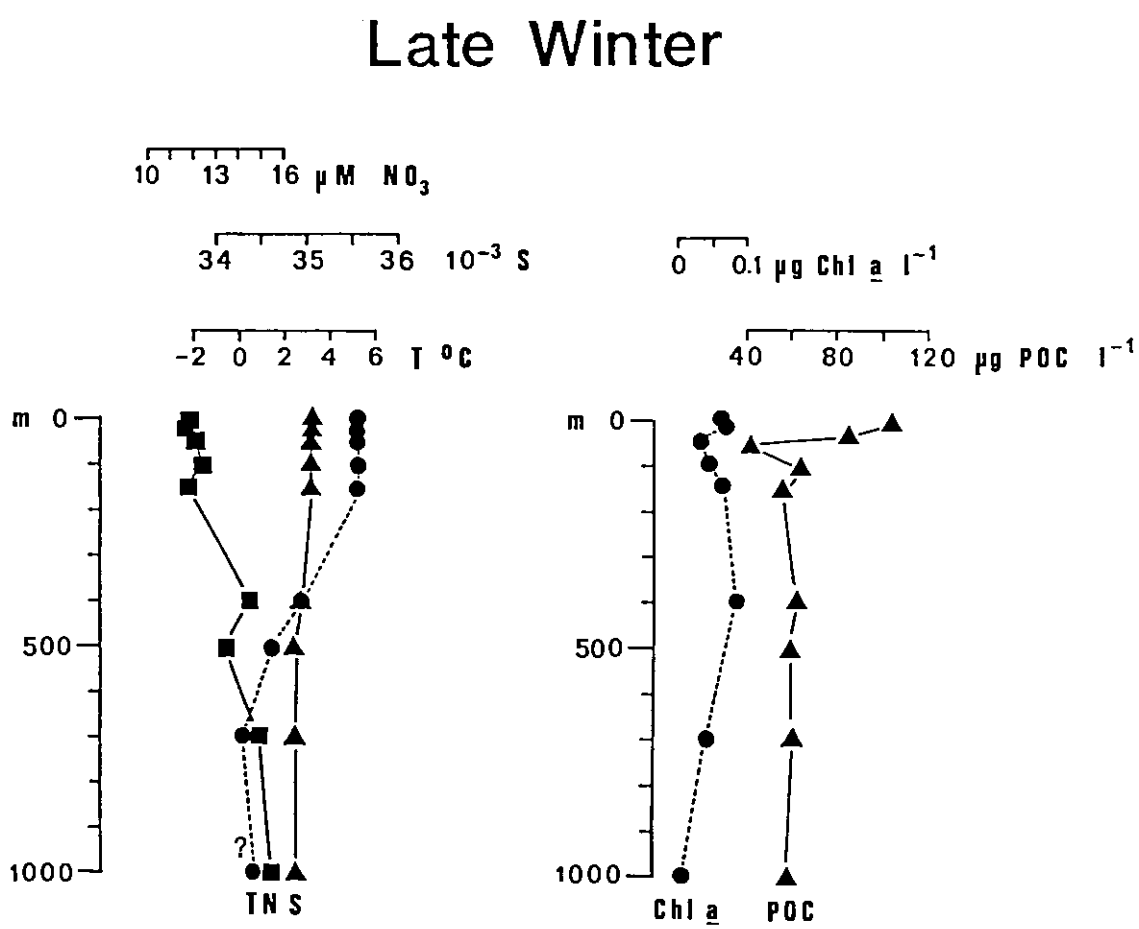


Figure 8. Vertical distribution of temperature (T°C), salinity (10^{-3} S) and concentrations of nitrate (µM), chlorophyll *a* (µg per liter) and particulate organic carbon (POC, µg per liter) on the Vøring Plateau from 9 February 1987. "?" indicates that temperature is probably < 0°C.

Late spring and early summer

The bodies of water on the Vøring Plateau in late May 1986 were Atlantic Water from the surface to midwater depths, Arctic Intermediate Water in midwater depths and Norwegian Sea Deep Water from the lower boundary of AIW to the sea-floor (Fig. 9). Nitrate concentrations were about 7 µM at the surface, increased rapidly to a value of 18 µM by 50 m, below which concentrations remained high. Values of over 18 µM may be overestimated by about 2 µM, as maximum nitrate concentrations in NSDW obtained from other expeditions were only about 16 µM. Chl. *a* concentrations of about 3 µg per liter at the surface declined to nearly 0 by 50 meters. Chl. *a* integrated from 0 to 100 m was 92.5 mg per m^2. Surface phytoplankton was dominated by diatoms (approx. 175 x 10^6 cells per liter) including *Corethron criophilum*, *Chaetoceros* spp. and *Nitzschia* spp. and small flagellates (< 6 µm; 65 x 10^6 cells per liter). This corresponded to about 1.57 and 0.33 mg C per liter. At 30 m depth the latter group was dominant. Coccolithophores (10 x 10^6 cells per liter) including *Emiliania huxleyi* and *Coccolithus pelagicus* were also numerous at the surface. Average primary production in May was 523 ± 107 mg C per m^2 per day (n = 5). (For further details concerning hydrography and phytoplankton development in May/June 1986 see Peinert *et al.* 1987.) Distribution of POC was similar in pattern to that for chl. *a*, which indicated the tight coupling between phytoplankton and suspended particulate organic carbon. Minimum values of about 100 µg POC per liter in deeper waters were about twice the minimum concentrations measured in February 1987, which indicates the higher background levels of suspended particulate organic matter in spring 1986. POC integrated from 0 to 100 m was 16.64 g per m^2.

Late Spring

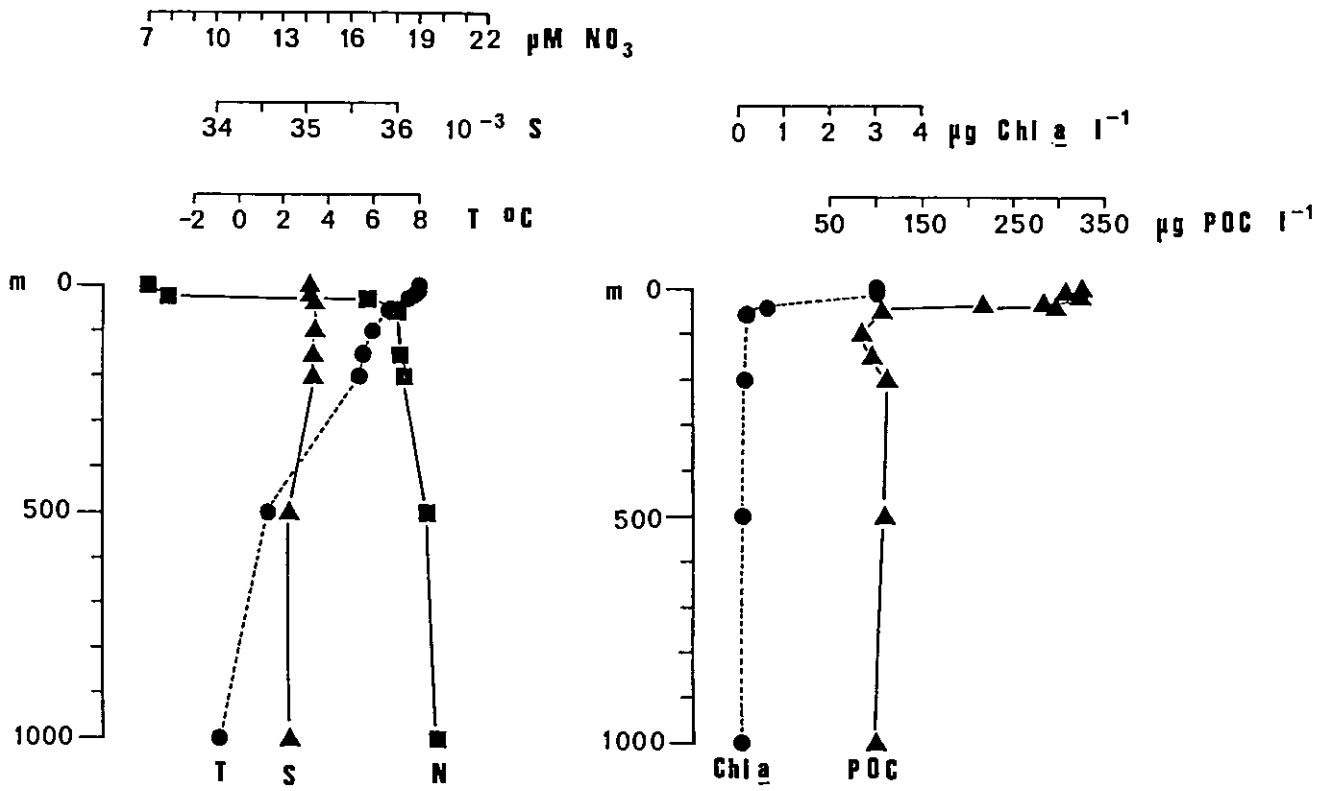


Figure 9. Vertical distribution of temperature (T°C), salinity (10^{-3} S) and concentrations of nitrate (µM), chlorophyll *a* (µg per liter) and particulate organic carbon (POC, µg per liter) on the Vøring Plateau from 29 May 1986.

By late June of the same year nitrate concentrations had declined to 5 µM. Integrated values for chl. *a* in the uppermost 100 m were roughly 20 % greater than those in late May. The corresponding increment in POC was about 100 %, which indicates the presence of large quantities of organic detritus. Phytoplankton composition at the surface was

dominated by large (6 - 30 µm in length) and small (< 6 µm) flagellates with concentrations of approx. 430 and 390 x 10^3 cells per liter. This corresponded to 7.2 and 0.4 µg POC per liter, respectively. Primary production was 330 ± 71 mg POC per m^2 per day (n = 4).

Fecal pellet numbers and carbon on the Vøring Plateau (Fig. 10) were generally concentrated at the surface, although on 30 May (Table 3) a distinct subsurface maximum at 25 m was recorded. By the end of June concentrations of fecal pellets in surface waters were reduced to about 10 % of values in May. The total fecal pellet POC also declined by the same magnitude.

Table 3. Suspended fecal pellet carbon (mg POC per m^2) (from Bathmann *et al.* 1987)

Depth (m)	29 May	30 May	4 June	24 June	30 June
0-100	475	430	27	30	33
0-250	620	580	73	67	60
1-1000	995	1330	135	132	125

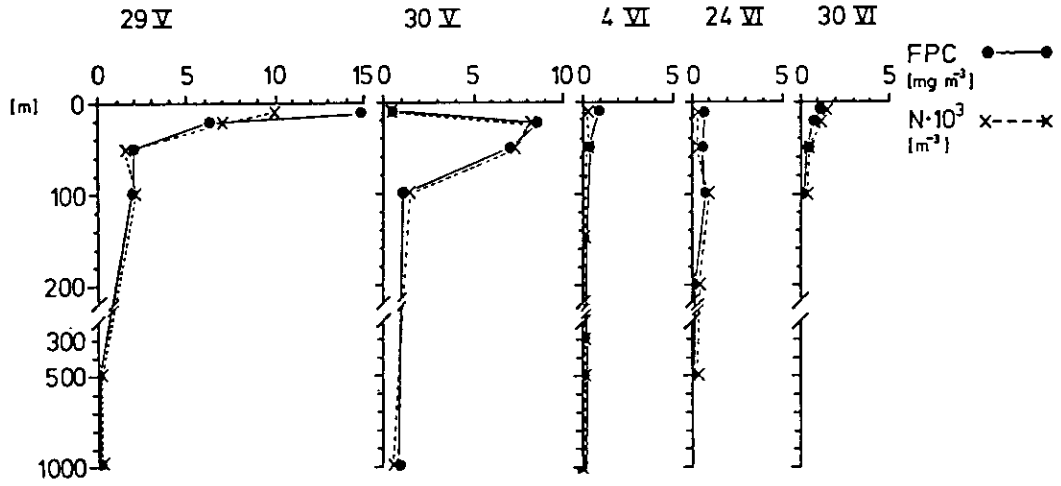


Figure 10. Vertical distribution of fecal pellet numbers (x) and carbon (•) in May (V) and June (VI) 1986 on the Vøring Plateau. (from Bathmann *et al.* 1987)

Summer

In late July 1987 only the physical parameters temperature and salinity (Fig. 11) were recorded. Water directly at the surface was characterized by a salinity of less than 35 x 10^{-3} S and a temperature of over 10°C; this thin layer was Norwegian Coastal Water (NCW) (Johannessen 1986). Atlantic Water was below this layer down to a depth of 400 to 500 m. A mixing zone (Arctic Intermediate Water) was found from depths of 500 to 600 m water, below which was Norwegian Sea Deep Water.

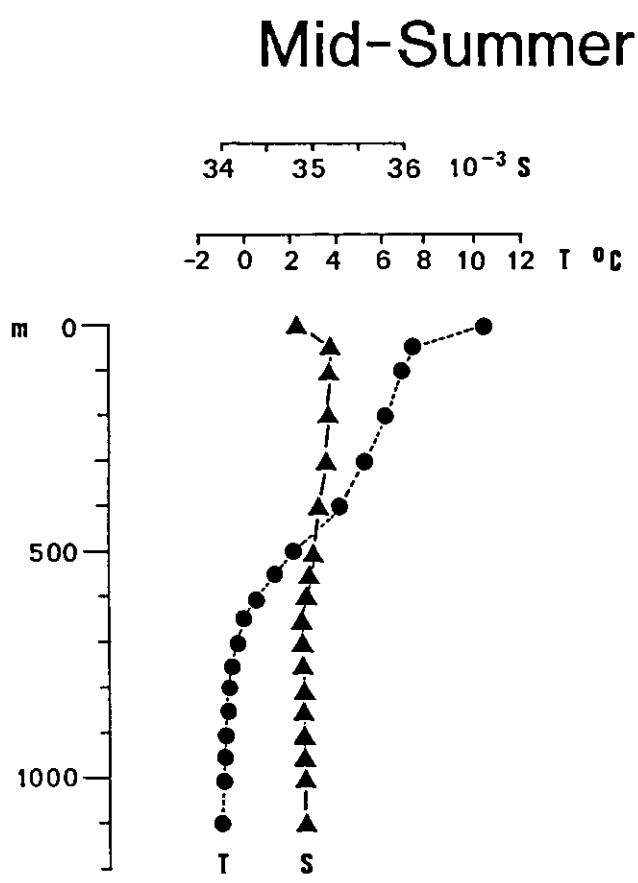


Figure 11. Vertical distribution of temperature (T°C) and salinity (10^{-3} S) on the Vøring Plateau from 30 July 1987.

In mid-August 1988 Norwegian Coastal Water (NCW) layered the upper meters of the water column (Fig. 12). The lower depth of NCW was usually about 20 m but varied, which indicated fluctuating eastward advection of NCW from coastal regions. Extending below the NCW layer down to about 500 m was Atlantic Water. A 150 to 250-m thick layer of Arctic Intermediate Water was at midwater depths, below which was Norwegian Sea Deep Water. The upper 15 m were deplete of nitrate, which however rapidly increased in concentration to approx. 12 µM by a depth of 50 m; by 1000 m nitrate had increased to almost 16 µM. It is noted that nitrite, ammonium and silicate in the upper 20 m were also detected in only minimum concentrations or were absent. Phosphate concentrations were generally low (< 0.2 µM) but not limiting for phytoplankton growth. Chl. *a* concentrations of about 0.2 µg per liter at the surface showed a subsurface maximum of about 0.6 µg per liter at 20 m, below which concentrations decreased rapidly to about 0 by 100 m depth. This subsurface maximum in chlorophyll was about 1.2 µg per liter on 19 August and by 31 August had declined to about 0.4 µg per liter. Concentrations of chl. *a* integrated from 0 to 100 m was 24.83 mg per m^2. Primary production for August was 373 ± 111 mg POC per m^2 per day (n = 12). Maximum concentrations of POC were measured at the surface and at a depth of 60 m. As observed for chl. *a*, minima for POC concentration were measured below about 100 m. However, distribution of chl. *a* and POC did not run parallel to one another, which indicated the substantial contribution of sources lacking chl. *a* to suspended particulate organic carbon. POC integrated from 0 to 75 m was 9.84 g per m^2.

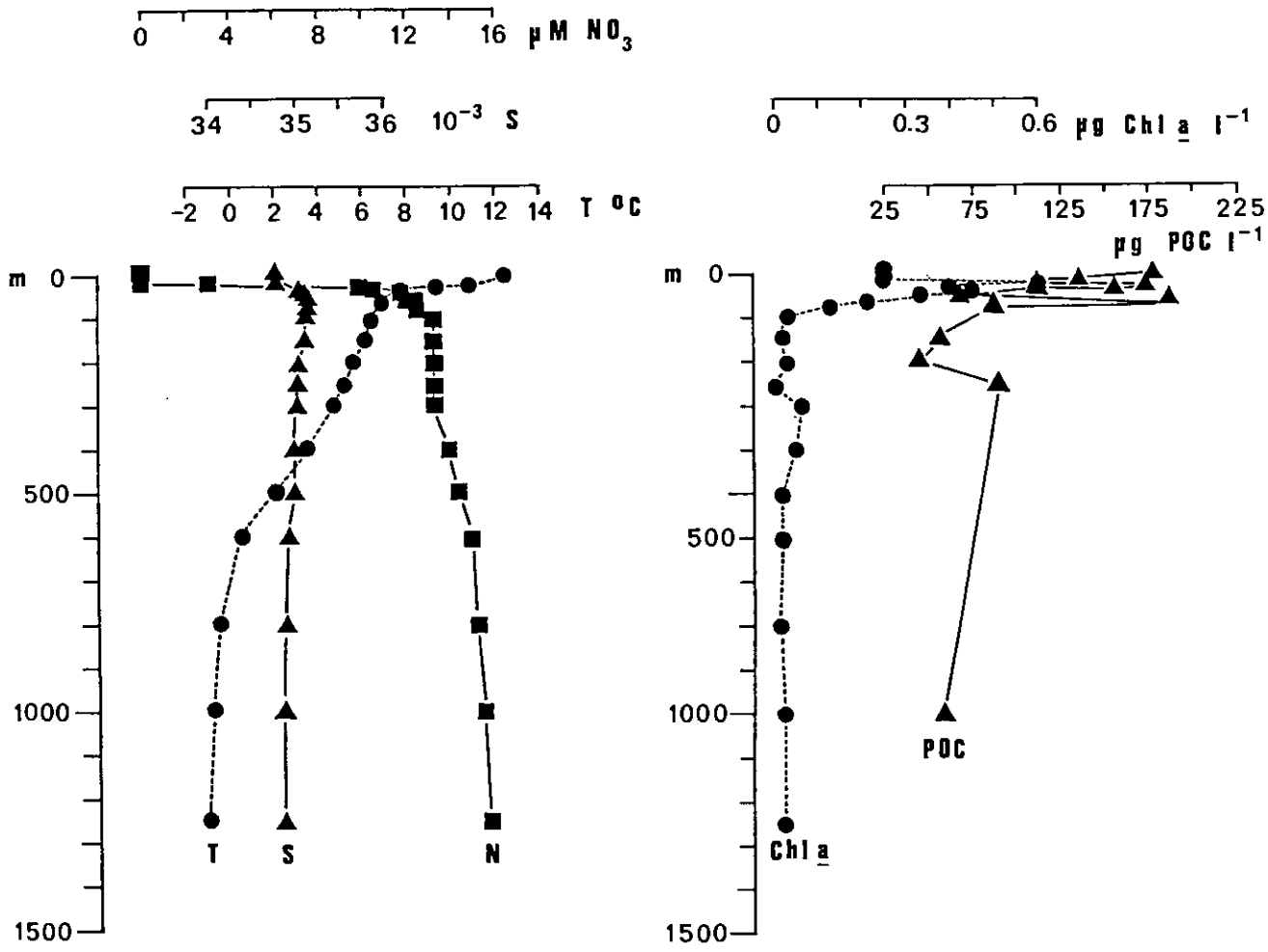


Figure 12. Vertical distribution of temperature (T°C), salinity (10^{-3} S) and concentrations of nitrate (µM), chlorophyll *a* (µg per liter) and particulate organic carbon (POC, µg per liter) on the Vøring Plateau from 13 August 1988.

Early winter

In early November 1987 relatively warm Norwegian Coastal Water layered surface waters (Fig. 13). Atlantic Water was below this layer to a depth of about 600 m. A layer of Arctic Intermediate Water was in the depth stratum of about 600 to 700 m, below which was Norwegian Sea Deep Water. Nitrate concentrations of about 10 µM at the surface increased gradually to about 16 µM by a depth of 1000 m. Chl. *a* concentrations of 0.3 µg per liter at the surface increased to almost 0.6 µg per liter at 50 m; this declined to about 0 µg by 100 m and remained low to depth. Chl. *a* integrated from 0 to 100 m was 57.66 mg per m^2.

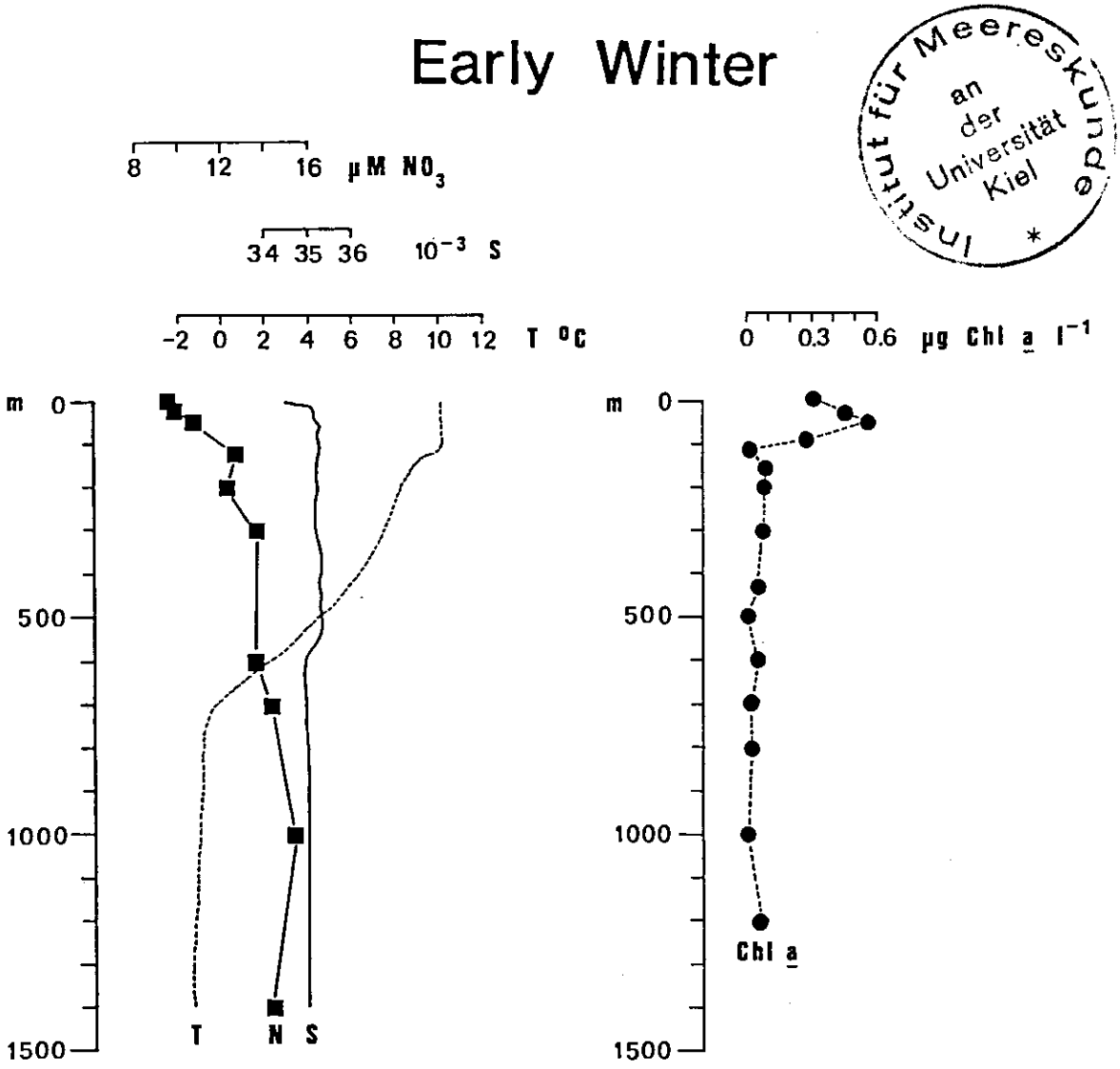


Figure 13. Vertical distribution of temperature (T°C), salinity (10^{-3} S) and concentrations of nitrate (µM) and chlorophyll *a* (µg per liter) on the Vøring Plateau from 6 November 1987.

3.1.2. Metazooplankton

Results from field studies on metazooplankton are presented in five sections: Total numbers and carbon biomass (section 3.1.2.1), Trophic distribution (section 3.1.2.2), Dominant groups (section 3.1.2.3), *Calanus finmarchicus* (section 3.1.2.4) and *Limacina retroversa* (section 3.1.2.5). Unless otherwise noted, results refer to zooplankters larger than 300 µm in the smallest dimension, i.e. retained by 200 or 300-µm nets. For all graphs in this section "Meters" represents the lower depth of the sampled water layer.

3.1.2.1. Total numbers and carbon biomass

Zooplankton numbers for the entire water column on the Vøring Plateau ranged from less than 50 000 in late spring to almost 500 000 individuals per m^2 in August (Fig. 14). The large values in August were confined to surface waters (Figs. 15 and 16). Generally, concentrations of individuals were highest at the surface during all seasons. Minimum concentrations occurred in midwater layers between about 200 and 600 m in late winter and late summer; these were followed by a resurge in numbers at depth. No such resurge was observed in May/June. From mid-May to late June (Fig. 17) the total concentrations of eggs, nauplii and copepodites (< 1.00 mm in length; from 64-µm net hauls) in the upper 100 m of the water column increased from about 100 000 to 1 000 000 individuals per m^2. Largest concentrations were near the surface.

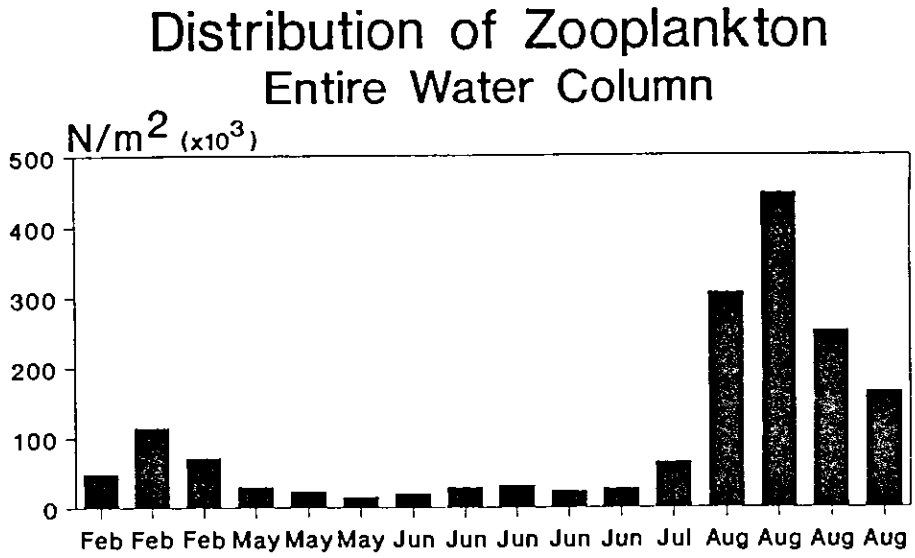


Figure 14. Abundance of metazooplankton numbers for the entire water column on the Vøring Plateau according to the month in which samples were collected. May and June samples were from 1986, February and July samples from 1987 and August samples from 1988.

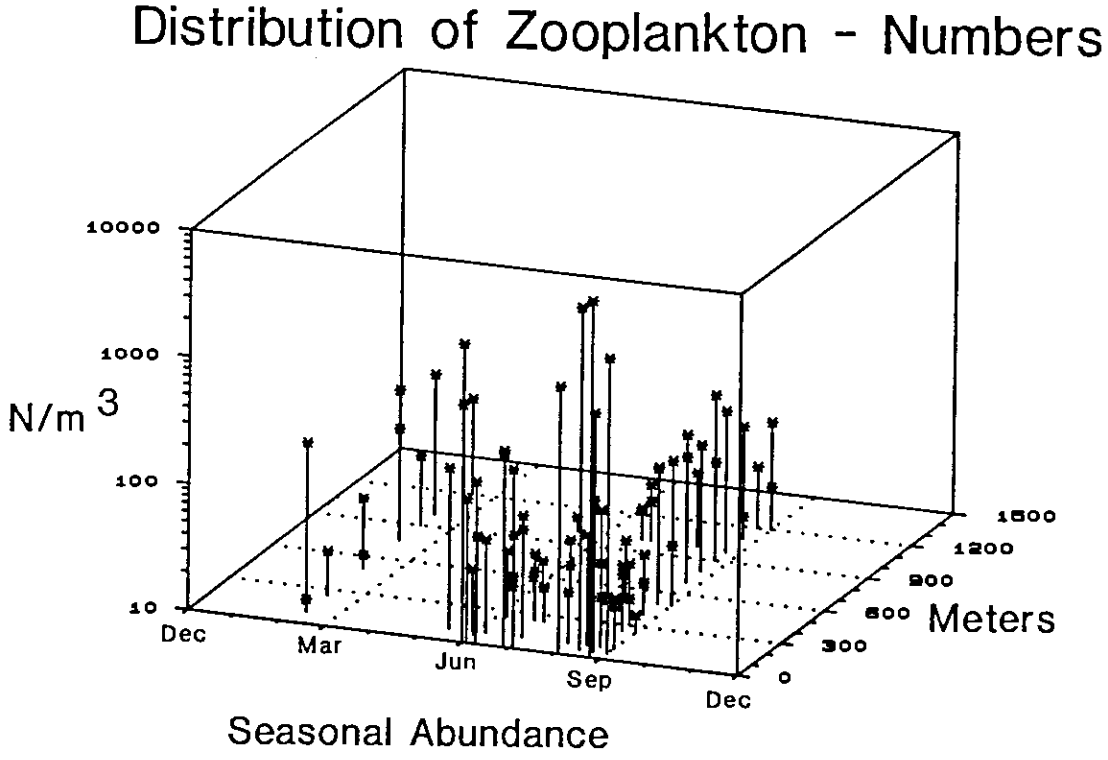


Figure 15. Seasonal distribution of metazooplankton numbers with depth for the entire water column on the Vøring Plateau. Data from samples collected from 1986 to 1988.

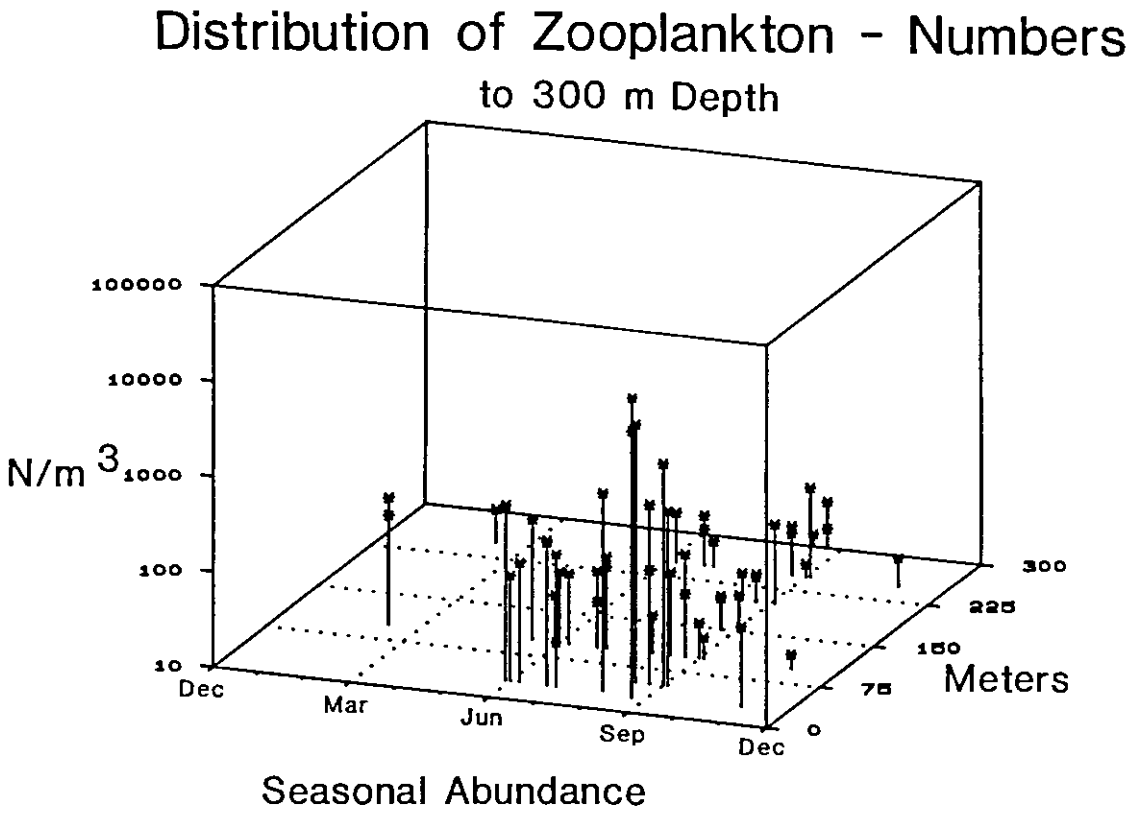


Figure 16. Seasonal distribution of metazooplankton numbers with depth for the upper 300 m of the water column on the Vøring Plateau. Data from samples collected from 1986 to 1988.

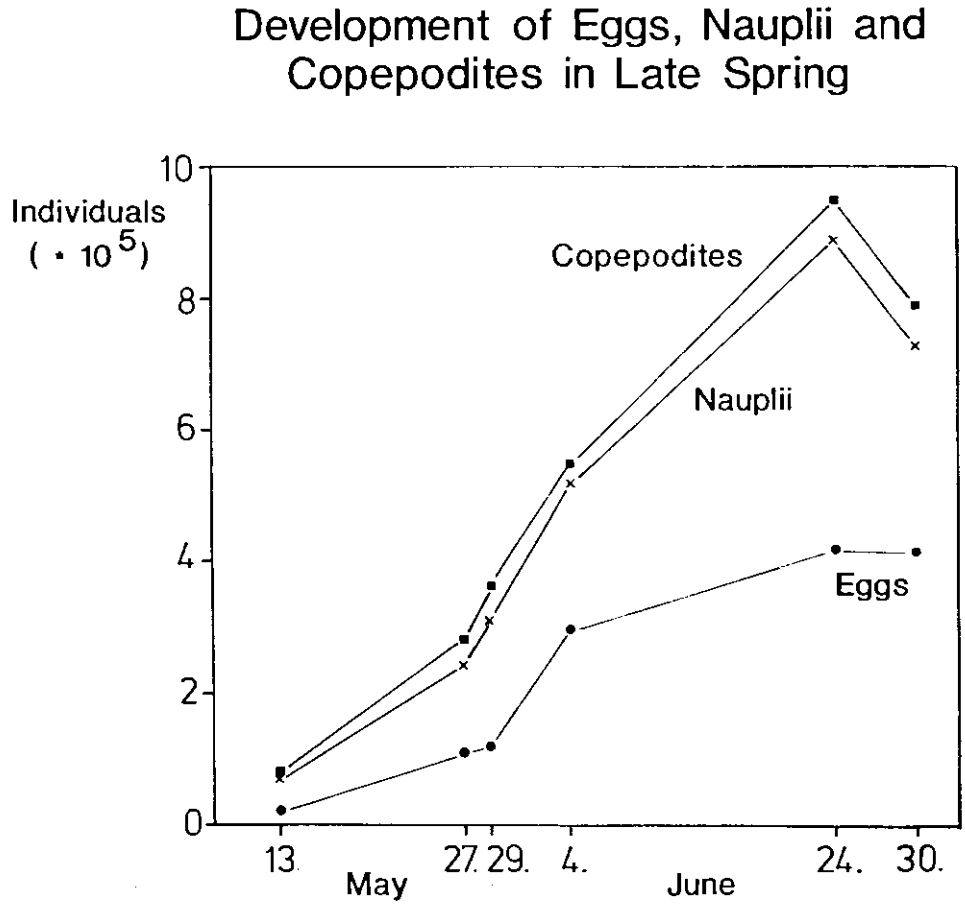


Figure 17. Abundance of eggs (•), nauplii (x) and copepodites (■) with a max. length of 1 mm for the upper 100 m of the water column on the Vøring Plateau in late spring/early summer. Values are presented cumulatively. Data from 1986.

The distribution of metazooplankton POC for the entire water column down to 1000 to 1200 m (Fig. 18) differed from that for numbers mainly in the relatively smaller peaks in August. With about 8 g POC per m^2 concentrations in late summer and late winter were about the same. In contrast to the peak numbers of individuals in August, the annual development of zooplankton carbon with depth (Fig. 19) peaked in May/June. Otherwise patterns were similar to those for distribution of numbers. Again, sharp concentration gradients (Fig. 20) were observed within the upper 300 m. In late spring to late summer the most abrupt reductions in biomass occurred at about a depth of 100 m.

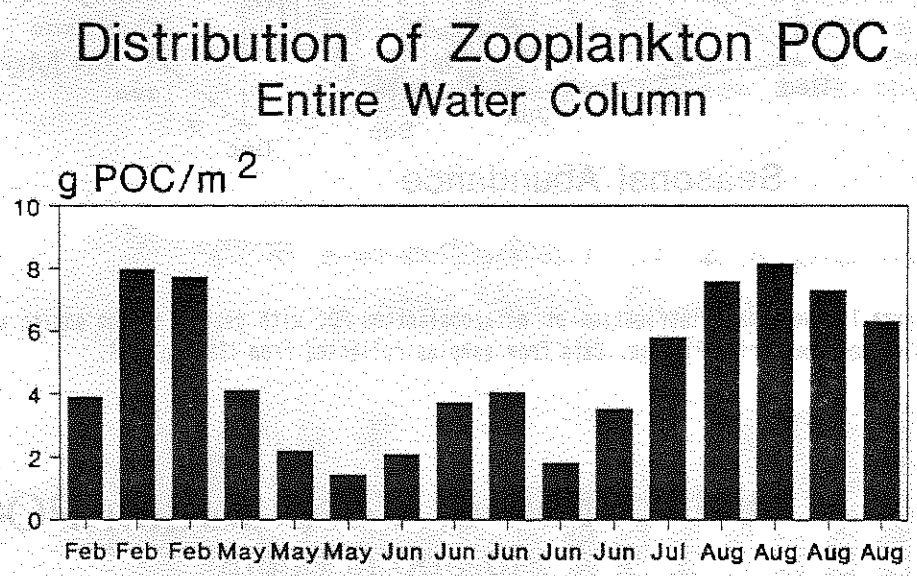


Figure 18. Abundance of metazooplankton POC for the entire water column on the Vøring Plateau according to the month in which samples were collected. May and June samples were from 1986, February and July samples from 1987 and August samples from 1988.

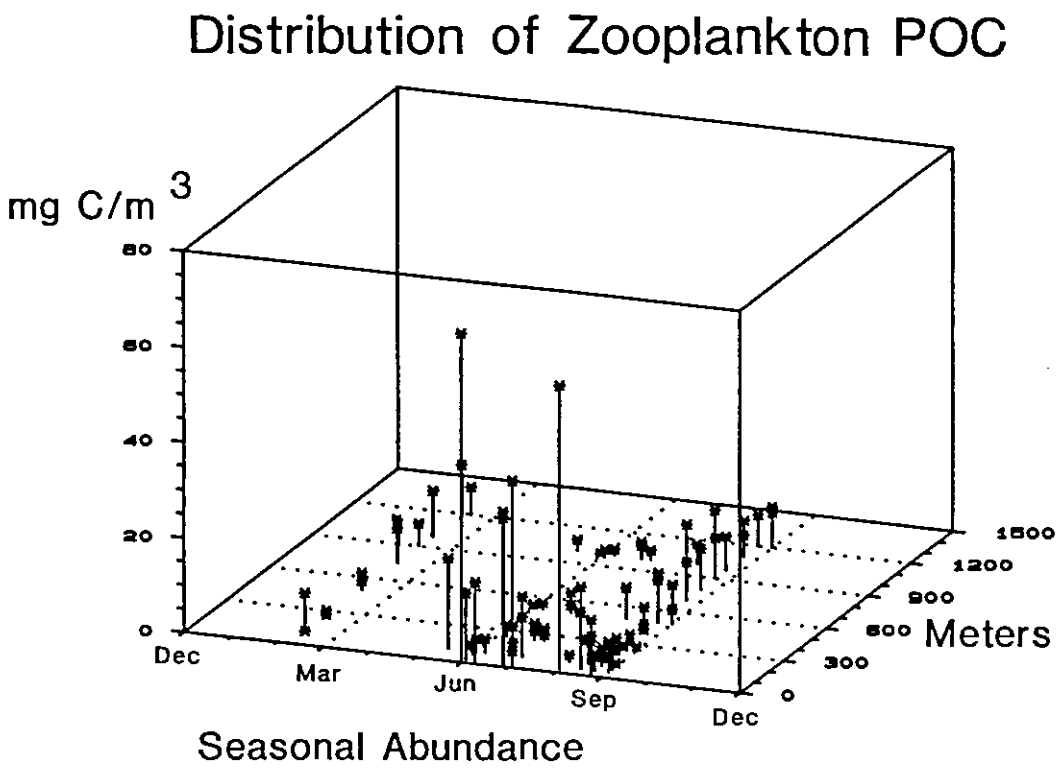


Figure 19. Seasonal distribution of metazooplankton POC with depth for the entire water column on the Vøring Plateau. Data from samples collected from 1986 to 1988.

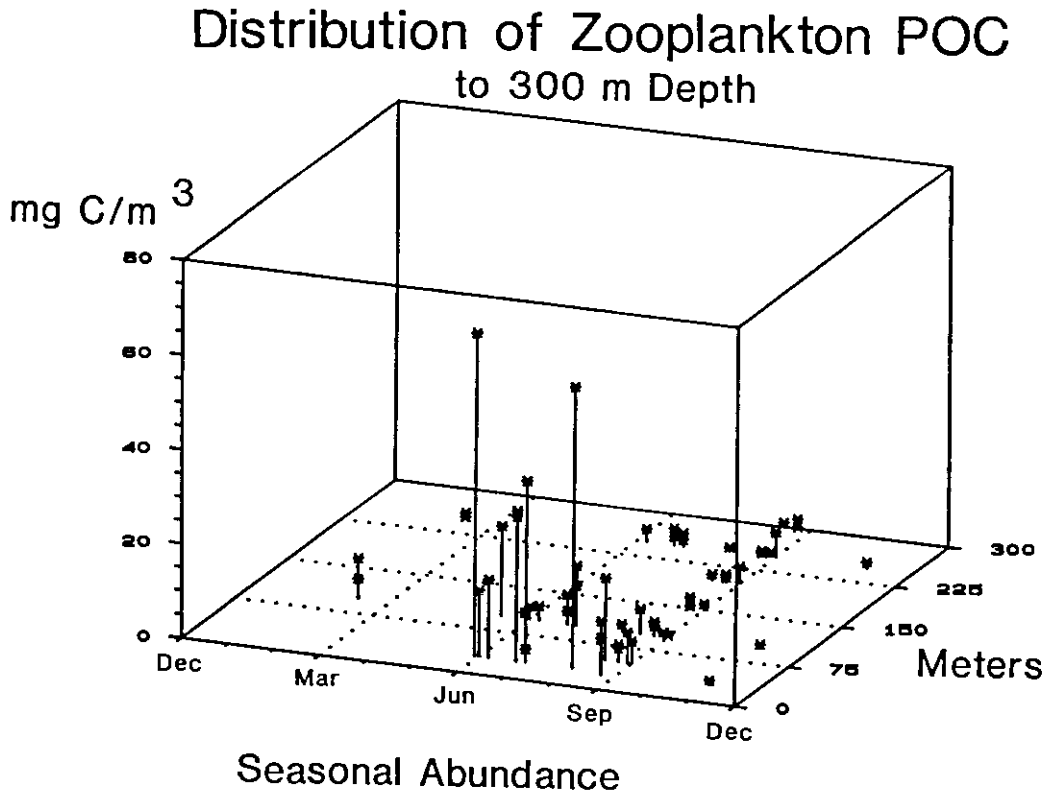


Figure 20. Seasonal distribution of metazooplankton POC with depth for the upper 300 m of the water column on the Vøring Plateau. Data from samples collected from 1986 to 1988.

3.1.2.2. Trophic distribution

The distribution of zooplankton according to trophic nature (Appendix 4) in the entire water column on the Vøring Plateau showed a predominance of herbivores, which from late summer to the following spring accounted for over 90 % of numbers (Fig. 21). In late spring, although absolute numbers did not increase, percentage contribution of omnivores and carnivores was between about 25 and 50 % of the total, an effect caused by the reduction in the numbers of herbivores, i.e. *Calanus finmarchicus* (section 3.1.2.4). In terms of carbon omnivores and carnivores accounted for large quantities of POC especially in August, when values attained about 4 g per m^2, half of total metazooplankton POC (Fig. 22) at this time. The generally larger sizes of omnivorous and carnivorous plankters relative to herbivores usually resulted in considerable percentage contribution to zooplankton POC.

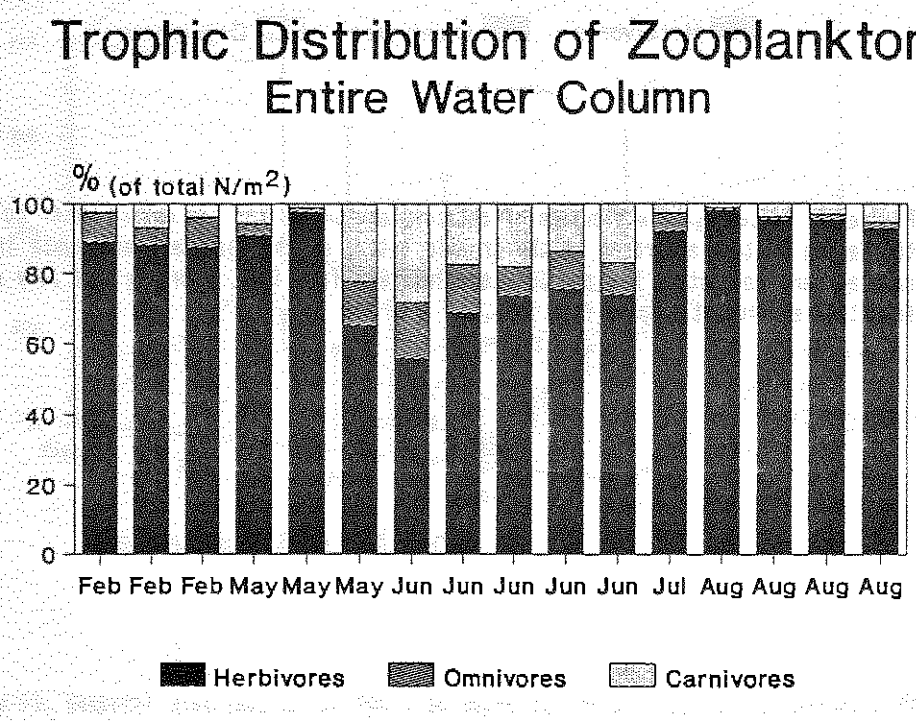


Figure 21. Percentage distribution of metazooplankton numbers for the entire water column on the Vøring Plateau according to the trophic nature of the plankters and month in which samples were collected. May and June samples were from 1986, February and July samples from 1987 and August samples from 1988.

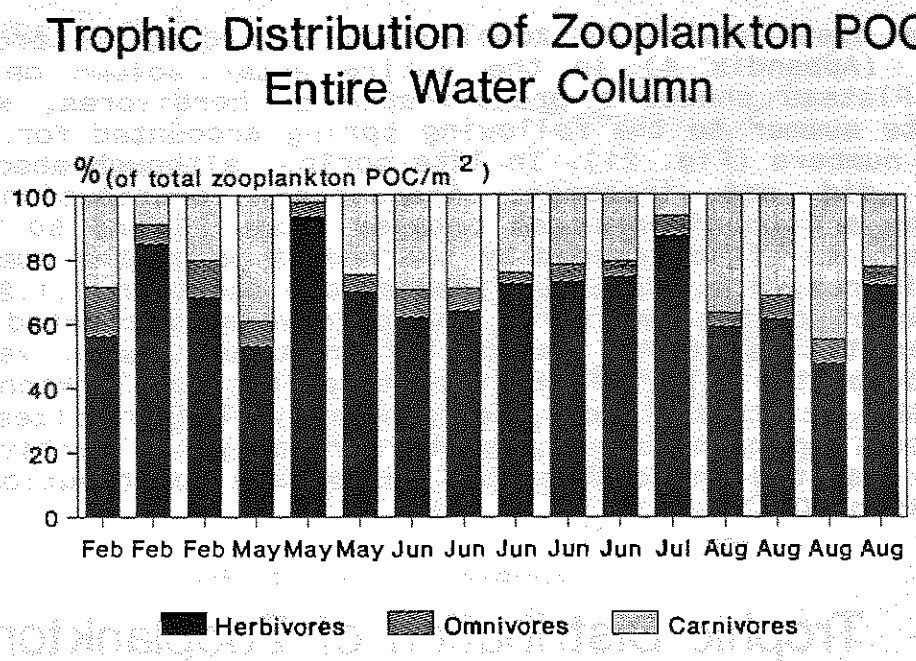


Figure 22. Percentage distribution of metazooplankton POC for the entire water column on the Vøring Plateau according to the trophic nature of the plankters and month in which samples were collected. May and June samples were from 1986, February and July samples from 1987 and August samples from 1988.

The vertical distribution of herbivore, omnivore and carnivore POC (Figs. 23, 24 and 25) was similar in pattern to that for total metazooplankton with peaks in surface waters in late spring and late summer; large concentrations at depth were also found in late summer. The amplitude of omnivore and carnivore POC concentrations during annual development was smaller than for herbivores, and differences in distribution with depth were also not as extreme as for herbivores. Further, in late summer highest concentrations of carnivore POC were in deep-water layers; the herbivore maximum was at the surface.

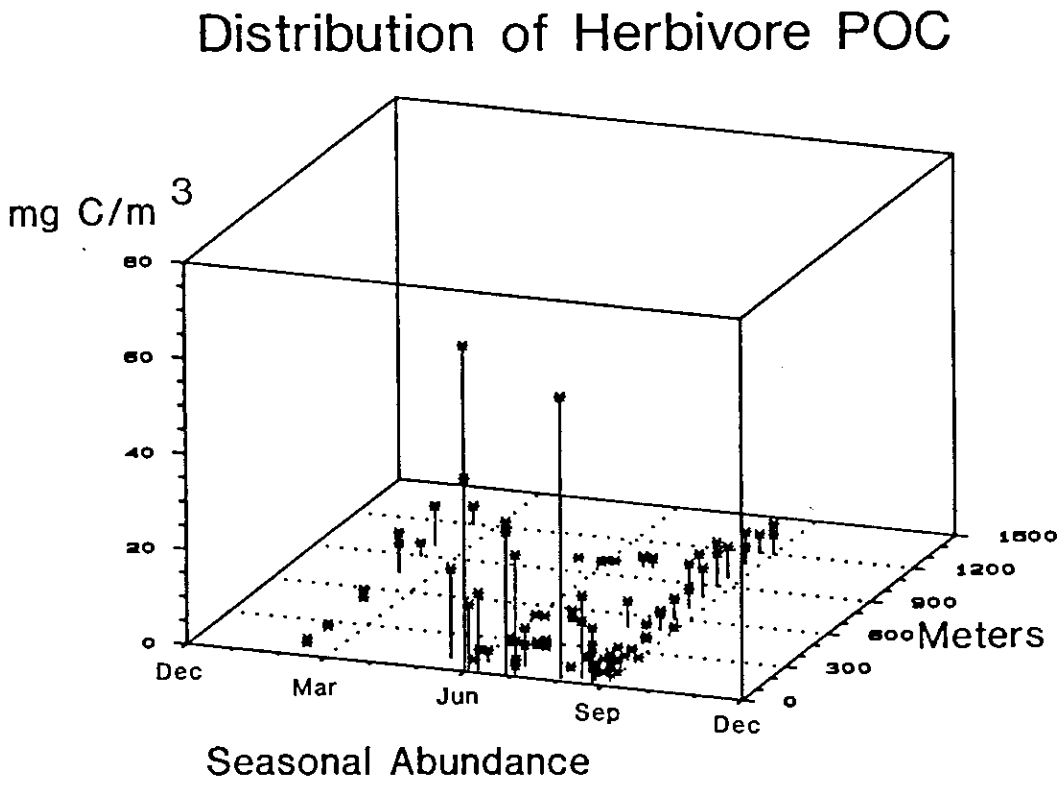


Figure 23. Seasonal distribution of POC with depth for herbivorous metazooplankton for the entire water column on the Vøring Plateau. Data from samples collected from 1986 to 1988.

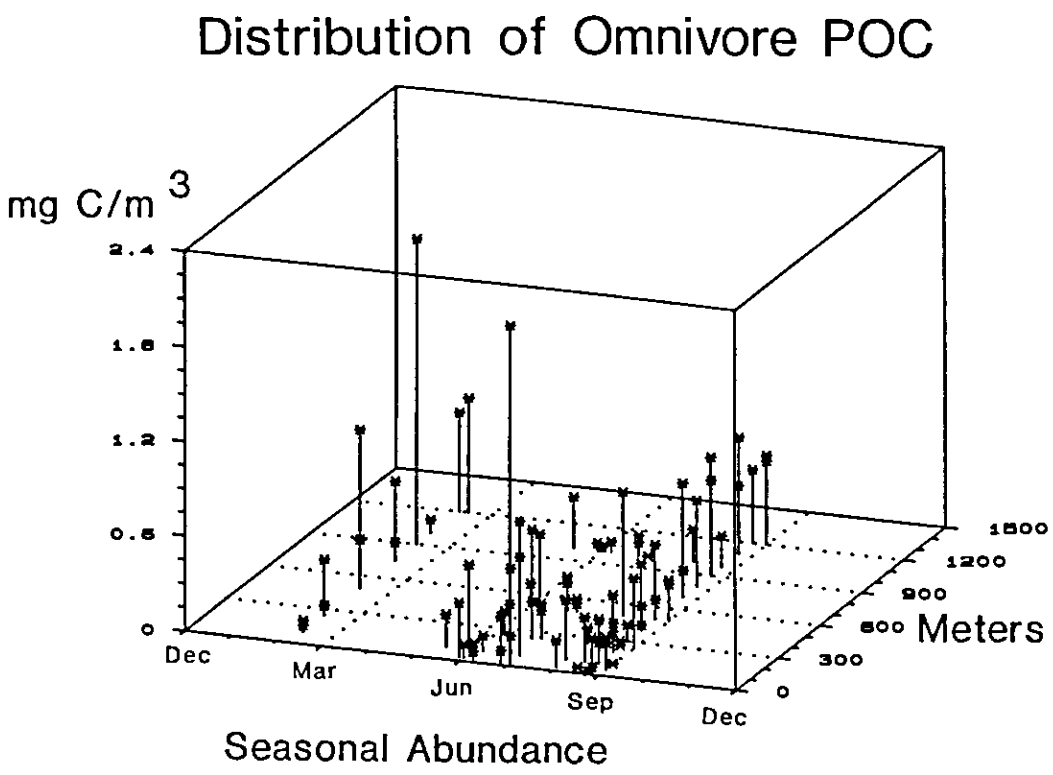


Figure 24. Seasonal distribution of POC with depth for omnivorous metazooplankton for the entire water column on the Vøring Plateau. Data from samples collected from 1986 to 1988.

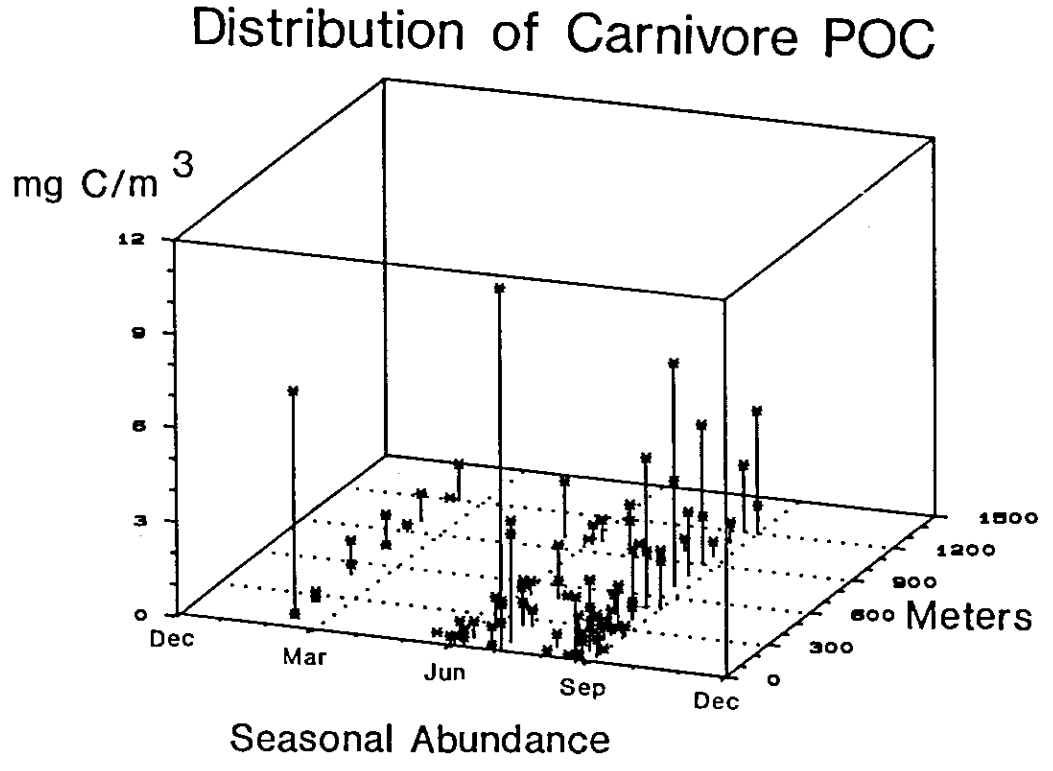


Figure 25. Seasonal distribution of POC with depth for carnivorous metazooplankton for the entire water column on the Vøring Plateau. Data from samples collected from 1986 to 1988.

3.1.2.3. Dominant groups

The percentage contribution of zooplankton groups to total metazooplankton number or POC (Appendices 5 and 6 for contributions of 5 % or more) in each sampled depth interval was calculated. Due to the large size of these data sets, only groups composing 10 % or more of numbers or carbon are presented graphically by season. See Table 4 for an interpretation of code numbers used in this section and in Appendices 5 and 6.

Late winter

The percentage of individual zooplankton groups relative to total metazooplankton number in late winter was dominated by *Calanus finmarchicus* copepodites, whose contribution approached 100 % in depths below 700 m (Fig. 26; see section 3.1.2.4 for details concerning *C. finmarchicus*). In surface layers the small copepod *Oithona spinirostris* (approx. 1.1 mm in length) was also a considerable component of metazooplankton numbers. The copepods *Metridia lucens* and *Pseudocalanus minutus* were present in smaller proportions.

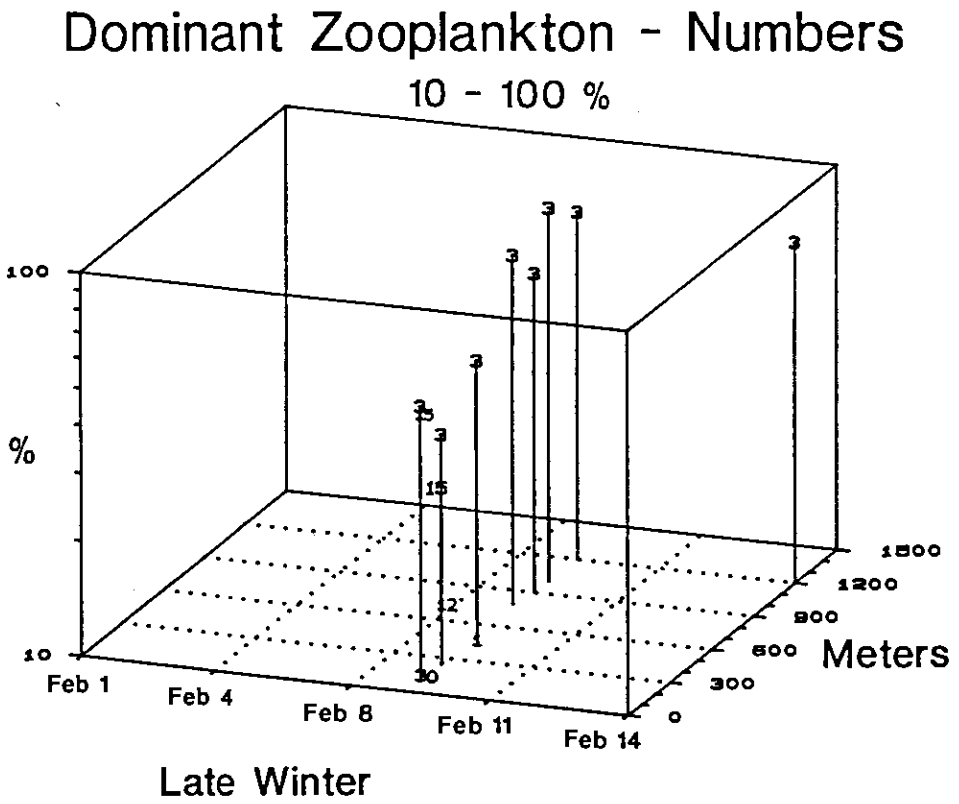


Figure 26. Late winter distribution of metazooplankton numbers with depth for dominant (composed > 10 % of numbers per sample) zooplankters for the entire water column on the Vøring Plateau. Data from 1987. See Table 4 for explanation of code numbers.

Table 4. Zooplankton groups accounting for 5 % or more of total metazooplankton number or carbon per sampling interval

Group	Code number
Copepods	
Calanus finmarchicus - adults	1
- copepodites CIV-V	3
Metridia longa - adults	6
- copepodites C IV-V	8
Metridia lucens - adults	11
- copepodites CIV-V	12
Oithona spinirostris - adults	15
Euchaeta norvegica - adults	17
- copepodites CI-III	18
- copepodites CIV-V	19
Euchaeta barbata - adults	20
- copepodites CI-III	21
- copepodites CIV-V	22
Euchaeta glacialis - adults	23
- copepodites CI-IV	24
Euchaeta sp. - copepodites CI-III	25
- copepodites CIV-V	26
Pseudocalanus sp. - adults	30
Calanus hyperboreus - adults	34
- copepodites CI-V	35
Aetideopsis rostrata - adults	47
- CI-V	48
Pleuromamma robusta - adults	55
- copepodites CIII-V	56
Heterorhabdus norvegicus - adults	60
- copepodites CI-V	61
other calanoid copepods (1.1-1.3 mm in length)	62
Others	
Limacina retroversa (pteropod)	75
Hyperoche medusarum (amphipod)	80
Thysanoessa sp. (euphausiid)	81
Eukrohnia hamata (chaetognath)	82
Conchoecia obtusata (ostracod)	87

The percentage contribution of *C. finmarchicus* copepodites to metazooplankton carbon was large at depth (Fig. 27). Otherwise, especially large zooplankters - euphausiids, ostracods (up to approx. 4 mm in length) and the large herbivorous copepod *Calanus hyperboreus* - dominated biomass in deeper waters. In depths above 600 m chaetognaths, amphipods and *C. finmarchicus* copepodites dominated biomass.

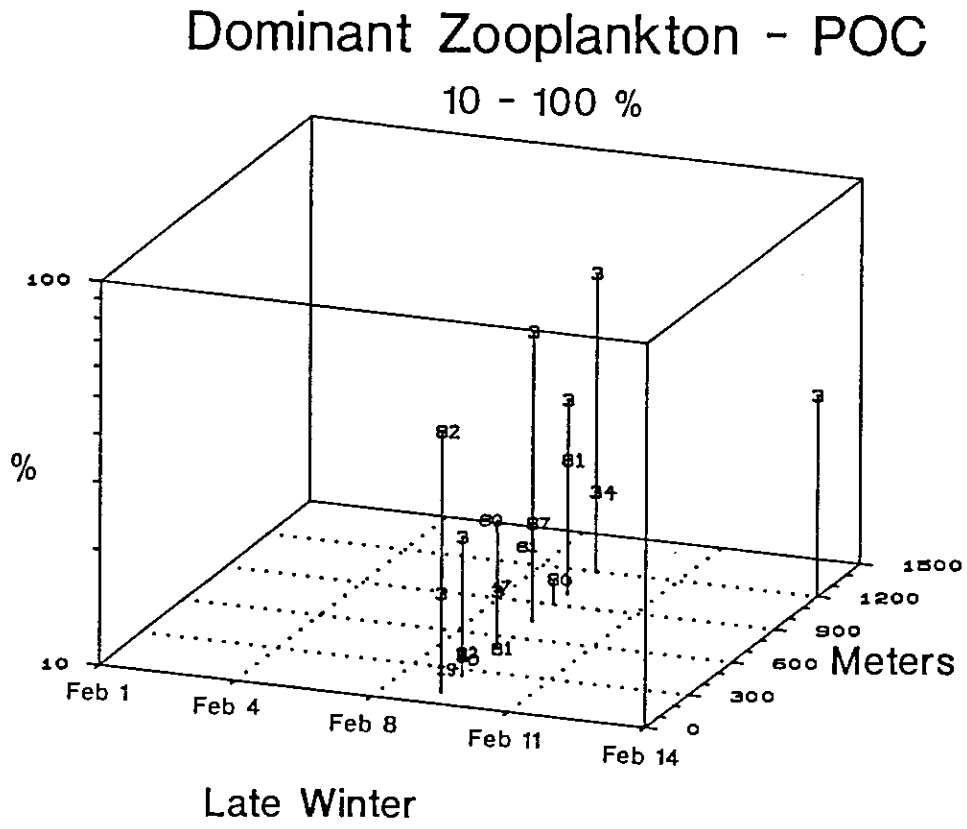


Figure 27. Late winter distribution of metazooplankton POC with depth for dominant (composed > 10 % of POC per sample) zooplankters on the Vøring Plateau for the entire water column. Data from 1987. See Table 4 for explanation of code numbers.

Late spring - early summer

Calanus finmarchicus adults dominated metazooplankton numbers throughout the water column but especially in surface waters (Fig. 28). In subsurface waters *Oithona spinirostris* was also common. Relatively high percentages of *Eukrohnia hamata* chaetognaths and *Euchaeta* sp. were sporadically encountered below 250 m depth. Ostracods were particularly abundant in midwater depths in late June. Notably, a large percentage of *C. finmarchicus* copepodites was present in late June/early July at greater depths.

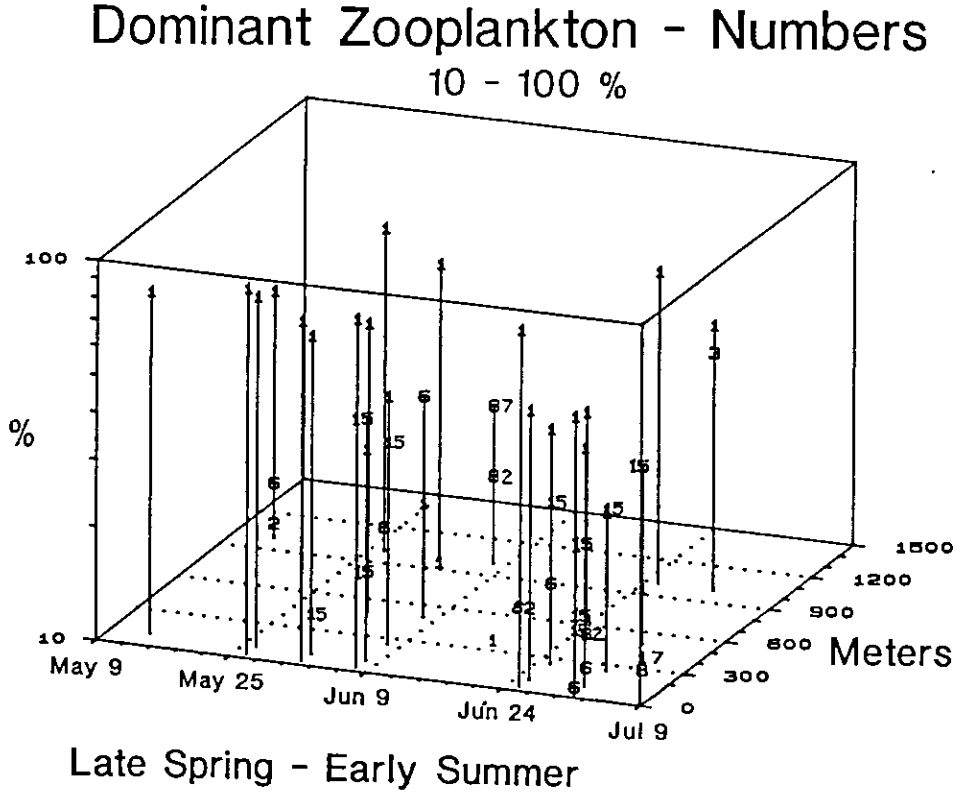


Figure 28. Late spring/early summer distribution of metazooplankton numbers with depth for dominant (composed > 10 % of numbers per sample) zooplankters for the entire water column on the Vøring Plateau. Data from 1986. See Table 4 for explanation of code numbers.

Percentage contribution to metazooplankton POC was generally similar in distribution to that for numbers except that *Oithona spinirostris* copepods lost and *Eukrohnia hamata* chaetognaths gained in importance as contributors to biomass (Figs. 29 and 30).

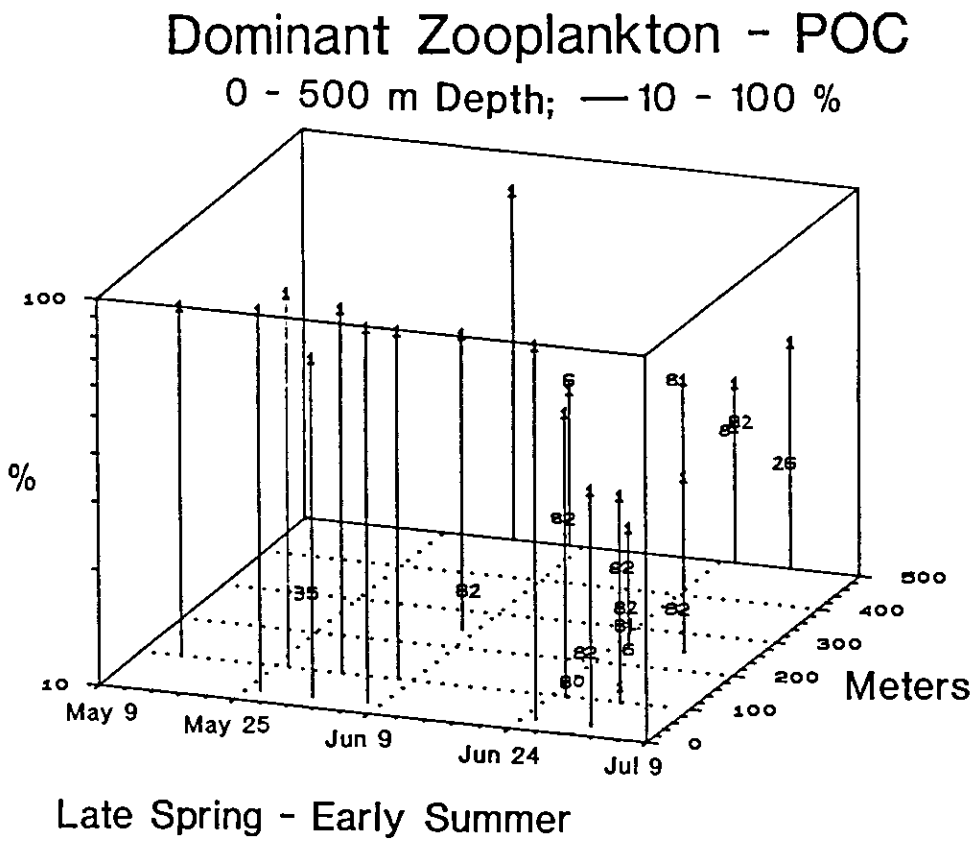


Figure 29. Late spring/early summer distribution of metazooplankton POC with depth for dominant (composed > 10 % of POC per sample) zooplankters for the upper 500 m of the water column on the Vøring Plateau. Data from 1986. See Table 4 for explanation of code numbers.

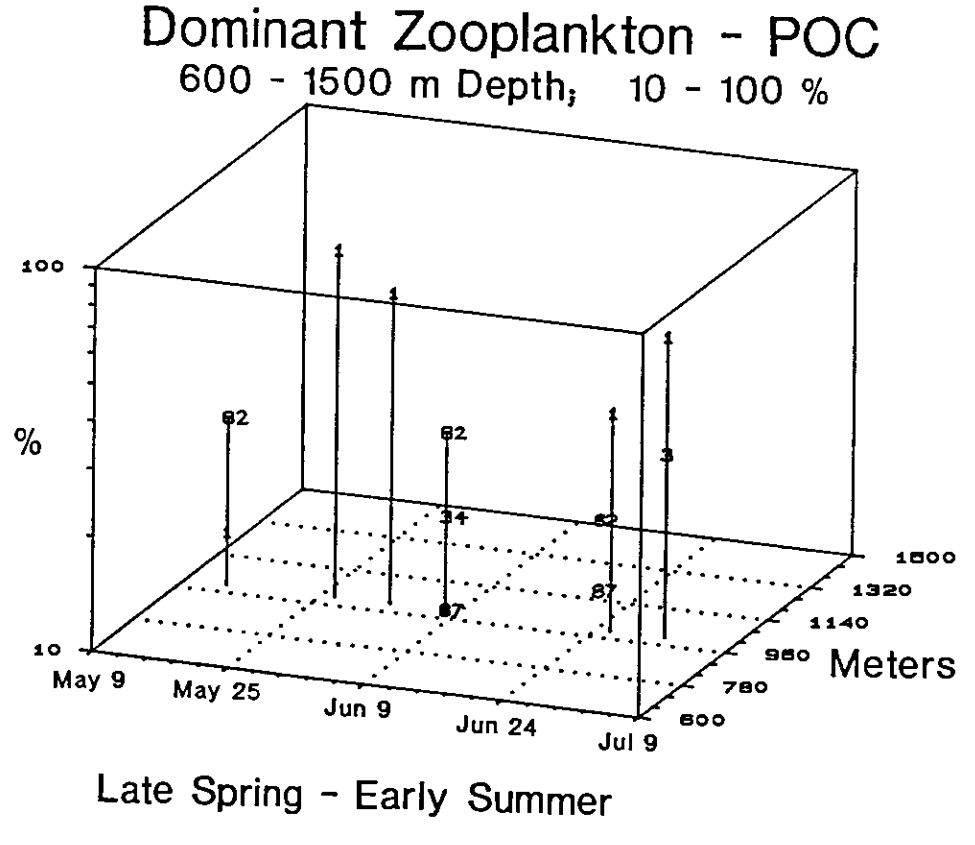


Figure 30. Late spring/early summer distribution of metazooplankton POC with depth for dominant (composed > 10 % of POC per sample) zooplankters below a depth of 500 m on the Vøring Plateau. Data from 1986. See Table 4 for explanation of code numbers.

Late summer

The percentage of numbers in surface waters in August (Fig. 31) was dominated by the euthecosomatous pteropod *Limacina retroversa*, whose contribution often approached 100 % of totals. The pteropod was not found in abundance in surface samples earlier in July or in depths below about 200 to 250 m (Fig. 32; see section 3.1.2.5 for details concerning *Limacina retroversa*). *Calanus finmarchicus* copepodites dominated numbers especially below about 500 m in depth (Figs. 32 and 33). Considerable percentages of *Oithona spinirostris* and chaetognaths above 750 m and of *Calanus hyperboreus* below 750 m were recorded.

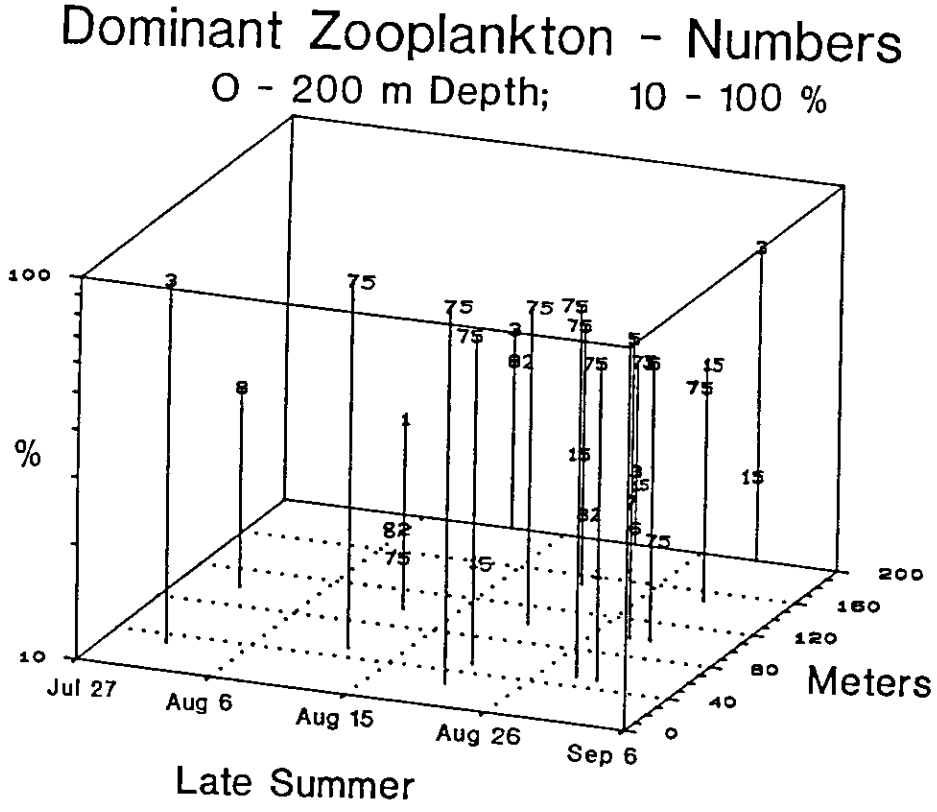


Figure 31. Late summer distribution of metazooplankton numbers with depth for dominant (composed > 10 % of numbers per sample) zooplankters for the upper 200 m of the water column on the Vøring Plateau. Data from 1988 except for late July 1987. See Table 4 for explanation of code numbers.

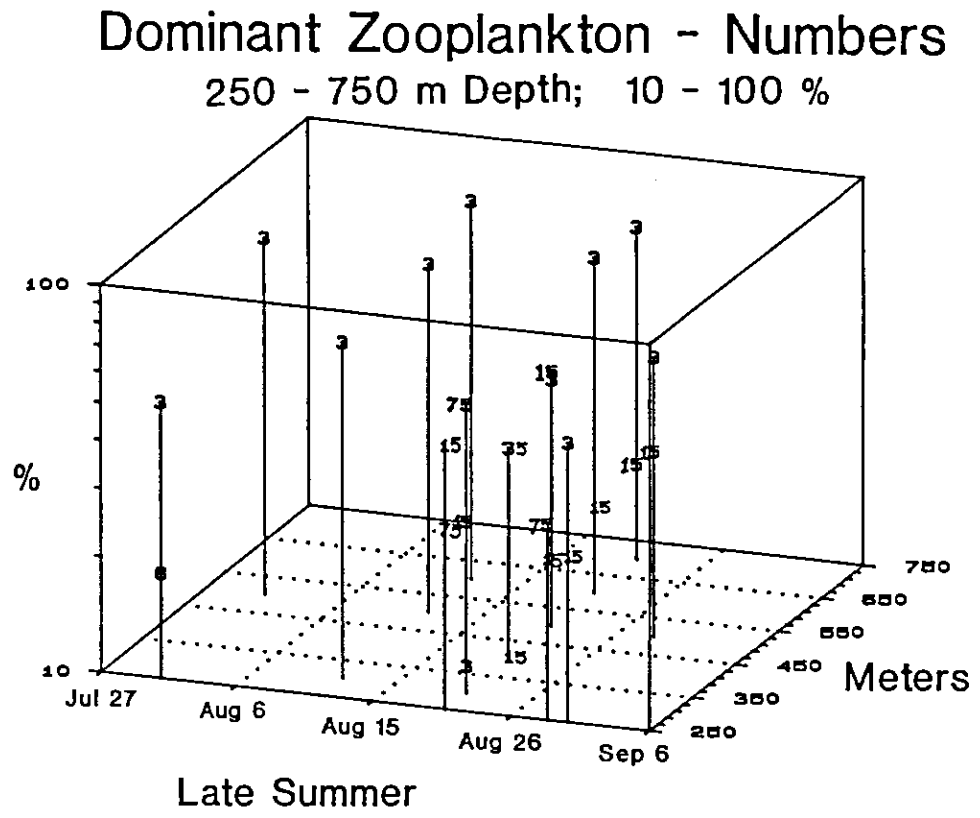


Figure 32. Late summer distribution of metazooplankton numbers with depth for dominant (composed > 10 % of numbers per sample) zooplankters for depths of 250 to 750 m on the Vøring Plateau. Data from 1988 except for late July 1987. See Table 4 for explanation of code numbers.

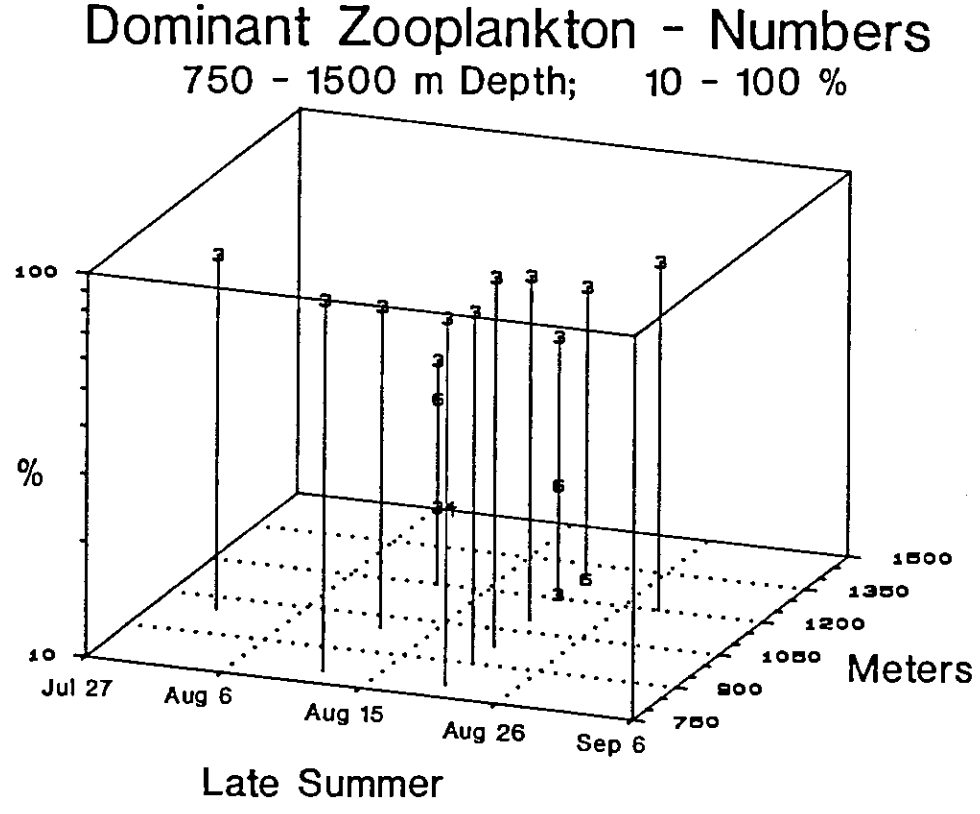


Figure 33. Late summer distribution of metazooplankton numbers with depth for dominant (composed > 10 % of numbers per sample) zooplankters for depths of 750 to 1500 m on the Vøring Plateau. Data from 1988 except for late July 1987. See Table 4 for explanation of code numbers.

Carbon-dominating zooplankton groups above 200 m depth in late summer were *Calanus finmarchicus* copepodites and adults, *Eukrohnia hamata* chaetognaths, euphausiids and other isolated zooplankters (Fig. 34). In midwater depths (Fig. 35) metazooplankton POC was dominated almost exclusively by *C. finmarchicus* copepodites and chaetognaths; at greater depths (Fig. 36) *Calanus hyperboreus* adults and copepodites also were important biomass contributors.

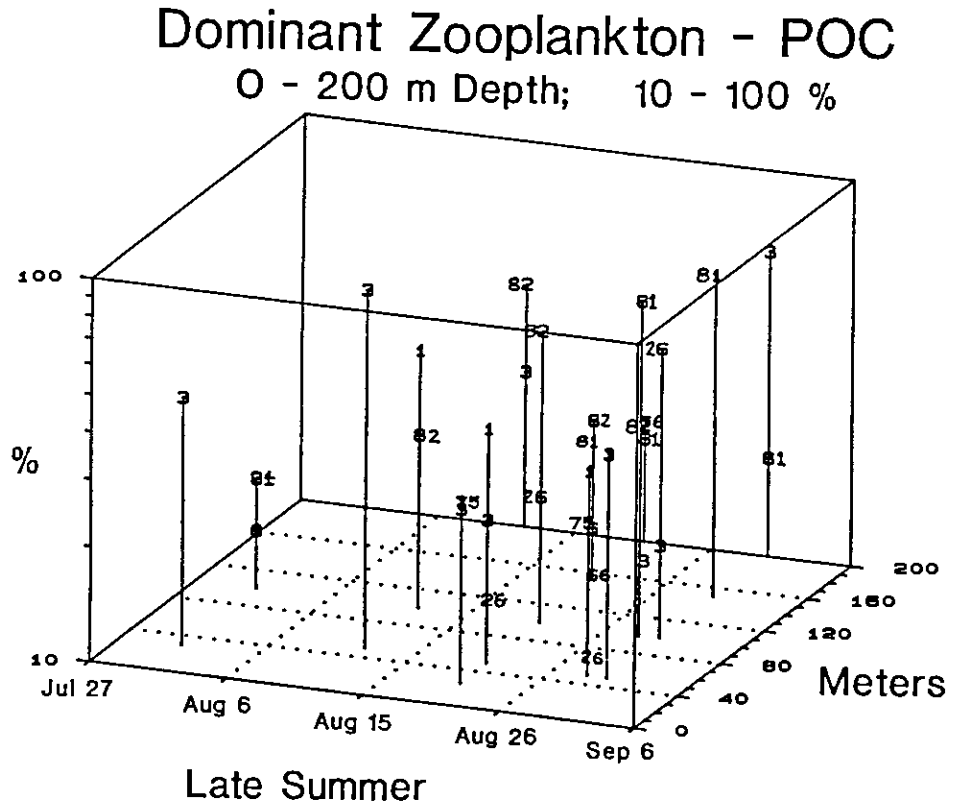


Figure 34. Late summer distribution of metazooplankton POC with depth for dominant (composed > 10 % of POC per sample) zooplankters for the upper 200 m of the water column on the Vøring Plateau. Data from 1988 except for late July 1987. See Table 4 for explanation of code numbers.

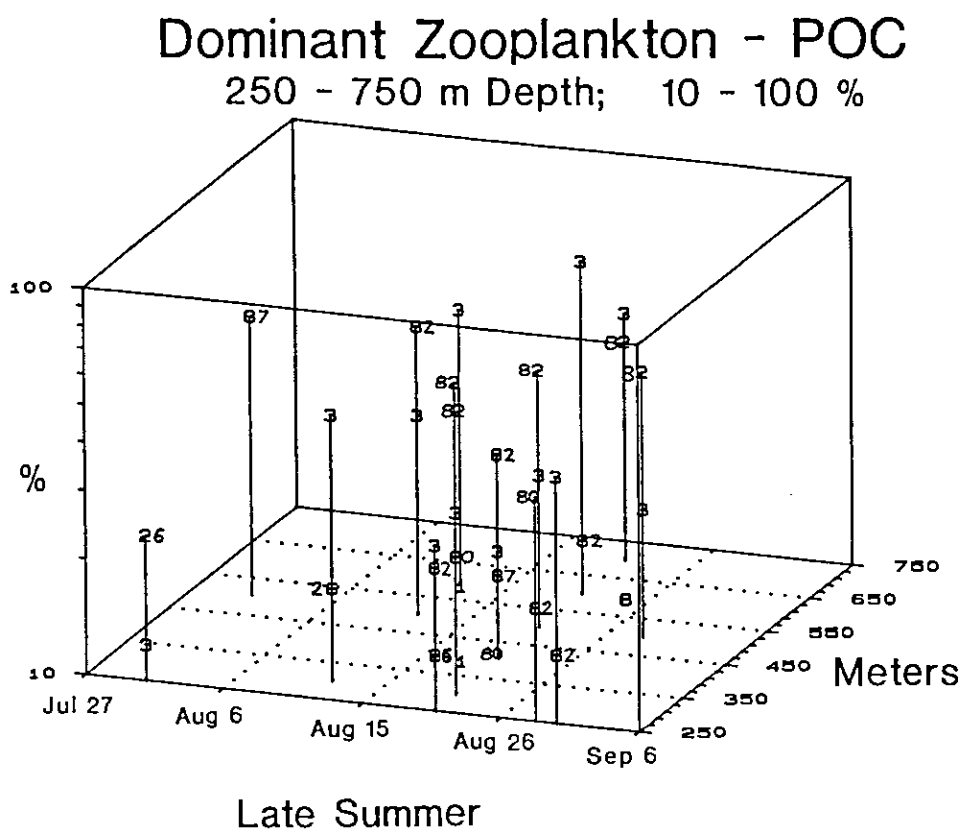


Figure 35. Late summer distribution of metazooplankton POC with depth for dominant (composed > 10 % of POC per sample) zooplankters for depths of 250 to 750 m on the Vøring Plateau. Data from 1988 except for late July 1987. See Table 4 for explanation of code numbers.

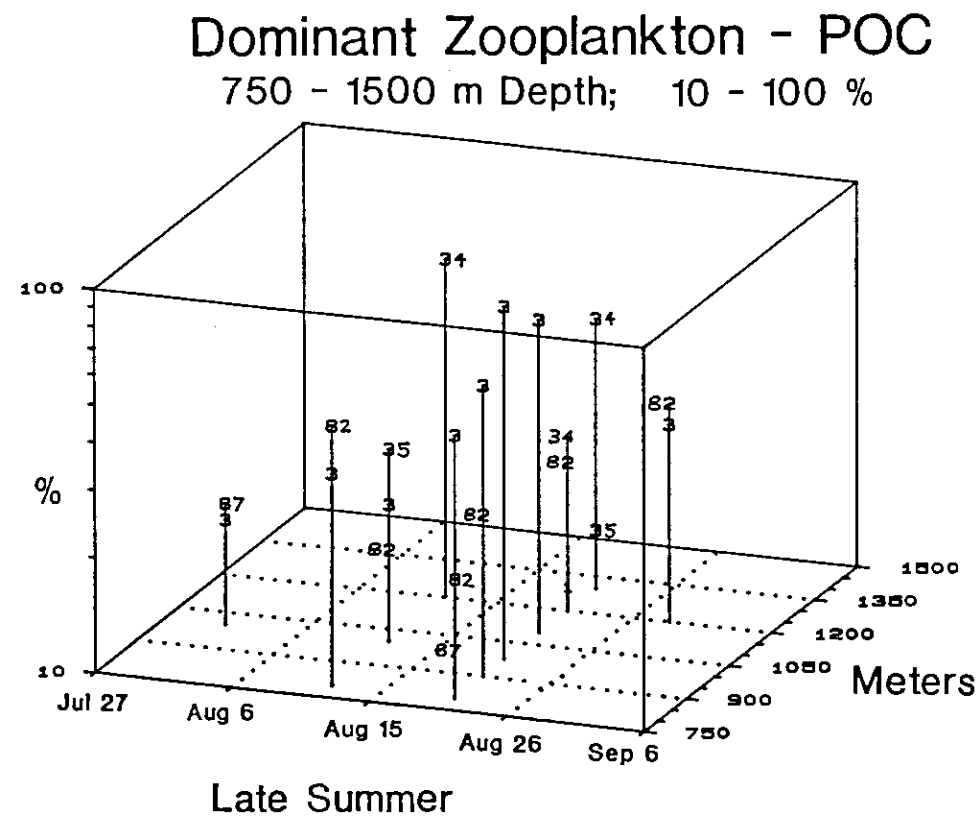


Figure 36. Late summer distribution of metazooplankton POC with depth for dominant (composed > 10 % of POC per sample) zooplankters for depths of 750 to 1500 m on the Vøring Plateau. Data from 1988 except for late July 1987. See Table 4 for explanation of code numbers.

Early winter

Zooplankton numbers in surface waters down to 250 m depth were clearly dominated by *Oithona spinirostris* (Fig. 37). Interestingly, a considerable portion of stocks at the surface consisted of *Calanus finmarchicus* copepodites.

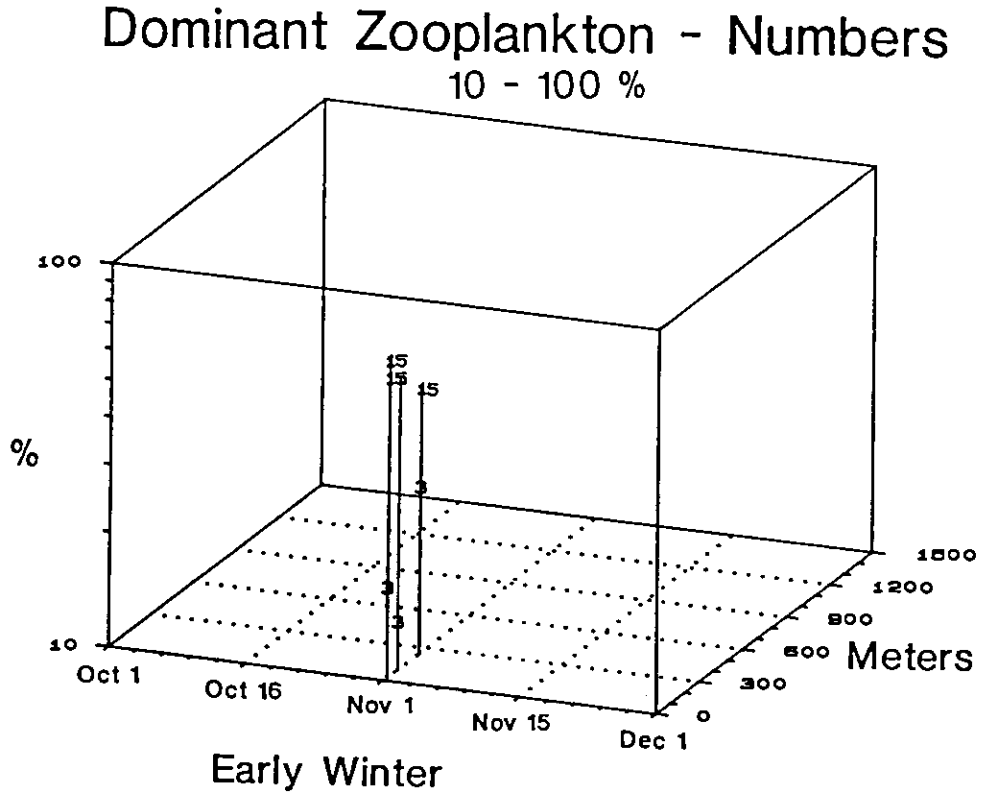


Figure 37. Early winter distribution of metazooplankton numbers with depth for dominant (composed > 10 % of numbers per sample) zooplankters for the entire water column on the Vøring Plateau. Data from 1987. See Table 4 for explanation of code numbers.

Metazooplankton carbon biomass was predominantly composed of *C. finmarchicus* copepodites, *Eukrohnia hamata* and *Euchaeta* spp. (Fig. 38).

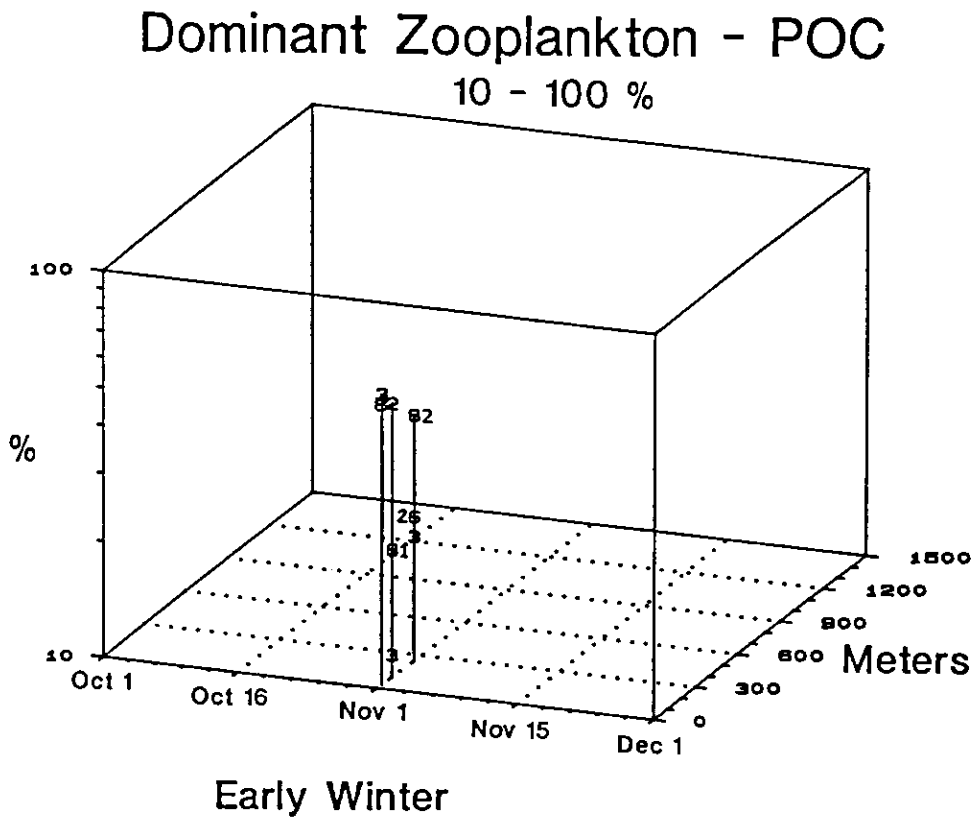


Figure 38. Early winter distribution of metazooplankton POC with depth for dominant (composed > 10 % of POC per sample) zooplankters for the entire water column on the Vøring Plateau. Data from 1987. See Table 4 for explanation of code numbers.

3.1.2.4. *Calanus finmarchicus*

The distribution of POC from *Calanus finmarchicus* adult females and copepodites (Appendix 7), which together composed nearly 100 % of total *C. finmarchicus* stocks during sampling, for the entire water column down to 1000 to 1200 m on the Vøring Plateau (Fig. 39) displayed maxima in late winter and late summer. With values of roughly 5 g POC per m^2 maxima were of similar magnitude during both seasons. In May/June adult females strongly dominated; at other times of the year copepodites composed the bulk *of C. finmarchicus* stocks. Concentrations of total *C. finmarchicus* carbon were highest in surface waters in late spring and summer (Fig. 40). Compared with total metazooplankton POC *C. finmarchicus* in May/June contributed most strongly in surface waters (values approached 100 %) and little in deep-water layers. In late summer percentage contribution was not generally as large at the surface but was considerable even in deep-water layers.

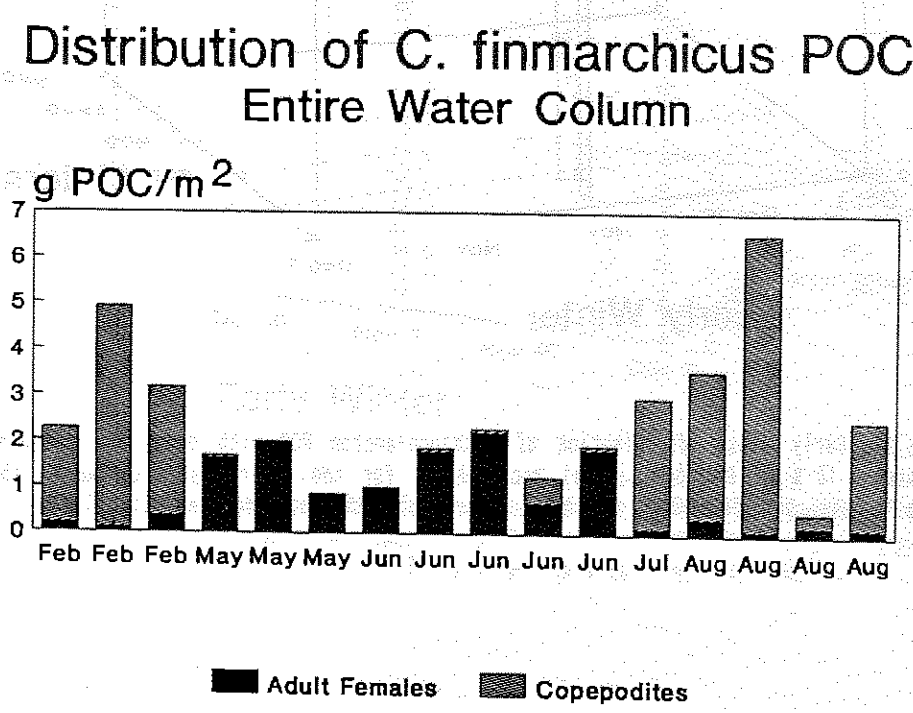


Figure 39. Abundance of *C. finmarchicus* POC for the entire water column on the Vøring Plateau according to the month in which samples were collected. May and June samples were from 1986, February and July samples from 1987 and August samples from 1988.

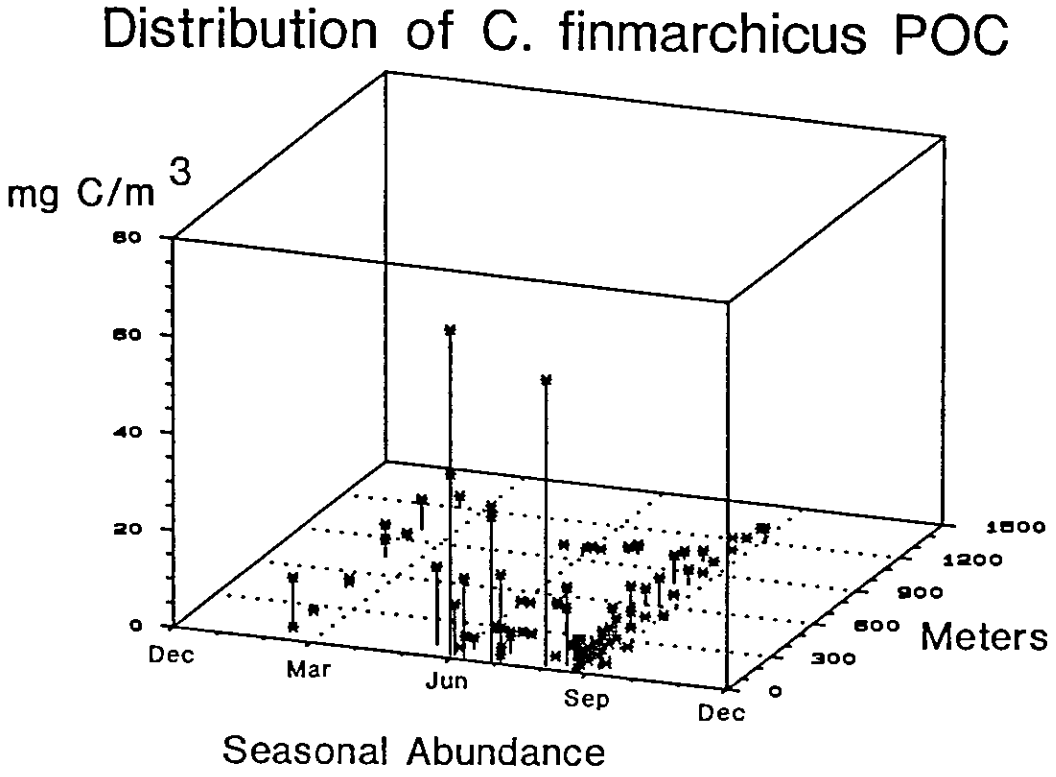


Figure 40. Seasonal distribution of *C. finmarchicus* POC with depth for the entire water column on the Vøring Plateau. Data from samples collected from 1986 to 1988.

In order to relate the distribution of *Calanus finmarchicus* to its life cycle it is more convenient to study numbers of individuals rather than biomass. This eliminates complications due to individual growth.

With little deviation in pattern the seasonal abundance of *C. finmarchicus* individuals per m^2 for the entire water column on the Vøring Plateau (Fig. 41) reflected that for carbon. *C. finmarchicus* copepodites were particularly abundant in late June.

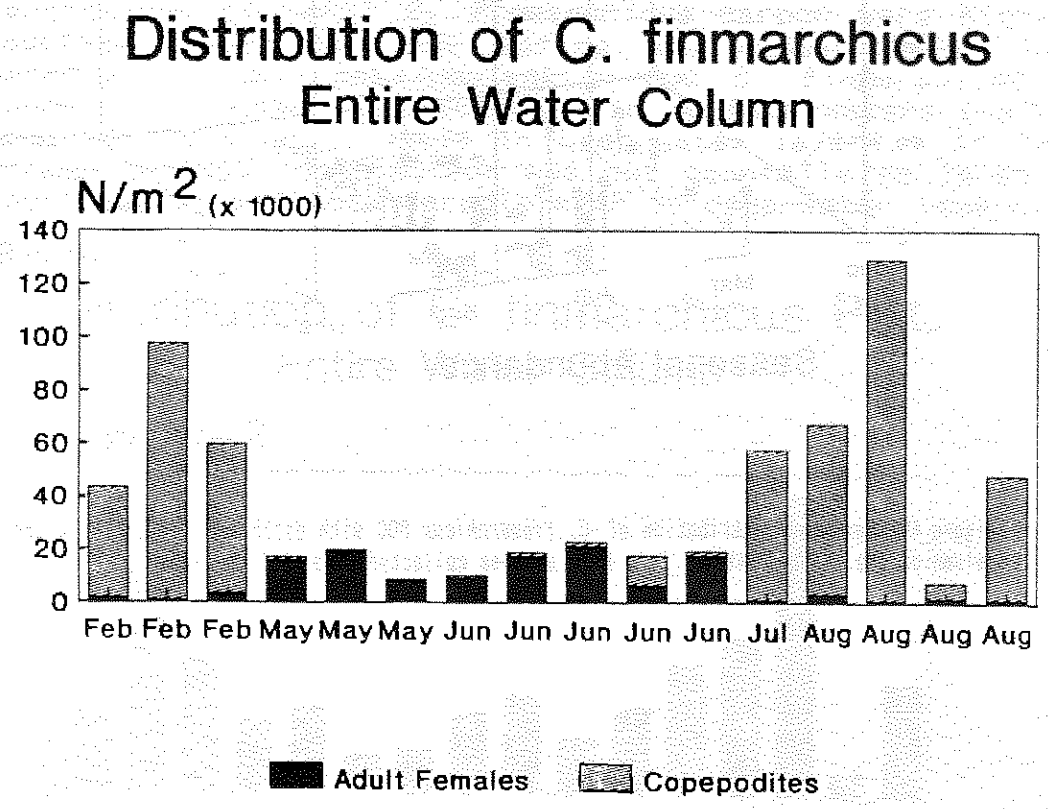


Figure 41. Abundance of *C. finmarchicus* numbers for the entire water column on the Vøring Plateau according to the month in which samples were collected. May and June samples were from 1986, February and July samples from 1987 and August samples from 1988.

The seasonal abundance of total *C. finmarchicus* numbers with depth (Fig. 42) was generally similar to that for *C. finmarchicus* POC. However, a distinct peak in numbers near the beginning of August was evident; the respective biomass peak was more subdued. Relatively high concentrations of this species were encountered in surface and deep-water layers in February and in mid-August and only near the surface in May/June.

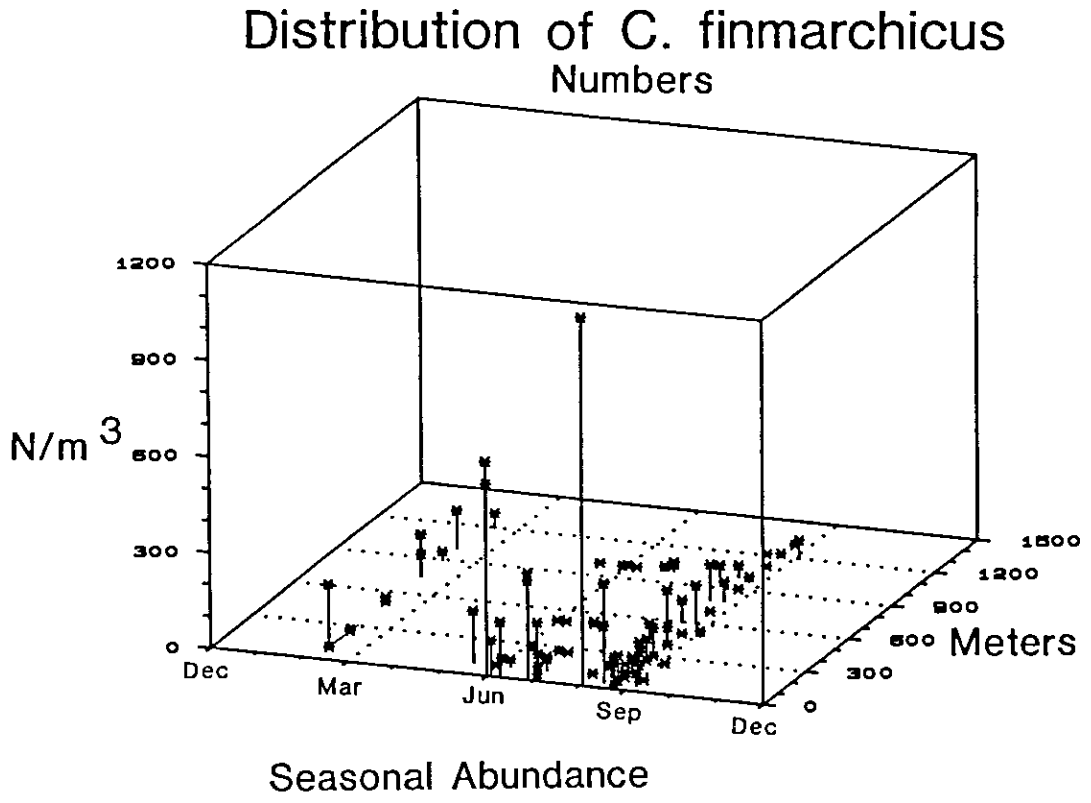


Figure 42. Seasonal distribution of *C. finmarchicus* numbers with depth for the entire water column on the Vøring Plateau. Data from samples collected from 1986 to 1988.

As described above, the stocks in February and mid-August were dominated by copepodites; these were particularly abundant in surface and deep-water layers (Fig. 43) at these times of the year. Interestingly, there was a minimum in copepodite concentrations between about 75 and 200 m in mid-August. In contrast, the high *C. finmarchicus* concentrations near the surface in May/June were primarily attributed to adult females (Fig. 44).

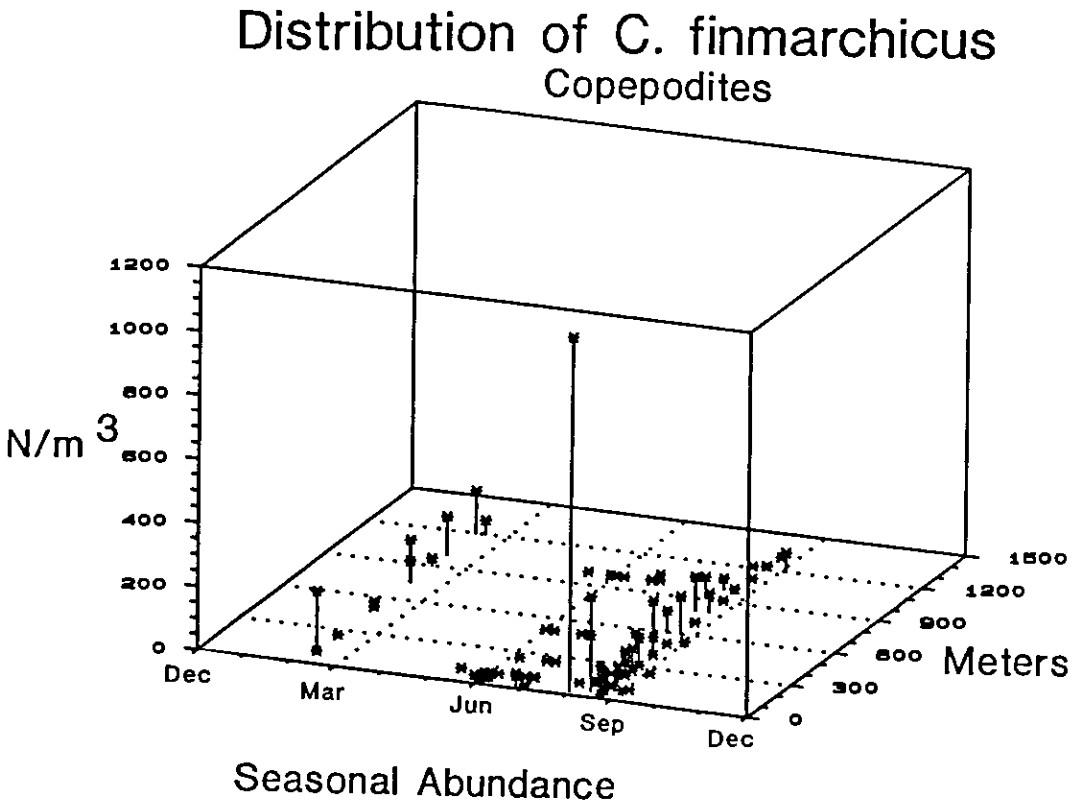


Figure 43. Seasonal distribution of numbers of *C. finmarchicus* copepodites with depth for the entire water column on the Vøring Plateau. Data from samples collected from 1986 to 1988.

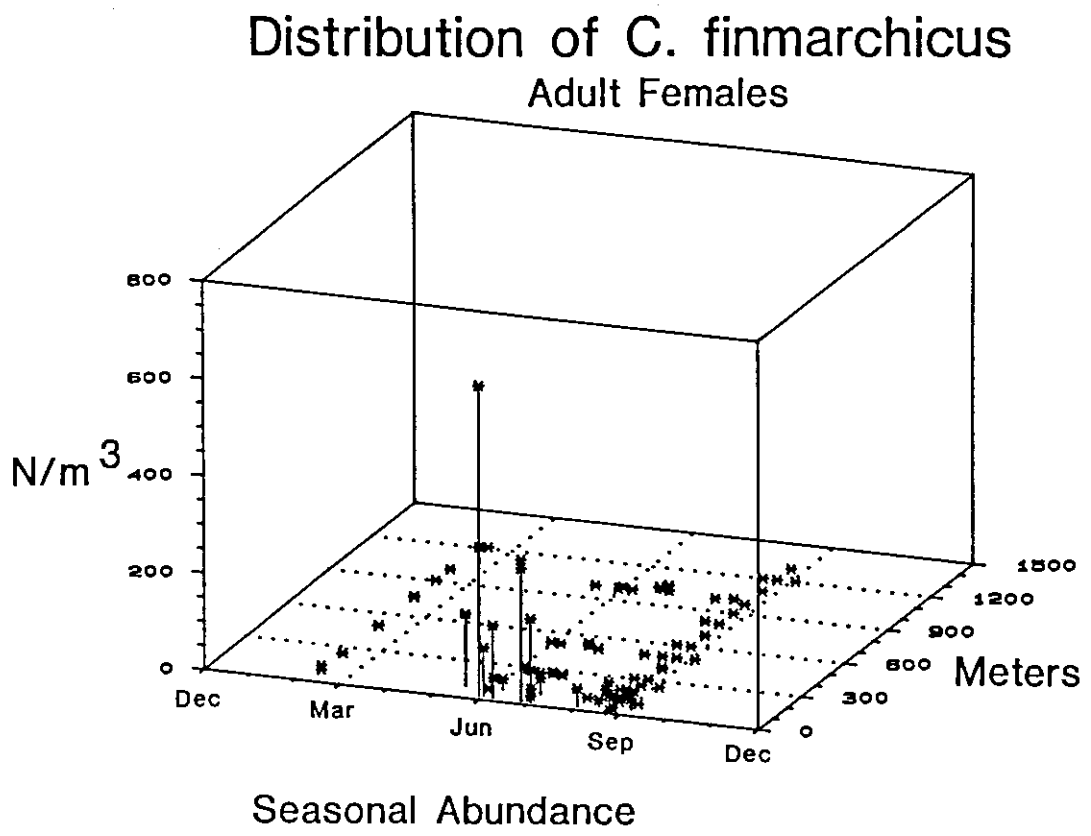


Figure 44. Seasonal distribution of numbers of *C. finmarchicus* adult females with depth for the entire water column on the Vøring Plateau. Data from samples collected from 1986 to 1988.

The major shifts in populational structure are more easily detected by looking at the period from late spring to summer. The May/June metazooplankton regime was dominated by adult female *Calanus finmarchicus* copepods (Fig. 45) near the surface. By mid-August populations of these adults had largely declined, although a small population remained at the surface. In contrast, the numbers of copepodites (Fig. 46) increased greatly and peaked in mid-August. This explains the temporal difference between observed peaks for numbers and carbon biomass. In May/June fewer but larger adult females represented a peak in *C. finmarchicus* biomass, but greater numbers of smaller copepodites composed a peak in concentration of individuals in August. Further, following an initial reduction of copepodite concentrations with increasing depth in August, there was a resurge in numbers between 400 and 900 m depth, below which concentrations declined to almost zero. Two weeks later at the end of August/early September copepodites were most abundant in the depth interval from 500 to 1200 m with smaller concentrations at the surface. In winter the bulk of *C. finmarchicus* copepodites remained in deep-water layers until February, when increments in surface concentrations were observed (see Fig. 43).

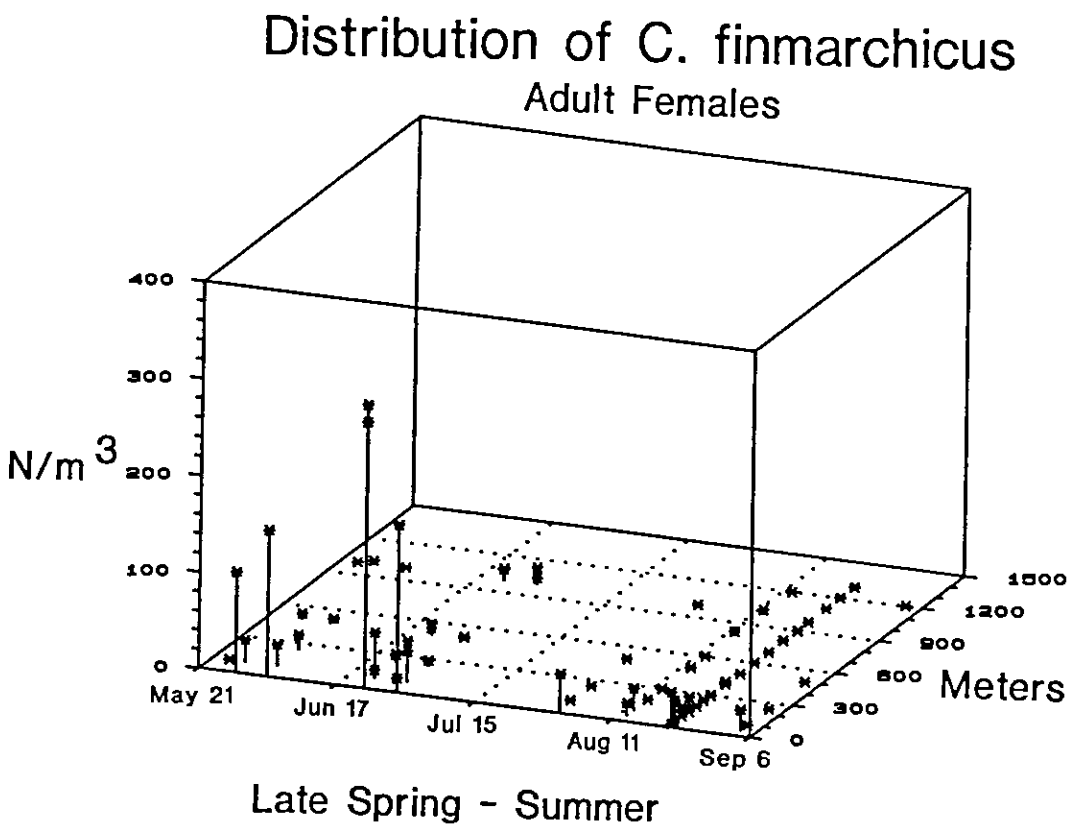


Figure 45. Late spring/summer distribution of numbers of *C. finmarchicus* adult females with depth for the entire water column on the Vøring Plateau. Data from samples collected from 1986 to 1988.

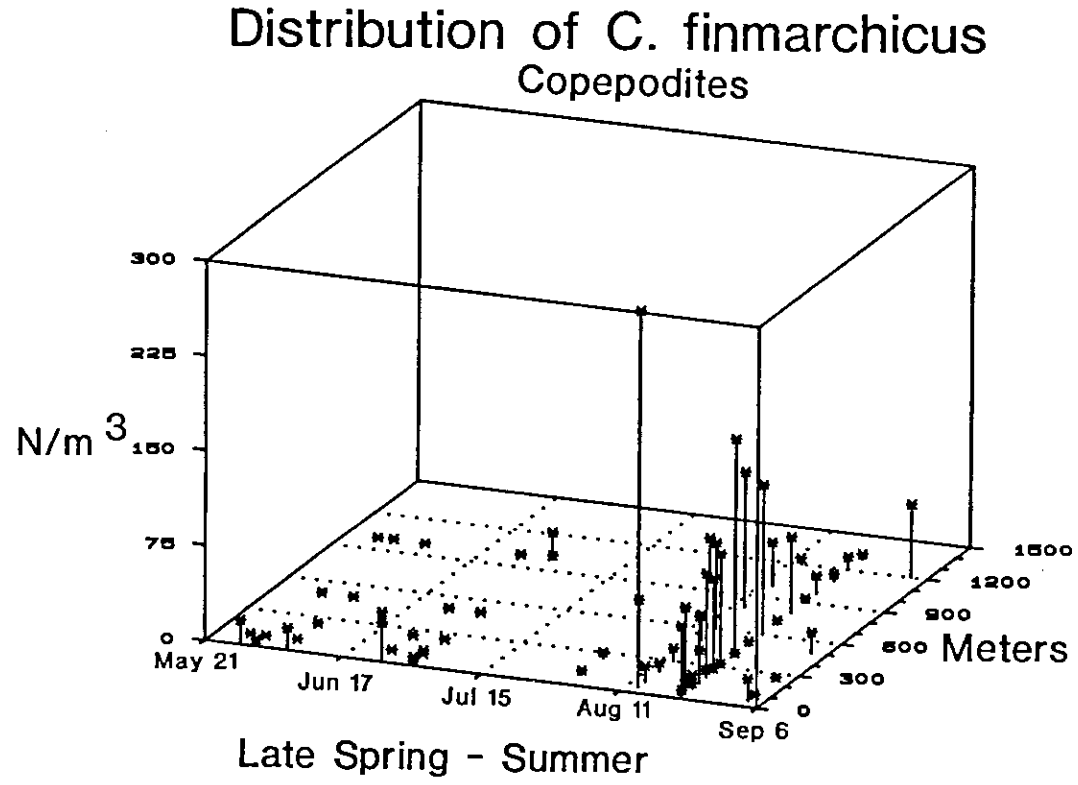


Figure 46. Late spring/summer distribution of numbers of *C. finmarchicus* copepodites with depth for the entire water column on the Vøring Plateau. Data from samples collected from 1986 to 1988.

The general pattern of development of *C. finmarchicus* individual numbers and the shift in dominance from adults to copepodites in the late spring/summer phase is presented in Fig. 47.

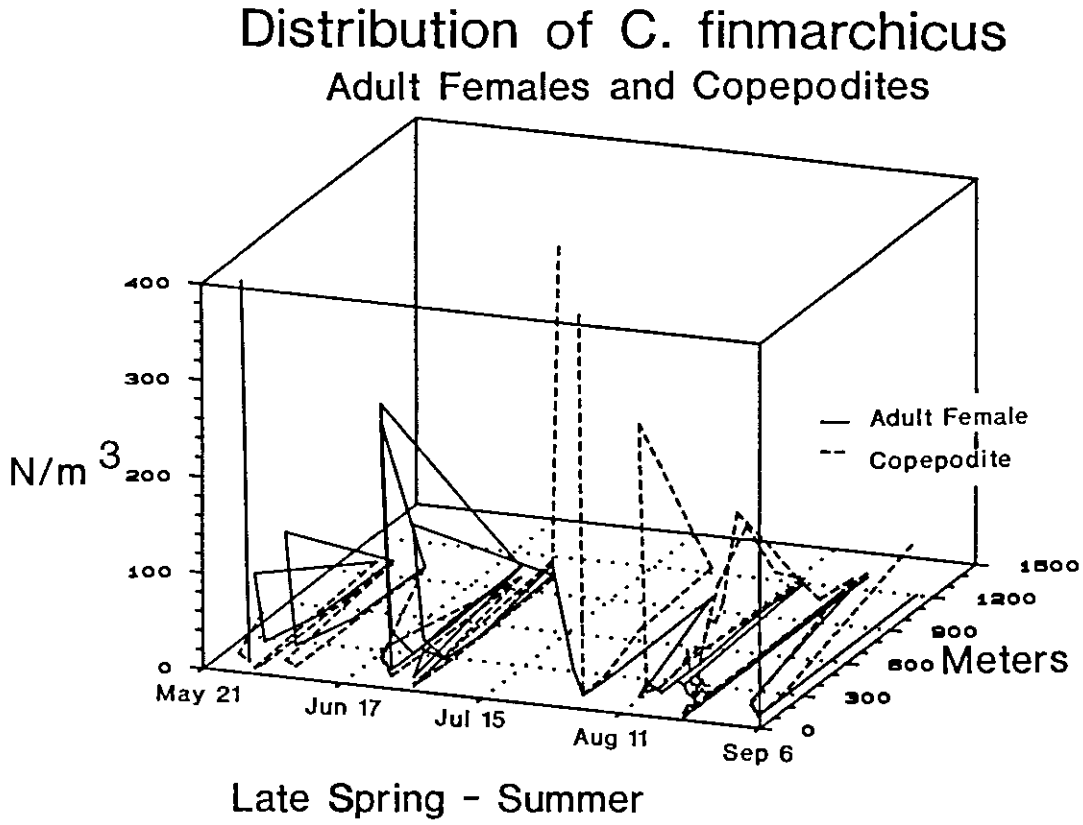


Figure 47. Late spring/summer distribution of numbers of *C. finmarchicus* adult females and copepodites with depth for the entire water column on the Vøring Plateau. Peak values in late May and late July are omitted. Data from samples collected from 1986 to 1988.

The concentrations of males were low throughout the investigation and generally ranged from about 0.0 to 0.3 individuals per m^3. However, in May and June concentrations of up to 6.0 and 2.1 individuals per m^3 were recorded in surface waters (above 100 m depth), respectively. In February a value of 1.8 per m^3 was measured for surface waters. These relatively high concentrations of male *Calanus finmarchicus* copepods corresponded temporally with peak values for copepodites in February and adult females in May/June. At other times of the year males were present but in negligible numbers.

3.1.2.5 *Limacina retroversa*

Except for relatively low numbers in February the euthecosomatous pteropod *Limacina retroversa* was encountered in considerable numbers only in August. Numbers for the entire water column on Vøring Plateau in this month were extremely high and attained values of up to 350 000 individuals per m^2 (Fig. 48). While the numbers of *L. retroversa* in the smallest size fraction decreased with time, larger individuals increased in abundance, which reflected growth of individuals within one month. Growth apparently was accompanied by considerable mortality, as total numbers also decreased.

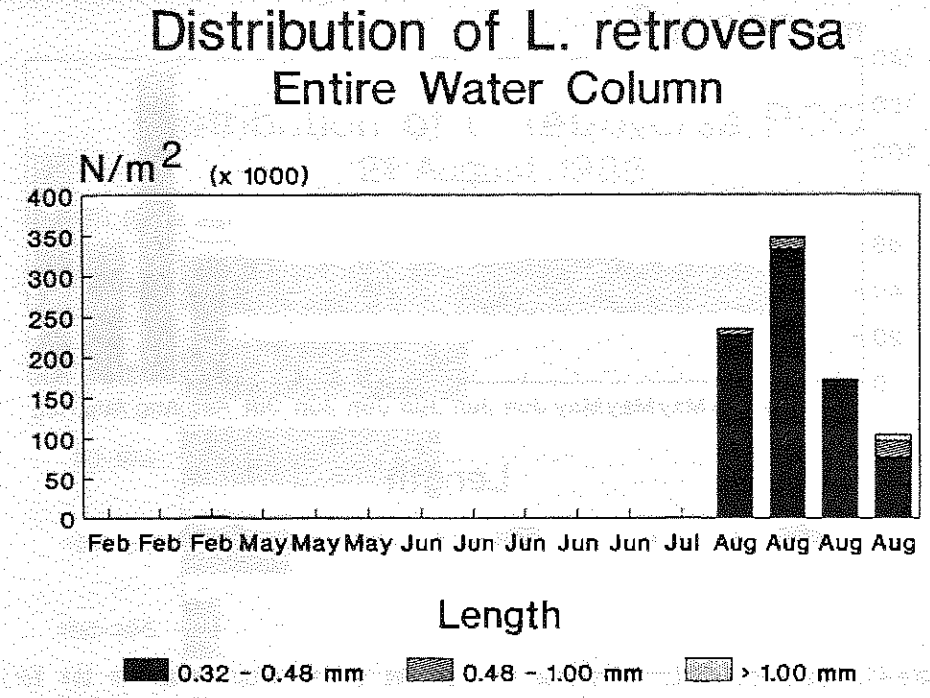


Figure 48. Abundance of *L. retroversa* numbers for the entire water column on the Vøring Plateau according to individual size and the month in which samples were collected. May and June samples were from 1986, February and July samples from 1987 and August samples from 1988.

The development of larger individuals is more easily detected from the distribution of carbon biomass for *Limacina retroversa* (Fig. 49). By the end of August over half of *L. retroversa* POC was attributable to pteropods larger than 0.48 mm in length. Interestingly, although carbon biomass was larger at this station than at the previous one (see Fig. 49), numbers were fewer (see Fig. 48). This, again, indicates substantial mortality during the development and increase in biomass of *L. retroversa* stocks.

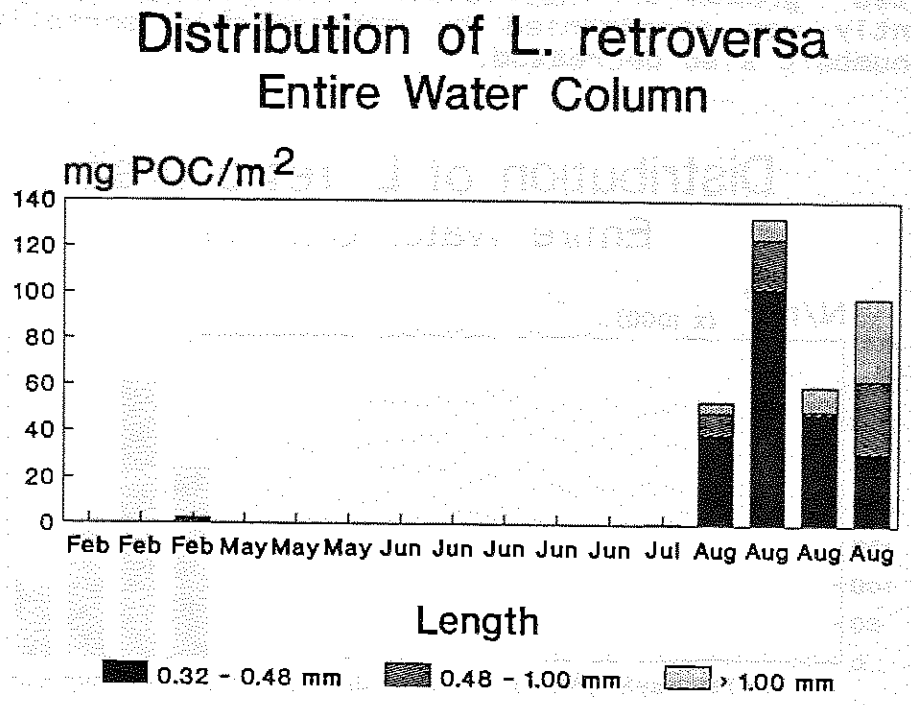


Figure 49. Abundance of *L. retroversa* POC for the entire water column on the Vøring Plateau according to individual size and the month in which samples were collected. May and June samples were from 1986, February and July samples from 1987 and August samples from 1988.

As the distribution of carbon within each of the three size fractions for *L. retroversa* mirrors that for the distribution of numbers for size categories, which is fully described below, *Limacina retroversa* POC shall not be illustrated in detail in this section. Only one example of typical vertical distribution of total *L. retroversa* POC is illustrated (Fig. 50). From a profile made on 21 August 1988 the sharp vertical gradient in POC distribution was readily detectable. About 30 times more *L. retroversa* POC was located within the uppermost 25 m of the water column than in the waters below. Within the depth stratum of 150 to 200 m total *L. retroversa* POC was only about 1/1000th of that in the uppermost 25 m. This sharp vertical gradient for the distribution of *L. retroversa* was typical for all water columns studied in August.

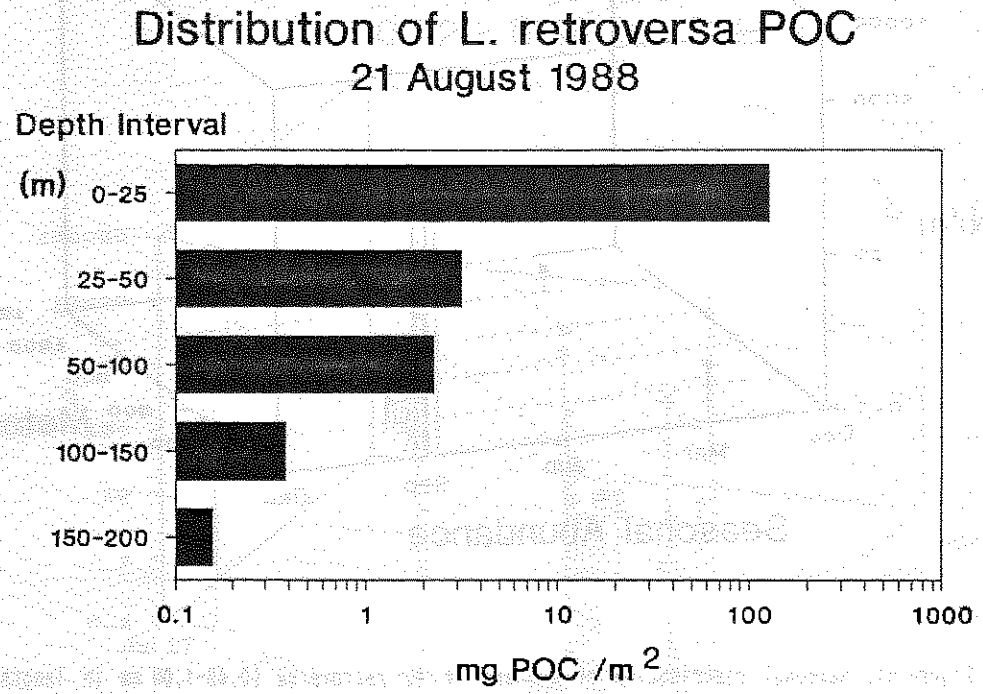


Figure 50. Vertical distribution of *L. retroversa* POC on the Vøring Plateau for the upper 200 m of the water column. Data from 21 August 1988.

The seasonal abundance in the vertical distribution of numbers of *Limacina retroversa* on the Vøring Plateau for all three size fractions showed large stocks in surface waters in August. Small (0.32 - 0.48 mm in length) and large (> 1.00 mm) individuals of *L. retroversa* were collected only in late summer. In February intermediate-sized individuals were collected in very small concentrations (Fig. 51).

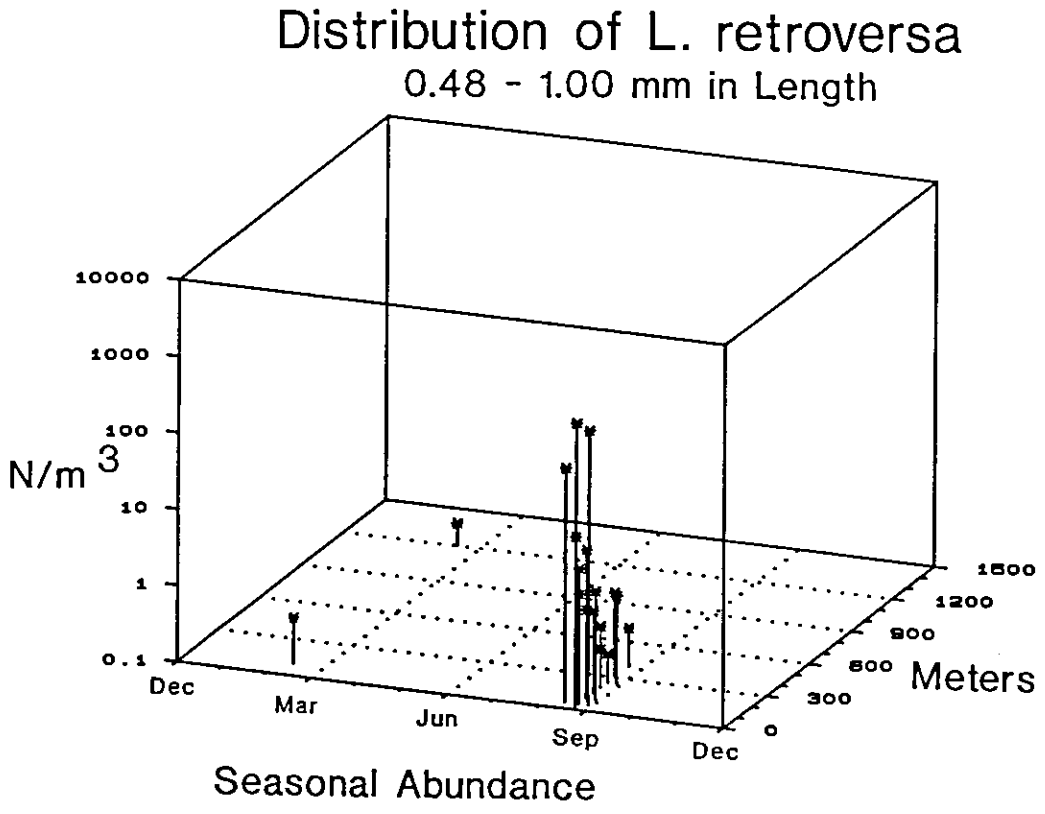


Figure 51. Seasonal distribution of numbers of *L. retroversa* (0.48-1.00 mm in length) with depth for the entire water column on the Vøring Plateau. Seasonal and vertical distribution of smaller (0.32-0.48 in length) and larger individuals (> 1.00 mm in length) was similar although no specimens were collected in February. Data from samples collected from 1986 to 1988.

A more detailed examination of the late August period reveals that concentrations of the smallest size fraction (Fig. 52) increased in August until about the 21st, after which concentrations appeared to be lower. However, surface concentrations (individuals per m^3) in the last profiles in late August (Fig. 53) were based on integrated hauls from 0 to 50 m (see Appendix 1); most previous surface hauls in late summer were from 0 to 25 m. As the vertical gradient for the distribution of *Limacina retroversa* was extreme, net hauls to greater depths yield noticeably smaller numbers per volume. Thus the calculated 10-fold reduction in "surface" concentrations in late August relative to concentrations in mid-August in effect represents about a 5-fold reduction, when integrated for the uppermost 50 m.

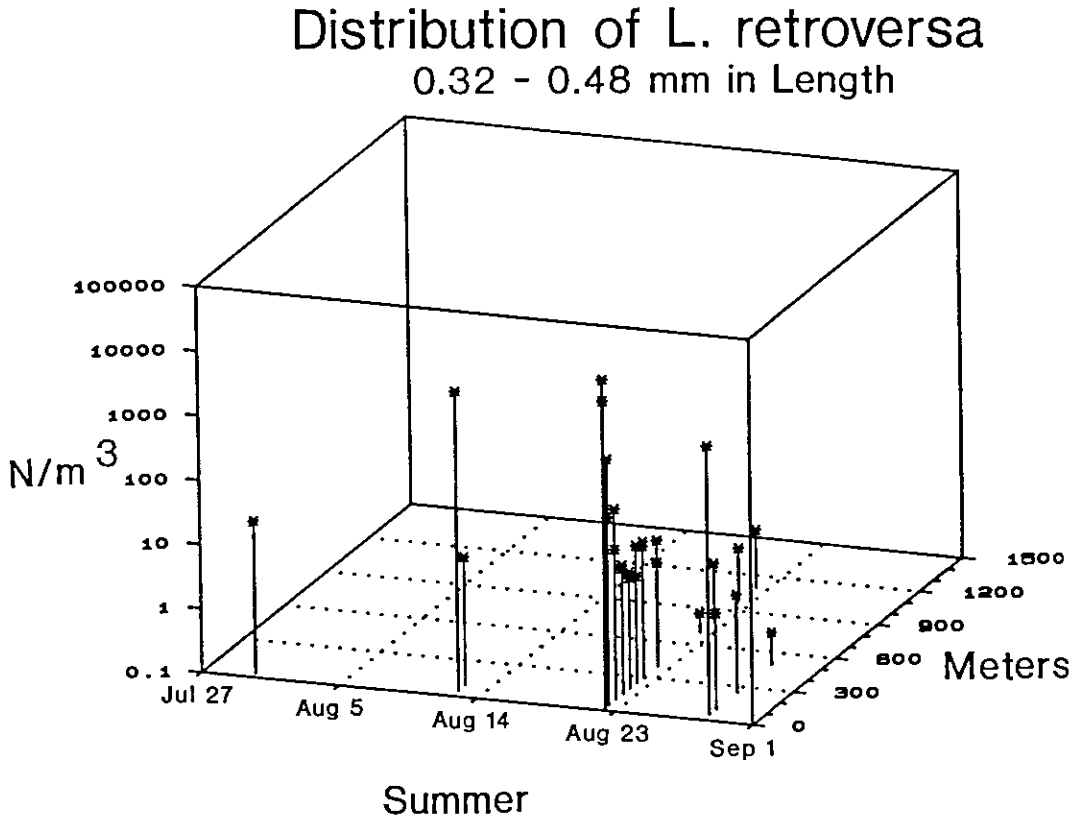


Figure 52. Summer distribution of numbers of *L. retroversa* (0.32-0.48 mm in length) with depth for the entire water column on the Vøring Plateau. Data from samples collected in 1988 except for July 1987.

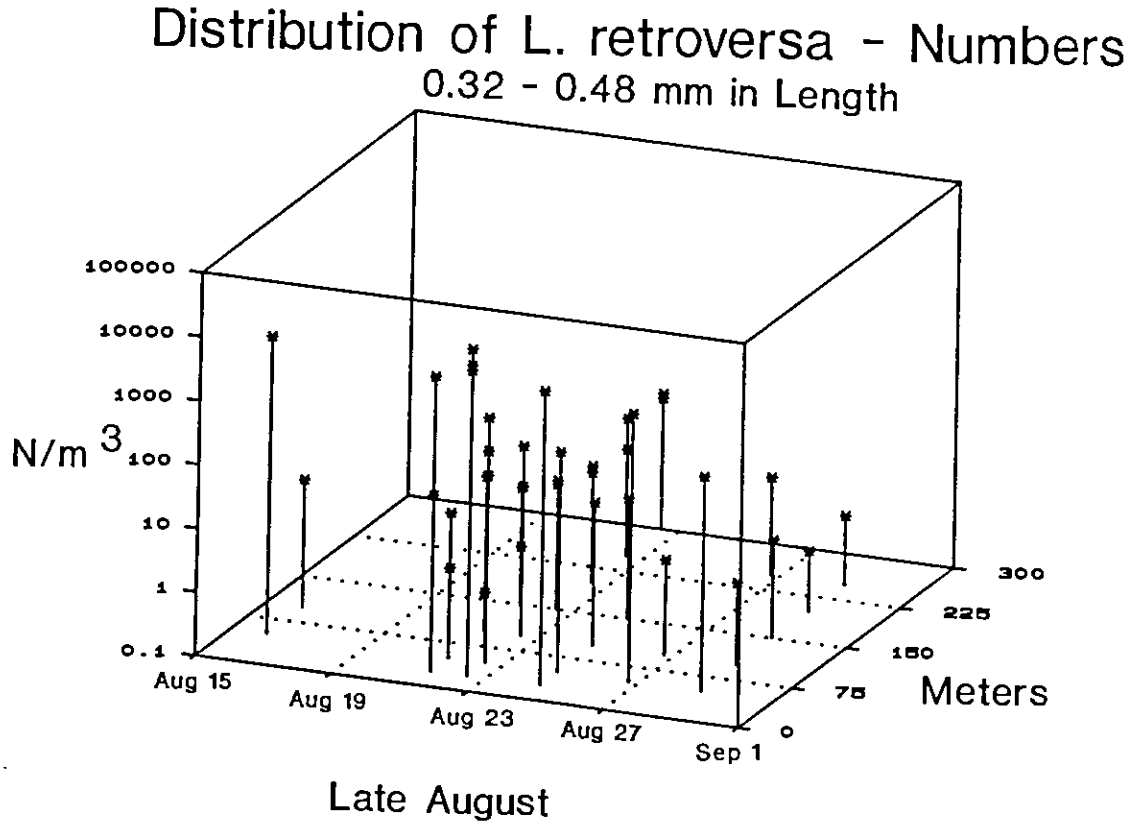


Figure 53. Late August distribution of numbers of *L. retroversa* (0.32-0.48 mm in length) with depth for the upper 300 m of the water column on the Vøring Plateau. Data from samples collected in 1988.

With concentrations of one to two orders of magnitude lower than for the smallest size fraction, intermediate-sized pteropods (Fig. 54) also increased in number from early to mid-August. Although calculated concentrations for surface hauls did not increase in late August due to the above-described dilution effect caused by deeper net hauls, concentrations of intermediate-sized pteropods in the uppermost 50 m in reality increased. In similar fashion large pteropods (> 1.0 mm in length) showed an increase in concentration during August (Fig. 55).

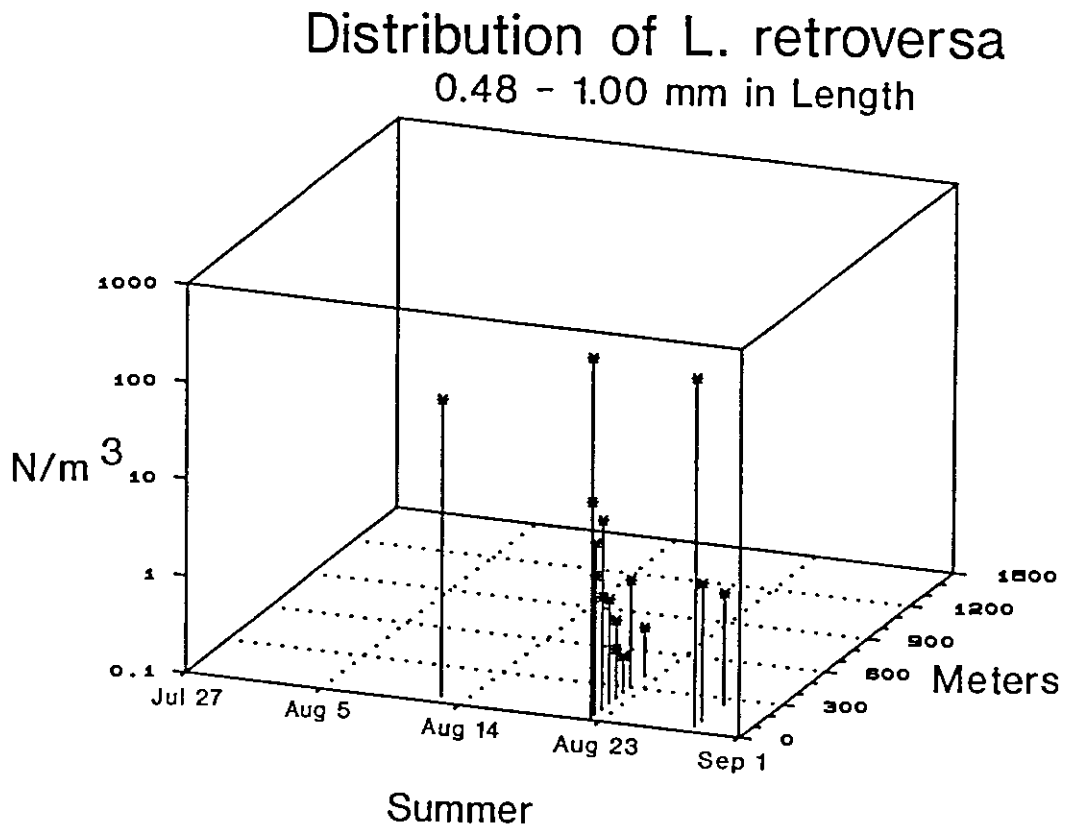


Figure 54. Summer distribution of numbers of *L. retroversa* (0.48-1.00 mm in length) with depth for the entire water column on the Vøring Plateau. Data from samples collected in 1988 except for July 1987.

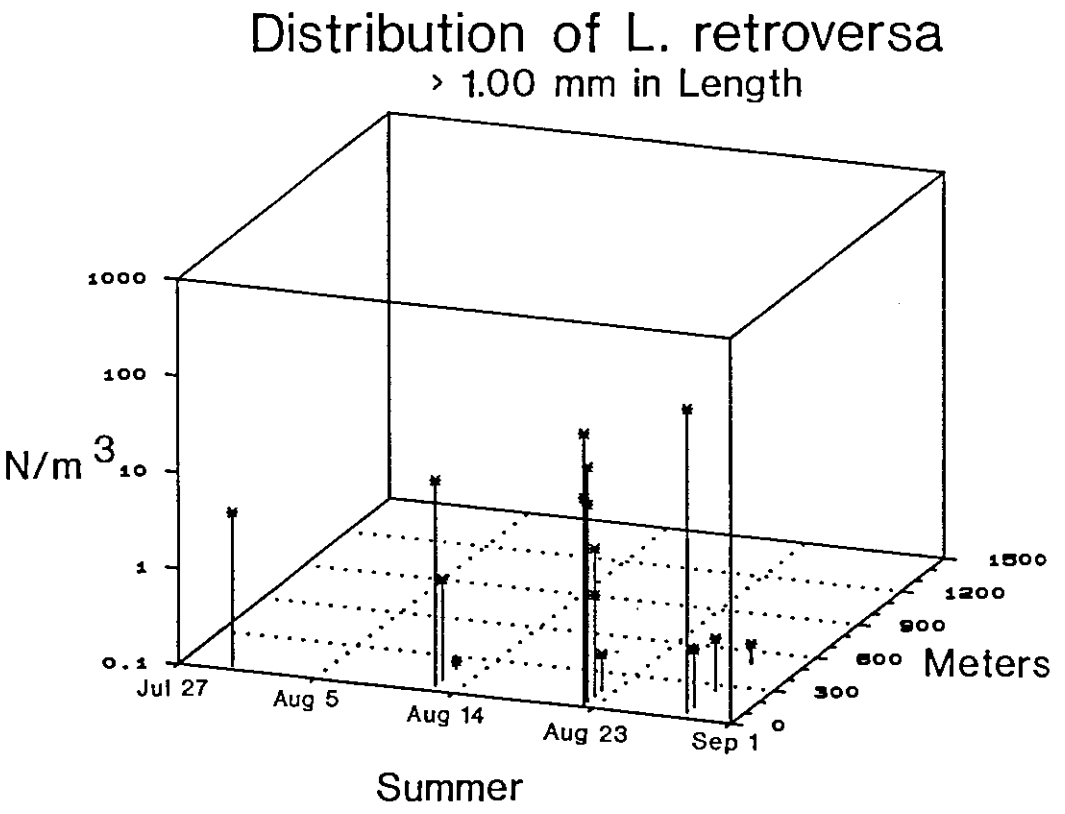


Figure 55. Summer distribution of numbers of *L. retroversa* (> 1.00 mm in length) with depth for the entire water column on the Vøring Plateau. Data from samples collected in 1988 except for July 1987.

Within a period of 75 hours 6 vertical net profiles were conducted in the immediate vicinity of a drifting sediment trap array (maximum trap depth of 100 m). Thus surface sampling during this period was presumably within the same body of water. Vertical distribution of small and intermediate-sized *Limacina retroversa* pteropods did not exhibit a diel pattern. In contrast individuals > 1.0 mm in length (Fig. 56) were most abundant in surface waters above 30 m from about 19.00 H to 3.00 H. From about 7.30 H to 15.00 H peak abundances were in the depth stratum of 30 to 60 m. Thus large individuals of *L. retroversa* appeared to migrate to the surface in the evening to descend again a few hours past midnight. Low concentrations at all depths at 7.30 H were also found for the smaller size categories and were presumably due to patchiness. However, the relative distribution in relation to depth is assumed to be representative of the larger stock.

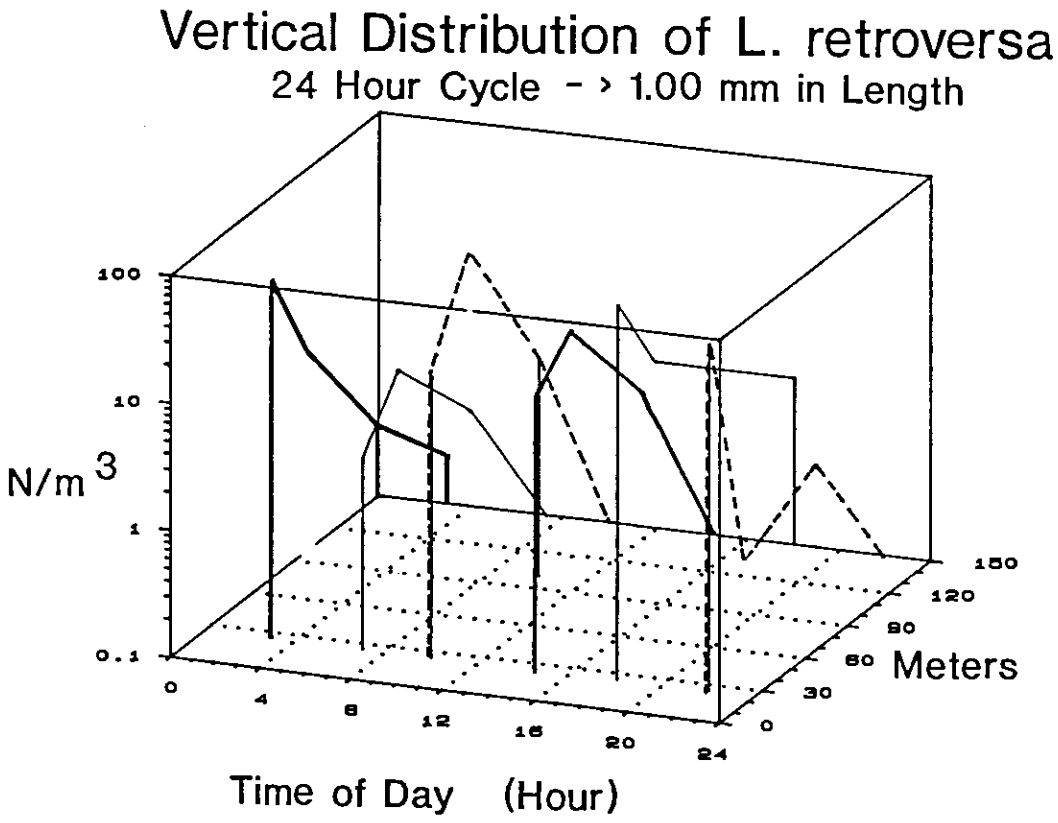


Figure 56. Diel pattern of distribution for *L. retroversa* (> 1.00 mm in length) with depth for the upper 150 m of the water column on the Vøring Plateau. Data were collected within 75 hours in the immediate vicinity of a drifting sediment trap array.

3.1.3. Sedimentation

Sedimentation for bulk parameters and biogenic components on the Vøring Plateau at a depth of 500 m in the years 1986 to 1988 is presented. Data from the period of May/June 1986, during which time sampling in three depths with high temporal resolution was conducted, are presented in detail. In addition, results from the series of deployments of free drifting traps at a depth of 100 m in August 1988 are provided.

Bulk parameters

The annual pattern of sedimentation on the Vøring Plateau at a depth of 500 m (Fig. 57) was characterized by

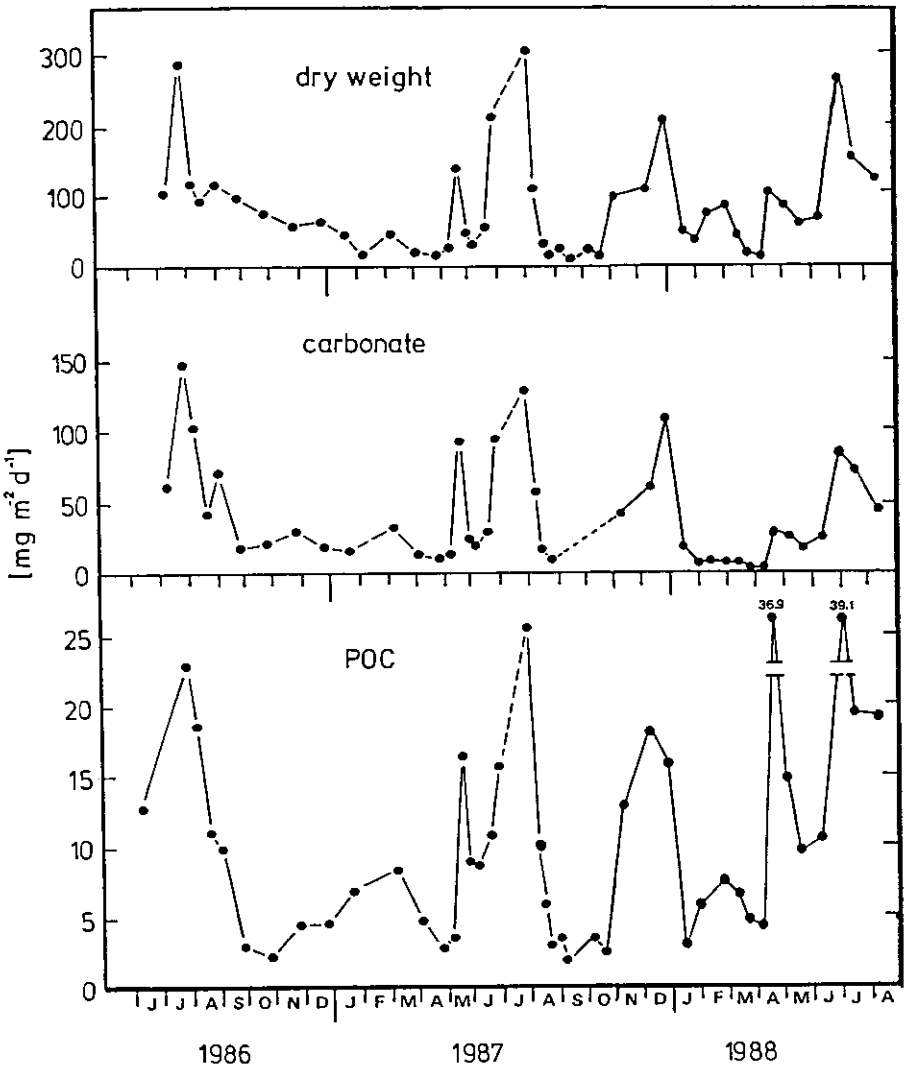


Figure 57. Daily sedimentation rates of total flux (dry weight), carbonate and POC at a depth of 500 m on the Vøring Plateau. Dotted lines indicate incomplete data. (from Bathmann *et al.* accepted; supplemented with data from 1988)

peak sedimentation rates of about 300, 100 - 150 and 25 - 35 mg per m^2 per day for dry weight, carbonate and POC in late summer for three consecutive years, respectively. A secondary peak was observed in late spring. A large peak in November/December of 1987 was recorded. A corresponding peak in 1986 did not occur.

Biological composition

Except for the periods in December 1987 and February and April 1988, during which time diatom sedimentation (predominantly empty valves and fragments) showed no peaks (Fig. 58), the annual pattern of sedimentation of this phytoplankton group was similar to that for dry weight. Thecae from tintinnids including *Favella* spp. and *Salpingella* spp. were characterized by high rates in July and little sedimentation at other times of the year. The sedimentation of tests from foraminifers including *Neogloboquadrina pachyderma* and *Globigerina bulloides* also showed increases in July but displayed peaks in winter 1986/1987 and April 1988 as well. Silicoskeletons from radiolarians including *Sagoscena* spp. and *Helotholus* spp. exhibited late summer peaks and relatively high sedimentation rates in winter 1986/1987 and April 1988. The late summer peak in 1986 was conspicuously recorded one month after that for foraminifers and tintinnids. Shells of *Limacina retroversa* pteropods (> 2 µm in length) were similarly characterized by peak sedimentation rates in late summer. A peak in April 1988 was evident. In 1986 the late summer peak was one and two months later than that for radiolarians and foraminifers, respectively.

All three categories of fecal pellets - copepod fecal pellets, oval fecal pellets and minipellets - exhibited increased sedimentation rates in late summer, early winter 1986 and late winter 1988. Note that oval fecal pellets in late summer 1986 displayed a maximum rate one month following that for copepod fecal pellets.

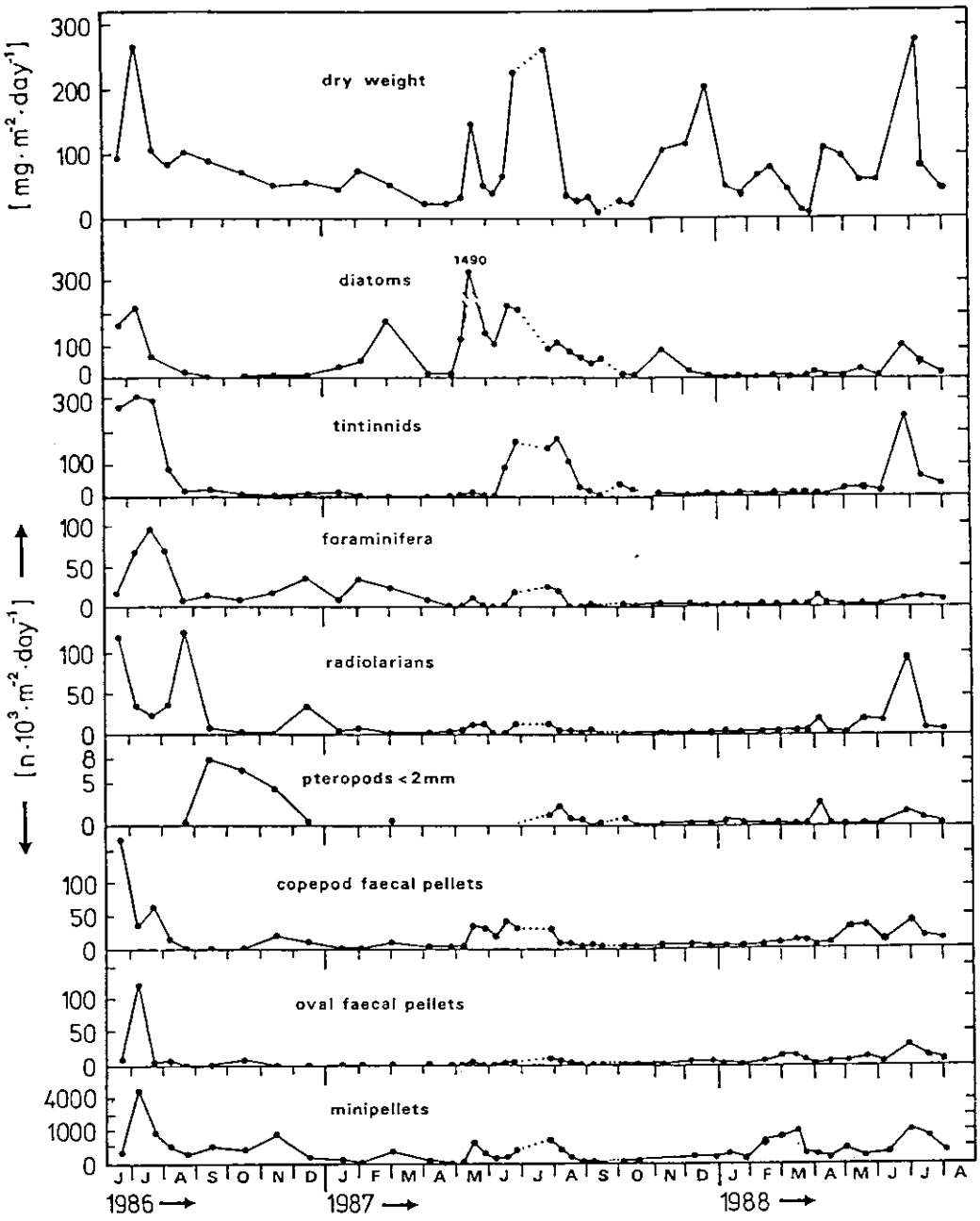


Figure 58. Daily sedimentation rates of total flux (dry weight), diatom fragments, tintinnid thecae, foraminifer tests, radiolarian silicoskeletons, pteropod (*L. retroversa*) shells, copepod fecal pellets, oval fecal pellets and minipellets at a depth of 500 m on the Vøring Plateau. Dotted lines indicate incomplete data. (from Bathmann *et al.* accepted; supplemented with data from 1988)

May/June 1986

The decrease in flux rates (Fig. 59) with depth was considerable as seen in May/June 1986. Rates for particulate organic carbon in late June were about 250, 100 and 50 mg per m^2 per day for depths of about 150, 300 and 1000 m, respectively.

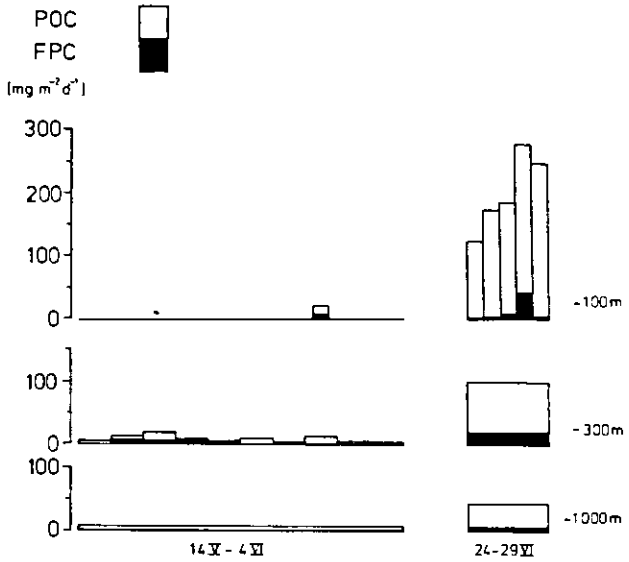


Figure 59. Daily sedimentation rates of particulate organic carbon and fecal pellet carbon for 3 depths in May and June 1986 on the Vøring Plateau. (from Bathmann *et al.* 1987)

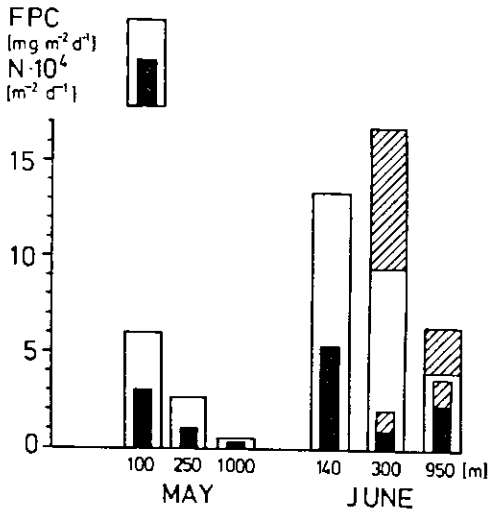


Figure 60. Average daily sedimentation rates of numbers (N, narrow bars) and fecal pellet carbon (FPC, wide bars) for May and June 1986 on the Vøring Plateau. White and black areas indicate copepod fecal pellets; shaded areas indicate oval fecal pellets.

Sedimentation rates were larger in June than in May. The amount of sedimenting fecal material was also considerably larger in late June. The flux of copepod fecal pellets (Fig. 60) progressively decreased with depth. In June large quantities of oval fecal pellets contributed substantially to pellet flux at 300 m and 950 m. The flux of fecal pellet carbon at 300 m relative to suspended material above the trap increased greatly from May to late June (Fig. 61). This was due to increased sedimentation rates coupled with lower concentrations of fecal pellets in the overlying water column (see Table 3).

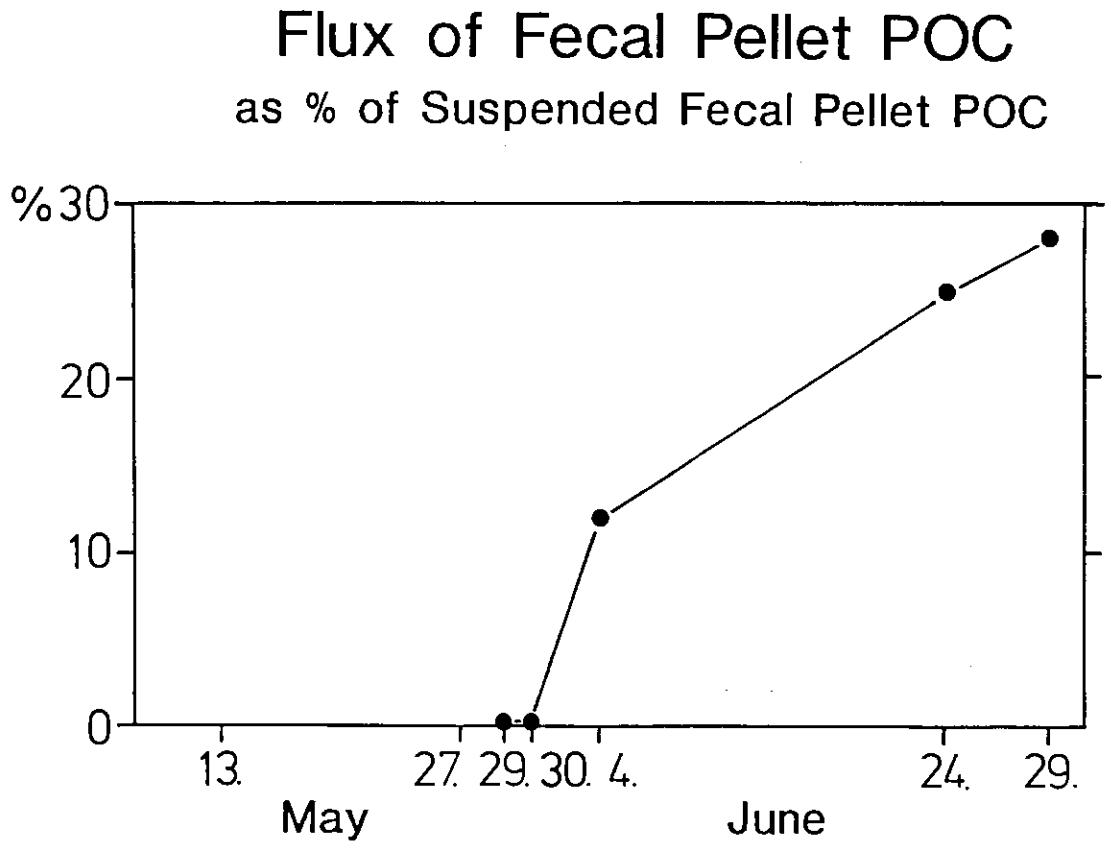


Figure 61. Percentage of daily sedimentation of fecal pellet carbon per m² at a depth of 250-300 m in May and June 1986 on the Vøring Plateau relative to suspended fecal pellet carbon per m² above the trap depth.

August 1988

Flux at 100 m from 19 to 31 August 1988 (Fig. 62) peaked from the 23rd to 25th with about 500 mg dry weight per m^2 per day. 50 % (by weight) or more of sedimented material was attributable to carbonate. The bulk of microscopically identifiable material was composed of shells from *Limacina retroversa*.

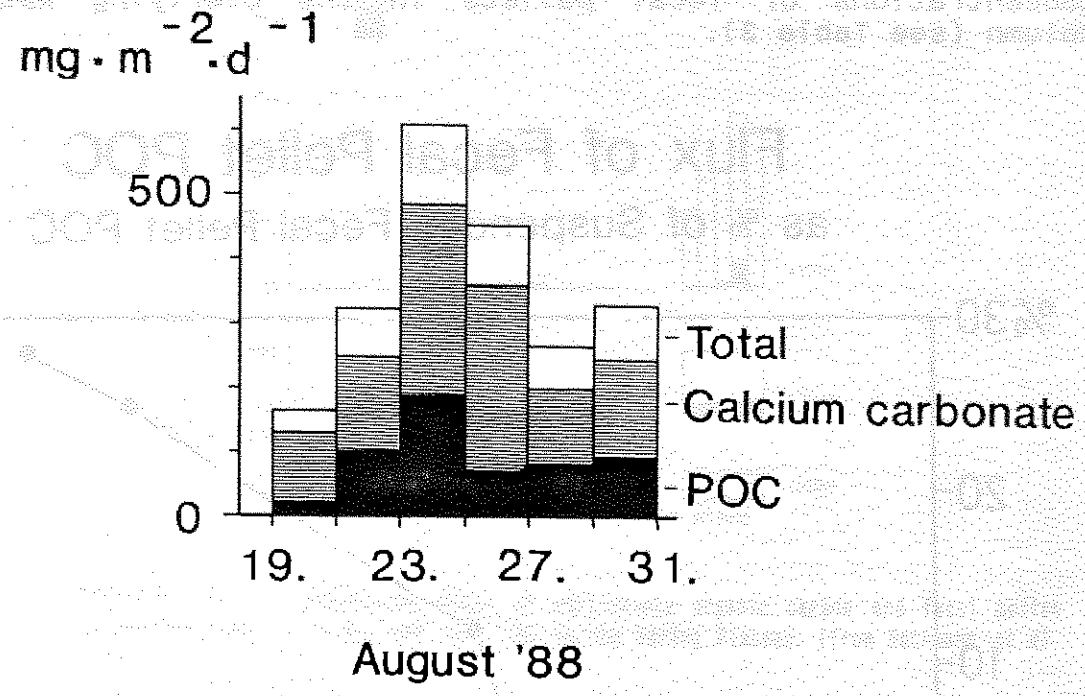


Figure 62. Daily sedimentation of total flux (dry weight), carbonate and POC at a depth of 100 m in late August 1988 on the Vøring Plateau. (from Bathmann unpublished)

3.2. Experimental Studies

Results from experimental studies are presented in two sections: Shipboard experiments (section 3.2.1) and Land-based laboratory investigations (section 3.2.2).

3.2.1. Shipboard experiments

Three major groups of results are presented in this section. Zooplankton feeding behavior and fecal material identification (section 3.2.1.1) is a summary of qualitative observations made during this study. Copepod grazing potential (section 3.2.1.2) addresses the feeding activity of copepods in winter. In Copepod-pteropod interactions (section 3.2.1.3) aggregate formation and sinking as well as a comparative analysis of copepod and pteropod feeding are presented.

3.2.1.1. Zooplankton feeding behavior and fecal material identification

A short summary of pertinent observations relative to feeding behavior of metazooplankters during incubation experiments is presented. The information may be helpful for other researchers who may conduct studies involving incubations with these plankters. Descriptions and photos of several types of copepod fecal pellets identified during experimentation are subsequently included.

Feeding behavior

Calanus finmarchicus: swim steadily; evenly distributed; overwintering diapausal copepodites did not feed

Pseudocalanus elongatus: swim steadily; congregate often near the middle or bottom of incubation vesicles

Centropages hamatus: swimming characterized by regular bursts of movement; congregate often at the surface of vesicles; attracted to light

Oithona similis: often float passively near or rest on the bottom of vesicles; capable of short bursts of very quick swimming

Acartia clausii: may swim steadily or in short bursts; often near the surface of vesicles; attracted to light

Euchaeta spp.: float passively; capable of short bursts of rapid swimming; prey (assuming that tightly held animals were prey) may include organisms much larger than itself, e.g. larger pteropods (*Clione retroversa*).

other carnivorous copepods: generally passive floaters capable of short bursts of rapid swimming

Limacina retroversa (euthecosomatous pteropod): charac-

terized by rapid swimming to the surface of vesicles and slower sinking to the bottom; production of large (up to 1 to 2 cm in diameter) adhesive aggregates

Thysanoessa sp. (euphausiid): rapid steady swimming especially when stimulated by light; also long nonmotile periods at the bottom of vesicles; robust

Hyperoche medusarum (amphipod): often float "helplessly" on the surface probably due to cohesion of the exoskeleton with the air-water interface; robust

Conchoecia obtusata (ostracod): steady swimmer; long inactive periods at the bottom of vesicles

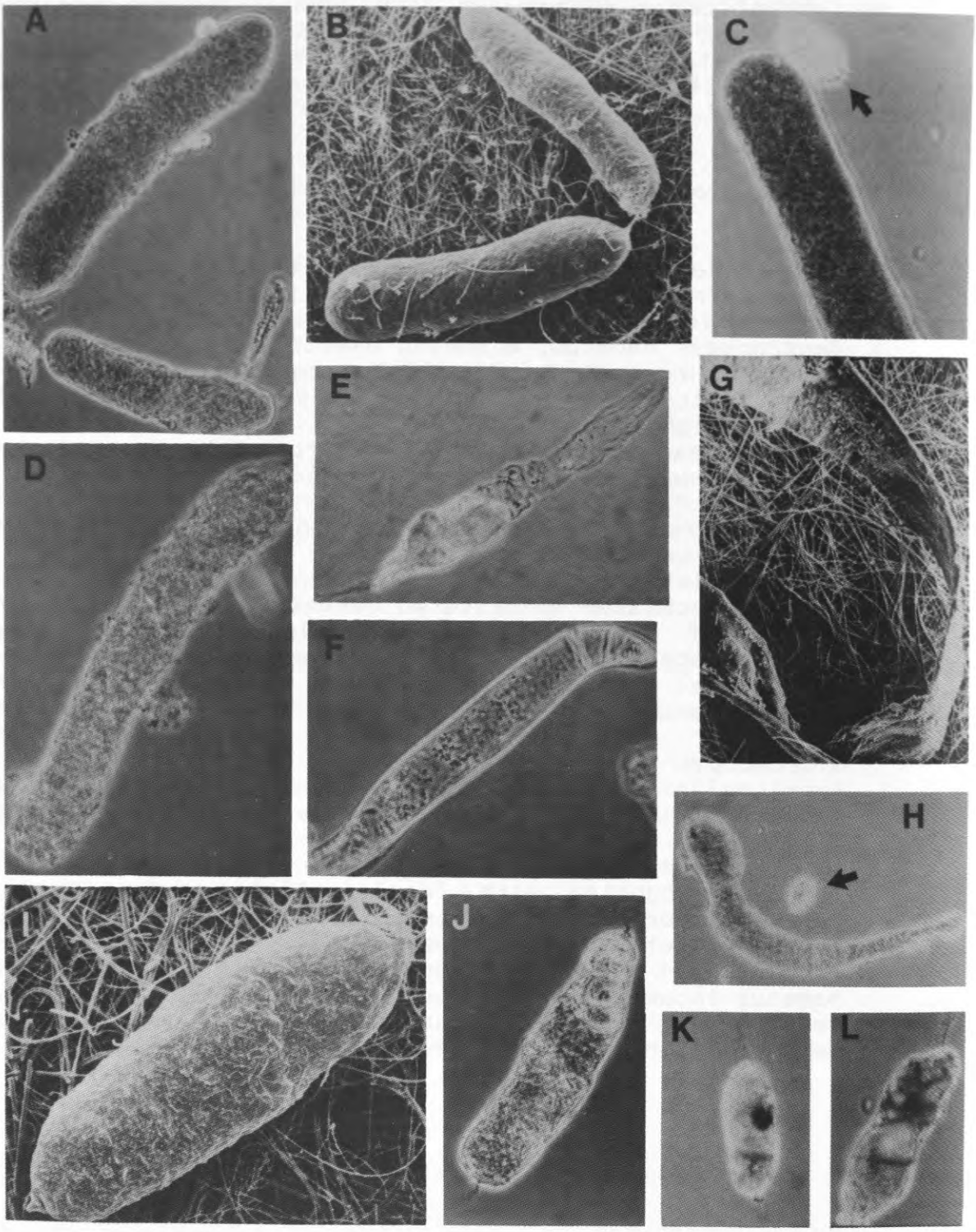
Variability in the forms of copepod fecal pellets

The photographs on the following page depict the variabiltiy in the forms of copepod fecal pellets. Explanations are provided below. The cylindrical form is the most "common" type of copepod fecal pellet, however a variety of other shapes can make identification difficult. The contents may also differ considerably in appearance. The small pellets (photos I, J, K and L) from *Centropages hamatus* may be "secondary" fecal pellets produced from the ingestion of fecal matter.

Explanation of photographs of fecal pellets on the following page:

A. Compact fecal pellets (longer pellet is approx. 200 µm in length) from *Centropages hamatus*; light microscopy.
B. Compact fecal pellets (approx. 200 µm in length) from *Centropages hamatus*; scanning electron microscopy.
C. Detail of compact fecal pellet from *Centropages hamatus*; arrow indicates a ciliate (probably *Euplotes* sp.) on the pellet; light microscopy.
D. Sparsely packed fecal pellet (approx. 650 µm in length) from *Calanus finmarchicus*; light microscopy.
E. Partially filled fecal pellet (approx. 200 µm in length) from *Centropages hamatus* incubated with fecal pellets; light microscopy.
F. Ghost pellet (approx. 320 µm in length) from *Centropages hamatus* incubated in filtered seawater; light microscopy.
G. Detail of collapsed ghost pellet from *Centropages hamatus*; scanning electron microscopy.
H. Bent fecal pellet (approx. 250 µm in length) from *Pseudocalanus elongatus*; arrow indicates a ciliate (probably *Euplotes* sp.) near the pellet; light microscopy.
I. Fecal pellet (approx. 90 µm in length) from *Centropages hamatus* incubated with fecal pellets; scanning electron microscopy.
J. Fecal pellet (approx. 70 µm in length) from *Centropages hamatus* incubated with fecal pellets; note "tail" - collapsed portion of peritrophic membrane - at both ends of the pellet; light microscopy.
K. Fecal pellet (approx. 50 µm in length) from *Centropages hamatus* incubated with fecal pellets; light microscopy.
L. Fecal pellet (approx. 50 µm in length) from *Centropages hamatus* incubated with fecal pellets; light microscopy.

Copepod fecal pellets



3.2.1.2. Copepod grazing potential

Overwintering *Calanus finmarchicus* copepodites (CV) collected from midwater layers in February on the Vøring Plateau did not graze on phytoplankton in incubation experiments. However, *C. finmarchicus* and *Metridia longa* copepods collected in surface waters were capable of active feeding (Fig. 63). Phytoplankton concentrations expressed both as cells and chl. *a* per liter in the seawater media of both experiments decreased significantly; reductions of phytoplankton in controls were minimal. Fecal pellets were produced during incubations (Fig. 64). For details concerning this experiment see Bathmann *et al.* (in press).

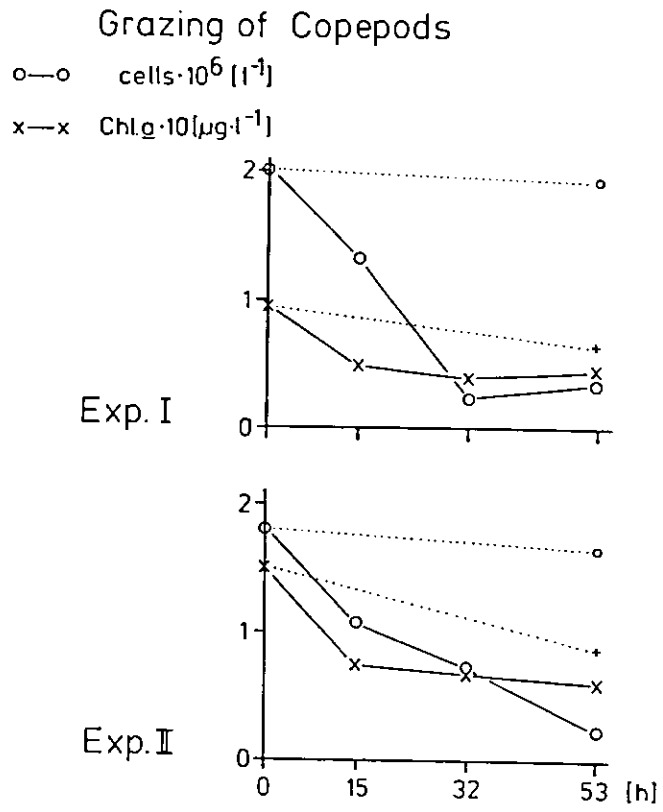


Figure 63. Grazing in winter by surface copepods. Two time series experiments for concentration of cells and chlorophyll *a* of natural phytoplankton during incubations with (continuous line) and without (dotted line) copepods. (from Bathmann *et al.* in press)

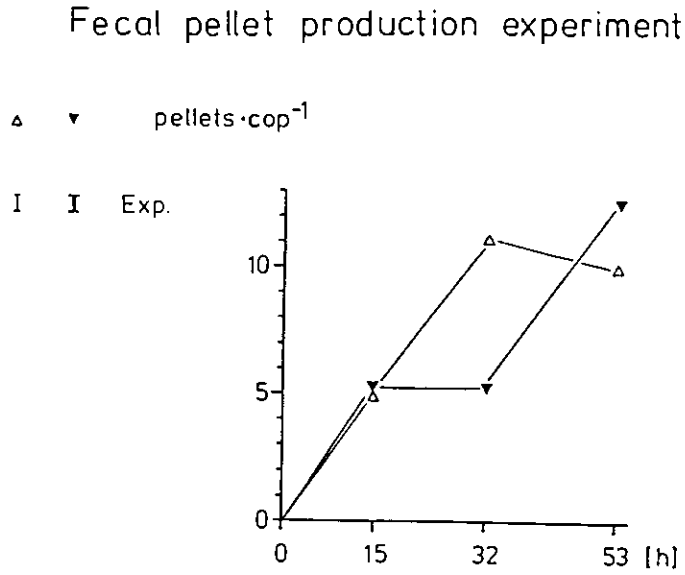


Figure 64. Fecal pellet production in winter by surface copepods grazing on natural phytoplankton. (from Bathmann *et al.* in press)

3.2.1.3. Copepod-pteropod interactions

Aggregate formation

The euthecosomatous pteropod *Limacina retroversa* formed aggregates during incubation experiments (Table 5).

Table 5. Influence of *Limacina retroversa* and *Calanus finmarchicus* on aggregate formation

Number/incubation		Number/liter (Volume (mm^3)/liter)			
		Size range in mm			
C.fin	*L.retr*	.4-.8	.8-1.2	1.2-1.6	1.6-2.0
0	0	15.00 (0.21)	5.00 (2.62)	1.67 (2.39)	0.00 (0.00)
0	0	4.17 (0.06)	3.33 (1.75)	0.83 (1.20)	0.00 (0.00)
0	5	68.33 (0.97)	17.50 (9.16)	6.67 (9.58)	1.67 (5.09)
0	5	55.83 (0.79)	25.00 (13.09)	3.33 (4.79)	2.50 (7.63)
0	10	79.17 (1.12)	29.17 (15.27)	12.50 (17.96)	4.17 (12.72)
0	10	85.83 (1.21)	25.83 (13.53)	8.33 (11.97)	2.50 (7.63)
5	5	53.33 (0.75)	19.17 (10.04)	6.67 (9.58)	1.67 (5.09)
5	5	41.67 (0.59)	15.00 (7.85)	5.00 (7.18)	0.83 (2.54)

The higher incidence of aggregates after incubations of *L. retroversa* with phytoplankton compared with controls with only phytoplankton was evident in numbers (Fig. 65) as well as in the volume of aggregates (Fig. 66). In the 1.2-l bottles used for incubation the volume of aggregates was about 30 mm^3 greater in the presence of 5 and 10 individuals of *L. retroversa* relative to controls.

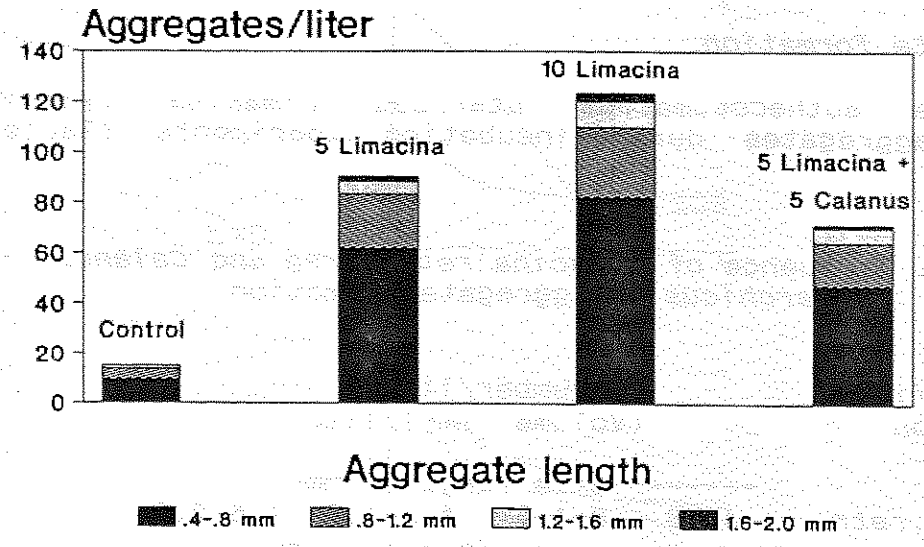


Figure 65. Average numbers of aggregates recovered after parallel incubations (24 h) in 1.2-l bottles of 5 or 10 individuals of *L. retroversa* with natural phytoplankton. In one case 5 individuals of *C. finmarchicus* were incubated with 5 *L. retroversa* and natural phytoplankton. The control was with phytoplankton only. Aggregates were grouped according to length (maximum linear dimension) in 4 size-categories.

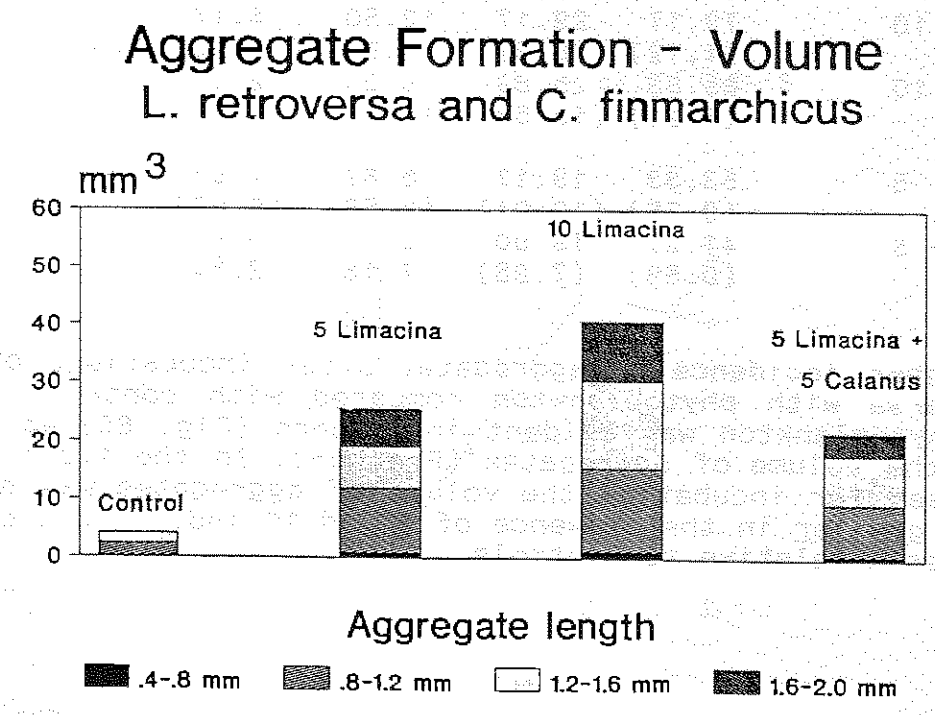


Figure 66. Average volumes of aggregates recovered after parallel incubations (24 h) in 1.2-l bottles of 5 or 10 individuals of *L. retroversa* with natural phytoplankton. In one case 5 individuals of *C. finmarchicus* were incubated with 5 *L. retroversa* and natural phytoplankton. The control was with phytoplankton only. Aggregates were grouped according to length (maximum linear dimension) in 4 size-categories.

This corresponded to about 2.5 mm^3 per individual per liter. When 5 individuals of *Calanus finmarchicus* were incubated with 5 *L. retroversa*, number and volume of aggregates were lower. Especially affected were the large aggregates, the cumulative volume of which in the largest two size categories was about 50 % smaller in the presence of copepods.

Feeding on small particles

The concentration of particles between 1 and 2 µm in diameter was distinctly smaller in experimental bottles with *Limacina retroversa* than in those with *Calanus finmarchicus* or controls containing only the phytoplankton food (Table 6, Fig. 67). Concentrations in incubations with *C. finmarchicus* and controls were similar. Thus, clearance of small particles of this size range was better by *L. retroversa* than by *C. finmarchicus*. There was no appreciable difference in clearance between incubations with 5 and 10

Table 6. Concentration of small particles (1 to 2 µm in diameter) after incubation with *Limacina retroversa* and *Calanus finmarchicus*

Individuals/ bottle		Chl.*a** (µg/l)	1-2 µm particles* ---(number/l)---	
L.retr	*C.finm*			Average
0	0	0.40	1098000	1036000
0	0	0.41	974000	
0	0	0.43	1033000	973500
0	0	0.40	914000	
0	5	0.36	1316000	1089500
0	5	0.38	863000	
0	10	0.34	1008000	874500
0	10	0.36	741000	
5	0	0.38	515000	539500
5	0	0.40	564000	
10	0	0.36	509000	509000
10	0	0.38	509000	
Average		0.38		
S.D.		0.02		

*Concentration after 21.5 h incubation

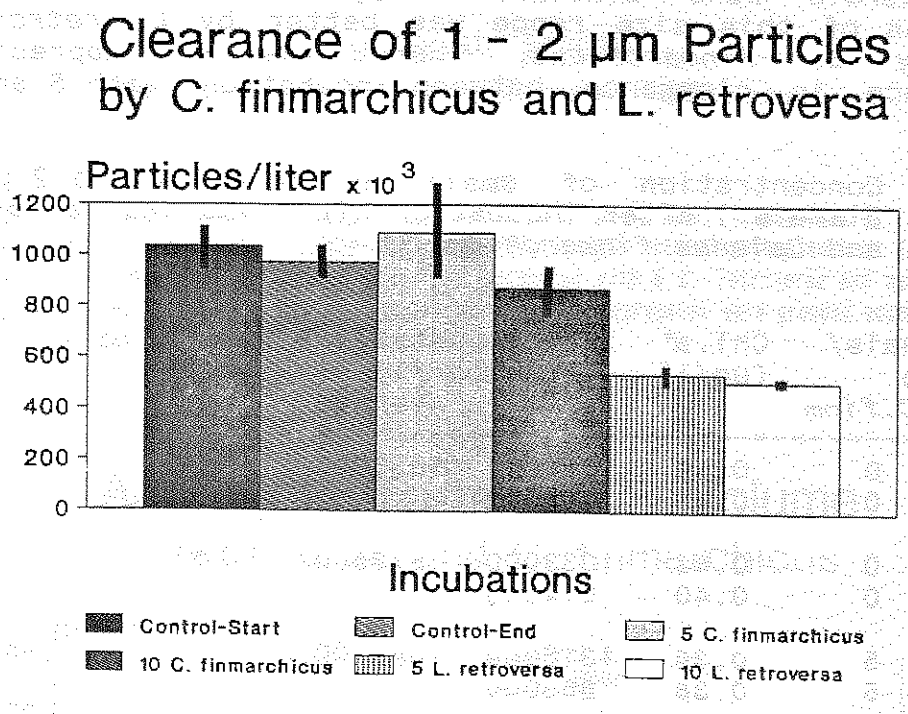


Figure 67. Average concentrations of small particles (1-2 µm in length) after parallel incubations (21.5 h) of 5 or 10 individuals of *C. finmarchicus* and 5 or 10 individuals of *L. retroversa* with filtered (2-µm membrane filters) phytoplankton. Controls were with phytoplankton only. Error bars indicate range of values.

individuals of *Limacina retroversa*. With about 520 000 particles per liter concentrations of small particles in *L. retroversa* incubations were about half of those in incubations with *C. finmarchicus* or controls. Applying the equation from Gauld (1951) for "volume of water swept clear", this corresponds to a clearance rate very close to 100 and 200 ml per pteropod per day for 10 and 5 individuals, respectively. This is higher than most values

reported for various copepods (e.g. Gaudy 1974, Schnack 1979, Huntley *et al.* 1983, Tande and Bamstedt 1985) and is somewhat lower than clearance rates often found for euphausiids (e.g. Morris 1984, McClatchie 1986, McClatchie 1988).

Sedimentation velocities

The average sinking velocities (Table 7) of fecal pellets of *Calanus finmarchicus* and aggregates of *Limacina retroversa* were about 50 and 300 m per day, respectively. Although the presented measurements were conducted *in vitro* at sea, the fecal pellet sedimentation velocities were in the range of those measured on land (see section 3.2.2.1).

Table 7. Sedimentation velocities of *L. retroversa* aggregates and *C. finmarchicus* fecal pellets

Calanus finmarchicus fecal pellets

	Length(µm)	Width(µm)	Volume(µm³)	m/s	
	480	80	2.41×10^6	41	
	800	80	4.02×10^6	29	
	800	80	4.02×10^6	63	
	600	80	3.02×10^6	83	
	720	80	3.62×10^6	64	
	600	60	1.70×10^6	29	
	400	40	5.03×10^5	36	
	640	100	5.03×10^6	neutral	buoyancy
	500	80	2.51×10^6	neutral	buoyancy
Average			2.98×10^6	49	
S.D.			1.29×10^6	19	

Limacina retroversa aggregates

	Length(µm)	Width(µm)	Volume(µm³)	m/s	
	560	400	7.04×10^7	82	
	6400	1600	1.29×10^{10}	480	
	700	500	1.37×10^8	144	
	400	200	1.26×10^7	48	
	4000	4000	5.03×10^{10}	1080	
	1600	1600	3.22×10^9	309	
	900	900	5.73×10^8	123	
	500	200	1.57×10^7	144	
	300	300	2.12×10^7	neutral	buoyancy
	600	200	1.88×10^7	neutral	buoyancy
Average			6.72×10^9	301	
S.D.			1.50×10^{10}	322	

3.2.2. Land-based laboratory investigations

Results from experimentation conducted in the laboratory on land are divided into three parts: Production and aging of fecal pellets (section 3.2.2.1) conducted in Tromsø, Norway, Coprophagy studies (section 3.2.2.2) conducted in Kiel and Coprorhexy studies (section 3.2.2.3) conducted in Bergen, Norway.

3.2.2.1. Production and aging of fecal pellets

Fecal pellet production and composition

The effect of food concentration on the production and composition of fecal pellets from *Calanus finmarchicus* adult females was not clear from this series of experiments. A calculation of the number of pellets produced per copepod per day (Table 8) revealed no correlation with food concentrations. Production rates ranged from about 30 to 190 fecal pellets per copepod per day with an average of 72.5 ± 41.1 (n = 20). This is equivalent to about 3 per hour and is in the lower range of values (about 3 to 6 per copepod per hour) reported by Marshall and Orr (1972) for *C. finmarchicus* copepods feeding on cultures.

Table 8. Production of fecal pellets by *Calanus finmarchicus* in relation to food concentration

Food concentration (ug Chl. *a*/l)	cop./l	pell.*/l	Pellet production (pell./cop./d)
0.99	59	4376	73
0.99	65	2003	30
1.11	44	1839	41
1.31	77	3194	41
1.31	82	2675	32
1.32	42	1872	44
1.32	42	5804	137
1.32	42	3170	76
1.32	45	2619	58
1.56	66	3324	50
2.41	50	2401	47
2.46	63	4311	67
3.18	43	3689	85
3.18	45	7157	159
3.22	68	4720	69
3.22	70	4740	67
3.22	73	3342	46
4.21	50	3392	67
4.21	69	13091	189
4.21	71	4308	60

Food concentration similarly did not appear to have an effect on dry weight or C:N ratio of fecal pellets in these experiments. Dry weight ranged from about 0.1 to 0.6 µg per pellet and C:N from about 3 to 12. The average of C:N values of suspended particles in the food supply was 7.5 ± 1.2 (n=5). These data are presented in Table 11 which summarizes biomass parameters for *C. finmarchicus* fecal pellets.

*Pellets were calculated from the number of intact pellets plus the total volume of fecal pellet fragments divided by the average volume of one pellet.

A negative correlation (r = - 0.42; n = 17) between the density of copepods and pellet production per copepod (Fig. 68) existed.

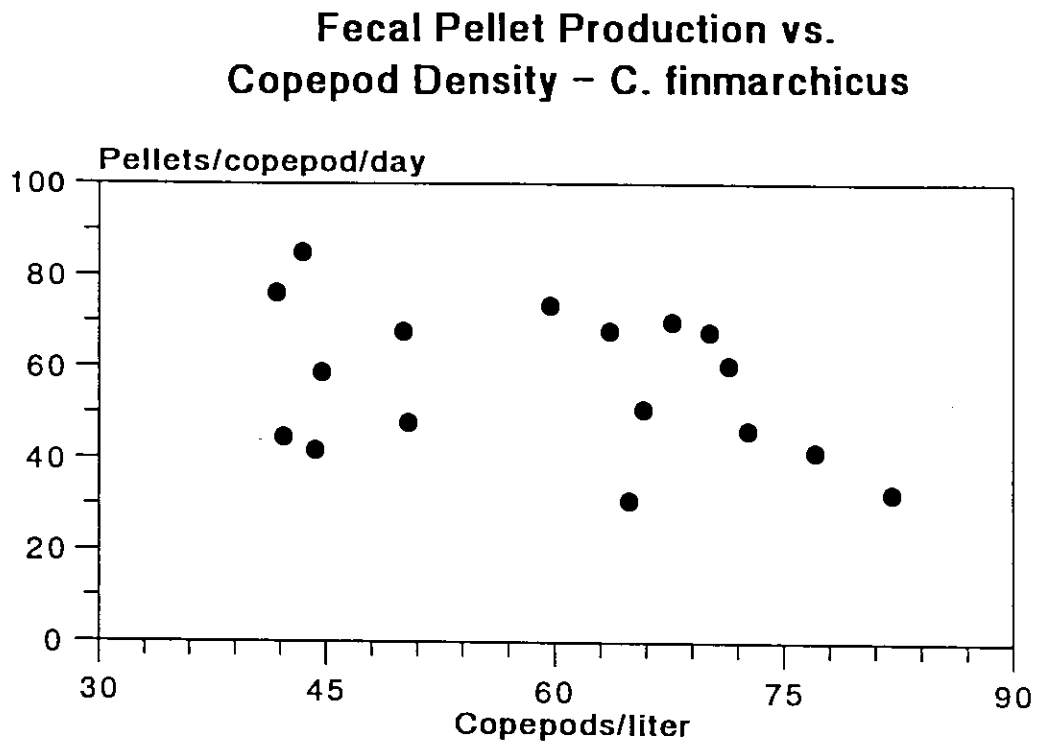


Figure 68. Numbers of fecal pellets per copepod per day recovered after incubations (24 h) of *C. finmarchicus* with natural phytoplankton in relation to copepod density (r=-0.42; n=17).

Aging of fecal pellets

In order to study the effect of bacteria and/or autolysis by digestive or phytoplanktonic enzymes on fecal pellet decomposition at 1 °C, fecal pellet volume (intact and fragmented pellets), POC, PON and sedimentation velocities were measured for intervals of 2, 3 and 5 days. Total volume of fecal material (Table 9) clearly exhibited a decrease over time. The number of intact pellets also decreased over time. Volumes of intact fecal pellets (Table 10) fluctuated erratically and averaged 1.12 ± 0.28 x 10^6 μm^3 (n = 340). By day 15 of the 20-d experiment (Fig. 69) many intact fecal pellets were lacking peritrophic

Table 9. Average volume of fecal material from *Calanus finmarchicus* vs. age

		Volume (μm^3)			Pellet*	
	Age (d)	Intact	Frag	Total	equivalent	N
A	0	3.18×10^8	2.09×10^9	2.41×10^9	2.14×10^3	569
	5	1.74×10^8	1.46×10^9	1.64×10^9	1.46×10^3	453
	10	2.97×10^7	1.36×10^9	1.39×10^9	1.24×10^3	397
	15	8.93×10^6	2.06×10^8	2.15×10^8	1.91×10^2	266
	20	4.24×10^7	9.54×10^8	9.96×10^8	8.86×10^2	284
B	0	7.40×10^8	4.34×10^9	5.08×10^9	4.52×10^3	602
	3	1.23×10^8	1.71×10^9	1.83×10^9	1.63×10^3	443
	6	5.71×10^6	1.27×10^9	1.28×10^9	1.14×10^3	345
	9	4.32×10^7	1.06×10^9	1.11×10^9	9.85×10^2	289
	12	1.79×10^7	1.02×10^9	1.04×10^9	9.22×10^2	297
C	0	1.60×10^8	1.20×10^9	1.36×10^9	1.21×10^3	351
	2	1.19×10^8	8.98×10^8	1.02×10^9	9.05×10^2	260
	4	9.80×10^7	8.19×10^8	9.17×10^8	8.16×10^2	204
	6	6.55×10^7	7.46×10^8	8.11×10^8	7.22×10^2	201
	8	4.79×10^7	9.93×10^8	1.04×10^9	9.26×10^2	255

*Pellet equivalent was calculated from the number of intact pellets plus the total volume of fecal pellet fragments divided by the average volume of one pellet.

Table 10. Average volume of intact *Calanus finmarchicus* fecal pellets vs. age

	Age (d)	Volume (μm^3)	S.D.	N
	0	9.77×10^5	6.46×10^5	72
	5	1.07×10^6	5.35×10^5	37
A	10	1.46×10^6	5.10×10^5	4
	15	1.61×10^6	7.38×10^5	6
	20	1.19×10^6	3.33×10^5	6
	0	1.27×10^6	9.86×10^5	78
	3	9.13×10^5	8.31×10^5	26
B	6	5.71×10^5		1
	9	8.14×10^5	5.52×10^5	12
	12	1.00×10^6	3.94×10^5	4
	0	1.20×10^6	1.06×10^6	35
	2	1.23×10^6	8.36×10^5	22
C	4	1.52×10^6	7.29×10^5	14
	6	1.24×10^6	9.65×10^5	10
	8	7.85×10^5	4.69×10^5	13

membranes. By day 20 almost all intact pellets lacked membranes. The amount of fragmented fecal material was considerably larger than that of intact fecal pellets for all three experiments (Figs. 69, 70 and 71). Increments in volume during the last sampling interval for two experiments (Figs. 69 and 71) were observed.

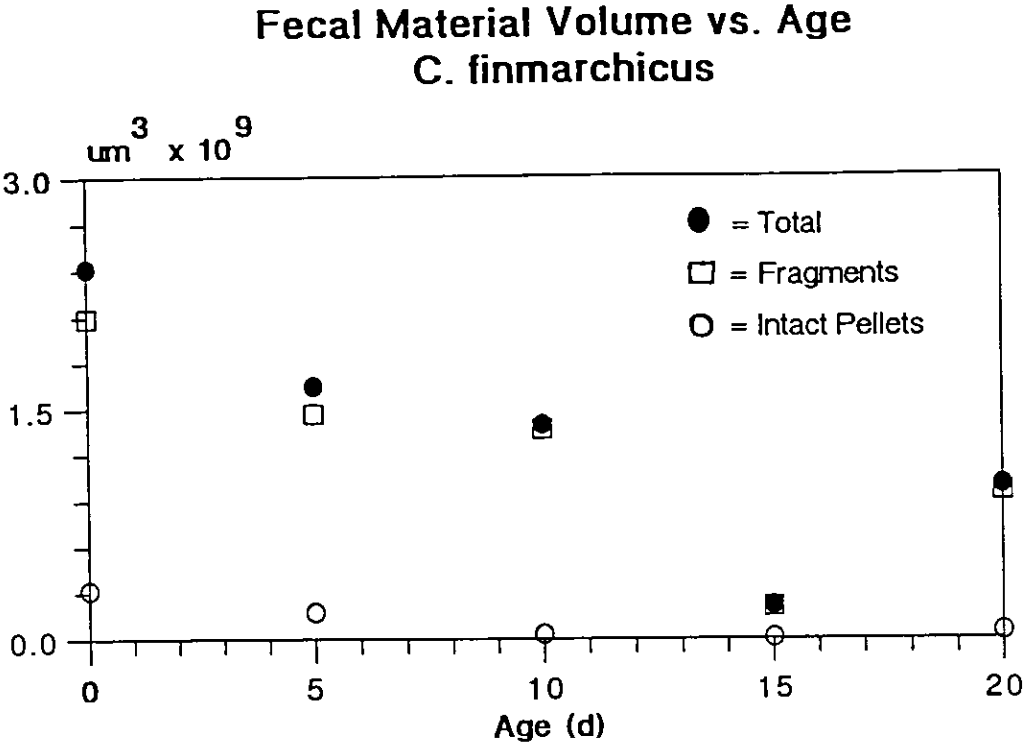


Figure 69. Volume of fragmented and intact *C. finmarchicus* fecal pellets and their total from aliquots in relation to age. Sampling interval and duration were 5 and 20 d, respectively.

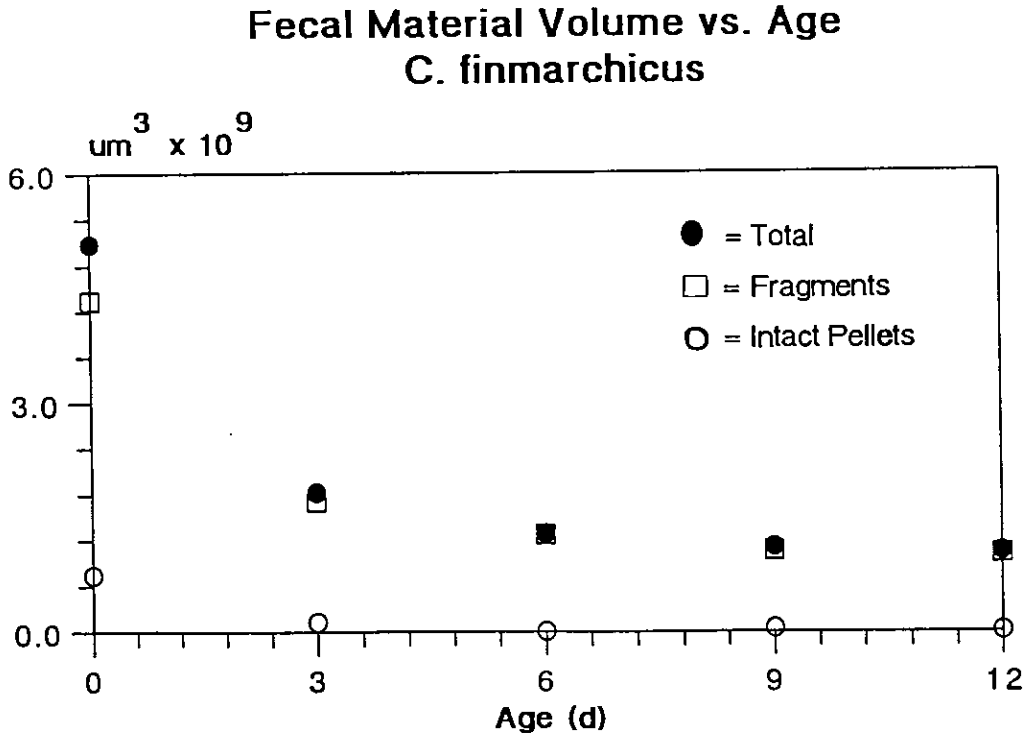


Figure 70. Volume of fragmented and intact *C. finmarchicus* fecal pellets and their total from aliquots in relation to age. Sampling interval and duration were 3 and 12 d, respectively.

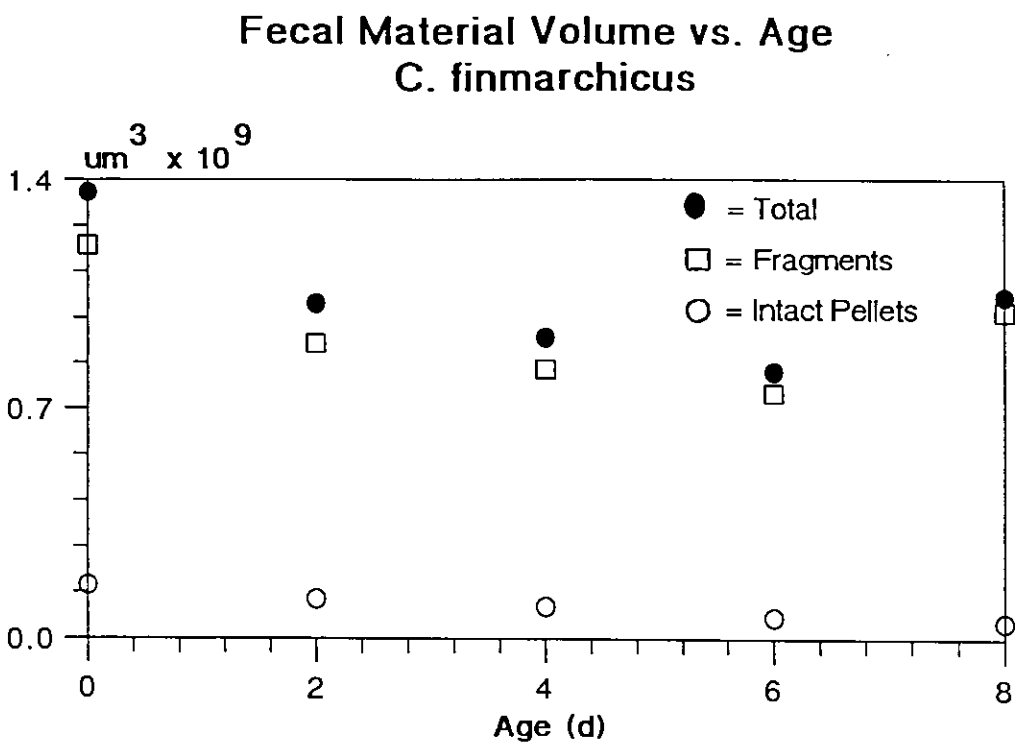


Figure 71. Volume of fragmented and intact *C. finmarchicus* fecal pellets and their total from aliquots in relation to age. Sampling interval and duration were 2 and 8 d, respectively.

Dry weight, POC and PON for *Calanus finmarchicus* fecal pellets in relation to food concentrations and age (Table 11) are summarized below. There was no distinct relationship between age and any of these three parameters.

Table 11. Biomass parameters for individual fecal pellets *Calanus finmarchicus* in relation to age and food supply

Age (d)	POC (µg)	PON (µg)	C:N (atoms)	Dry weight (µg)	POC(%DW)	Food (µg Chl.a/l)
0	0.064	0.010	7.49	0.530	12.20	-
0	0.176	0.042	4.89	1.529	11.54	-
0	0.184	0.044	4.85	1.503	12.30	-
1	-	-	8.56	-	12.45	-
1	-	-	6.95	-	22.49	-
1	-	-	4.88	-	-	-
1	0.014	0.003	4.13	0.074	18.72	4.21
1	0.034	0.013	3.04	0.282	12.16	4.21
1	0.035	0.010	3.83	0.159	22.27	2.46
1	0.035	0.011	3.65	0.152	23.19	0.99
1	0.047	0.006	8.98	0.157	30.21	3.18
1	0.047	0.011	4.79	0.227	20.98	4.21
1	0.056	0.006	10.53	0.190	29.65	1.32
1	0.062	0.014	5.14	0.338	18.50	1.56
1	0.084	0.008	12.13	0.422	19.96	1.32
1	0.087	0.009	11.13	0.316	27.81	3.18
1	0.088	0.012	8.44	0.572	15.49	2.46
1	0.089	0.017	6.07	0.511	17.57	1.32
1	0.093	0.013	7.82	0.519	17.97	1.32
1	0.126	0.021	6.89	0.509	24.80	1.11
2	-	-	6.65	-	17.96	-
2	0.282	0.049	6.64	2.237	12.61	-
2	0.478	0.118	4.70	5.090	9.40	-
3	0.160	0.029	6.25	1.334	12.02	-
4	0.274	0.060	5.31	1.929	14.23	-
5	0.279	0.050	6.42	1.695	16.50	-
6	0.226	0.058	4.48	3.496	6.47	-
6	0.264	0.045	6.77	1.797	14.70	-
8	0.181	0.043	4.85	1.700	10.68	-
8	0.224	0.084	3.09	8.325	2.69	-
9	0.274	0.044	7.19	1.751	15.66	-
10	0.196	0.027	8.45	1.753	11.19	-
12	0.260	0.055	5.43	2.493	10.45	-
15	1.071	0.247	5.06	12.822	8.36	-
20	0.223	0.049	5.28	2.201	10.17	-
Average	0.155	0.033	6.34	1.460	19.83	
S.D.	0.106	0.026	2.18	1.701	17.55	
N	30	30	34	30	34	

With an average of 1.460 µg per pellet dry weights of individual fecal pellets varied over a range of one order of magnitude. Variations were greatest for one-day old fecal pellets. Average content of particulate organic carbon and nitrogen per pellet was 0.155 and 0.033 µg, respectively, and covered a similarly wide range. For POC this corresponds to an average of about 20 % of dry weight. The high values for POC, PON and dry weight for 15-day old fecal pellets are probably unrealistic and have not been included in calculating averages and standard deviations.

C:N values in older fecal pellets (> 1-day old) were surprisingly low with an average value of 6.3. Variation, again was greatest in one-day old pellets. No distinct pattern with age was evident.

Sedimentation of fecal pellets

Sedimentation velocities of intact fecal pellets from *Calanus finmarchicus* oscillated erratically in relation to age in three experiments (Table 12). Assuming that the surface friction of sedimenting pellets did not change with increasing age, specific weights of older intact pellets were not significantly different from freshly produced pellets. This was also indicated in dry weight measurements, as described above.

Table 12. Sedimentation velocities of *Calanus finmarchicus* fecal pellets in relation to age

Exp	Age(d)	m/d	S.D.
A	0	46.75	22.07
	5	19.65	9.76
	10	13.70	6.03
	15	30.25	11.49
	20	41.10	9.95
B	0	34.40	13.20
	3	16.55	9.52
	6	17.55	7.27
	9	22.40	13.29
	12	32.90	10.34
C	0	20.00	8.17
	2	20.25	10.13
	4	35.30	8.65
	6	30.95	8.56
	8	34.11	7.98

N= 20 for all values

A summary of all measurements of sinking velocities of *Calanus finmarchicus* fecal pellets in relation to age (Fig. 72) illustrates that velocity of intact pellets was independent of age. Values ranged from about 10 to 90 m per day. Average sedimentation velocity from all measurements was 33.7 m per day (see Table 13). Sedimentation velocity of *C. finmarchicus* fecal pellets was also independent of volume (Fig. 73).

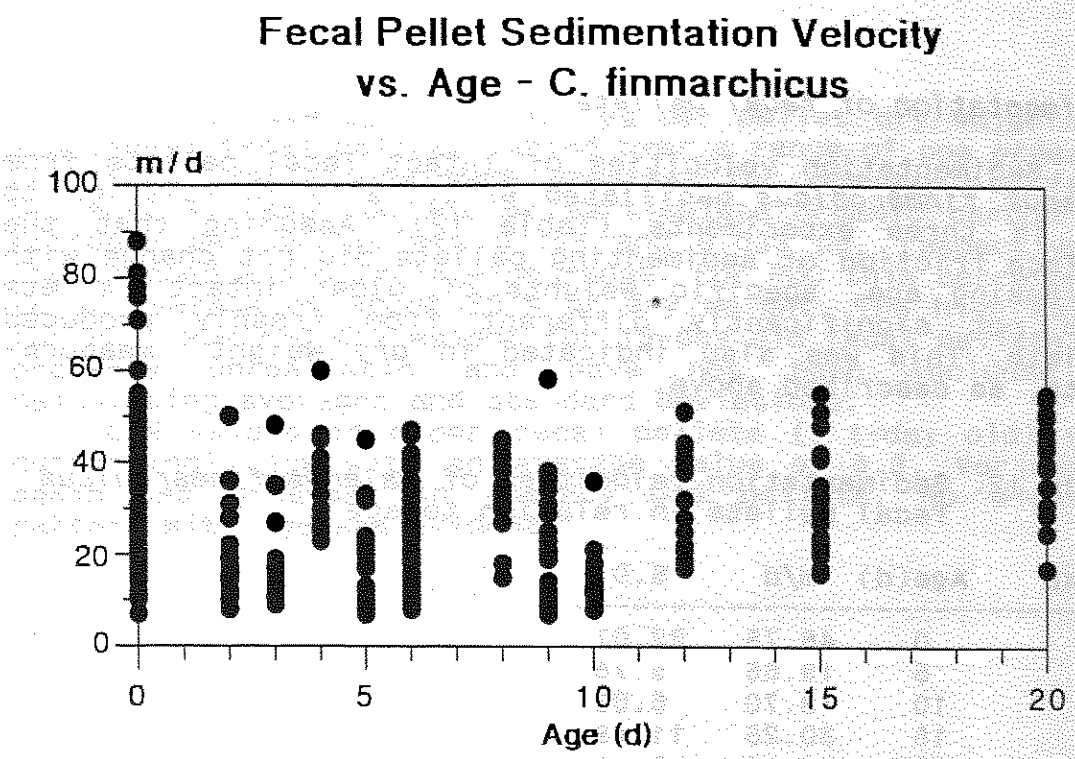


Figure 72. Sedimentation velocity in relation to age of *C. finmarchicus* fecal pellets.

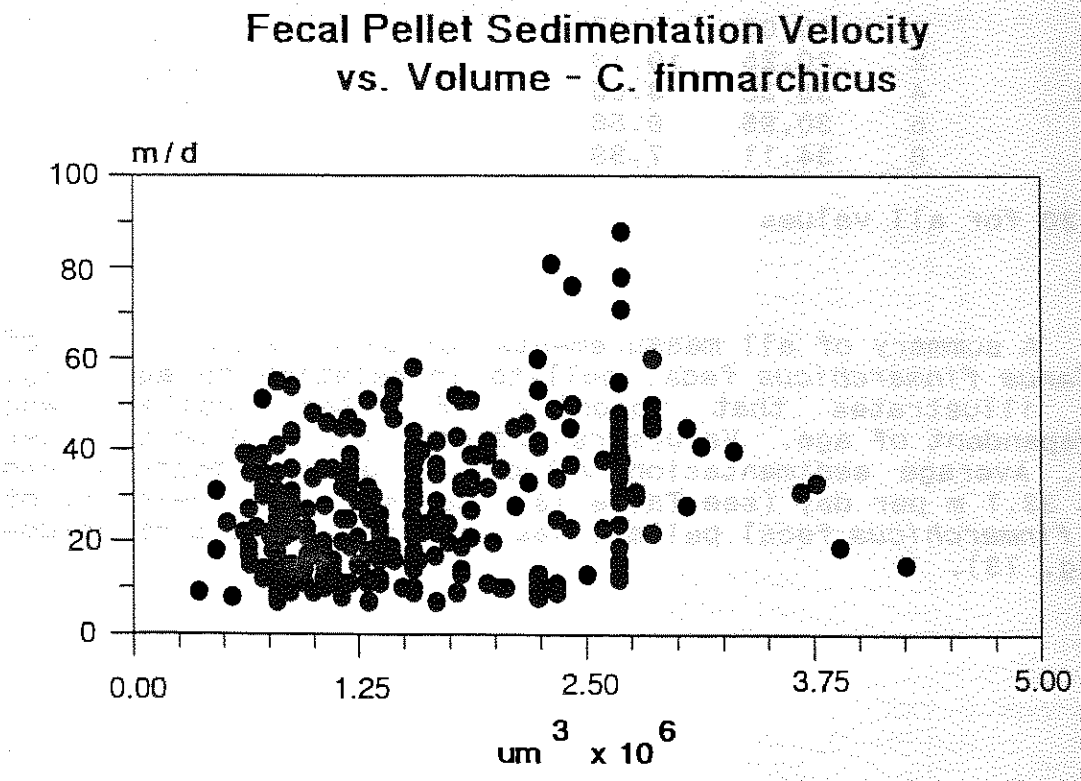


Figure 73. Sedimentation velocity in relation to volume of *C. finmarchicus* fecal pellets.

With an average of 49.4 and 94.9 m per day average sinking velocities of *Calanus hyperboreus* fecal pellets and krill (*Thysanoessa* sp.) fecal strings* were significantly larger than for *Calanus finmarchicus* fecal pellets (Table 13). Sedimentation velocities reflected size (volume) of the fecal types. The particularly large standard deviation for measured sinking velocities for krill fecal strings is attributable to the wide range of volumes of the measured fecal strings within this group. Presuming that the average velocities measured at sea for *Limacina retroversa* aggregates (see Table 7) are comparable with land-based measurements, a significant relationship between average volume and sinking velocity for 4 groups of particles - fecal pellets/strings from *Calanus finmarchicus*, *C. hyperboreus*, *Thysanoessa* sp. and aggregates from *Limacina retroversa* - exists (Fig. 74). Note that due to the break in the x-axis, the significance of the correlation is not immediately evident in Fig. 74.

Table 13. Average sedimentation velocities and volumes of 0 to 1-day old *Calanus finmarchicus*, *Calanus hyperboreus* and *Thysanoessa* sp. fecal pellets

Zooplankter	Sed.Velocity + S.D. (m/d)	Volume + S.D. ($\mu m^3 \times 10^6$)
Calanus finmarchicus N = 60	33.7 ± 19.0	1.79 ± 0.83
Calanus hyperboreus N = 15	49.9 ± 19.9	3.36 ± 0.66
Thysanoessa sp. N =15	94.4 ± 98.4	12.94 ± 14.41

*As fecal material from euphausiids is broken into open-ended cylinders after attaining a certain length, it is referred to as fecal strings to differentiate it from the encapsulated fecal pellets of e.g. copepods.

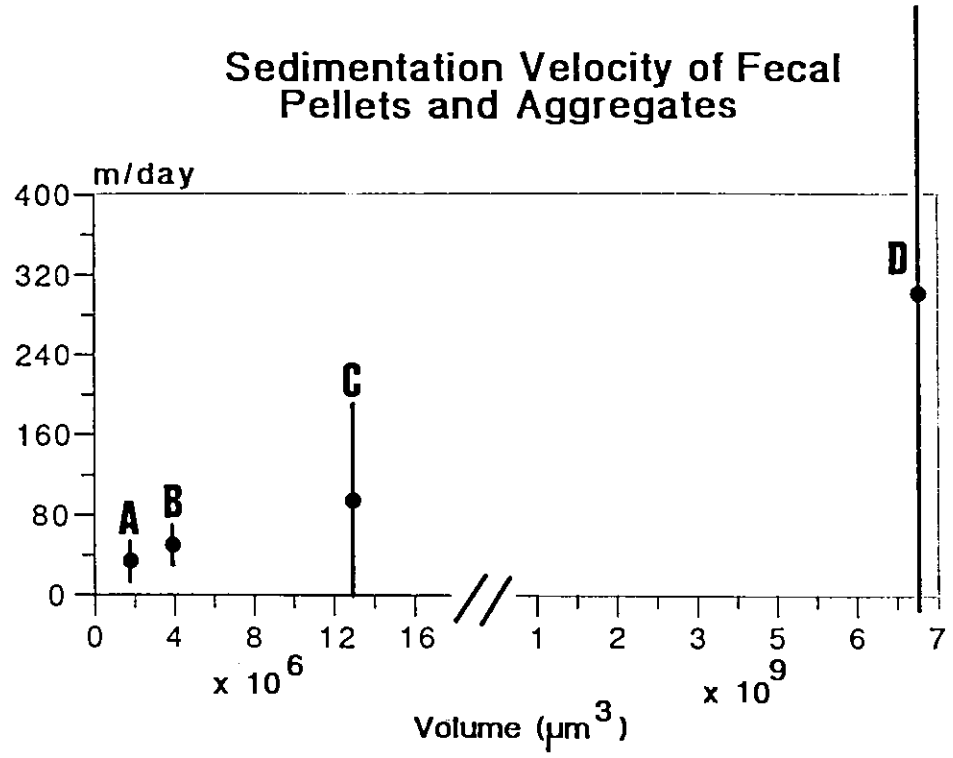


Figure 74. Average sedimentation velocity in relation to average volume of *C. finmarchicus* (A) and *C. hyperboreus* (B) fecal pellets, *Thysanoessa* sp. fecal strings (C) and mucous aggregates from *L. retroversa* (D) (r=0.9985, n=4). Error bars indicate standard deviation.

3.2.2.2. Coprophagy studies

Clearance rates and ^{14}C-labelling

Incubating *Centropages hamatus* with fecal pellets resulted in a reduction in the number of fecal pellets by about 55.5 ± 15.5 % (n = 34) by the end of incubations (28 h) with copepods as opposed to 7.6 ± 5.0 % in controls (n = 19) (Fig. 75). Note that all points in Fig. 75 are included in the calculation for the presented regression. These results can also be expressed as clearance rates (Frost 1972). Clearance rate, although usually used for expressing the filtration of small, abundant, homogeneously distributed particles, e.g. phytoplankton (Gauld 1951), may be used as a measure of the probability of encounter for larger food particles (Landry 1981). Compared with fecal pellet concentration (Fig. 76), clearance rates were relatively constant with values of about 10 to 20 ml per copepod per day for the concentrations of fecal pellets used in these experiments. This agrees with rates measured for similarly sized copepods feeding on phytoplankton (Poulet 1974).

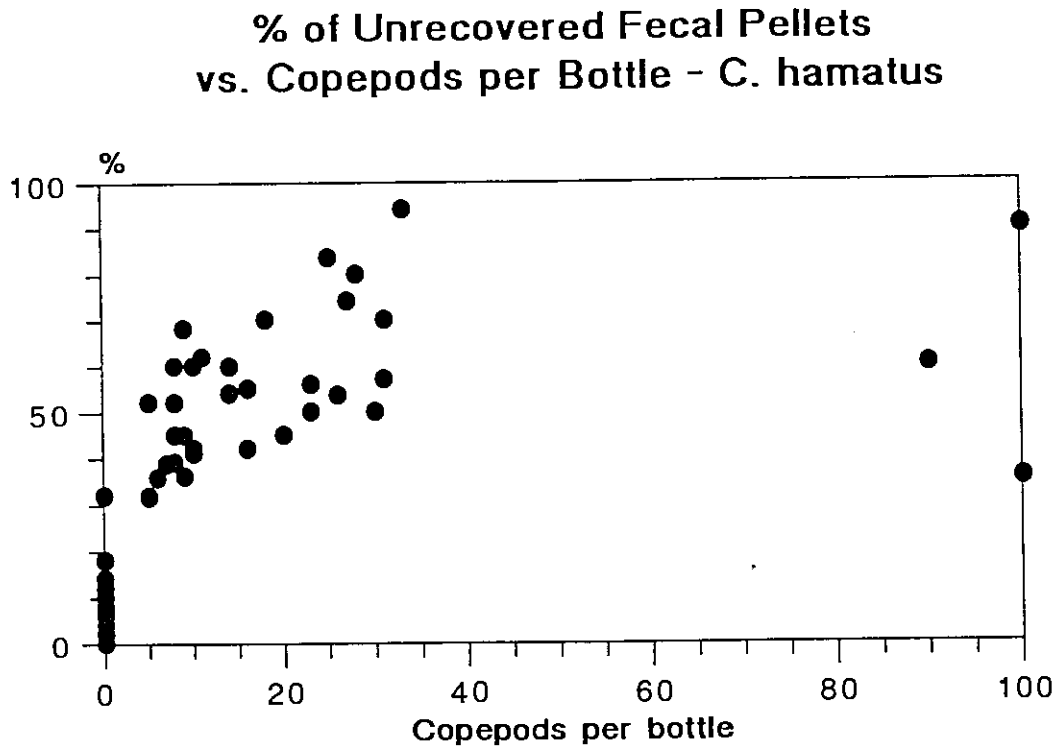


Figure 75. Percentage of unrecovered fecal pellets after incubation (28 h) with *C. hamatus* in relation to copepod density (r=0.60; n=53). Note that for coprorhexy incubations with copepods and for controls without copepods the average values are 55.5±15.5 (n=34) and 7.6±5.0 % (n=19), respectively.

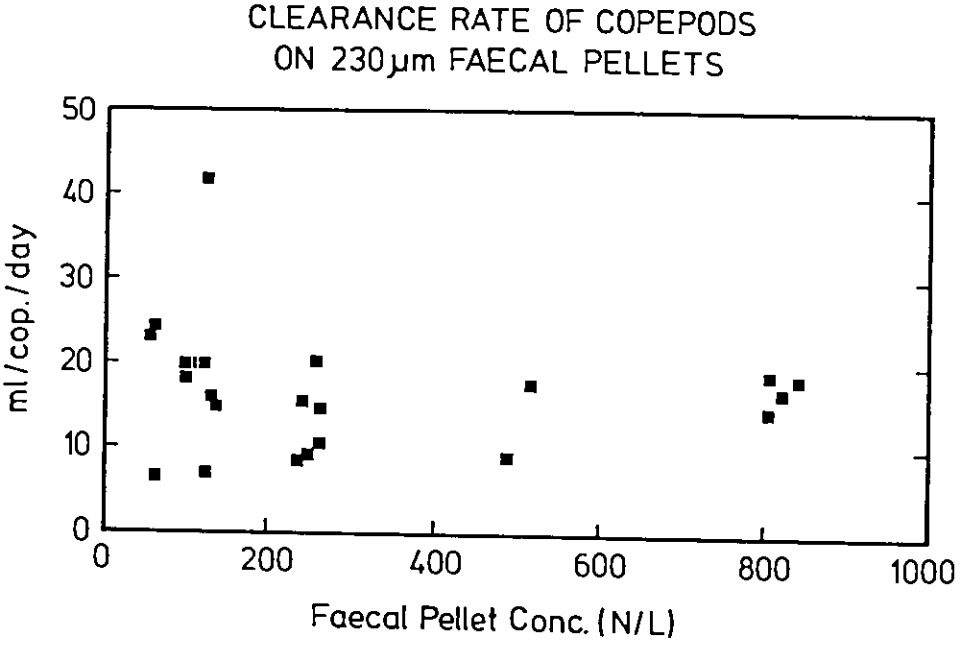


Figure 76. Clearance rate of *C. hamatus* copepods in relation to fecal pellet concentration. (from Lampitt *et al.* in press)

In ^{14}C-labelling incubations the presence of copepods resulted in a shift of ^{14}C from the fecal pellet to the detrital fraction, as shown for two experiments in Fig. 77a and b. Smaller increases in ^{14}C also occurred in the copepod and dissolved carbon fractions. When $^{14}CO_2$ was measured separately, values for 2-h and 28-h control incubations were similar. Released $^{14}CO_2$ was 1.2 ± 0.4 % after 28 h. In the presence of copepods the $^{14}CO_2$ pool in these experiments was larger with 4.3 ± 0.7 %; the difference between control and copepod incubations of 3.1 % presumably reflects respiration by these animals.

It is noted that in comparison with the above results, in incubations involving fragmented (homogenized) pellets less ^{14}C was recovered in the copepod body pool (1.1 ± 0.5 %). Further, the release of labelled CO_2 in the presence of copepods increased over control values by only 1.3 %.

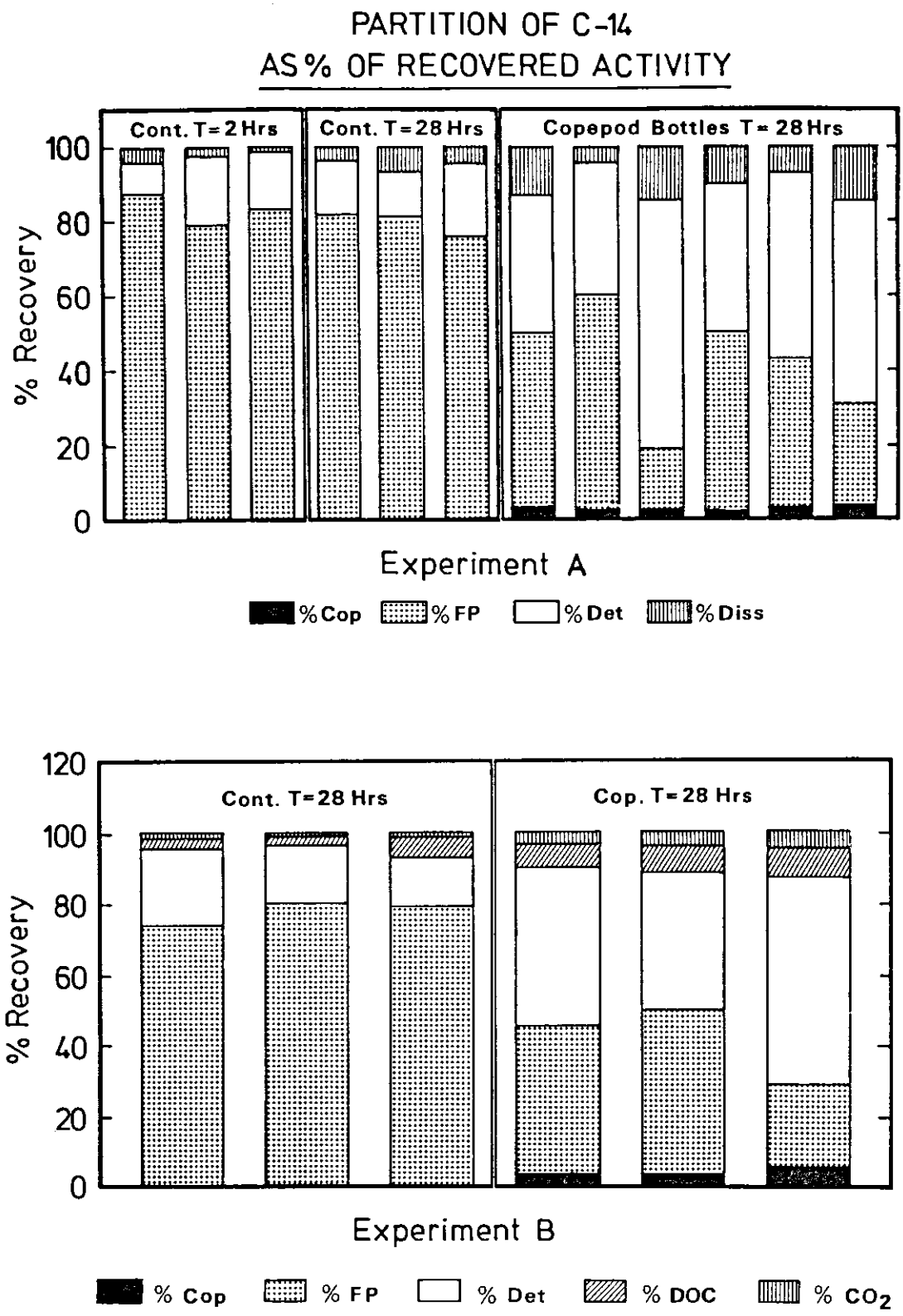


Figure 77. Distribution of ^{14}C activity in various pools from two experiments with and without *C. hamatus* copepods. Activity is expressed as a percentage of that recovered. In experiment A some of the control bottles were analysed after only 2 h in addition to those analysed after 28 h. In experiment B the dissolved pool was subdivided into DOC and CO_2. (from Lampitt *et al.* in press)

^{14}C probably was introduced to detrital and dissolved carbon pools before incubation, as the percent of recovered dissolved carbon (Fig. 78) in controls after only 2 h of incubation was fairly high (2.0 ± 1.1 %) relative to the values after 28 h (4.6 ± 1.8 %). Percent recovered ^{14}C in the dissolved fractions after incubation with copepods doubled (9.7 ± 3.4 %). Considering the 2-h control values to be a baseline, release of labelled carbon was about 3 % in controls and about 8 % in incubations with copepods. Thus 5 % of the recovered dissolved carbon pool can be attributed to the presence of copepods.

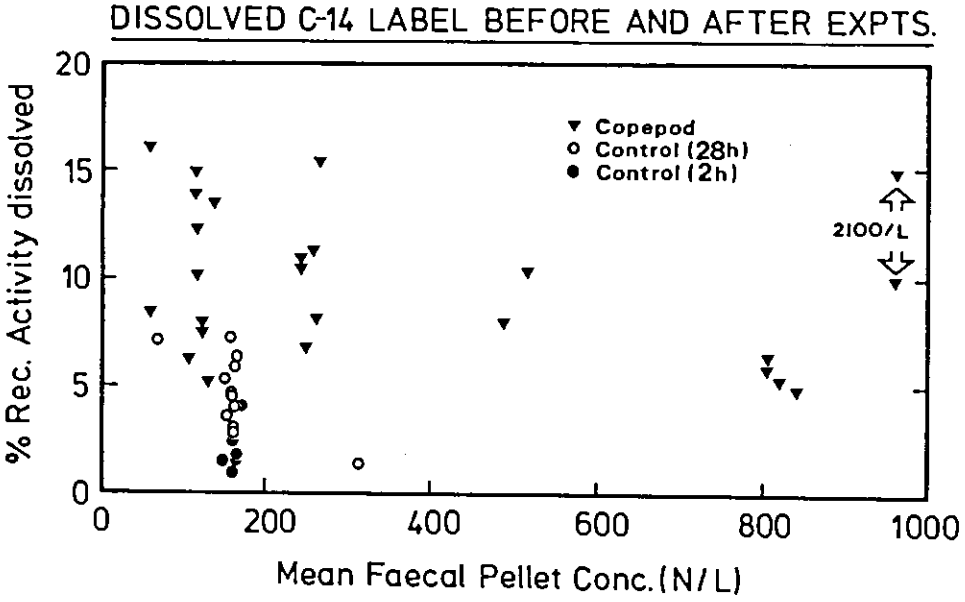


Figure 78. Percentage of ^{14}C activity recovered in the dissolved phase (<0.45 µm) as a function of mean fecal pellet concentration. Control bottles contained no copepods; incubation was 2 and 24 h for T_0 and T_t, respectively. (from Lampitt *et al.* in press)

The percentage of ^{14}C in the detrital fraction of particulate organic carbon (POC) did not vary with the number of fecal pellets used in incubations (Fig. 79). In 2-h and 28-h controls the contribution of detritus to POC was 9.4 ± 6.0 and 14.8 ± 4.7 %, respectively. This contribution increased greatly to 54.7 ± 14.7 % in the presence of copepods.

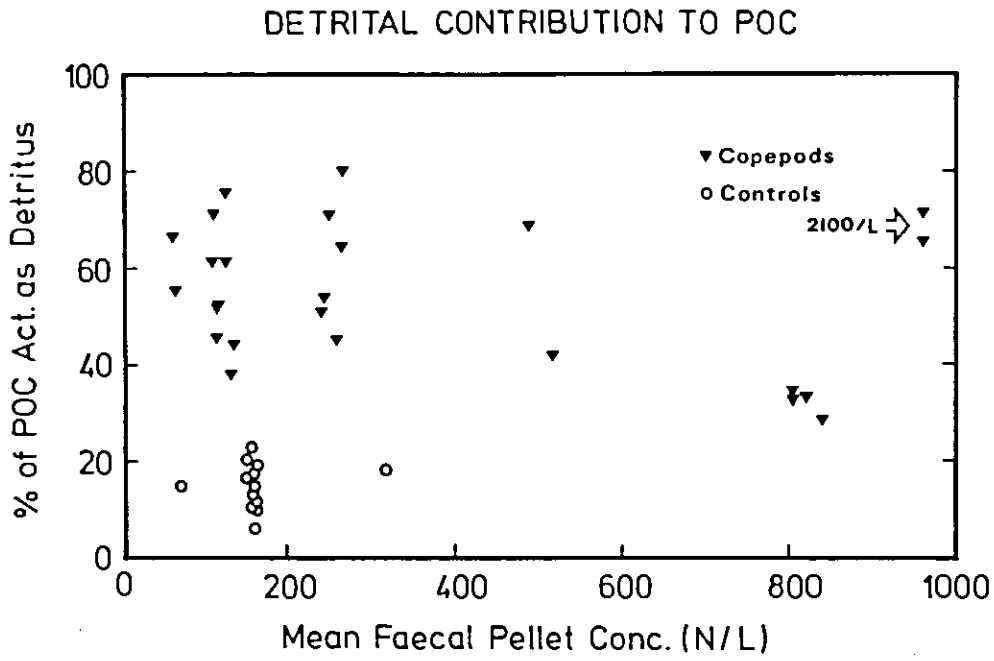


Figure 79. Percentage of ^{14}C activity recovered as non-fecal detritus as a function of mean fecal pellet concentration. Control bottles contained no copepods. (from Lampitt *et al.* in press)

The fraction of label recovered in copepod bodies did not correlate with fecal pellet concentration (Fig. 80). With a mean value of 2.5 ± 1.0 % the copepod fraction of labelled carbon was very small.

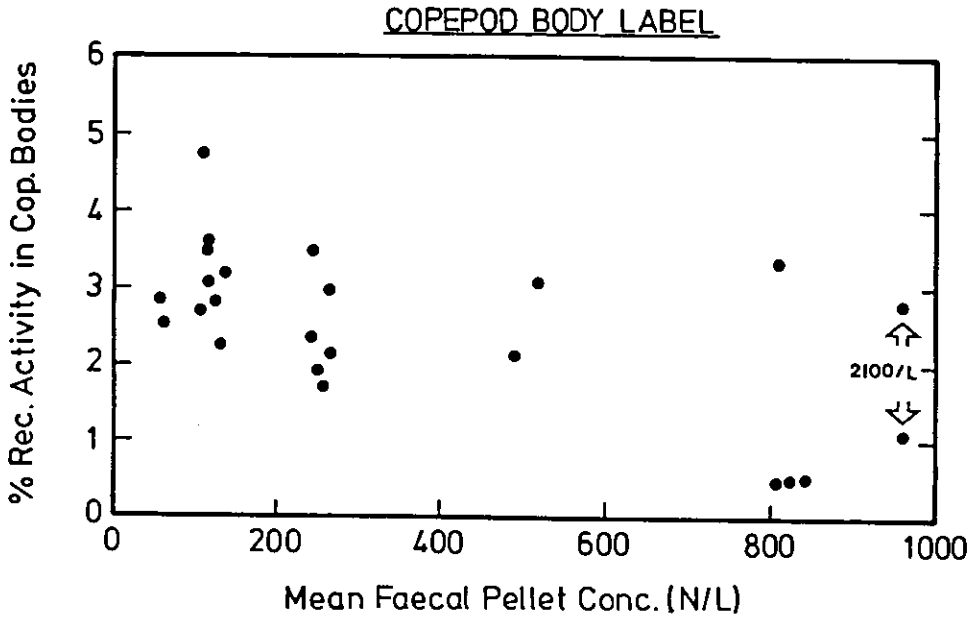
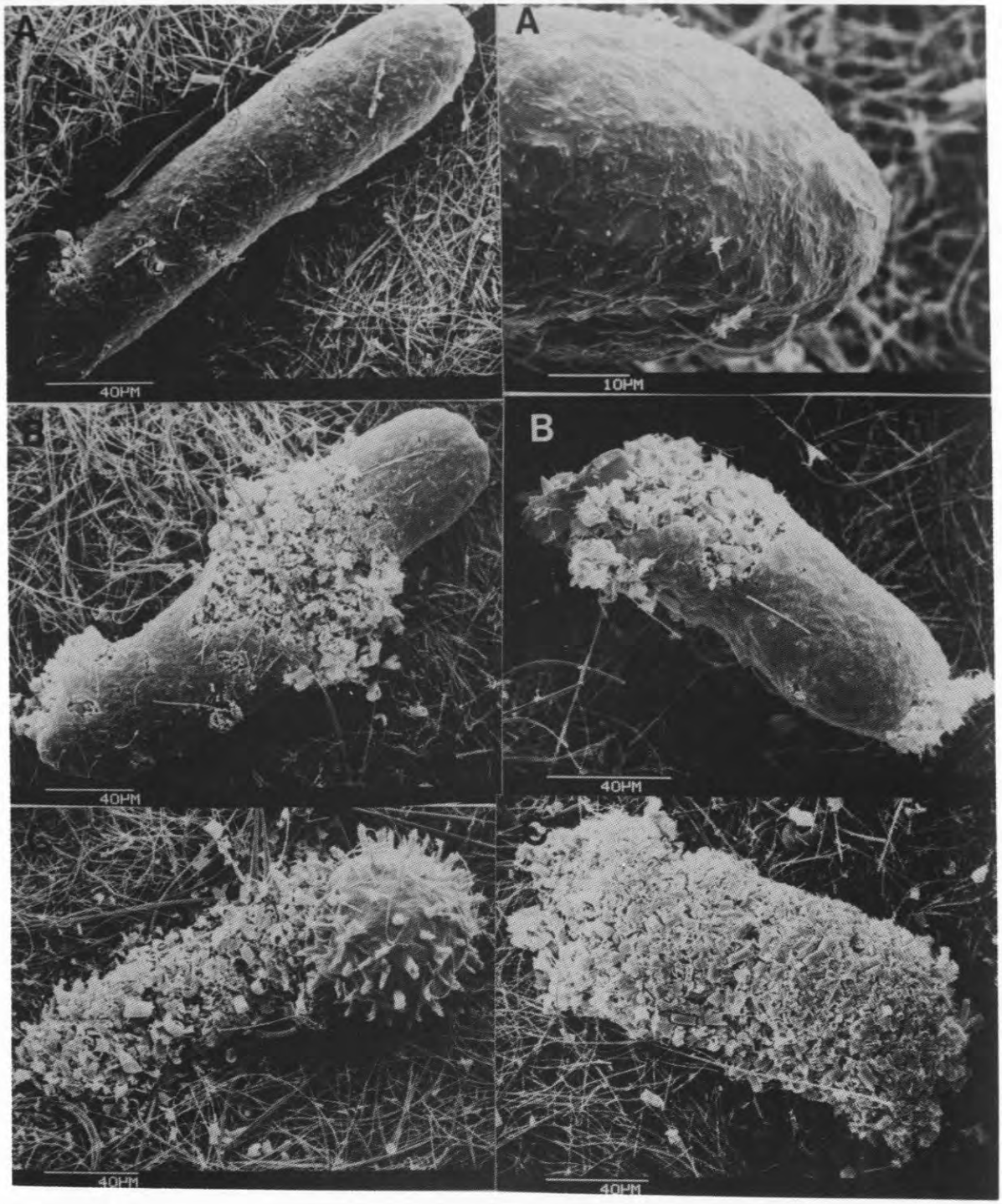


Figure 80. Percentage of ^{14}C activity recovered in the bodies of the *C. hamatus* copepods as a function of mean fecal pellet concentration. Control bottles contained no copepods. (from Lampitt *et al.* in press)

Scanning electron microscopy

The electron micrographs on the next page depict freshly produced *Centropages hamatus* fecal pellets (A) and pellets incubated (24 h) without (B) and with (C) *C. hamatus* copepods. Freshly produced fecal pellets (A) were intact and evidenced almost no damage to the peritrophic mambrane. Although handling and incubation damaged the fecal pellets incubated without copepods (B), the peritrophic membrane of the fecal fragments was intact. However, in the presence of copepods the degree of damage was substantially greater (C); the peritrophic membrane was completely or largely lacking. (The spinose egg is from *C. hamatus*.) The implication is that the first step in the coprorhexic process is the removal of the peritrophic membrane.

Scanning electron micrographs of freshly produced *Centropages hamatus* fecal pellets (A) and pellets incubated (24 h) without (B) and with (C) *C. hamatus* copepods



3.2.2.3 Coprorhexy studies

A convenient basis for comparing size-frequency distributions is cumulative percentages. In the graphs presented here the percentage contribution of each particle to total surface area, S, and total volume, V, is presented cumulatively (y-axis of graphs) and logically terminates at 100 % for any one incubation for the respective parameters. Individual particles are differentiated by volume (μm^3) and presented from smallest to largest volumes (x-axis of graphs). V_{s50} and V_{v50} (Table 14) are the volumes of the individual particles corresponding to 50 % of the total surface area and total volume of particles per liter, respectively.

The size-frequency distribution of particle volume (Fig. 81a) and surface area (Fig. 81b) for coprorhexy incubations of fecal pellets with *Acartia clausii* differs from that of its theoretical counterpart, Control-*Acartia* (combined results from controls with only fecal pellets and only copepods), in values for V_{v50} and V_{s50}. V_{v50} for Control-*Acartia* and the coprorhexy incubations is 0.330 and 0.140, respectively, which corresponds to a reduction of 58 %. The corresponding values for V_{s50} are 0.043 and 0.030, which is a reduction of 30 %. These differences resulted from the shift to smaller particles when *Acartia* was incubated with pellets. Further, the ratio of total volume to total surface area per liter, V:S, was 20 % lower in the coprorhexy incubation, indicating the relative increase in surface area of these particles. Since the seawater medium was composed of relatively small particles, as indicated by the lowest V_{v50} and V_{s50} values, and particles of the medium are overrepresented in the control (see section 2.3.2 - *Coprorhexy study* for explanation), in reality the shift to smaller particles with larger cumulative surface area was greater than represented here.

The size-frequency distribution of particles for *Pseudocalanus elongatus* (Figs. 82a and b) incubated with pellets differed primarily from that of Control-*Pseudocalanus* in V_{s50} and V:S, which are 42 and 15 % lower in the coprorhexy incubation, respectively (Table 14). These observations reflected the shift to smaller particles and relative increase in the total surface area as compared with the more conservative total volume. Again, since particles of the seawater medium were relatively small, the fraction of small particles in the theoretical control is overrepresented. Hence, the shift to smaller sizes in the coprorhexy incubation was greater than here depicted.

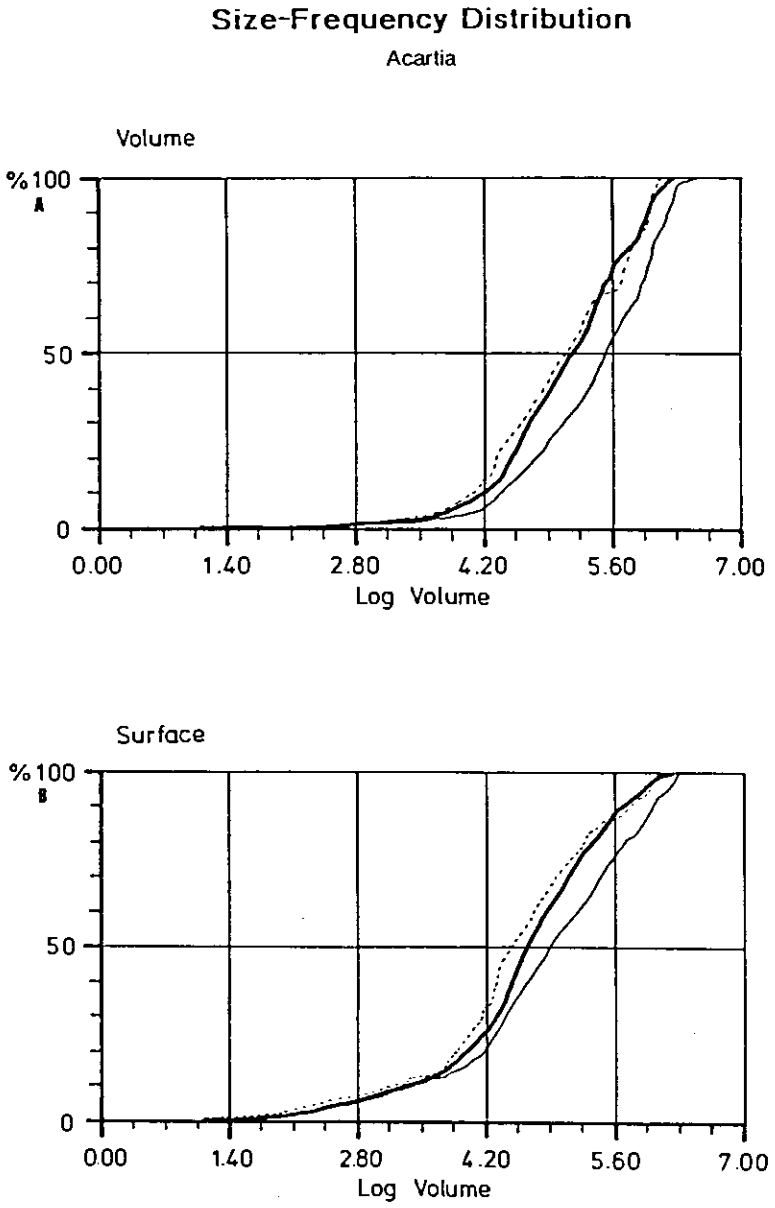


Figure 81a,b. Size-frequency distribution of volumes (A) and surface areas (B) of particles in the coprorhexy incubation (thick line) with *Acartia clausii* and fecal pellets, Control-*Acartia* (thin line; see text) and the seawater medium (dotted line). For both parameters the percentage contribution of individual particles to totals for all particles is cumulatively presented versus logarithmic values of the individual volumes of particles. (from Noji *et al.* submitted)

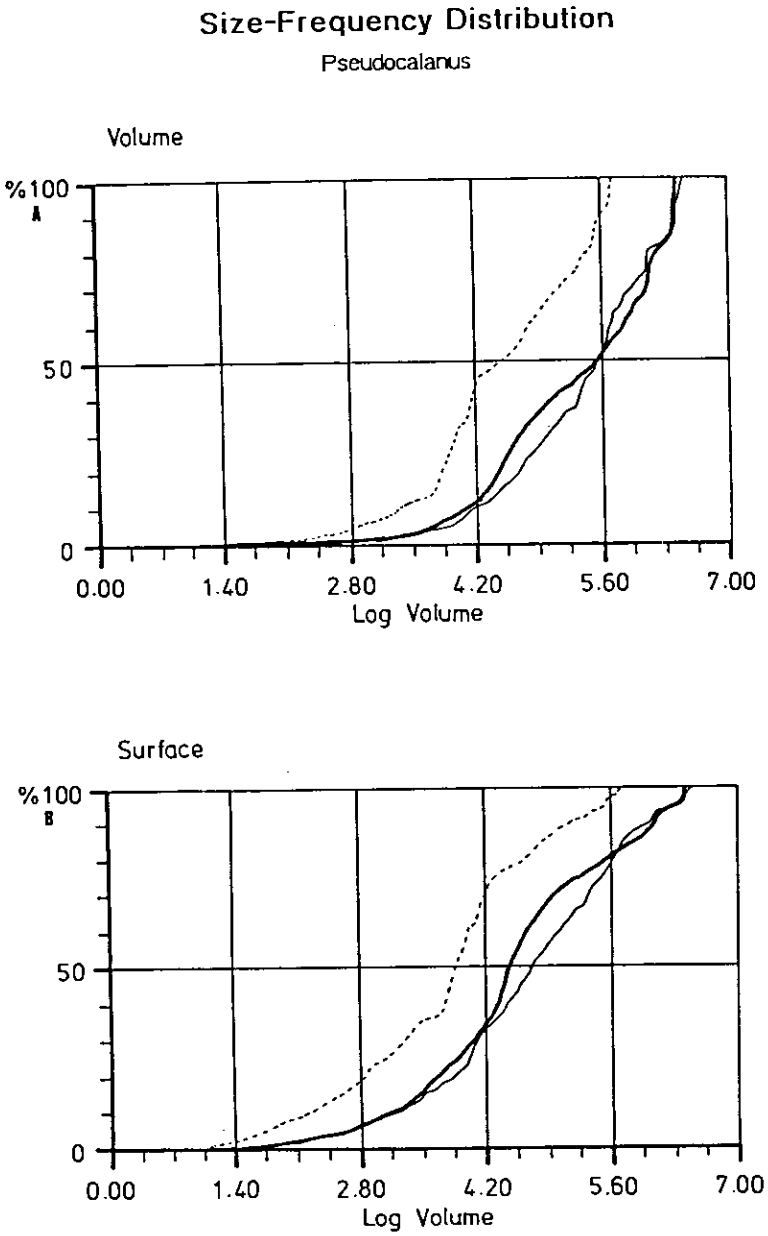


Figure 82a,b. Size-frequency distribution of volumes (A) and surface areas (B) of particles in the coprorhexy incubation (thick line) with *Pseudocalanus elongatus* and fecal pellets, Control-*Pseudocalanus* (thin line; see text) and the seawater medium (dotted line). See Figure 81 for explanation of axes. (from Noji *et al.* submitted)

As for the other two experiments, the distribution of particles for *Calanus finmarchicus* incubated with fecal pellets as compared with that of Control-*Calanus* showed a higher concentration of small particles (Figs. 83a and b). V_{V50}, V_{S50} and V:S from the coprorhexy incubation were 74, 51 and 20 % lower, respectively (Table 14). Although total particle volume per liter was similar, surface area was larger in the coprorhexy incubation. The presence of these copepods with fecal pellets again resulted in a general reduction in particle size relative to the control. No loss of particulate material was recorded.

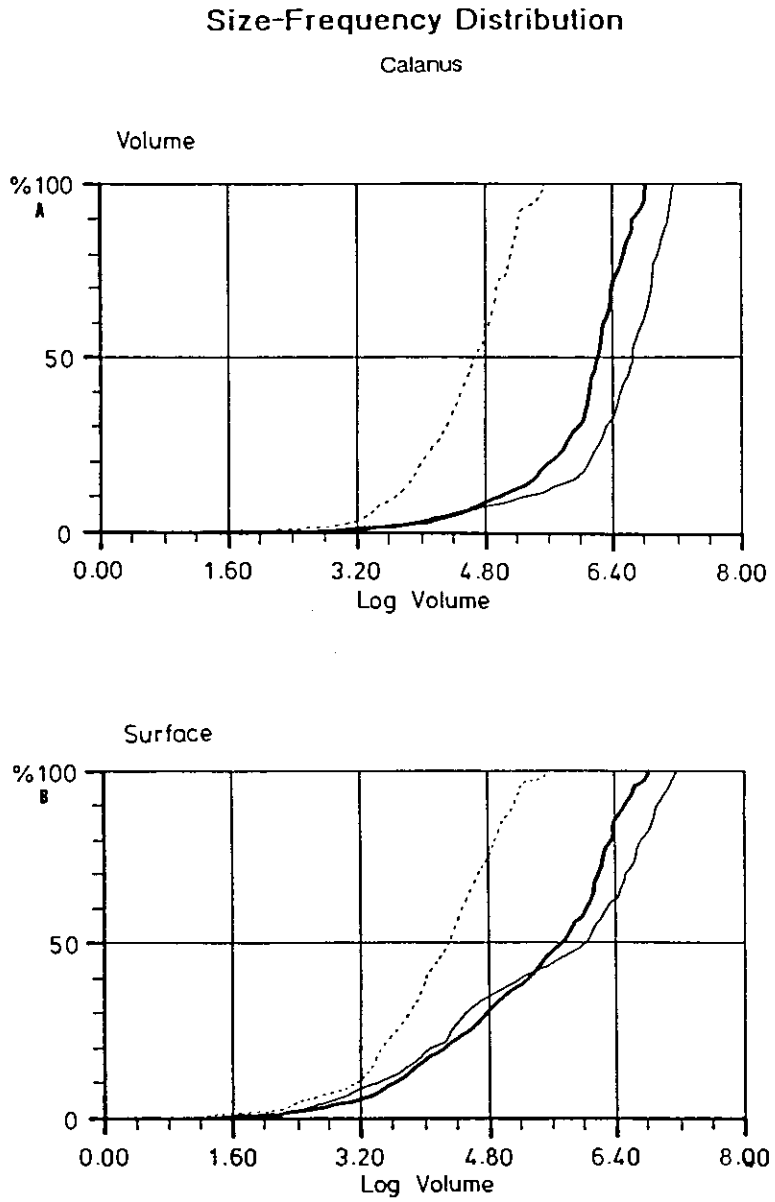


Figure 83a,b. Size-frequency distribution of volumes (A) and surface areas (B) of particles in the coprorhexy incubation (thick line) with *Calanus finmarchicus* and fecal pellets, Control-*Calanus* (thin line; see text) and the seawater medium (dotted line). See Figure 81 for explanation of axes. (from Noji *et al.* submitted)

Table 14. Total volume (V) and total surface area (S) of all particles, V:S, and size (volume) of individual particles corresponding to 50 % of total volume (V_{V50}) and total surface area (V_{S50}) (see text) at the end of incubations (21.5 h) during the coprorhexy study.

Experiment	V ($\mu m^3 \times 10^9$)	S ($\mu m^2 \times 10^6$)	V:S	V_{V50} ($\mu m^3 \times 10^9$)	V_{S50} ($\mu m^3 \times 10^9$)	N
Acartia						
-coprorhexy	3.7	552.9	6.7	0.140	0.043	1560
-control	2.8	332.8	8.4	0.330	0.080	1691
-seawater	0.8	124.2	6.4	0.120	0.030	383
Pseudocalanus						
-coprorhexy	1.7	232.8	7.3	0.350	0.030	939
-control	1.2	141.2	8.6	0.350	0.052	368
-seawater	0.4	98.3	4.1	0.032	0.007	325
Calanus						
-coprorhexy	5.4	407.8	13.2	1.610	0.570	719
-control	6.2	370.0	16.6	4.460	1.160	923
-seawater	0.5	96.8	4.7	0.045	0.019	244

4. Discussion

The results from this study shall be discussed in five main parts. **Experimental studies** (section 4.1) discusses the implications of findings from the experimental work conducted during this study. The particular importance of aggregation and disaggregation is a major theme in this section. An introduction to the processes involved in the **Flow of particulate matter in the pelagial** (section 4.2) with emphasis on the regulation of sedimentation by zooplankton is then provided. This section is designed to provide the reader with an understanding of the fundamental processes involved in the regulation of sedimentation. With these processes as a foundation, the **Seasonal influence of zooplankton on sedimentation in the Norwegian Sea** (section 4.3) analyzes the different seasons of the year with respect to zooplankton distribution and sedimentation on the Vøring Plateau. The importance of hydrography on the seasonal distribution of the major herbivores is also discussed. Lastly, **Annual perspective** (section 4.4) draws upon the major findings from the detailed analyses of the individual seasons and considers them within in the more coherent framework of an annual cycle. The particular importance of carnivory is also addressed.

4.1. Experimental studies

A discussion of the major experimental findings is presented according to the chief processes addressed. **Copepod grazing potential** (section 4.1.1) in winter is thoroughly discussed in Bathmann *et al.* (in press) and is presented here only summarily. In **Pteropod-copepod interactions** (section 4.1.2) clearance of small particles and aggregate formation are discussed primarily in terms of their influence on zooplankton biology. The sections on **Fecal pellet production** (section 4.1.3), **Fecal pellet composition in relation to age** (section 4.1.4) and **Sedimentation velocities of fecal pellets and mucous aggregates** (section 4.1.5) address the importance of fecal pellets in influencing the quantitative and qualitative characteristics of vertical flux. A comparison with mucous aggregates is also made with respect to sedimentation velocities. The studies on fecal pellet ingestion and fragmentation are described in **Coprophagy** (section 4.1.6) and **Coprorhexy** (section 4.1.7), respectively. The latter section includes a discussion on the advantages of image-analysis as an analytical tool in studies of particle dynamics. Further, possible impetus behind the process of coprorhexy and the its implications for the vertical flux of particles are presented.

4.1.1. Copepod grazing potential

As described in section 3.2.1.2, surface stocks of copepods dominated by *Calanus finmarchicus* were capable of active feeding in winter. This fact is particularly important with respect to enhanced seasonal phytoplankton growth in late winter/early spring. Presumably these stocks of active copepods immediately respond to increases in primary production; intensified grazing may hinder the accumulation of phytoplankton biomass. This shall be addressed again in section 4.4.

4.1.2. Pteropod-copepod interactions

Aggregate formation

As described in section 3.2.1.3 fewer mucous aggregates were present after incubations of *Limacina retroversa* pteropods with *Calanus finmarchicus* copepods as compared with incubations of *L. retroversa* alone. This must have been due to either (1) inhibited formation of aggregates due to food competition or behavioral effects or (2) ingestion or fragmentation of aggregates by the copepods. If fragmentation were a process of importance, then a major portion of fragments must have been smaller than 0.4 mm in length (the lower limit of analysis), since no increase in either number or total volume of aggregates in the 0.4 to 0.8 mm size range of the mixed species-incubation was evident. Determent of aggregate formation by pteropods due to the presence of copepods merits further study.

The process of the formation of the mucous aggregates during these experiments is unknown. However, there are three possibilities: (1) rejection of captured food, (2) egestion and (3) loss of mucous nets. *Limacina retroversa* has been described as a ciliary feeder, which eliminates undesirable material including "larger and looser particles" via ciliary movements below its wings (Morton 1954). The concept of the ciliary feeding technique for *L. retroversa* has since been updated, as described below. However, the rejection mechanism may be tenable. Although not specifically reported by Morton, the rejected particles were probably rich in mucous, as this is the transport medium for captured particles. Rejected particles embedded in mucous represent a form of aggregate, which would presumably adhere to other particles to form larger aggregates. Alternatively, aggregates could be fecal products of the pteropods. Unfortunately, there is no reported description of *L. retroversa* fecal material, although Bruland and Silver (1981) describe fecal coils for the pteropod *Corolla spectabilis*. The coils however do not correspond to the appearance of the aggregates from these experiments. Further, digestion of phytoplankton would lead to a

measurable decrease in the chlorophyll *a* concentration of particles (including the aggregates); no significant reduction in chlorophyll *a* of the particles in the incubations with *L. retroversa* was evident. Hence, it may be unlikely that aggregates were fecal in nature. More recently mucous nets have been observed to be the mode of particle capture for many pteropods including *L. retroversa* (Gilmer 1974, Gilmer and Harbison 1986). The net can be several cm in diameter for an adult. Moreover, they noted that nets were discarded upon disturbance of the feeding animals. Nets lost during incubation or material rejected before ingestion are the most likely candidates for the aggregates formed during these experiments.

Feeding on small particles

Compared with *Calanus finmarchicus* copepods, *Limacina retroversa* pteropods were better able to clear particles of 1 - 2 µm in diameter (section 3.2.1.3). The ability of *L. retroversa* to clear very small particles is most probably due to its mucous net-technique of food capture (described above in the discussion on *Aggregate formation*), although pore-size of the net may also restrict the size of filterable particles (Bruland and Silver 1981). In contrast *Calanus finmarchicus* filters particles with the aid of microsetae on feeding appendages (e.g. Schnack 1975). The spacing of microsetae may limit the lower size range of filterable particles to about 2 µm in diameter (Bartram 1981)* Thus, while the net-feeding pteropods are capable of feeding on particles smaller than 2 µm in diameter, *C. finmarchicus* may be forced to find larger food particles or starve. This offers a distinct advantage for *L. retroversa* in pelagic regimes characterized by small phytoplankters - a situation which is often encountered in "regenerating" production systems. This shall be addressed again in section 4.3.

*Koehl and Strickler (1981) reported that the bristled appendages of the calanoid copepod *Eucalanus pileatus* do not filter particles but act as paddles propelling parcels of particle-containing water to be captured by the second maxillae. This would imply that the lower size range of filterable particles is not necessarily determined by the spacing of microsetae. Perhaps there exists another factor in limiting the lower size of particles filtered by copepods. Other studies (Cowles and Strickler 1983, Price *et al.* 1983, Price and Paffenhöfer 1986) support this observation for some copepod species.

4.1.3. Fecal pellet production

It is acknowledged that a direct relationship generally exists between food concentration and ingestion/egestion rates by copepods (e.g. Gauld 1951, Marshall and Orr 1972). This was not evident from experiments conducted during this study (section 3.2.2.1). However, high concentrations of copepods were used in incubations since the chief purpose of the experiments was to collect fecal material for morphological and biochemical studies. With values of about 40 to 60 individuals per liter the densities of *Calanus finmarchicus* copepods in these experiments were one to two orders of magnitude greater than surface concentrations in the Norwegian Sea during the copepod annual maximum. Such "crowding" may lead to reductions in measured feeding rates. Accumulation of metabolites may, for example, retard feeding (Roman and Rublee 1980). Further, high densities of copepods result in intensive reprocessing of suspended particles, including fragmentation and ingestion of fecal material. Intensive reprocessing in these experiments probably masked any relationship between food concentration and ingestion/egestion. Such reprocessing was also reflected in decreasing estimates for fecal pellet production rate with increasing copepod density. This shall be discussed in detail in sections 4.1.6 and 4.1.7.

4.1.4. Fecal pellet composition in relation to age

Morphology

During experiments on the changing composition of *Calanus finmarchicus* fecal pellets in relation to age (section 3.2.2.1), the total volume of fecal material as well as number of intact fecal pellets decreased over periods of one to three weeks. This indicates a loss of particulate material or disaggregation of fecalia to microscopically unidentifiable fecal detritus due to microbial respiration and remineralization. Lingering digestive enzymes from the consumer or autolytic phytoplanktonic enzymes may also play a role.

Thus microbial or autolytic processes may degrade fecal matter at temperatures characteristic of arctic and subarctic waters on a time-scale of weeks. This is comparable to findings by Honjo and Roman (1978) who measured the decomposition of the peritrophic membrane of copepod fecal pellets to be 20 days at 5°C. The time-scale for disaggregation may be shorter if turbulent stress is considered. For benthic fecal pellets Taghon *et al.* (1984) documented enhanced pellet disintegration during sedimentation relative to age. However, if handling during the present experimentation represents a form of mechanical stress similar in effect to hydrographic stress, then

disaggregation and degradation times on the order weeks may be realistic. This is decidedly slower than for the process of coprorhexy which shall be discussed in section 4.1.7.

Although there was a net decrease in the volume of microscopically identifiable fecal material during these experiments, a small resurge in volume during the last sampling interval for two of the experiments was observed. This was presumably due to loosening of material over long periods of time leading to increases in the size of fecal fragments. This effect may be aggravated by handling of the samples during preparation for microscopy.

Biochemical composition

As the composition (e.g. Bathmann *et al.* 1987, Voss in prep.) and compactness of fecal pellets (Bathmann *et al.* 1987, personal observations) vary with food quantity and quality, one would normally expect a correlation between food concentration and fecal pellet content. This was not true for the collated results obtained during this study (section 3.2.2). However, as described above, assuming that intensive reprocessing including fragmentation of material occurred in the present experiments, it is not surprising that no distinct relationship between food concentration and the content of *C. finmarchicus* fecal pellets was observed.

The carbon content of fecal pellets measured during this study generally agreed with values in the literature. For example, with values of about 20 %, POC content (as % of dry weight) was similar to that for copepod fecal pellets measured by Johannes and Satomi (1966). This was also similar to values for flocculent aggregates (Herndl and Peduzzi 1988).

The results for dry weight, POC and PON content of *Calanus finmarchicus* fecal pellets (section 3.2.2.1) indicate that content increased after an age of one day. In the absence of protozoans rapid bacterial growth in or on fecal material (Johannes and Satomi 1966) would be the only reasonable explanation for this phenomenon. At temperatures of approx. 18°C maximum concentrations of bacteria may be reached within hours, after which numbers decline. Although the experimental temperatures for incubations in the present study were about 1°C, it is still conceivable that dense bacterial concentrations may be achieved within a day. An increase in the particulate content of fecal pellets is possible if the source of DOM for bacterial growth is outside of the fecal pellet. As bacterial growth on fecal pellets is largely due to attached bacteria (Jacobsen and Azam 1984, Wille 1988), access to external DOM sources should be no hindrance. Alternatively, if the freshly produced fecal pellet contains a large DOM component, subsequent bacterial growth may convert the dissolved component to POM. The latter process seems more likely, as it is difficult to imagine why bacteria should colonize a

fecal pellet if the substrate were not a food source. More detailed experimentation on this process would be required to quantify the effect. It is, however, noted that substantial increases the carbon content of benthic fecal pellets have been attributed to bacteria (Peduzzi and Herndl 1986).

The wide range in C:N values for pellets may be a combined effect of the utilization of ingested material by consumers and the above-mentioned bacterial colonization. One expects that nitrogen of ingested fresh phytoplankton is utilized by the metazooplanktonic consumer at a faster rate relative to carbon (Downs and Lorenzen 1985). Excreted particulate material should thus be comparatively poor in nitrogen leading to C:N ratios higher than those of fresh phytoplankton cells (Redfield *et al.* 1963). Downs and Lorenzen (1985), for example, reported C:N values of 7.5 in fecal pellets from *Calanus pacificus* feeding on diatoms with a C:N ratio of 6.1. However, rapid bacterial colonization of fecal pellets also influences C:N ratio of the pellets. As described above, colonization is very rapid. This is of importance, as the largest variations in C:N were for the "freshly produced pellets", which were up to one-day old. As bacteria fix greater amounts of nitrogen relative to carbon, i.e. C:N ratio for bacteria of about 3 (Fukami *et al.* 1985) as compared to a DOC:DON ratio of about 7 in open-ocean waters (Sugimura and Suzuki 1988), increasing bacterial biomass lowers the C:N ratios of fecal pellets. For example, Fukami *et al.* (1985) found that increases in PON due to bacterial colonization on flocculent aggregates were accompanied by lowered C:N ratios. Further, if the food source for bacterial growth is POM from the aggregates, then selective enrichment of bacterial PON implies the selective release of excess DOC from the aggregate; this has been documented by Herndl and Peduzzi (1988). Although the work was conducted on nonfecal aggregates, their studies should have application for fecal material as well.

Thus, the particularly large variation of C:N ratios in "younger" pellets in the present investigation is probably due to varying degrees of bacterial colonization during the initial phase of rapid bacterial growth. Some of these pellets may have been only sparsely colonized while others may have hosted maximum concentrations of bacteria. Further, the less sporadic and somewhat low C:N ratios of about 5 to 7 for older fecal pellets (> 1-day old) may reflect a relatively stable bacterial community (Peduzzi and Herndl 1986) which is established after the decline of the initial high densities.

4.1.5. Sedimentation velocities of fecal pellets and mucous aggregates

With values of between about 15 and 55 m per day, the range of sedimentation velocities for *Calanus finmarchicus* fecal pellets agreed with reported values from other studies (e.g. Bienfang 1980). Within the relatively narrow spectrum of *C. finmarchicus* fecal pellet sizes, no relationship between volume and sedimentation velocity was observed. However, over the wider range of volumes for fecal pellets of *C. finmarchicus* and *Calanus hyperboreus*, fecal strings of *Thysanoessa* sp. and mucous aggregates of *Limacina retroversa* a distinct positive relationship was observed. The range of sedimentation velocities was about one order of magnitude - from 30 m per day for *C. finmarchicus* fecal pellets to about 300 m per day for mucous aggregates. This is not surprising as velocity is a function of volume if density of the particles is not a factor (e.g. Komar *et al.* 1981), and the volumes of the aggregates were generally much larger than those of the *C. finmarchicus* fecal pellets. In addition, the mucous aggregates may have lower drag coefficients, i.e. may cause less friction during sinking, which increase sinking velocities. For example, marine snow aggregates of similar size exhibited much lower sedimentation velocities (Alldredge and Gotschalk 1988).

In general the relationship between the size and sinking velocity of particles is reflected in these velocity measurements, although the "behavior" of particles in the ocean is certainly different from that *in vitro* (e.g. Alldredge *et al.* 1987). Moreover, the importance of large particles as vehicles of vertical flux (e.g. Karl *et al.* 1988, Suess 1988) is emphasized by the high velocities of mucous aggregates as well as fecal pellets. The importance of large particles in pelagic systems shall be discussed more fully in section 4.2.

4.1.6. Coprophagy

As described in section 3.2.2, copepods reduced the number of intact fecal pellets during incubations. Clearance rates of intact fecal pellets were similar to those measured using phytoplankton (Poulet 1974). High values for clearance rate at low fecal pellet concentrations may have been an artefact, as an "overlooked" pellet at the end of incubation in this case may represent a substantial percentage of the total available particles, i.e. fecal pellets. No reductions in clearance rates were observed with increasing fecal pellet concentrations; in contrast saturation effects are usually observed when copepods feed on high concentrations of phytoplankton (e.g. Lam and Frost 1976, Lampitt and Gamble 1982).

The initial impression from these results is that copepods ingested fecal pellets. One might conclude that coprophagy was the active process effecting fecal pellet reduction. However, tracing the flow of carbon using radioisotopes showed that this conclusion would be premature. Although the interpretation of radiotracer incubations is difficult (Conover and Francis 1973), it is possible if one can account for all pathways of carbon flow. In these experiments the source of ^{14}C was fecal pellets, and all carbon pools - fecal pellets, copepods, detritus and DOC and CO_2 - were measured. If there is no appreciable uptake of free dissolved carbon, then the flow of ^{14}C can be traced. Uptake of DOC in these incubations would be accompanied by respiration and release of CO_2. By quantifying released CO_2 by bacteria, one can at least approximate potential DOC uptake. This is possible as the potential autotrophic processes capable of assimilating dissolved CO_2 - photosynthesis and chemosynthesis - were presumably inoperative in these incubations. Scanning electron microscopy showed that fecal pellets contained no intact phytoplankton cells, and therefore the first means of uptake was unlikely. The existence of chemoautotrophic uptake of dissolved $^{14}CO_2$ was very improbable, as this process can only occur in an anoxic environment. Uptake of free $^{14}CO_2$ released through respiration inherently implies that the potential assimilators, the bacteria, are free swimming and, hence, are in an aerobic environment.

With these considerations assimilation rates for copepods may be approximated from the results of the ^{14}C-labelling experiments presented in section 3.2.2.2. Assuming that microbial respiration* was the same in controls and incubations with copepods, assimilation of carbon by copepods was the amount of dissolved carbon released from the copepods plus the amount incorporated into the bodies. The first component is equal to the difference between dissolved ^{14}C values for the incubations with and without copepods. Thus,

$$\text{Assimilation} = {}^{14}C_{\text{dissolved (copepods-control)}} + {}^{14}C_{\text{copepod bodies}},$$

and in terms of recovered radioisotope

$$= 4\% - 2\% + 2.5\%$$
$$= 4.5\%.$$

*The measured value of 1.2 ± 0.4 % after 28 h was notably similar to findings from Jacobsen and Azam (1984), who attributed a 1.6 % recovery of ^{14}C in the form of CO_2 to bacterial respiration after incubating fecal pellets from *Calanus pacificus*.

Thus 4.5 % of ^{14}C at the end of incubation was assimilated by the copepods. This may also be expressed in terms of carbon. In this investigation a mean dry weight of 0.29 ± 0.16 µg per pellet with a mean volume of 0.239 ± 0.078 x 10^6 μm^3 was measured, i.e. a specific weight of 1.20 which compares well with findings by Komar *et al.* (1981) of 1.23. If we assume that 20 % of dry weight was in the form of POC, as indicated from other studies (e.g. Johannes and Satomi 1966, this study - section 3.2.2.1), then carbon content per fecal pellet was 58 ng. If 4.5 % of this carbon was assimilated by the copepods, then with an average of 45 copepods per liter and a range of fecal pellet concentrations from 100 to 800 per liter, assimilation rates are 6 to 46 ng POC per copepod per day in these incubations.

In order to assess the assimilation rate in terms of daily requirements, the following estimates may be made. Since an adult female *Centropages hamatus* copepod has a carbon content of approx. 5 µg (Johanssen unpublished data), respiratory requirement was estimated to be about 1.4 µl O_2 or 440 ng POC per day (Ikeda 1970). The highest rates (46 ng POC per copepod per day) of estimated assimilation obtained from these experiments covered only about 10 % of these requirements. Further, even if POC content of fecal pellets were greater than the assumed 20 % of dry weight, the effect would not account for the difference between measured assimilation and respiratory demands. For example, if a POC content of 40 instead of 20 % of fecal pellet dry weight is assumed, calculated assimilation still covers only 20 % of respiratory requirements. Hence, although there was more than enough POC, i.e. 580 to 46 400 ng POC per liter according to the above assumptions, in the form of fecal material to cover respiratory demands, copepods did not utilize enough of the available fecal pellet carbon to meet their daily requirements. In fact they utilized only a very small fraction of the fecal carbon despite the fragmentation of about half of the pellets to smaller assumably more easily filterable pieces.

In light of this fact, the absence of any evidence for "feeding" saturation (section 3.2.2.2) is not surprising. In these incubations the percentage of recovered intact fecal pellets did not increase even when very large numbers of pellets were introduced to the bottles. Such saturation effects are observed when copepods feed on high concentrations of phytoplankton (e.g. Lam and Frost 1976, Lampitt and Gamble 1982). One would only expect this effect, if copepods were actively ingesting the fecal material in these experiments; they did not do this.

In summary the results show that copepods are capable of rapidly fragmenting intact fecal pellets to microscopically unidentifiable particles. The process has been named "coprorhexy" - the fragmentation of fecal material (Lampitt *et al.* in press). In contrast, "coprophagy" (e.g. Paffenhöfer and Knowles 1978) - the ingestion of fecal material - occurred but was minimal in this study. Until now the major mechanisms leading to fecal pellet disaggregation in the ocean have been considered to be turbulent stress, microbial decomposition and coprophagy. Coprorhexy represents another feasible mechanism which disaggregates fecal pellets and thereby enhances their further recycling by zooplankton and bacteria. Moreover, the fragmentation of fecal pellets via coprorhexy operates on a time-scale of hours rather than of days to weeks as measured for decomposition of the peritrophic membrane by bacteria (Honjo and Roman 1978, Wille 1988).

4.1.7. Coprorhexy

Image-analysis

Image-analysis, the analytical tool employed for this series of experiments, offers several advantages over other methods of particle analysis. The major advantages over manual methods, using eyepiece micrometers, are speed and precision (Estep *et al.* 1986). When compared with other electronic particle counters such as the Coulter Counter, the advantages are primarily associated with measurement of a continual spectrum instead of size increments, selectivity according to visible properties, e.g. length:breadth ratio, and operator intervention. The possibility of intervention eliminates many of the difficulties encountered using other electronic systems (Harbison and McAlister 1980, Baretta and Malschaert 1985). Problems associated with the "dead time", i.e. time of the processing of electrical pulses, of some electronic particle counters (Kersting 1985) are avoided. Moreover, the operator sees all particles - an aid for interpreting grazing and other experiments (Bakker *et al.* 1985); the "black box" aspect of particle numeration is minimized. The disadvantage to image-analysis is the slight increase in time needed to perform operations when compared with electronic particle counters such as the Coulter Counter.

Size-frequency distributions

Total volume of particles in coprorhexy incubations (incubations of copepods with fecal pellets; section 3.2.2.3) as compared with theoretical (Control-genus) data sets (combined data from incubations of only fecal pellets and only the seawater medium) was either larger (30% larger for *Acartia* and 40% for *Pseudocalanus* experiments) or almost constant (< 15% difference in *Calanus* experiment). The important point is that no substantial reductions in total volume of particles were recorded. If we assume that the density of particles was constant in these experiments*, then volume is essentially a parameter for organic content. Since there were no substantial reductions in total volume in coprorhexy incubations, particulate fecal matter apparently was largely conserved. Hence, no appreciable trophic utilization, i.e. ingestion, assimilation and respiration or remineralization, of particles presumably occurred.

The major effect of copepods on particle composition in fecal pellet incubations was a shift to smaller size which led to an increase in total surface area. The increased proportion of smaller particles in the coprorhexy incubations could result from (1) the removal of large particles and (2) the introduction of small particles. The large particles removed must have been fecal material. The small particles introduced could have had two sources: the copepods and the fecal pellets. If the particles were of copepod origin, significant loss of skeletal or other bodily parts must have been a response to increased concentrations of particles, i.e. fecal pellets. To my knowledge loss of fine skeletal material, for example by abrasion, during feeding has not been documented although it is conceivable. If the small particles were fecal in nature, then the fragmentation of fecal pellets, coprorhexy, explains the findings. Other zooplankton grazing studies (e.g. Ayukai 1987) relying on the microscopic numeration of intact fecal pellets attributed pellet loss to coprophagy; these conclusions may have been premature although noteworthy. I believe that coprorhexy was the chief moderator of change in the particle size-distribution in these experiments, although loss of fine bodily parts from copepods may have contributed to the observed effects. As material was essentially conserved, the fragmentation of fecal pellets explains the observed shift to smaller particles in the size spectra, which in turn resulted in increased total surface area of particles due to the simple geometrical relationship involved.

*Density of fecal material appeared to increase in other experiments (section 4.1.4) over periods of many days to weeks. However, in the present incubations (21.5 h) it may be justified to assume that density was constant.

The biological function of coprorhexy and implications for sedimentation

Although copepods can be very dextrous when handling food items, at present the mechanics involved in the removal of the membrane are not known. Research with the aid of high speed cinematography should be conducted to tackle this unknown.

The impetus behind coprorhexy may be feeding. As peritrophic membranes of fecal pellets are rapidly colonized by bacteria, and colonization may be facilitated by sinking through the water column (Jacobsen and Azam 1984), copepods may intercept sinking pellets and graze the membrane along with attached microbial flora. Reingestion of substances such as chitin, a glucose amine and major component in the structure of the peritrophic membrane of copepods (Yoshikoshi 1988, Yoshikoshi and Ko 1988), may be of nutritional importance. The more refractory material within the peritrophic membrane may be left uneaten. Fecal pellets, which are stripped of an enveloping peritrophic membrane, are presumably more liable to fragmentation by other means, the most likely being further manipulation by zooplankters or protozoans and turbulence. Moreover, coprorhexy offers an ecological explanation for the existence of "ghost pellets" - fecal pellets with little or no visible content. Such pellets are also attracted by microbes (personal observations) and may thus represent a food source for zooplankton.

Although the mode and impetus behind coprorhexy are poorly understood, some of the consequences are readily predictable. The most obvious consequences are an additional food source for the zooplankton, increased residence time of material due to reductions in sinking velocities of the smaller particles and increased substrate for microbes due to enlarged surface area. They each have an effect on remineralization and respiration of the material and thus flux rates of organic particles in the ocean. Another possible effect is the oxygenation of anaerobic microenvironments (Gowing and Silver 1983, Alldredge and Cohen 1987, Sieburth *et al.* 1987) should they exist within fecal pellets of these sizes. In fecal pellets (0 to 1-day old) from *Calanus finmarchicus* as well as from *Pseudocalanus elongatus*, anaerobic was greater than under aerobic bacterial activity (I. Martinussen personal communication), indicating the possible existence of anoxia within these pellets. These were preliminary experiments and should be considered with caution. However, if the results are valid then sudden flushing of fecal material with oxygen could conceivably lead to an increase in microbial respiration and remineralization of fecal material due to the energetic advantages of aerobic respiration of certain organic complexes such as protein (Meyer-Reil 1983). Similar effects

have been observed in sediments (Graf *et al.* 1983, Meyer-Reil 1983, Graf 1989).

The reduction of particulate organic matter from surface to midwater and deep layers in the ocean has been a topic of recent fervent interest (Cho and Azam 1988, Karl *et al.* 1988, Sasaki *et al.* 1988, Suess 1988). Coprorhexy represents a mechanism explaining the elusive fragmentation process in the conversion of large, fast-sinking particles to small, "suspended" particles, the precursors to the microbially mediated transition from particulate to dissolved organic matter.

4.2. Flow of particulate matter in the pelagial

In order to provide the reader with the proper background for discussion of the presented findings, a short overview of the Production and fate of biogenic particles (section 4.2.1) is presented. Emphasis is given to the Influence of zooplankton on sedimentation (section 4.2.2) in terms of zooplankton-regulated processes which enhance and inhibit vertical flux and influence its quality.

4.2.1. Production and fate of biogenic particles

Pelagic production of biogenic particles and their fate are influenced by a myriad of factors. The two comprehensive categories "physical environment" and "biology" (Fig. 84) contain the manipulators of the quality, quantity and distribution of biomass. The biological response of organisms to regular changes in the physical environment (e.g. Nixon 1988) is the first link in a chain of processes. Internal biological mechanisms also regulate biology; such biorhythms are, however, based on physical cycles such as diel periodicity (Bary 1967). Perturbations in the pattern of biological responses are caused by inconsistency in the cycle of physical changes. For example, sudden turbulent breakdown of a summer thermocline due to storms or a particularly "warm spring" or "cold winter" modifies the pattern of biological responses. The physical environment of an organism may also change when the organism migrates. For the purposes of examining the influence of zooplankton on sedimentation, the relationship between physical environment and biology is considered to be predominantly but not exclusively monodirectional. Counterexamples to this assumption are microscale environments, i.e. an individual plankter and its immediate fluid environment (Woods and Onken 1982, Strass and Woods 1988, Wolf and Woods 1988), enclosed or semi-enclosed mesoscale environments, e.g. plankters in strongly stratified near-surface waters, and megascale environments on geological time scales, e.g. the global stock of plankton and its influence on climate (McCarthy *et al.* 1986). In comparison, the units of the biological apparatus, i.e. all living things, are decisively interactive; biological interaction induces biological perturbations, which induce further perturbations in an endless network. This may function on an interorganismal, e.g. grazing, or intraorganismal level, e.g. ontogenetic changes in feeding strategy. For example, intensive local carnivory of herbivorous zooplankton by a fish swarm inevitably affects the accumulation of phytoplankton stocks.

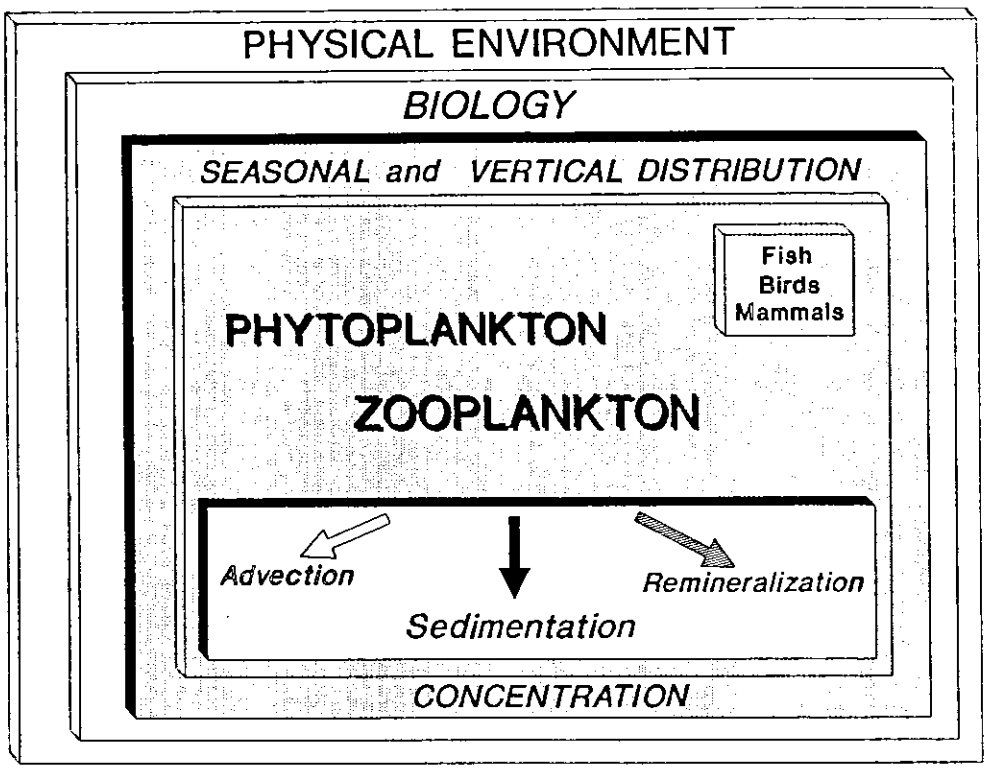


Figure 84. Schematic representation of the factors regulating the pelagic production of biogenic particles and their fate.

A pattern of the seasonal distribution of plankton is the result of a recurring pattern of temporal changes on an annual time-scale in the physical environment, e.g. light and temperature, and the network of biological responses of the plankton to these changes. Vertical distribution of plankton is primarily the spatial expression of biological adaptations to relatively stable hydrographical conditions modified by diel rhythms (and other rhythms of relatively high frequency such as the lunar cycle) and interactions between organisms. Seasonal and vertical distribution may exert a reciprocal influence on one another. The magnitude of the biological component, of which the emphasis in this study is on the concentration of plankton, is the end-product of the network of interactions. Other units - fish, birds and mammals - are of course integral members of the

pelagial and may be important in this network (e.g. Miller *et al.* 1985).

On a global scale pelagic biomass has three possible fates. It may be respired, remineralized or it may sediment out of the pelagial. Biological mechanisms of export out of the pelagial, such as effected by birds which may feed on pelagic organisms, are exceptions to this general rule. Advection is also an alternative fate, if the spatial scale is restricted, i.e. if boundaries are drawn between separate regimes within the pelagial.

Pelagic respiration/remineralization and sedimentation of particles are strongly and inversely related. Respiration results in the consumption of POM to fulfill energetic demands. Remineralization is the conversion of particulate organic matter (POM) and particulate inorganic matter (PIM) to its dissolved components. Diminishing particulate matter due to respiration and remineralization naturally results in decreasing vertical flux. Conversely, if the proportion of particulate matter sedimenting out of the water column increases, less material is available for satisfying organisms' energetic demands and conversion to dissolved components via pelagic remineralizing processes. Generally, this study addresses the organic fraction (POM) of sedimenting particulate matter. However, the production and sedimentation of biogenic inorganic substances such as calcium carbonate are also strongly influenced by zooplankton and, thus, PIM shall also be discussed in special cases.

4.2.2. The influence of zooplankton on sedimentation

The influence of zooplankton on sedimentation can be explained within the framework of the above-described scenario. Zooplankton can quantitatively enhance sedimentation through processes which contribute to particle production and especially the production of large particles. Large particles generally have faster sinking rates (e.g. Komar *et al.* 1981, this study - section 3.2.1.3) and have been recognized as the main vehicles of vertical flux (e.g. McCave 1975, Bishop *et al.* 1977, Suess 1988, Karl *et al.* 1988, Cho and Azam 1988). Zooplankton can inhibit sedimentation by remineralizing particulate organic matter and fragmenting large particles to smaller ones (Lampitt *et al.* in press, Noji *et al.* submitted). This is discussed in detail below. Furthermore, zooplankton can qualitatively influence sedimentation by discriminant feeding, selective utilization of ingested particles and processes associated with the biological and physicochemical properties such as diffusion boundaries of fecal material.

4.2.2.1. Zooplankton-regulated processes which enhance sedimentation

There are two main forms, which can enhance vertical flux and are produced by the zooplankton. These are the zooplankters themselves (or parts of zooplankters) and aggregates.

Cadavers and hard bodily parts belong to the first category. As metazooplankters and armoured protozooplankters (Bodungen 1989) may be considered to be fast-sinking particles in the pelagic system, they represent potential vehicles of rapid vertical transport. A dead organism will probably sink* unless gas or lipid reserves are a relatively abundant component of its structure. Unfortunately, cadavers are very difficult if not impossible to differentiate from "swimmers" - zooplankters which have actively swum into sediment traps (a topic intensively discussed in the recent NSF-GOFS workshop entitled "Sediment Trap Vagaries" in November 1988 in Ocean Springs, Mississippi, U.S.A.; see also Lee *et al.* (1988)). In some cases, however, it is possible to deduce whether zooplankters in sediment trap material are most probably swimmers or entered as cadavers. For example, a surface-dwelling herbivore collected by a sediment trap at a depth of 3000 m is likely to have sedimented to that depth as a dead organism. However, this may not be verifiable. Similar to cadavers, hard bodily parts represent large particles; they are often associated with large specific weights which enhance sinking velocities. Hard bodily parts of zooplankters may originate from cadavers, swimmers or may be discarded by living zooplankters. Typically they are the remains of zooplankton most prominent in sediment trap material, as hard bodily parts are often digestion-resistant POM and PIM and therefore not susceptible to rapid degradation. For example inorganic calcite and aragonite are main components of foraminifers and pteropods, respectively, and may be found in large quantities in trap material. Similarly, inorganic silica from radiolarians is often present in trap material whereas plasma from these organisms is either unidentifiable or recycled in the water column. Importantly, the source for the production of biogenic inorganic particles produced by zooplankton is in dissolved material and not ingested particulate material. Hence, in this case the zooplankton contributes directly to production of particles which

*Personal observations indicate for example that dead overwintering *Calanus finmarchicus* CV copepodites, which are rich in lipids, sink very slowly. In contrast, dead pteropods of *Limacina retroversa*, which are characterized by their calcareous shells, sink extremely rapidly. However, recently it has been shown that dead organisms and other particles at abyssal depths may actually be buoyant and cause considerable upward flux (Smith *et al.* 1989).

sediment. In contrast, the main component of exuviae from crustaceans is organic and is the product of the turnover of ingested particulate material; in this case the hard bodily parts are composed largely of chitin.

"Aggregates", the second group of sedimentation-enhancing particles produced by zooplankton, is an encompassing term for a collection of particles forming a unit (Guralnik 1968). Two types of aggregates shall be considered here: fecal material and mucous aggregates.

Fecal material - strings from krill (e.g. Moore 1931, Bodungen 1986, Clarke *et al.* 1988), oval pellets from amphipods (personal observations), cylindrical pellets from copepods (e.g. Gowing and Silver 1983, Bathmann *et al.* 1987), coils from doliolids and pteropods (Silver and Bruland 1981), large fecal mats from salps (Bruland and Silver 1981, Iseki 1981, Madin 1982, Matsueda *et al.* 1986), etc. - is traditionally considered to be an important vehicle of vertical flux (e.g. Gauld 1957, Fowler and Small 1972, Hoffmann *et al.* 1981, Lorenzen and Welschmeyer 1983, Fowler *et al.* 1987). Contribution of fecal material by weight to vertical flux has been recorded to range from about 1 % (Pilskaln and Honjo 1987) to over 90 % (Bathmann *et al.* 1987). The effectiveness of fecal material as a form of sedimenting particle is largely dependent upon its sedimentation velocity, which has been measured *in vitro* to range from about 30 to 3000 m per day (Smayda 1969, Angel 1984 for a review; see also section 3.2.1.3). Velocity may depend upon the diet of the pellet producers; diet affects composition and density of the fecal pellets which influence sinking velocity (Bienfang 1980, Dagg and Walser 1986, Voss in prep.). If these measurements are applied to the natural environment, then fecal material produced at the surface on the Vøring Plateau may reach the sea-floor (at a depth of 1200 to 1400 m) after a period ranging from less than one day to over one month. Due to the ideal conditions under which such sedimentation velocity measurements should be conducted, i.e. no turbulence and no physical gradients in the seawater medium, such sinking velocities may be considered to be maxima. In the ocean a sinking fecal pellet may be decelerated by hydrographic conditions (Alldredge *et al.* 1987) and perhaps by buoyancy mechanisms, e.g. gas (Krause 1981) produced in microenvironments (Gowing and Silver 1983) within the fecal pellet or physiological mechanisms such as ion-exchange (Smayda 1970) by ingested viable phytoplankters. These mechanisms may not be evident or functional during laboratory experimentation. Further, fecal pellets may be colonized by microbes (e.g. Jacobsen and Azam 1984, Alldredge *et al.* 1986, Nagasawa and Nemoto 1988) or intercepted by larger organisms and ingested or fragmented during their descent (discussed below). Hence, the effectiveness of fecal pellets as vehicles of vertical flux of particulate as well as dissolved organic matter (Poulet *et al.* 1986 describe the possible vertical tranport

of DON in fecal pellets) is dependent upon specific conditions of the physical and biological environment.

It is noted that the site of fecal pellet production is neither restricted to the surface of the ocean nor need the producer be a herbivore to exert an enhancing effect on sedimentation. For example omnivores or detritivores in midwater layers (e.g. copepod activity in midwater layers described by Sasaki *et al.* 1988) may "repackage" small particles into large pellets (this study). Similarly, carnivores may consume buoyant zooplankton which results in the production of sinking fecal material*.

Mucous aggregates, as for fecal pellets, can represent large particles with high sinking velocities (see section 3.2.1.3). In contrast to typical flocculations of "marine snow" (e.g. Lampitt 1985, Alldredge and Gotschalk 1988), mucous aggregates, as defined here, are particles entrapped in mucus. Diatom aggregates microscopically appear to be encased in a sheath (Bodungen personal communication) possibly of mucus and may serve to transport cells quickly to deep water layers (Smetacek 1985). Amongst the zooplankters, appendicularians and doliolids apparently can produce mucus (Alldredge *et al.* 1986) and these may serve as seeds for aggregates. To my knowledge the only other documentation of mucous aggregates produced by metazooplankton is that of discarded mucous feeding veils formed by pteropods** (observed *in situ* by Gilmer and Harbison 1986). The production of mucous aggregates with high sinking velocities by the pteropod *Limacina retroversa* (section 3.2.1.3) was documented in experiments during the presented study. With measured sinking velocities of almost 500 m per day (one order of magnitude greater than for *Calanus finmarchicus* fecal pellets) they represent an extremely important mode of vertical transport of particles.

In combination with the forms described above vertical migration may also promote the vertical transport of particles. This is particularly true on a daily basis for some surface feeding herbivores, although in theory it may apply to the entire water column in a process known as the "ladder of vertical migrations" - (Vinogradov 1962). It is well documented, for example, that *Calanus finmarchicus* copepods may vertically migrate up to about 100 m per day to feed at night near the surface, where phytoplankton concentrations are often high, to return to deeper water layers at dawn (e.g. Krause 1981). Longer diel migrations of

*For example, chaetognath fecal pellets can be large, compact and sink quickly (personal observations).

**Feeding veils have been documented for thecate heterotrophic dinoflagellates (Jacobson and Anderson 1986) and, if discarded, may be a type of small "mucous" aggregate.

hundreds of meters have been documented for euphausiids (Everson 1982, Sameoto *et al.* 1987), often an important component of "deep scattering layers" - discrete layers of organisms acoustically detected via echo-sounding and often exhibiting diel patterns of vertical movement (Hopkins *et al.* 1978). Such movements are usually related to feeding; diel patterns in gut content have for example been documented (Dagg and Walser 1987). Such migrators inevitably "pump" material to deeper water layers by ingesting material at the surface and egesting at least a part of this material in deeper water layers (Longhurst and Harrison 1988). This phenomenon is not yet well investigated. However using techniques for estimating *in situ* grazing rates - a method which demands much vigilance (Head 1988, Head *et al.* 1988) - Simard *et al.* (1985) showed that the gut fullness of diurnally migrating copepods feeding in surface waters was larger during their post-feeding descent. In their study migration in fact occurred twice per night; the nonfeeding phase was speculated to be necessary for the regeneration of digestive enzymes. Restoration of the digestive epithelium which is purported to be a component of fecal pellets (Yoshikoshi 1980, Nott *et al.* 1985) could also be a reason for the nonactive phase. Regardless, it may be deduced that some copepods excrete part of their ration in depths greater than in those of its ingestion (speculated for large copepods by Emerson and Roff (1987)).

Theoretically this could be a source of error in the interpretation of analyses of data collected with sediment traps deployed in near-surface waters. For example, copepods feeding at a subsurface maximum located at a depth of 30 m would need perhaps 30 minutes (Marshall and Orr 1972) to descend to a depth of 50 m. Measurements of egestion rates on copepods with full guts suggest that about one-half of gut contents may be egested within 30 minutes of cessation of feeding, and the bulk of the rest of gut contents may be egested over the following 12 hours at temperatures of about 5 to 10°C (e.g. Simard *et al.* 1985, Christoffersen and Jespersen 1986, Dagg and Walser 1987, Dam and Petersen 1988). A sediment trap in a depth of 50 m would thus collect a maximum of about 50 % of fecal material produced by these copepods after feeding had ceased. This could lead to considerable errors in interpreting the flow of particulate organic matter in these water layers. Placement of sediment traps below the zone of large primary production and intensive diurnal migrations by herbivores alleviates the problem.

On an annual time-scale, seasonal vertical migrations which are a part of the life cycle of certain zooplankton species, e.g. *Calanus finmarchicus* (e.g. Wiborg 1976a,b), enhance sedimentation as well. The mode, however, is indirect. Such zooplankters, whose growth is primarily fueled by material in waters near the surface, migrate to greater depths to overwinter in a diapausal stage of low metabolic activity (Hirche 1983, Båmstedt and Tande 1988)

until the next season of enhanced phytoplankton growth, i.e. spring. These overwinterers are liable to predation (e.g. Yen 1983; discussed in section 4.4) and presumably physiological "malfunctions" in exceptional cases during dormancy resulting in mortality. Cadavers and fecal material from carnivores in deep water layers are the results. These "newly produced" nonliving particles will sediment.

4.2.2.2. Zooplankton-regulated processes and mechanisms which inhibit sedimentation

Two main processes which inhibit sedimentation are practiced by zooplankters. The first is the ingestion and utilization of particulate organic matter. The second is the destruction of fast-sinking aggregates.

The utilization of particulate organic matter is probably the chief means by which zooplankton inhibits the vertical flux of particles. Utilization, as defined here, is the ingestion, anabolism, catabolism and respiration of material. The assumption is that particles being utilized would otherwise sediment. Basically, particles assimilated by the zooplankton are anabolically incorporated for growth and maintenance of physiology, catabolically decomposed to inorganic waste products or respired as an energy source to fuel these processes. This fraction of utilized particulate material cannot sediment except perhaps at some later point in time in the form of zooplanktonic material.

Logically, the timing of phytoplankton and zooplankton populational growth is of considerable importance for this process. Latitudinal differences in models of plankton regimes (for reviews see Cushing 1975 and Heinrich 1962) in the Atlantic provide a good example of the importance of this timing. In Arctic regions characterized in spring by new production regimes of short and intensive plankton growth, the stock of zooplankton typically attains maximum size after the phytoplankton bloom is well established. There is a "delay" in grazing upon the phytoplankton, a large proportion of phytoplankton biomass is not utilized by herbivores and senescing phytoplankton stocks may culminate in sedimentation events (e.g. Peinert *et al.* 1987). In temperate zones this pattern may be modified; zooplankton grazing may be intense during enhanced phytoplankton growth and sedimentation may be suppressed (described in detail in section 4.3.3). Tropical zones are based largely upon regenerated production and exhibit only small amplitude in the annual cycle of the development of phytoplankton, zooplankton and sedimentation. Zooplankton grazing is relatively intense throughout the year and sedimentation of organic material is small relative to primary production but seasonal. In a comparative analysis of energy flow over the continental shelf in three regimes - a tropical, temperate and subarctic system - data from Høpner-Petersen and Curtis (1980)

indicate that the ratio of zooplanktonic to zoobenthic production changes from about 6:1 in the tropical system to 1:1 for the subarctic system. Although there are questions as to applicability of some of the data used in the calculations, the study illustrates the trend toward larger input of pelagic organic material to the benthos, i.e. sedimentation, for systems in higher than for systems in lower latitudes. Specific physiological adaptations and limitations of organisms to considerably different physical environments often associated with latitude (e.g. Clarke 1987, Ikeda 1970) can modify the simplified scenario above but cannot be addressed in detail within this study.

Many physical perturbations arising in pelagic systems cause large mismatches in the timing of primary and secondary production. Upwelling of nutrient-rich water to an otherwise nutrient-deplete euphotic zone fuels intensive primary production which cannot be fully utilized by zooplankton at least in the region of phytoplankton production. The accumulated phytoplankton may sediment. Similarly, storms which break down near-surface pycnoclines in summer may lead to the sudden introduction of nutrients from deeper water layers which, again, fuels primary production. Zooplankton stocks are not "prepared" for such a burst in primary production and phytoplankton accumulation may culminate in mass sedimentation.

It may be argued that catabolic wastes (e.g. ammonium) arising from utilization of POM by zooplankton are biologically recycled and promote growth of phytoplankton, which potentially may sediment. This indirect reasoning, however, is not acceptable, as the generation of catabolites is most probably coupled with consumption of the phytoplankton. Moreover, one of the key messages from the importance of timing in the regulation of sedimentation is that large vertical flux occurs when there is a mismatch between autotrophy and heterotrophy. If an equilibrium between primary and secondary production exists, suspended matter will be recycled within the pelagial. Any process which slows the accumulation of phytoplankton biomass will promote the establishment of such an equilibrium. The catabolism of phytoplanktonic biomass by zooplankton and renewed uptake of released nutrient salts by autotrophs is such an equilibrium-promoting process.

The second chief zooplankton-regulated means of inhibiting sedimentation is the destruction of aggregates. This is a new concept and only the destruction of copepod fecal pellets (termed coprorhexy) has been well documented (Lampitt *et al.* in press, Noji *et al.* submitted). As coprorhexy and its implications have been discussed in depth, the reader is referred to section 4.1.7 for more information. However, three main points should be emphasized. Firstly, the fragmentation of aggregates need not be limited to copepods and their fecal pellets. Destruction (or inhibition of their production) of mucous

aggregates, for example, has been suggested by preliminary experiments in this study. All large zooplankters are conceivably capable of fragmenting aggregates including fecal pellets, mucous aggregates and marine snow. Secondly, the fragmentation mechanism can be very fast. The coprorhexic mechanism appears to work on a time-scale in the order of hours. Microbial decomposition of the peritrophic membranes of fecal pellets, in contrast, seems to operate on a scale of days to weeks (Honjo and Roman 1978). Thus fragmentation of aggregates to finer particles by zooplankton may be much more important than fragmentation by microbes (Cho and Azam 1988). Thirdly, the quintessential aspect of the fragmentation of aggregates with regard to vertical flux lies in the resultant longer residence time of POM. Longer residence time of slowly sinking POM allows more complete utilization of material by other organisms, especially microbes. The fragmentation mechanism has been considered to be necessary for microbial remineralization of organic particles in the ocean (Lochte and Turley 1988, Karl *et al.* 1988, Suess 1988), although large DOC release has been measured from intact flocculent aggregates (Herndl and Peduzzi 1988).

4.2.2.3. Zooplankton-regulated processes which influence the quality of sedimenting particles

Zooplankton influences the quality of sedimenting material through discriminant feeding on suspended particles, the selective utilization of ingested material and the biological and physicochemical properties of fecal material. Another important influencing factor is of course the quality of sedimenting zooplankton bodies and remnants. This however is strongly coupled to the above discussion on "cadavers and hard bodily parts", and it is presumably self-evident that the composition of zooplankton stocks will influence the composition of sedimenting zooplankters and their corporal rests. Therefore although this is an important aspect of the influence of zooplankton on sedimentation, further detailed discussion on this topic shall be reserved for specific examples presented in the forthcoming section (4.3).

Zooplankton influences the quality of sedimenting material through discriminant feeding on suspended particles. The process of discrimination between different particles by copepods is well documented for neritic (e.g. Donaghay and Small 1979) as well as oceanic copepods (Huntley *et al.* 1983, Barthel 1986, 1988). If food items are selected, then, biogenic material is enriched in fecal material. Moreover, refractory biogenic material is particularly enriched (Gauld 1957). The reason for this is simply that much nutritious POM is part of a larger biological unit, e.g. coccolithophores and intact diatoms,

containing biogenic inorganic or refractory organic material, which will not be biologically utilized. This is discussed in more detail below. The sedimentation of such material is enhanced through transport in fecal material. For example the enhanced transport of coccoliths (e.g. Bathmann *et al.* 1987, Samtleben and Bickert 1989) and diatom valves and frustules (e.g. Schrader 1971, Ferrante and Parker 1977, Haberyan 1985) via fecal pellets has been reported. An important aspect of discriminant feeding is the trophic nature of zooplankters. Excreted material of herbivores is largely phytogenous, whereas that of carnivores is largely zoogenous. This seemingly banal observation is important, as the spatiotemporal distribution of zooplankton is heterogeneous. As the distribution of active herbivorous feeders is coupled to phytoplankton stocks, the quality of sedimentation particularly in surface waters is strongly influenced by the sinking aggregates including fecal material formed by these herbivores, i.e. a relatively large phytogenous component in vertical flux can be expected. Similarly, carnivores feeding for example in midwater depths will enhance the sedimentation of zoogenous material.

The selective utilization of ingested material is a process based on the physiological demands of the zooplankters. Materials essential for these demands will be "extracted" by zooplankters from the pool of fine POM and less nutritional material will be excreted. This changes the quality of particles; the fraction of less preferable material increases. Similarly, certian elements may be selectively utilized. A larger proportion of nitrogen than carbon may be extracted from ingested material; an increase in the C:N ratio of material is the result (as explained in section 4.1.4). Other substances fulfilling the physiological demands of the consumer will also be selectively extracted. Although different organisms may have differing nutritional requirements and abilities to assimilate ingested POM, the overall result is that the nutritional value of sedimenting fecalia is generally lower than that of suspended food sources.

Processes which occur on and within sinking particles can be equally important for the quality of sedimenting material. These processes depend upon the biological and physicochemical properties of the particles. Fecal material and other aggregates may be particularly important in this respect, as they represent potential microenvironments. Conditions within aggregates may be considerably different from and independent of those of its immediate environment. Generally aggregates may possess autonomous production systems (Prezelin and Alldredge 1983) and are often characterized by large bacterial colonization (Fellows *et al.* 1981, Alldredge and Cohen 1987, Herndl 1988) which in marine snow may result in a cycle of microbially moderated

aggregation and disaggregation (Biddanda and Pomeroy 1988).

Some fecal pellets may possess a particularly effective physical barrier in the form of a peritrophic membrane which inhibits exchange processes. Freshly produced fecal pellets are presumably anaerobic but encounter strong oxygen diffusion gradients upon egestion. Large pellets (e.g. from large amphipods) may maintain the anaerobic state for several days. Further, as described in section 4.1, anaerobic bacterial activity has been measured in fecal pellets from *Calanus finmarchicus* and *Pseudocalanus elongatus*. Microenvironments within fecal pellets (Gowing and Silver 1983) and other aggregates may affect the aggregates' contents in ways uncharacteristic of the surrounding water. The enrichment of nitrogen relative to carbon by attached or endemic bacteria (see section 4.1) is a simple example of microenvironment-specific modification. Evidence for the deposition of sulphur by green bacteria in sediment trap material (probably in anaerobic aggregates of senescent *Phaeocystis pouchetii* colonies or *Calanus hyperboreus* fecal pellets) has been found and is an example of biological modification made possible by the particular physicochemical properties of the aggregates (M. Vernet personal communication; P. Wassmann personal communication).

The preservation/dissolution of material within aggregates, especially fecal pellets, may also be influenced by the particular physicochemical properties of the pellets. Similar to the effect of reduced diffusion of oxygen across the peritrophic membrane, it has been speculated that the enhanced vertical transport of silica within fecal pellets (Ferrante and Parker 1977, Haberyan 1985) was due to suppressed diffusion (Schrader 1971) between the interior and exterior of the pellets. This results in the build-up of silicate concentrations within the pellets and inhibited dissolution of diatom valves. Notably intact phytoplankton cells also can be present in fecal pellets (Fowler and Small 1983). This is primarily a result of digestion-resistance generally associated with superfluous feeding or armoured phytoplankters, spores and cysts. However, suppressed diffusion may also play a role in hindering the dissolution of these cells. In contrast, it has been speculated that certain species of coccolithophores dissolve more easily in fecal pellets than do others (Samtleben and Bickert 1989). The properties of the pellets determining dissolution were, however, not evident.

The properties of aggregates from zooplankters may affect sedimenting particles in one more way. Depending upon the consistency and morphology of sinking particles, they may passively sweep suspended particles along with them during descent. Smetacek (1985) mentions the possibility of this mechanism for mass sinking of diatoms. I speculate that the passive collection of particles occurs for many sedimenting spinose and adhesive objects. For example the spinose eggs of *Acartia* sp. and *Centropages hamatus*

collected *in situ* are very often covered with detritus (personal observations). Further, detritus almost always adhered to the mucous aggregates of *Limacina retroversa* collected during incubation experiments conducted during this study. The addition of material to mucous aggregates (or other adhesive or spinose particles) produced by the zooplankton will modify the composition of the sinking particle. Moreover, objects prone to collect detritus serve as potential seeds for marine snow. Increasing the size of aggregates via passive collection during sedimentation probably increases the sinking velocities of these aggregates. In this respect, passive sweeping of suspended particles also enhances sedimentation. Depending upon the particular properties of each aggregate, increasing size and sinking speed will eventually produce turbulent stress of such magnitude that the aggregate may be torn apart.

4.2.2.4. Summary

The production and fate of biogenic particles in the pelagial depend upon a network of biological responses to changing conditions in the physical environment. Although this is a reciprocal relationship, within this study "biology" can usually be viewed as being subordinate to "physical environment". Products of this network are the spatiotemporal distribution and concentration of plankton stocks, for which there are three possible fates: advection, sedimentation and respiration/remineralization. On a global scale advection is not a source or sink.

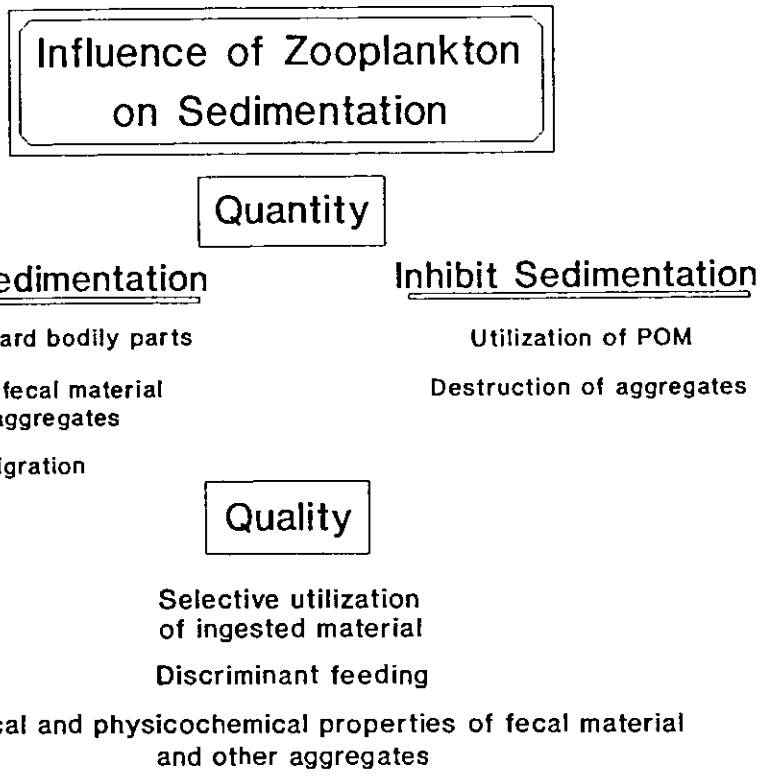


Figure 85. Zooplankton-regulated means which enhance or inhibit vertical flux of particles and influence their quality.

The influence of zooplankton on sedimentation (Fig. 85) is quantitative and qualitative. As large particles are the prime vehicles of vertical flux, zooplankters enhance rates of sedimentation through their contribution of cadavers, hard bodily parts and aggregates including fecal material to sedimenting material. This may be promoted by vertical movements of zooplankton stocks. Enhanced sedimentation has large implications for the deposition of material in sediments and, hence, for the global carbon cycle. Zooplankton-regulated processes which inhibit sedimentation are the physiological utilization of POM and destruction of aggregates. These must play an important role in the microbial loop. In addition, the composition of sedimenting material is influenced by zooplankton through the composition of zooplankton stocks, selective metabolic utilization of ingested material, discriminant feeding and the biological and physicochemical properties of fecal material and other aggregates.

4.3. Seasonal influence of zooplankton on sedimentation in the Norwegian Sea

A short discussion of the importance of hydrography for the seasonal distribution of zooplankton on the Vøring Plateau is presented (section 4.3.1). Thereafter, results from the field investigations shall be analyzed in terms of the described zooplankton-regulated means of influencing sedimentation (section 4.2). The dominant modes of influence exerted by the zooplankton change over the annual cycle, and thus field results shall be discussed according to season. In addition, a short note on the interpretation of field data has been included.

A note on the interpretation of field data

The accuracy and precision of sediment traps in quantifying the vertical flux of particles is a theme of ongoing controversy. Good reviews of trap dynamics with emphasis on sediment trap construction and variations in hydrographical conditions exist (e.g. Gardner 1980, Blomqvist and Håkanson 1981, Staresinic *et al.* 1982, Gardner *et al.* 1983, Bloesch 1988), and the reader is referred to these works for an analysis of this method of quantifying the flux of particles in the ocean. Generally it may be stated that especially with the aid of supplementary pelagic and experimental data, results from sediment trapping provide valuable information on the quality as well as quantity of sedimenting material. It remains the best tool we have for estimating the vertical transport of matter to the deep-sea.

Although continual measurements for sedimentation were made via sediment trapping over three years, pelagic data were momentary recordings from the specific situation encountered during the respective expeditions. This is of course a traditional dilemma for biological oceanographers; much or all data collecting is logistically restricted to a few precious research expeditions in the oceanic area of interest. Very often data from different years are used to reconstruct a seasonal cycle. In my opinion this is a legitimate method of data analysis and indeed often the only recourse open to ecologists, who are interested in understanding biological patterns in specific pelagic systems. However, if this approach is used, as it is here, two methodological tenets should always be applied. Firstly, corresponding data from different years should be stringently compared if they exist. Secondly, one must apply utmost caution and reason to avoid "overinterpreting" results. I am aware of these tenets and have analyzed the data accordingly.

4.3.1. Seasonal abundance of metazooplankton in relation to hydrography

The purpose of this study is to assess the means of influence of zooplankton on sedimentation and not to conduct a detailed analysis of the composition of zooplankton stocks in relation to hydrography in the Norwegian Sea. For more information on the latter the reader is referred to reviews in the literature (e.g. Østvedt 1955, Wiborg 1955, Wiborg 1976a,b, Hansen 1960, Ljøen 1962, Lie 1968). However, in light of the importance of advective processes on the size and composition of zooplankton stocks, especially of the main herbivores strongly influencing sedimentation in the Norwegian Sea, a short characterization of the metazooplankton stocks in relation to dominant currents is presented. The possible effects of the latter on an annual scale are discussed.

As described by Hansen (1960) and others, the metazooplankton stocks in the Norwegian Sea can be separated into four groups characterized by hydrography. Neritic stocks from nearshore waters, e.g. the Faeroes and Shetlands, Atlantic Water stocks, arctic-subarctic stocks from the East Icelandic Current and indigenous stocks in waters of the Norwegian Sea proper contribute to the composition of zooplankton. The hydrographical features of the respective bodies of water affect the vertical and horizontal distribution of plankton. For example, *Calanus hyperboreus* and *Metridia longa* of the arctic-subarctic regime are associated with a body of cold water, which results in a distribution of these species in predominantly deep water in the Norwegian Sea. In contrast, *Limacina retroversa* is characteristic of Atlantic Water, warmer than East Icelandic Current Water, and is accordingly distributed primarily in surface waters. The input of different plankters from different sources in conjunction with the prevailing conditions for growth in the Norwegian Sea contributes to the large variation in size of metazooplankton stocks.

Atlantic Water is introduced with the Norwegian Atlantic Current which flows in through the Faeroe-Shetland Channel with the North Atlantic Current (e.g. Johannessen 1986). Off northern Norway the Norwegian Atlantic Current divides into two main arms - the North Cape Current which flows into the Barents Sea and the West Spitsbergen Current which flows along southwestern Spitsbergen and either further into the Arctic or southwestward with the East Greenland Current. Large *Calanus finmarchicus* and *Limacina retroversa* stocks are thus transported from the Atlantic into the Norwegian Sea with the Norwegian Atlantic Current in spring and late summer, respectively. The size of *C. finmarchicus* and *L. retroversa* stocks depends largely upon their history in the North Atlantic.

Because of the specific life-strategies of these two species, the most important herbivores on the Vøring Plateau, their fates are very different. As described in section 3.1.2.5, the size of *L. retroversa* stocks peaks in late summer. These plankters remain at the surface during their life-cycle. A portion of the stocks may recirculate in the gyre system associated with the Norwegian Basin (Swift 1986), however the bulk may be transported northward with the Norwegian Atlantic Current into the Barents Sea or in a northwesterly direction toward Spitsbergen and Greenland. With near-surface current velocities of about 5 to 10 cm per second (Deutsches Hydrographisches Institut 1980), zooplankton stocks could be advected from the Vøring Plateau to the entrance of the Barents Sea within about two to four months. The *L. retroversa* stocks probably perish in these regions, as their northernmost distribution does not extend into these arctic latitudes (e.g. Spoel 1967). Hence, massive mortality is probably the fate of most of the pteropod stock encountered during this study.

Calanus finmarchicus has a much different fate. As described previously, a small population remains in surface waters; this population must be advected northward or recirculate in the Norwegian Sea. However, the bulk of the spring/summer stock, which migrates to great depths to overwinter in a phase of diapause, is below 500 or 600 m in Norwegian Sea Deep Water. A portion of this body of water flows southward into the North Atlantic, but the bulk of NSDW circulates internally in the Norwegian Sea (Swift 1986). Overwinterers in this deep water are not advected out of the system *en masse*. Those which are advected southward may be rerouted into the region with the North Atlantic Current in late winter/early spring, when seasonal migration to surface waters commences. It may be speculated that this offers distinct advantages in maintaining an indigenous stock of *C. finmarchicus*. If this is the case then the overwintering tactic may provide a conservative element in the pelagic biology in the Norwegian Sea.

4.3.2. The influence of zooplankton on sedimentation in late winter

Primary production in February was extremely low as were concentrations of suspended chl. *a* and POC, which decreased with increasing depth. This is not surprising as the light climate in late winter in this area is characterized by only a couple of hours of sunlight per day. Metazooplankton stocks, in contrast, were large and carbon biomass of these stocks was among the largest recorded throughout the year. However, about half of this metazooplankton POC was in the form of diapausal CV copepodites of *Calanus finmarchicus* in depths below 500 m, i.e. they had no active influence on sedimentation. These copepods were probably prey to omnivorous and carnivorous copepods and chaetognaths. Carnivores were particularly abundant at depth. In surface waters, however, active herbivorous *C. finmarchicus* copepodites and isolated adults of both sexes and carnivorous *Eukrohnia hamata* chaetognaths dominated carbon biomass of metazooplankton.

From experiments with these surface plankters it was shown that *C. finmarchicus* actively fed on a supplemental phytoplankton food supply (sections 3.2.1.2 and 4.1). In order to roughly assess the minimum grazing pressure of these active copepods on the sparse phytoplankton stocks, we may conservatively estimate *C. finmarchicus* carbon biomass to be about 1 g per m^2 in the upper 100 m of the water column. For the purpose of simple calculations concerning material utilization by metazooplankton, an ingestion rate of about 25 % of body weight per day at ambient temperatures for *Calanus finmarchicus* was assumed (Tande and Båmstedt 1985, Barthel 1988). If the rate of incorporation of ingested material is 45 % of body weight per day (Copping and Lorenzen 1980), then a theoretical metabolic food demand of about 100 mg C per day is estimated if copepods are actively growing. Alternatively, if a respiration rate of 4 % of body carbon per day (Ikeda and Skjoldal 1989) is assumed, metabolic demands are only about 40 mg C per day. I do not intend to budget the flow of material. However I wish to emphasize that as primary production was estimated to be about 15 mg C per m^2 per day, metazooplankton stocks were potentially capable of metabolizing all primary production in late winter.

Sedimentation rates, as evidenced by values at a depth of 500 m for dry weight, carbonate and particulate organic carbon, exhibited slight increases in February but were generally low in late winter. With maximum sedimentation rates for POC of about 7 mg C per m^2 per day, roughly half of primary production was remineralized or invested in higher trophic levels within the upper 500 m of the water column. A portion of the sedimented material was in the form of fragments of small diatoms at the time the pelagic data for late winter were collected. Although the contribution of diatom fragments to sedimented POC was negligible, their

presence does verify the active primary production measured in late winter. Large fecal pellets were notably scarce in sediment trap material. As the *Calanus finmarchicus* copepods were probably consuming phytoplankton stocks at a rate about equal to primary production, i.e. up to 15 mg C per m^2 per day, the bulk of phytoplankton was converted to fecal matter, dissolved organic and inorganic matter or respired. DOC and DIC (as dissolved CO_2) may comprise up to almost 50 % of carbon flow during copepod metabolism (Copping and Lorenzen 1980). It can be stated with reasonable certainty that a large portion (about half according to primary production and sedimentation trap data) of phytoplankton biomass was remineralized in the upper 500 m of the water column. The bulk of the rest sedimented as fragmented fecal material.

Especially in light of the scarcity of fresh phytoplankton, it may be expected that the dominant copepod *Calanus finmarchicus* coprophagically and/or coprorhexically exploited fecal pellets, a potentially important food source at this time of year. Following *Calanus finmarchicus* in abundance of individuals in surface waters were the copepods *Oithona spinirostris* and *Metridia lucens*. The genera *Oithona* (Lampitt 1978, Turner 1984) and *Metridia* (Haq 1967) are generally considered to be carnivorous and/or omnivorous. Due to its ability to capture particles raptorially as well as by filtration (Haq 1967), the latter is well adapted to the relative paucity of food during late winter in that it may feed on intact fecal pellets or the microbial flora associated with them, fragmented fecal material or phytoplankton cells. *O. spinirostris* may also be well adapted to feeding on pieces of fecal material, although the finest particles may escape capture.* The increase in the flux of detrital POC (without any indication of increases in other biological components except for a non-compensatory peak in minipellets) in late winter of 1988 can thus be theoretically explained by a large input of fragmented, microscopically unidentifiable fecal material.

In late winter of 1988 the flux of minipellets also increased noticeably. The origin of minipellets (Gowing and Silver 1985) is suspected to be small gelatinous zooplankters, radiolarians and/or other protozooplankters. As the more or less spherical pellets are small (from 3 to 50 µm in diameter according to Gowing and Silver 1985), they presumably do not sediment over long distances; rather they are subject to physical and biological degradation or consumption. Hence, recorded increases in sedimentation rates probably reflect high minipellet production rates near the depth of collection. If a large portion of the fine sedimenting material at 500 m depth was fecal in nature, then it is likely that the minipellets represent reingested,

*On the other hand, preliminary experiments with *Calanus finmarchicus* fecal pellets and *Oithona similis* copepods showed no evidence for coprophagy or coprorhexy.

repackaged feces. Gelatinous plankton was not collected in February in this depth layer; the source of fecal pellets was thus probably protozoans. Unfortunately, the microplankton assemblage at these depths has not yet been analyzed. Although the effect was probably confined to midwater depths, the minipellets represent a morphological and biochemical restructuring of sedimenting material. Moreover, they most likely increased local flux rates in these depths.

4.3.3. The influence of zooplankton on sedimentation in late spring/early summer

Phytoplankton stocks dominated by small naked flagellates (diatoms and coccolithophores were numerous but probably composed less than 15 % of phytoplankton carbon biomass) had developed considerably by late spring and primary production ranged from 200 to 700 mg C per m^2 per day and averaged about 500 mg C per m^2 per day in May 1987. Phytoplankton was apparently in good physiological state with assimilation numbers (Harrison and Platt 1980) of 1 to 2 mg C per mg chl. *a* per hour, nutrients were plentiful and hydrographical and light conditions were favorable for phytoplankton growth. Despite these conditions, a large accumulation of phytoplankton did not occur. (For more information concerning the general development of hydrography, plankton and sedimentation of POC and photopigments see Peinert *et al.* 1987.) The inhibition of the development of a large bloom was due to intensive grazing by metazooplankton. In May the metazooplankton stock dominated by *Calanus finmarchicus* adult females was moderate with values ranging from about 2 to 4 g C per m^2 and averaging about 3 g C per m^2 for herbivores, which were distinctly concentrated in surface waters. These were accompanied by relatively large carbon biomasses of carnivorous and omnivorous metazooplankters. Again, by applying the assumptions for rates of ingestion and incorporation described in section 4.3.2, an estimate of about 300 mg C per day can be calculated as the amount of POC required to fuel metazooplankton metabolism. It may be concluded that metazooplankton metabolic needs in May were somewhat less than were supplied by primary production.

Hence, although sedimentation increases in late spring, the intensive utilization of phytoplankton by metazooplankton prohibits the occurrence of large sedimentation events. Drifting sediment traps in depths of 100 m recorded flux rates of only about 30 to 150 mg C per m^2 per day. The larger rates roughly correspond to the amount of material not utilized by metazooplankton in the above calculation, if the average rate of primary production (500 mg C per m^2 per day) is applied, and supports the suggestion that metazooplankton limited sedimentation rates in May. Further, as intact or fragmented phytoplankton cells contributed very little to flux at all trap depths (100, 300 and 1000 m) in comparison with fecal pellets and detritus, it is likely that the bulk of sedimented material was fecal. It is noted that the flux of diatom valves and fragments does indeed show increments in late spring/early summer. The peak was particularly large in 1988. However, their contribution to organic material flux was small.

Less than 2 % of suspended fecal pellets was collected in the uppermost sediment trap per day in May; at 1000 m depth pellets sedimented in trace amounts. Thus, the bulk of fecal pellets was fragmented, incorporated by the zooplankton, remineralized or respired. *Oithona spinirostris* in large numbers in subsurface waters may have contributed significantly to this process. Roughly it can be estimated that in May about 1/4 of primary production sedimented as fragmented fecal material and 3/4 was incorporated by the metazooplankton or remineralized.

The situation changed in late June in 1986. Primary production and concentrations of suspended particulate matter at the surface decreased, e.g. from peak chl. *a* concentrations of 3 in late May to about 1 to 2 µg per liter in late June. Further, although integrated values for chl. *a* in the upper 100 m increased by 20 %, corresponding values for POC increased by 100 %. This indicates the intensive turnover of phytoplankton biomass by zooplankton grazing from late May to late June. Major changes in the populational structure of *C. finmarchicus* also occurred. The concentrations of *Calanus finmarchicus* adult females at the surface decreased slightly but were still dominant, and a large portion of the *C. finmarchicus* stocks in late June was in the form of diapausal CV copepodites in depths below 500 m. Sedimentation rates increased, e.g. about 100-fold for POC.

The increase in sedimentation is related to changes in the physiological state and populational structure of *Calanus finmarchicus*. The changes led to a reduction in grazing pressure. Grazing pressure exerted by the surface stock of *C. finmarchicus* dominated in late June by adult females (Figs. 53 and 54) was presumably less intense for two reasons: concentrations of adult females decreased slightly and the physiological state of these copepods was presumably poor in comparison with their state in May. The latter presumption is based on the facts that (1) the increasing numbers of eggs in spring stabilized in early summer which indicates the completion of spawning, (2) after the period of spawning, which may endure for several weeks (Østvedt 1955, Lie 1965, Tande 1982, Hopkins *et al.* 1984), spent females will probably die within a relatively short time and (3) adult females are relatively scarce in late summer (discussed in section 4.4). It is suggested that *Calanus finmarchicus* was reproductively active throughout spring and into early summer. The new cohort exerted large grazing pressure on phytoplankton stocks and developed into a large stock of CV copepodites by late spring, the bulk of which migrated to depth starting in June. During the migration the copepods presumably do not feed or produce fecal pellets. The copepodites in deeper water layers represent the overwintering diapausal stage in the life-cycle of *Calanus finmarchicus*. They remain inactive until late winter/early spring and, hence, do not actively affect

particulate flux. The old cohort in the form of adult females also fed intensively in May but grazing pressure from these copepods probably became progressively weaker as females spawned and presumably stopped feeding. By late June the first signs of increasing mortality of the old cohort of adult females were evident by the lower concentrations in surface waters. Intact adult females were, however, not found in considerable numbers in sediment traps deployed at this time. Presumably their cadavers are recycled in the water column. Many CV copepodites of *C. finmarchicus* were in trap material; these were presumably "swimmers" which entered the traps during this annual vertical migration to depth.

The result is less intensive utilization and recycling of material by metazooplankton in near-surface waters, which leads to increased vertical flux of POM. This is also reflected in the increasing flux of intact copepod fecal pellets collected in sediment traps despite presumably low rates of production of fecal pellets. Due to the populational restructuring of the *C. finmarchicus* stocks, coprorhexy and/or coprophagy were less important processes and did not inhibit sedimentation to the degree they did a month earlier.

It is noted that coccoliths and some diatom rests were the only identifiable components of the otherwise hyaline copepod fecal pellets both suspended and sedimented. Fecal pellets have been speculated to be one of the chief vehicles of vertical transport for coccoliths in the Norwegian Sea (Samtleben and Bickert 1989). The pellets were sparsely packed and no rests from the main autotrophs, naked flagellates, were identifiable. Hence, in late spring/early summer copepod utilization of organic material and the packaging of hard bodily parts in fecal pellets enhance the flux of PIM.

In late June/July 1986 large numbers of oval fecal pellets were collected in traps in midwater and deep-water layers. These are attributed to ostracods, which have been collected in deep waters in the Norwegian Sea (Wiborg 1955) and were particularly abundant in the midwater depth stratum in which the intensive sedimentation of the oval fecal pellets occurred. Other producers of large oval fecal pellets, e.g. amphipods, were not abundant at this time. The pellets contained compact detritus and some crustacean rests. The large size and compactness of the pellets undoubtedly result in high sedimentation velocities (e.g. Urrére and Knauer 1981). Hence, feeding by this species of ostracod leads to the packaging of (probably) copepod fecal material and copepod bodily parts into larger fast-sinking particles; flux is enhanced. The midwater depths at this time represented a zone of sedimentation acceleration. Vertical zonation in the pelagic biology is typical of the Vøring Plateau and has been reported for other open-ocean systems (Karl and Knauer 1984).

Larger concentrations of tintinnids, foraminifers and radiolarians were also collected in net hauls in late June (unpublished data). Thus, a shift in the composition of heterotrophs from metazooplankters to protozoans accompanied the restructuring of *C. finmarchicus* population. Such shifts to protozoans following intensive grazing by larger zooplankton stocks has been indicated in other studies (e.g. Stegmann and Peinert 1984, Noji *et al.* 1986). The flux of tintinnid thecae, foraminifer tests and radiolarian silico-skeletons was greater in late spring/early summer for all years studied. Notably, although plasma was visible in the tests of foraminifers in traps at 100 and 300 m, none was found in traps at 1000 m. Dead or dying foraminifers may serve to transport material to subsurface water layers, in which particulate organic matter is utilized; only inorganic tests remain to sediment to greater depths. The necrophiles utilizing this material may be bacteria, protozoans or metazooplankters.

4.3.4. The influence of zooplankton on sedimentation in mid-summer

Pelagic data collected in mid-summer are limited to metazooplankton collections in late July 1987. Analysis of the pelagic situation is, hence, based largely on sediment trap findings.

Metazooplankton stocks were somewhat larger but similar in composition compared with stocks in late June 1986. During mid-summer sedimentation rates are the highest of the year and average about 25 mg C per m^2 per day in 500 m. Moreover, the composition of sedimenting microscopically identifiable material exhibited unique features in comparison with other seasons. Peaks in hard bodily parts of foraminifers and radiolarians and thecae from tintinnids were generally but not always recorded. Interestingly, in June to July 1986 foraminifers and radiolarians exhibited inverse patterns of sedimentation rates, and in 1988 a peak in radiolarian flux but none for foraminifers was recorded. Without supplementary pelagic data it is difficult to assess this pattern. The possibility of competitive feeding leading to the suppression of the development of one group or the other is a consideration and is worthy of further study. The causes of interannual variation in biological systems are often puzzling. However, the interannual similarity within this data is the importance of heterotrophic protozooplankters for summer sedimentation. It may be assumed that protozooplankters were amongst the chief heterotrophs in near-surface waters of the summer system. Further, they apparently were also abundant in midwater layers, as peaks in minipellets were also recorded. However, *Calanus finmarchicus* was also active in near-surface waters and contributed to vertical flux through fecal pellet production, which is relatively high in mid-summer, even though a large portion of the *C. finmarchicus* stock was overwintering in deeper water layers.

It is speculated that the relatively high sedimentation rates associated with mid-summer are a result of less intensive secondary production and less fragmentation of particles by the metazooplankton. As described in section 4.3.3, the restructuring of the *Calanus finmarchicus* stocks, i.e. vertical migration of copepodites to depth, is the probable cause of increased sedimentation rates. Assuming that the activity of *C. finmarchicus* stocks in mid-summer is reduced as described for the stocks at the surface in late June, metazooplankton-regulated mechanisms which inhibit sedimentation may still be less effective than they are in early spring. The effect is a high sedimentation rate, provided primary production does not decrease significantly which is unlikely as rates later in August were similar to those in May. The speculated increases in protozooplankton stocks in near-surface waters are probably due to the relaxed grazing pressure by metazooplankton. A large input of hard bodily parts from these protozoans to vertical flux

results. The increase in sedimentation also provides a larger food supply for protozoans in midwater layers, where minipellets are produced.

4.3.5. The influence of zooplankton on sedimentation in late summer

The production regime in late summer is much different from the regime in spring. Phytoplankton production in the upper 20 m in mid-August 1988 was largely based on regenerated nutrient salts. Ranging from 180 to 560 and averaging about 320 mg C per m^2 per day primary production was similar to that in spring 1986. Concentrations of suspended particles throughout the water column were lower than in spring, e.g. chl. *a* decreased from maximum concentrations of 3 in spring to about 0.6 µg per liter in late summer. New production occurred in subsurface waters, i.e. below a depth of about 20 m, where nitrate was not depleted. The composition of metazooplankton in terms of numbers in this regenerated production system is dominated by the euthecosomatous pteropod *Limacina retroversa*, which shows very strong gradients in vertical distribution. Highest concentrations of these pteropods in near-surface waters reflect the herbivorous nature of these pteropods. Its contribution to carbon biomass was also considerable. However, metazooplankton POC in the surface waters was still dominated by the larger herbivores *Calanus finmarchicus* (CV copepodites) and *Thysanoessa* sp.* as well as carnivorous chaetognaths. In deeper waters large stocks of *C. finmarchicus* copepodites were accompanied by considerable POC contribution by *Calanus hyperboreus* and the carnivorous chaetognath *Eukrohnia hamata*. *C. hyperboreus* and certain chaetognaths are characteristic of deep waters in the eastern Norwegian Sea (Wiborg 1955). The dependence of juvenile chaetognaths on high food densities has been shown (Sullivan 1980). Their feeding must influence sedimentation in deeper waters (discussed in section 4.4).

*Due to the sampling technique, very large fast-swimming zooplankters including krill such as *Thysanoessa* sp. were probably not quantitatively collected. However, due to their relatively large numbers in collections, it is valid to conclude that they were quite abundant.

Sedimentation rates in late summer are about the same as in late spring with 10 mg C per m^2 per day at a depth of 500 m. Again, the bulk of sedimenting organic material was diverted to secondary production, remineralized or respired in the water column. There were few intact fecal pellets in sediment trap material in 500 m and I assume that coprorhexy and coprophagy by *Calanus finmarchicus* copepodites in surface waters and considerable numbers of *Oithona spinirostris* in subsurface waters also play important roles in the inhibition of flux in late summer. By far the most common microscopically identifiable component of sedimented material was calcareous shells from *L. retroversa*. The contribution of the shells to carbonate flux is very large in late summer and composed up to about 50 % of flux (by weight) in 100 and 500 m, assuming that the bulk of carbonate in sediment traps originated from *L. retroversa*. This assumption is justified, as the small coccolithophores and foraminifers, the other carbonate sources in the pelagial, were present in the water column in relatively small quantities. Further, Honjo *et al* 1988 showed that carbonate flux of particles larger than 1 mm in this area in late summer increases significantly; this could only originate from pteropods.

Considering only the latter half of August, carbonate flux at a depth of 100 m peaked between the 23rd and 25th, after which flux decreased slightly. As mortality rates are high during the development of *Limacina retroversa* stocks (Almogi-Labin *et al* 1988; section 3.1.2.5), the increase in flux is a direct result of the sedimentation of cadavers of *L. retroversa*. One other conceivable means of carbonate input, however, existed for the trapped material in 100 m. As large individuals of *L. retroversa* appeared to migrate from depths of about 100 m to near-surface waters at night to descend again at dawn, they represent potential "swimmers" in sediment trap material. Migration has been documented for euthecosomatous pteropods off the Florida coast (Wormuth 1981), although migrations of over 100 m were not recorded for *L. retroversa* (Wormuth 1985). This may overestimate vertical flux of pteropods and aragonite (the chief form of inorganic carbonate component of the shells), as has been observed by Harbison and Gilmer (1986b) for near-surface sediment trapping and *Limacina* spp.. However, as a large percentage of sedimented carbonate in the present study was in the size fraction < 1.0 mm in diameter, and small pteropods in this investigation did not display evidence of diurnal migration, the input of swimmers is probably relatively small. The reason for vertical migration of large individuals of *L. retroversa* is probably feeding in the higher concentrations of phytoplankton and POC in surface waters. Migratory escape from predators (e.g. fish swarms) could also be a factor (Wright *et al* 1980, Vuorinen 1987); this cannot be analyzed here. Temperature probably did not influence the vertical distribution of *L. retroversa* as was speculated for the plankton regime in an Atlantic

gyre by Beckmann *et al.* (1987).

Mucous aggregates were also common in the upper (100 m) sediment traps. Unfortunately these aggregates could not be selectively quantified in terms of organic content. As discussed in section 4.1.2, such aggregates may be discarded feeding veils produced by *Limacina retroversa*. If this is true, then their presence in trap material indicates that loss of mucous feeding veils is a natural phenomenon as opposed to losses through *in situ* (Gilmer and Harbison 1986) or *in vitro* (this study) experimental manipulation. The reasons for this behavior are difficult to deduce. However, since *L. retroversa* is purportedly capable of rejecting particles before ingestion (Morton 1954)*, one could speculate that entire feeding veils are rejected if undesirable particles are captured. Unusual situations of large turbulent stress could alternatively tear the veils away from their hosts. In any case, mucous aggregates represent a form enhancing sedimentation in late summer. One fate of these aggregates, as indicated from experimentation, could be destruction by copepods - a process similar to coprorhexy. However, as determined with scanning electron microscopy, mucous aggregates similar in size and appearance (network of fine filaments) to the aggregates in sediment trap samples and from experiments were found on the sediment surface on the Vøring Plateau in late August (P. Jensen personal communication). Detritus was often found on the exterior of aggregates which indicates their adhesiveness. Further, according to Jensen this was not a single observation but true for all of about 15 studied sediment cores (taken using a multicorer, i.e. surface sediment was undisturbed). These aggregates are presumably from *L. retroversa*. Thus the chief fate of these aggregates may be sedimentation to great depths. In one sense, this is not surprising as the measured sedimentation velocities of the aggregates were very high, i.e. generally higher than for copepod or krill fecal pellets. On the other hand, the loss of feeding veils appears to be a highly inefficient and wasteful process if it occurs regularly. This is the first report of the possible mass sedimentation of such veils; further research is required to understand the causes for loss of feeding veils and their contribution to vertical flux.

*This may also be a misinterpretation of observations. Morton was not aware of the importance of feeding veils for pteropod biology, and the observed rejection of individual inedible particles may not necessarily occur *in situ*.

4.3.6. The influence of zooplankton on sedimentation in early winter

The plankton regime in November 1987 was still productive as evidenced from chl. *a* concentrations of about 0.3 to 0.6 µg per liter in the upper 50 m of the water column. Only data for metazooplankton in the upper 300 m are available and showed that metazooplankton stocks were small and carbon biomass was dominated by chaetognaths and *Calanus finmarchicus* CV copepodites. Isolated adult females of these herbivorous copepods were also present in collections as well as *C. finmarchicus* nauplii. As it is not reasonable to assume that the nauplii are refugees from spring, summer or fall secondary production, it is concluded that a small surface population of *C. finmarchicus* copepods remained reproductively active throughout winter. With the presence of considerable phytoplankton in winter, maintenance of such winter activity is a reasonable behavior, as indicated by the presence of *C. finmarchicus* stocks in February (section 4.3.2).

Sedimentation in early winter was recorded for two years with very different results. In 1986 total flux corresponded to an annual minimum; in 1987 there was a peak approaching the maximum yearly rate measured in mid-summer. As phytoplankton production in 1987 was still considerable, as described above, it must be concluded that relatively large quantities of POM escaped the fates of recycling and respiration and sedimented. The presence of moderate numbers of diatom valves and rests in sediment trap material in November supports this conclusion. However, as few intact fecal pellets were recovered in trap samples, coprorhexy was still intensively operative. The abundance of *Oithona spinirostris* in subsurface waters may be an important factor in this process. The winter situation in 1986 was much different. Although pelagic data are not available, microscopic data of sedimented material revealed that foraminifers and radiolarians must have been abundant in November/December, as evidenced by secondary peaks in the sedimentation of their hard bodily parts. The flux of minipellets was also relatively large, indicating active protozoan feeding in midwater depths. Moreover, very large flux rates of *L. retroversa* shells were measured in November 1986. This pteropod is restricted to the surface of Atlantic Water (Østvedt 1955). Thus heterotrophic metazooplanktonic pteropods fed in surface waters and protozoans scavenged particles in the midwater layers (perhaps in the surface waters as well) in early winter 1986. The zooplanktonic network of POM utilization was quite operative in winter 1986 and vertical flux was inhibited.

A possible reason for this interannual variation in winter protozoan and metazooplankton stocks and, hence, sedimentation* may be sought in the spring and summer months. Again, if the magnitude of the sedimentation of planktonic hard bodily parts reflects the abundance of the contributing organisms, then foraminifers, radiolarians and pteropods were present in high concentrations in summer in 1986 and were relatively scarce in 1987. The protozoan stocks apparently declined in fall, however it is conceivable that their resurge in December of 1986 was attributable to an abundant supply of active refugee organisms from summer stocks, which rapidly responded to increases in food supply. The increase in food availability in this case could result from reduced grazing pressure due to the decline in pteropods in fall. Depressed but continued growth of phytoplankton would increase available food for surface stocks of protozooplankton. A deterioration in pteropod stocks could moreover result in a surge in the rain of fine sedimenting particles which otherwise would be ingested near the surface. This rain could fuel protozoan growth in deeper water layers. The higher flux rates of minipellets in midwater layers in winter of 1986 relative to 1987 support this hypothesis. I must emphasize that at the present this scenario is conjecture. However, I believe that the concepts presented here are tenable.

*Outbursts of sedimentation of lithogenic particles in winter in the Norwegian Sea (Honjo *et al* 1988) have been documented as well. The authors presume that these were due to the advection of particles with the southward flow of cold water from the Barents Sea through the Storfjord Trough and not to biological causes.

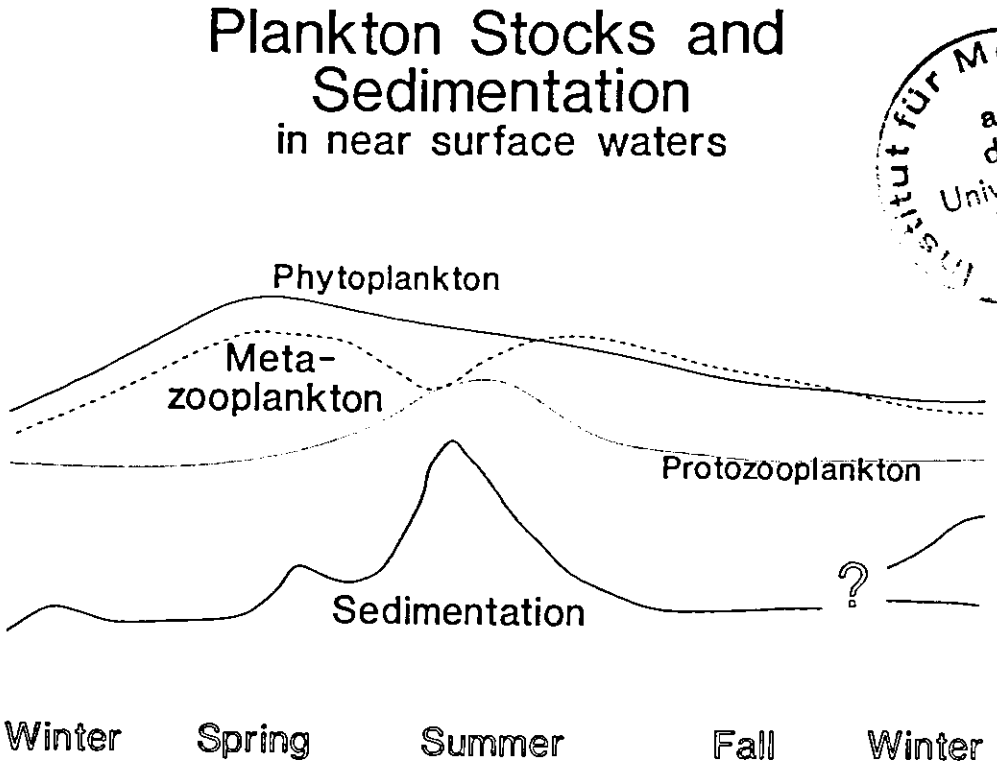
4.4. Annual perspective

The analyses of the development of the pelagic system for the individual seasons on the Vøring Plateau (Fig. 86) shall be summarized. Moreover, interseasonal processes and findings from other studies are discussed. Emphasis is given to the development of metazooplankton stocks and their influence on the vertical flux of particles. With respect to the phytoplankton the presented cycle is preliminary. As more information especially on phytoplankton dynamics on the Vøring Plateau becomes available, this picture will undoubtedly be modified. However, at present I hope that this perspective of the seasonal development of plankton and sedimentation can at least serve as a foundation for further investigations.

The pelagial is a system of relatively little production early in the year. In late winter primary production is at an annual minimum as are concentrations of suspended POM. The vertical flux of particles, however, although low is still considerable and even exhibits secondary peaks which may include diatom valves and fragments. Considering the low production of the system in late winter, the magnitude of sedimentation is at first surprising. However, metazooplankton stocks in surface waters are not yet fully developed. Although a population of actively feeding *Calanus finmarchicus* copepods ingests the bulk of produced phytoplankton, the recycling network of POM utilization is not as effective as later in the year. Thus relative to the concentration of suspended POM, large amounts of organic particles escape recycling in the water column. This material sediments. Active protozooplankters in midwater layers feed upon this fine sedimenting material.

The size of the active *Calanus finmarchicus* stocks in late winter is most probably decisive for the development of the spring phytoplankton (Bathmann *et al.* in press). Within the classical model for temperate oceanic copepods in the Atlantic (Heinrich 1962, Cushing 1975), according to which delayed grazing on spring phytoplankton due to slower development of herbivorous metazooplankton leads to a large accumulation of autotrophic biomass, active herbivorous copepods in winter represent a buffering mechanism. They are not subject to ontogenetic delays in feeding ability and respond immediately to increased phytoplankton production. This may aid to hinder the development of spring phytoplankton stocks, as has been suggested for the plankton regime in spring of 1986. The situation may be comparable to that in the North Pacific where winter/early spring grazing and small spring phytoplankton stocks are regular features (e.g. Evans and Parslow 1985, Vidal and Smith 1986, Frost 1987). It is however noted that the necessity of copepod grazing in controlling phytoplankton stocks in the North Pacific has recently been questioned (M. Angel personal communication).

A



B

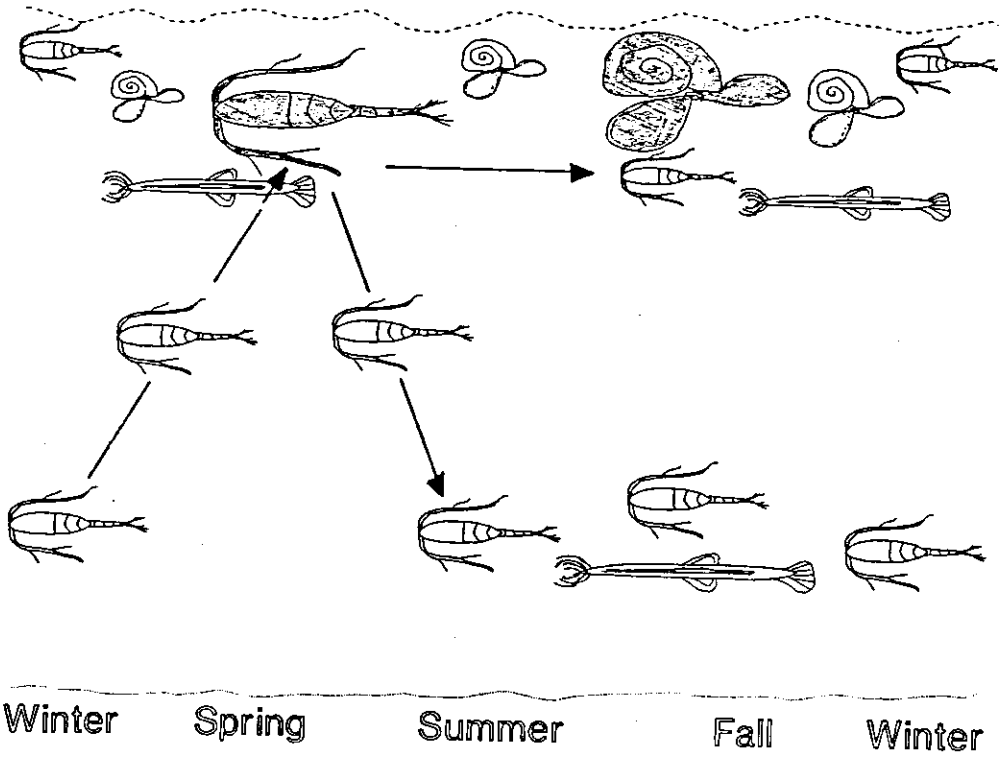


Figure 86. (A) Schematic representation of the seasonal abundance of phytoplankton, protozooplankton and metazooplankton stocks in near-surface waters and sedimentation on the Yøring Plateau. (B) The distribution and abundance of major groups of metazooplankton; copepods represent *C. finmarchicus*, pteropods represent *L. retroversa* and chaetognaths represent carnivores; size of characters indicate relative abundance within the group.

The bulk of herbivore stocks migrates to the surface as *Calanus finmarchicus* CV copepodites in late winter/early spring (Hansen 1960, Lie 1968). The migration commences in February on the Vøring Plateau, as evidenced by small but increased concentrations of adult males in this month. The increase in males was also observed by Lie (1968), who recorded much larger proportions (about 5 % by number) of males relative to the entire surface population of *C. finmarchicus*. However, the main migration of overwinterers may occur about a month or two later. Development to adults occurs during feeding at the surface (Marshall and Orr 1972, Tande and Hopkins 1981) and is followed by intense spawning in about April. Developmental time from egg to CV copepodite may take from about 1½ to 3 months (Hansen 1960). Spawning and growth of stocks continues until about June, when maximum metazooplankton biomasses in surface waters are attained (e.g. Wiborg 1976a, this study).

In 1986 the size of zooplankton stocks in the upper 100 m was comparable to those in previous years (Lie 1968, Peinert *et al.* 1987). It is important to note that the size and occurrence of maxima in metazooplankton stock may vary considerably from year to year (e.g. Lie 1968). The timing and magnitude of the late spring peak will determine the intensity of grazing on spring phytoplankton stocks. The presence of moderately sized zooplankton stocks during the onset of enhanced spring phytoplankton growth will retard the accumulation of phytoplankton stocks and their sedimentation, especially if the physical climate, e.g. stratification of the water column and light conditions, is not optimal for growth (Bathmann *et al.* in press).

As spawning and the development of *Calanus finmarchicus* stocks including nauplii, copepodites and adults are active well into late spring, the bulk of the increased production by phytoplankton stocks, dominated by small naked flagellates, small diatoms and coccolithophores, is well utilized by metazooplankton. The coupling between autotrophs and heterotrophs is tight. Although phytoplankton stocks become larger, most of their biomass is converted to fecal pellets and fecal detritus. Sedimentation is somewhat larger than in late winter but low relative to the much improved growth of phytoplankton stocks. Due to the very high concentrations of copepods in surface waters, coprorhexy and perhaps coprophagy by *Calanus finmarchicus* are probably the key processes inhibiting sedimentation in late spring.

Although phytoplankton stocks, whose composition shifts to larger flagellates, are still fairly large, by early summer the bulk of the new generation of *Calanus finmarchicus* CV copepodites migrates to midwater layers to overwinter in a diapausal state. Mass vertical migration leads to a discoupling of the autotroph-heterotroph relationship, and increased sedimentation is the result. With less intense fragmentation of fecal pellets due to the declining metazooplankton stocks a pulse of fecal pellets and fecal detritus

sediments; this pulse is strong enough to evoke a rapid response in benthic activity (Graf 1989). Much of this sinking material is also "repackaged" by zooplankton in midwater layers and large, fast-sinking fecal pellets originating from these plankters may accelerate sedimentation. A portion of the *C. finmarchicus* stock, however, does not migrate but remains reproductively active at the surface. A second annual spawning of *C. finmarchicus* has been observed in other years in the Norwegian Sea (Østvedt 1955, Lie 1965) and in Norwegian fjords (Matthews *et al.* 1978, Båmstedt 1988) as well. The presence of these surface stocks after the annual vertical migration of the bulk of CV copepodites to depth enhances the recycling of POM by zooplankton.

With the decline of the herbivorous copepod stocks at the surface, protozoan populational growth increases. This may be due to reduced grazing pressure on the protozoans and fast growth rates. These small heterotrophs apparently do not utilize suspended POM as intensively as the large herbivorous metazooplankters. The result is maximum sedimentation of the year. Metazooplankton (e.g. Sasaki *et al.* 1988), protozoans (e.g. Frost 1987) and bacteria (e.g. Cho and Azam 1988, Hagström *et al.* 1988, Karl *et al.* 1988) in midwater layers are able to utilize a considerable portion of sedimenting material in summer.

With less competition for food by herbivorous *Calanus finmarchicus* copepods in surface waters and possibly decreased "predation" by these copepods on small juveniles of other herbivores (an effect reported for *Neocalanus cristatus* by Green and Landry 1988), stocks of the pteropod *Limacina retroversa* rapidly grow in mid- to late summer and attain massive concentrations of individuals close to the surface. In some years this build-up may already transpire in June (Wiborg 1955). Each of these herbivores hence have a specific and different temporal niche during their annual development, a pattern often true of herbivorous copepods (e.g. Vidal and Smith 1986). The seeding population for this explosion in growth is probably a refugee component of isolated *L. retroversa* individuals, which survive throughout the year, as evidenced by the presence of moderately sized individuals of this pteropod in late winter as well as the introduction of new stocks from the North Atlantic. Late summer conditions favor rapid growth of *L. retroversa* over that of *Calanus finmarchicus*, which was still present in surface waters in late summer. The reason for this may be the ability of *L. retroversa* to collect very small particles with the aid of mucous veils. In regenerating systems, such as the surface waters on the Vøring Plateau in late summer, phytoplankters are typically small in size (Margalef 1978, Smetacek 1988). Although individual growth is not particularly fast (5 months has been reported by Redfield (1939) for attainment of maximum size), populational growth of *L. retroversa* can be extremely rapid. These pteropods are hermaphrodites; the smaller forms are predominantly male in gonadal composition and larger forms possess progressively

more female tissues (Hsiao 1939a,b). Once ovulation in an individual commences it is continuous and individuals become progressively more fecund (Redfield 1939). This strategy permits a rapid increase in the population once a certain minimum concentration of mature functional "females" is present. In addition, for certain species of pteropods aberrant forms capable of particularly rapid and plentiful production of eggs (Spoel 1962, 1967) have been documented. No such form has as yet been identified for *L. retroversa*, but the possibility cannot be excluded, especially since new aspects of the physiology and behavior of pteropods are still being discovered. The increase in herbivore stocks results in the reduction of the vertical flux of particles, which are characterized by detritus, calcareous pteropod shells and mucous aggregates. The large *L. retroversa* population presumably declines, when phytoplankton production decreases.

The large stock of pteropods accompanied by high concentrations of protozooplankters may but need not persist into early winter. The size of these stocks probably depends partially upon the size of the seeding populations for these groups and the quality and abundance of food in winter. The interannual variation in the size of these stocks results in large differences in the intensity of the utilization of suspended organic particles. If utilization is small, relatively large rates of sedimentation may result. If utilization is large, vertical flux may approximate the recorded annual minima.

The conditions in winter may be particularly important for the success or failure of certain active herbivores (Colebrook 1985). *Calanus finmarchicus* and *Metridia longa* copepods in surface waters in winter depend largely upon the small production of phytoplankton in the winter months as the chief food supply of high quality. Additional food sources such as detritus (Heinle *et al.* 1977, Newell 1984) probably greatly facilitate the phytoplankton food supply under the unfavorable winter conditions (Kleppel *et al.* 1988). Carnivory even amongst "herbivores" such as described for krill (Price *et al.* 1988) may also be a recourse for some metazooplankters. However, these are certainly alternative measures for most herbivores. If the survival rate of these active herbivores is high in winter, then their ability to regulate spring phytoplankton will be greater. Further, the mortality rate of diapausal *C. finmarchicus* copepodites in deeper water layers is presumably important in determining the size of spring herbivore stocks. Mortality of overwinterers may largely depend upon the predation rate of carnivores, e.g. chaetognaths and *Euchaeta norvegica*, which are particularly abundant in the depths of the overwintering stock of diapausal *C. finmarchicus* copepodites. Small chaetognaths, for example, may depend on high densities of prey organisms for growth (Sullivan 1980) and *Euchaeta* spp. may feed voraciously when prey is abundant (Yen 1983). Considering the chemosensory adeptness of some

metazooplankters during predation (Poulet and Marsot 1980), one might expect that mortality due to carnivory is large. However, the concentrations of CV copepodites in late winter appear to be similar to those in late summer, which may indicate that losses are not large during winter diapause. As carnivores also locate prey via mechanoreception (Zaret 1980, Yen 1985), the motionlessness of diapausal *C. finmarchicus* copepods may be a passive defense. A high survival rate of inactive overwinterers in general has been suggested by Miller *et al.* (1984).

It is noted that one nonplanktonic carnivorous group has not been discussed. The effect of fish may be important in controlling metazooplankton stocks and thereby indirectly influence sedimentation in the Norwegian Sea, one of the most productive oceanic areas in terms of fisheries. A direct relationship between the size of cod and metazooplankton stocks in the Norwegian Sea has for example been suggested by Wiborg (1976b). An analysis of the possible effects of herbivorous fish stocks is not within the scope of this investigation. However their influence may be considerable. Predation by fish should especially be considered in energy flow budgets of the Norwegian Sea.

5. Conclusion

In this study a combination of research in the laboratory and in the field shows that sedimentation in the Norwegian Sea is influenced strongly by the metazooplankton. Quantitatively the zooplankton exerts a net inhibiting effect on the vertical flux of particles to the deep-sea. The extent of losses of potentially sedimenting particulate organic material from the euphotic zone to midwater depths is about two orders of magnitude on the Vøring Plateau in the Norwegian Sea. The predominating inhibition of vertical flux is, however, tempered with distinct annual quantitative and qualitative patterns. Further, these fundamental patterns vary from year to year.

Interannual variations as well as seasonality in the pattern of sedimentation are results of a complex network of biological interactions in response to the changing physical environment. As the responses of plankters are categorically different, seasonal and vertical distribution of organismal groups in the pelagial are evoked. Each group can influence the vertical flux of ambient particles in characteristic ways. Hence, patterns of sedimentation arise.

The trophic structure of the plankton as well as the timing of the occurrence of the individual components are decisive in determining the mode and effectiveness of zooplankton-moderated regulation of flux. Life-cycles and feeding strategies of the plankton are of particular importance. This regulation may be grouped into three types: mechanisms and processes which enhance, inhibit and qualitatively modify sedimentation. The utilization of POM by metazooplankton is an extremely compelling process in the reduction of the vertical flux of particles. The fragmentation of large fast-sinking particles coupled with remineralizing and respiratory processes is also particularly important in the Norwegian Sea. In contrast, the contribution of metazooplankters to the stock of large particles, i.e. hard bodily parts, fecal material and mucous aggregates, locally enhances sedimentation. These forms are the zooplanktonic contributions most prevalent in sedimented material. Distinct qualitative patterns in sedimentation due to regulation by the zooplankton are effected by discriminant feeding, selective utilization of ingested material and modifications of sinking material due to the biological and physicochemical properties of aggregates, e.g. fecal pellets, formed by the animals.

The influence of zooplankton on sedimentation may not be strong in regimes characterized by very short intensive seasons of primary production such as in the high Arctic and/or if the system is shallow. In tropical waters, in contrast, this influence is indeed very powerful. From the present study it is evident that in temperate regimes such as on the Vøring Plateau in the Norwegian Sea the

zooplankton may also be the prime component in the regulation of the vertical flux of material to the deep-sea.

Concluding remarks

Lastly, I wish to emphasize that research in the field and research in the laboratory are complimentary approaches to science. They are interactively stimulating, the one providing new provocations for the other in an endless cycle. The themes of experimentation originate in the gaps of our understanding of the mosaic called, in this case, pelagic biology. Experimentation provides some of the "missing pieces" and simultaneously changes our perception of the mosaic - the paradigm; new questions arise. One of the goals of the marine ecologist should be to find some rhyme and reason between findings from the field and those from the laboratory. I have attempted to do that in this study.

6. Summary

The aim of this study was twofold - to identify the metazooplankton-regulated processes which regulate sedimentation and to assess the influence of metazooplankton stocks on sedimentation on the Vøring Plateau in the Norwegian Sea. The first endeavor was approached largely with the aid of experimental findings. The central theme of most of the experimentation was the production and destruction of aggregates, especially fecal pellets. The second is based on the application of these findings and reports in the literature to field data collected during expeditions on the Vøring Plateau and recorded continuously with sediment traps over a period of nearly three years. The study was conducted within the Sonderforschungsbereich (special research project) 313 - "Sedimentation in the European Nordic Seas" - at the University of Kiel, Federal Republic of Germany. The author was a member of the subproject "Flux of Particles from the Pelagial".

The field investigation was conducted from November 1985 to February 1989 on and within the vicinity of the Vøring Plateau (67° 44'N, 05° 55'E) in the eastern Norwegian Sea. During six expeditions data on the hydrographical conditions, primary production and concentrations of nutrient salts, suspended particles including POC and chlorophyll *a*, phytoplankton, metazooplankton and fecal pellets were collected. Metazooplankton was analyzed according to species in most cases, length, and for copepods sex and developmental stage. Carbon content of metazooplankton stocks was estimated from conversion factors in the literature and carbon analyses in the laboratory. In addition, data on the vertical flux of particles (total flux, POC, chlorophyll *a*, carbonate and microscopical composition) were collected using moored and free-drifting sediment traps. The author collected the metazooplankton data.

Experimentation was conducted at sea, in Tromsø and Bergen in Norway and in Kiel. The central themes of experimentation were grazing by *Calanus finmarchicus* in winter, feeding and aggregate formation by the pteropod *Limacina retroversa*, fecal material identification, production, composition and aging of *C. finmarchicus* fecal pellets, sedimentation velocities of fecal material from selected zooplankters and mucous aggregates from *L. retroversa*, coprophagy and coprorhexy by neritic and oceanic copepods.

Results from field investigations showed that the spring plankton regime in May was based on new and regenerated production while the late summer regime was strongly regenerating. With values of about 400 to 500 mg C per m^2 per day primary production during this period was one order of magnitude higher than in the winter months. In terms of carbon metazooplankton stocks exhibited maxima of about 8 g C per m^2 for the entire water column in winter and late summer. Peak values in terms of numbers were found in late summer. However, in surface waters peaks in biomass occurred in late spring/early summer and late summer. Sharp vertical gradients in copepod fecal pellets with maximum concentrations near the surface existed.

The seasonal distribution of metazooplankton with depth showed that CV copepodites and adult females of the herbivore *Calanus finmarchicus* dominated surface waters in mid-spring. Adults presumably spawned at this time and earlier in late winter/early spring, and by late spring a new generation of CV copepodites was abundant in surface waters, which were however still dominated by adult females. In early summer the bulk of the new generation of copepodites migrated to depths below 500 tO 600 m to overwinter in a diapausal state until the return migration in late winter. In late summer *C. finmarchicus* copepodites were still present in surface waters, but metazooplankton stocks were dominated by the herbivorous euthecosomatous pteropod *Limacina retroversa*. At other times of the year this herbivore was scarce. Throughout the year the abundance of carnivorous zooplankters with depth reflected that of herbivores.

Sedimentation rates were characterized by an annual summer peak of about 300 and 25 mg per m^2 per day for total flux and POC, respectively, at a depth of 500 m. Sedimentation in winter was very large in one year and minimal in another. In the year of low winter rates, winter and summer flux was associated with a relatively large input of hard bodily parts from foraminifers and radiolarians and thecae from tintinnids. Generally sedimentation rates for copepod fecal pellets were highest in late spring; rates for minipellets were highest in mid-summer. Lowest sedimentation rates for POC were recorded in mid-autumn.

Major findings from experimentation were:

- Surface copepods in winter dominated by *Calanus finmarchicus* could feed actively when offered phytoplankton food
- *Limacina retroversa* was better able to clear small (1 to 2 µm in diameter) particles than was *C. finmarchicus*.
- *L. retroversa* formed mucous aggregates, which were probably discarded feeding veils.
- *C. finmarchicus* fecal pellets exhibited large variations in organic content and C:N ratios. The latter was presumably a combined result of utilization of essential elements by the copepod consumers and bacterial colonization after fecal pellet production.
- Fecal material was decomposed by bacteria on a time scale of weeks at 1°C.
- Average sedimentation velocities of fecal material from *C. finmarchicus*, *C. hyperboreus* and *Thysanoessa* sp. were about 35, 50 and 95 m per day, respectively. Sedimentation velocities for mucous aggregates were one order of magnitude higher.
- Coprophagy, the ingestion of fecal material, was a minor process during incubations of copepods with fecal pellets and appeared to cover only about 10 % of respiratory demands.
- Coprorhexy, the fragmentation of fecal material, was the dominant process leading to the destruction of fecal pellets in incubations. The process functions on a time scale of hours.

From these findings and from reports in the literature, the influence of zooplankton on sedimentation may be presented in three categories: Processes which

- enhance sedimentation including the production of cadavers, hard bodily parts, fecal material and other aggregates and vertical migration,
- inhibit sedimentation including zooplanktonic utilization of POM and the destruction of aggregates and
- influence the quality of sedimentation through discriminant feeding, selective utilization of ingested material and biological and physicochemical properties of fecal material and other aggregates.

Sedimentation on the Vøring Plateau is strongly influenced by zooplankton. Throughout the year the bulk of phytoplankton production is ingested by the zooplankton and is respired, remineralized or sediments as fecal material. Fecal material is intensively recycled by bacteria, protozoans and metazooplankton often at midwater depths. Based on primary production rates and sedimentation rates at a depth of 500 m, losses in POC of one order of magnitude in the spring and summer months and much smaller losses in winter can be attributed to recycling. Peaks in sedimentation are results of major modifications in the composition and distribution of metazooplankton stocks. This results in

decoupling of the usually strongly recycling effect of zooplankton on suspended and sinking particles. This is true even during the initiation of enhanced annual phytoplankton growth in spring. The ability of surface copepods in late winter to quickly respond to increases in food supply at this time of year is presumably important in limiting accumulation of phytoplankton stocks. The large pool of fecal material in spring is mostly fragmented to suspended or slowly sedimenting fecal detritus by coprorhexy. In early summer less intensive recycling of particles by the zooplankton results from the migration of *C. finmarchicus* copepodites to depth; a fecal pellet pulse in sedimentation occurs. Intensive repackaging of sedimenting material in midwater depths is reflected in the production of large oval fecal pellets probably from ostracods and minipellets from protozoans. In mid-summer sedimentation is large and characterized by an increase in the flux of hard bodily parts from protozooplankters. It is speculated that the zooplankton in mid-summer is characterized by increasing proportions of protozoans which cannot reduce the sedimentation of large particles as well as does the metazooplankton. By late summer the developing stocks of *L. retroversa* intensify the recycling of material and reduce flux rates. Pteropod feeding may be the reason for the concomitant decrease in protozoan stocks. These pteropods feed by means of mucous veils which probably permit them to feed more effectively on the small particles characteristic of regenerating systems. However, some feeding veils are discarded and appear to sink rapidly to great depths; they are a potential source of food for the benthos. The large stocks of pteropods may decline in the fall or persist into early winter, and winter sedimentation rates are high or low, respectively. In the second case, the decline of winter pteropod stocks may be followed by a resurge in protozoan stocks.

The study conclusively shows that the zooplankton exerts a dominant influence on sedimentation on the Vøring Plateau in the eastern Norwegian Sea. The net effect is to inhibit vertical flux of particles, assuming that particles especially phytoplankton stocks would otherwise sediment. However, this is tempered by spatiotemporally heterogeneous zooplankton-regulated processes which enhance sedimentation. The result is distinct quantitative and qualitative annual patterns in sedimentation. These fundamental patterns vary from year to year.

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Appendix 1. Vertical metazooplankton hauls. Expedition, station, date, time of day (UTC), depth interval and net type.

Expedition	Sta.	Date (time)	(Net type - mesh size) Depth interval in meters	
POS 128/1	166	13 May 86 (14.00-14.45) 67°43.37'N 05°57.20'E (1260 m depth)	(Apstein-300 µm; -50 µm) 0-1000	0-30 30-100
	168	14 May 86 (1.00-2.20) 67°09.82'N 06°59.56'E (1406 m)	(Apstein-300 µm) 0-100 0-1000	
POS 128/2	247	27 May 86 (0.15-1.45) 67°33.00'N 06°29.82'E (1445 m)	(Apstein-300 µm; -50 µm) 0-30 0-100 0-1000	0-30 30-100
	259	29 May 86 (13.30-15.00) 67°42.35'N 06°08.89'E (1305 m)	(Apstein-300 µm; -50 µm) 0-30 0-100 0-500 0-1000	0-30 30-100
	268	30 May 86 (12.40-14.00) 67°43.21'N 03°46.04'E (1271 m)	(Multinet-200 µm) 0-30 30-60 60-100 100-150	150-200 200-400 400-600 600-800 800-1000
	276	1 June 86 (7.30-8.31) 68°00.00'N 02°90.00'E (1700 m)	(Multinet-200 µm) 0-30 30-100 100-250 250-500 500-1000	
	282	4 June 86 (11.00-12.00) 67°43.40'N 05°57.42'E (1250 m)	(Multinet-200 µm) 0-30 30-100 100-250 250-500 500-1000	(Apstein-50 µm) 0-30 30-100

Appendix 1 (continued)

Expedition	Sta.	Date (time)	(Net type - mesh size) Depth interval in meters	
MET 2/1	63	24 June 86	(Multinet-64 µm)	(Apstein-50 µm)
		(1.30-1.50)	0-25	0-30
		67°44.41'N	25-50	30-100
		05°54.09'E	50-100	
		(1245 m)	100-150	
			150-200	
		(3.30-4.30)	(Multinet-200 µm)	
			0-30	
			30-100	
			100-250	
			250-500	
			500-1000	
	65	24 June 86	(Multinet-200 µm)	
		(12.00-13.05)	0-30	
		67°38.94'N	30-100	
		05°48.87'E	100-250	
		(1430 m)	250-500	
			500-1000	
	69	25 June 86	(Multinet-200 µm)	
		(4.15-5.13)	0-30	
		66°59.91'N	30-100	
		07°45.00'E	100-250	
		(990 m)	250-500	
			500-900	
	82	29 June 86	(Multinet-200 µm)	
		(23.15-0.16)	0-30	
		68°13.80'N	30-100	
		02°32.24'E	100-250	
		(2390 m)	250-500	
			500-1000	
	86	30 June 86	(Multinet-200 µm)	(Apstein-50 µm)
		(15.20-16.40)	0-30	0-30
		67°44.40'N	30-100	30-100
		05°54.36'E	100-250	
		(1241 m)	250-500	
			500-1000	
	92	30 June 86	(Multinet-200 µm)	
		(23.20-0.25)	0-30	
		67°39.23'N	30-100	
		05°48.44'E	100-250	
		(1427 m)	250-500	
			500-1000	

Appendix 1 (continued)

Expedition	Sta.	Date (time)	(Net type - mesh size) Depth interval in meters
MET 2/1	96	1 July 86 (10.00-10.53) 67°00.22'N 07°49.18'E (939 m)	(Multinet-200 µm) 0-30 30-100 100-250 250-500 500-850
POS 137	175	9 Feb. 87 (4.00-5.15) 67°37.60'N 05°48.70'E (1435 m)	(Multinet-200 µm) 0-250 250-500 500-750 750-1000 1000-1200
			(Apstein-300µm) 0-100
	176	9 Feb. 87 (12.54-13.19) 66°59.36'N 07°44.60'E (980 m)	(Multinet-200 µm) 0-100 100-250 250-500 500-750 750-900
	186	14 Feb. 87 (6.00-6.30) 67°37.07'N 05°49.36'E (1436 m)	(Multinet-64 µm) 0-50 50-100 100-150 150-250 250-500
	188	16 Feb 87 (12.00-13.00) 65°32.00'N 00°07.30'W (3700 m)	(Multinet-200 µm) 0-1200 1200-2000 2000-2400 2400-2800
VAL 61	4	30 July 87 (15.23-16.35) 67°36.27'N 04°28.44'E (1210 m)	(Multinet-200 µm) 0-30 30-100 250-500 500-1000

Appendix 1 (continued)

Expedition	Sta.	Date (time)	(Net type - mesh size) Depth interval in meters
POS 142	1155	1 Nov. 87 (10.40-10.53) 67°48.00'N 06°00.40'E (1307 m)	(Multinet-64 µm) 0-50, 50-100, 100-150, 150-200, 200-250
	1157	1 Nov. 87 (12.14-12.30) 67°46.60'N 05°59.80'E (1285 m)	(Multinet-200 µm) 250-500
	1158	1 Nov. 87 (13.33-13.48) 67°46.80'N 05°59.50'E (1296 m)	(Multinet-200 µm) 500-650, 650-800, 800-1000, 1000-1200
	1159	1 Nov. 87 (14.20-14.31) 67°47.30'N 05°59.00'E (1298 m)	(Multinet-200 µm) 0-30, 30-100, 100-250
	1191	6 Nov. 87 (20.44-21.15) 67°39.30'N 05°49.10'E (1425 m)	(Multinet-200 µm) 0-500, 500-800, 800-1000, 1000-1200, 1200-1400
	1196	7 Nov. 87 (9.50-10.30) 68°00.00'N 02°41.00'E (1680 m)	(Multinet-200 µm) 0-150, 150-400, 400-700, 700-1000, 1000-1300
MET 7/3	459	13 Aug. 88 (15.40-17.00) 67°45.11'N 05°30.57'E (1269 m)	(Multinet-200 um) 0-50, 50-100, 100-200, 200-300, 300-500, 400-600, 600-800, 800-1000, 1000-1200

Appendix 1 (continued)

Expedition	Sta.	Date (time)	(Net type - mesh size) Depth interval in meters	
MET 7/4	469	20 Aug. 88 (4.49-6.44) 67°35.90'N 05°15.39'E (1400 m)	(Multinet-200 µm)	
			0-25	250-300
			25-50	300-400
			50-100	400-500
			100-150	500-700
			150-200	700-900
			200-250	900-1100
				1100-1300
	474	20 Aug. 88 (22.03-22.12) 67°35.55'N 05°20.58'E (1413 m)	(Multinet-200 µm)	
			0-25	
			25-50	
			50-100	
			100-150	
	475	21 Aug. 88 (00.53-2.55) 67°35.39'N 05°21.03'E (1416 m)	(Multinet-200µm)	
			0-25	250-300
			25-50	300-400
			50-100	400-500
			100-150	500-700
			150-200	700-900
			200-250	900-1100
				1100-1300
	477	21 Aug. 88 (12.57-14.33) 67°43.29'N 05°47.93'E (1254 m)	(Multinet-200 µm)	
			0-25	250-300
			25-50	300-400
			50-100	400-500
			100-150	400-600
			150-200	600-800
			200-250	800-976
				976-1200
	478	21 Aug. 88 (18.05-18.12) 67°39.04'N 05°47.18'E (1425 m)	(Multinet-200 µm)	
			0-25	
			25-50	
			50-150	
			150-200	

Appendix 1 (continued)

Expedition	Sta.	Date (time)	(Net type - mesh size) Depth interval in meters
MET 7/4	489	23 Aug. 88 (9.52-9.56) 67°46.64'N 06°00.21'E (1293 m)	(Multinet-200 µm) 0-25 25-50 50-100 100-150
	534	31 Aug. 88 (6.50-7.00) 67°25.83'N 07°26.78'E (1664 m)	(Multinet-200 µm) 0-50 50-100 100-150 150-200 200-250

Appendix 2. Carbon conversion factors for individual metazooplankters

Group	stage	µg C	(body length)	Reference
Copepods				
Aetideopsis rostrata	Assume same as for *C. armatus* by length			Shih & Stallard (1982)
Chiridius tenuispinus	"			
Chiridius armatus	C V f	140	(2.67 mm)	Bakke & Volderhang (1978)
	C V m	225	(2.67 mm)	
	C VI f	295	(3.28 mm)	"
	C VI m	270	(3.00 mm)	"
	C VI	400	(3.8-4mm)	approximation
	C VI	550	(5.00 mm)	"
Calanus finmarchicus	[1]C IV-V	50	(2.0 mm)	Robertson (1968)
	[1]C V	50	(2.0 mm)	"
	C VI f	103 ± 28		Hopkins *et al.* (1984)
	C VI m	63 ± 15		
C. hyperboreus	[1]C IV	226		Conover and Corner (1968)
	[1]C V	857		
	[1]C VI f	1625		"
Euchaeta barbata	C VI f	2854	(10.6 mm)	this study
	C VI m	assume same as for *E. norvegica*		
E. glacialis	C VI f	assume same as for *E. norvegica*		
E. norvegica	C I-III	20	(1.6-2.4 mm)	approximation
	C IV	230		Bamstedt (1975)
	C V	520		"
	C VI f	1615		"
	C VI m	810		"
Heterorhabdus norvegicus	C III-V	assume same as for *Metridia lucens* by length		
	C VI	181		
Metridia longa	C IV-V	26 ± 10		Hopkins *et al.* (1984)
	C VI f	57 ± 9		
	C VI m	45		approximation
Metridia lucens	C IV-VI	15		approximation
Microcalanus sp.		25		approximation from Bathmann 1986
Oithona sp.		0.96	(1 mm)	Johanssen (unpubl.)

Appendix 2. (continued)

Group	stage	Conversion µg C (body length)	Reference
Pleuromamma robusta		Assume same as for *C. armatus* by length	
Pseudocalanus elongatus		3.61 ± 1.04 (1 mm)	(Bathmann 1986)
Rhincalanus nasutus		$\log_{10}$(µg C)=4.3 $\log_{10}$(mm)-0.47	Mullin and Brooks (1967)
Spinocalanus sp.		2.5	approximation
Undinopsis bradyi		Assume same as for *C. armatus* by length	
Pteropods			
Limacina retroversa		8.1 (1.0 mm)	Bathmann (1986)
		72.9 (2.0 mm)	Bathmann (1986)
		$C = 4/3\ \pi\ (L/2)^3 * 0.002$	approximation
Cliona retroversa		$C = \pi\ (L/2)^3 * 0.001$	approximation
Others			
Conchoecia obtusata		35.00 (1.1-2 mm)	this study
		74.23 (2-2.6 mm)	"
		200.00 (2.6-3 mm)	"
		317.11 (3-3.8 mm)	"
		500.00 (>3.8 mm)	approximation
Hyperoche medusarum		28.25 (1.6 mm)	this study
		75.30 (3.2 mm)	"
		200 (4-6 mm)	approximation
		1000 (6-9 mm)	"
		1500 (9-14 mm)	"
		3500 (>14 mm)	"
Thysanoessa sp.		$^2C = 33.5\ (0.4\ L)^{2.77}$	Matthews and Herstad (1977)
Chaetognaths (based on *Sagitta elegans*)		$^1C = 0.000032\ L^{3.3}$ note: good agreement with Bathmann (1986) for 12 mm	Matthews and Herstad (1977)
decapod larvae		assume same as for *Thysanoessa* sp.	

Appendix 2. (continued)

Group	Conversion stage	µg C (body length)	Reference
appendicularians	assume same as for chaetognaths		
ctenophores	C = 0.838 * diameter (mm)$^{2.62}$ (assume diameter = 0.7 * L)		Schneider (1986)
salps	15.0	(5.0 mm)	approximation
	30.0	(6.0-7.5mm)	"
	70.0	(10.0 mm)	Bathmann (1986)
	150.0	(15.0 mm)	approximation
polychaetes (based on *Tomopteris helgolandica*)	[1]C = 0.0225 * L$^{1.36}$		Matthews and Herstad (1977)

C = carbon content
L = body length in mm
[1] assuming POC = 50 % of Dry Weight
[2] assuming POC = 50 % of Dry Weight and a carapax length : body length ratio of 4 : 10
[3] volume * 0.11; according to the volumetric conversion after Edler (1979) used for estimating phytoplankton POC

Appendix 3. Sediment trap deployments on Vøring Plateau.

Designation	Duration of deployment	Depth	Collecting interval	Preservative
VP 1	14 May-	250 m	2.0 d	chloroform
	4 June 1986	950 m	22.0 d	chloroform
VP 1a	4 June-	140 m	2.5 d	chloroform
	20 June 1986	300 m	16.0 d	chloroform
VP 1b	24 June-	140 m	1.0 d	chloroform
	29 June 1986	300 m	5.7 d	chloroform
		1000 m	5.7 d	chloroform
VP 2	2 July 1986-	500 m	14.5-	mercury chloride
	4 Feb. 1987		29.0 d	
VP 3	18 Feb.-	500 m	10.0-	mercury chloride
	20 Oct. 1987		30.0 d	
VP 3a	22 Oct.-	500 m	10.0 d	mercury chloride
	1 Nov. 1987	1000 m	10.0 d	mercury chloride
VP 4	1 Nov. 1987-	500 m	10.0-	mercury chloride
	19 July 1988		20.0 d	
		1100 m	260 d	mercury chloride
VP 4a	13 Aug. 1988-	100 m	3.0 d	mercury chloride
	8 Sep. 1988	250 m	3.0 d	mercury chloride
		500 m	21.0 d	mercury chloride
		1000 m	21.0 d	mercury chloride
DR 1	26 May 1986	100 m	14.0 h	chloroform
DR 2	27-28 May 1986	100 m	24.0 h	chloroform
DR 3	29 May 1986	100 m	17.0 h	chloroform
DR 4	29-30 May 1986	100 m	36.5 h	chloroform
DR 5	31 May-	100 m	9.0 h	chloroform
	1 June 1986			
DR 6	19-21 Aug. 1988	50 m	47.5 h	mercury chloride
		100 m	47.5 h	mercury chloride
DR 7	21-23 Aug. 1988	50 m	48.0 h	mercury chloride
		100 m	48.0 h	mercury chloride
DR 8	23-25 Aug. 1988	50 m	49.0 h	mercury chloride
		100 m	49.0 h	mercury chloride

Appendix 3. (continued)

Designation	Duration of deployment	Depth	Collecting interval	Preservative
DR 9	25-27 Aug. 1988	50 m	46.5 h	mercury chloride
		100 m	46.5 h	mercury chloride
DR 10	27-29 Aug. 1988	50 m	47.0 h	mercury chloride
		100 m	47.0 h	mercury chloride
DR 11	29-31 Aug. 1988	50 m	49.5 h	mercury chloride
		100 m	49.5 h	mercury chloride

VP = moored deployments at 67° 44'N, 05° 55'E; 1250 m
DR = free-drifting deployments within 50 nautical miles of same position

Appendix 4. Trophic distribution of metazooplankton number and POC

Depth interval			N/m2				mg C/m2			
Upper	Lower	Date	Total	Hrb	Omn	Crn	Total	Hrb	Omn	Crn
0	100	13-May-86	18496	16827	632	1038	1902.39	1878.99	20.46	2.93
100	1000	13-May-86	11819				2205.00	307.70	293.79	1603.90
0	30	27-May-86	20797	20300	271	226	2048.80	2031.51	10.24	7.06
30	100	27-May-86	2164				91.00	19.85	37.19	33.74
100	1000	27-May-86	1443				53.00	0.00	44.30	8.29
0	30	29-May-86	3835	3383	90	361	417.09	406.71	2.55	7.83
30	100	29-May-86	3913	1534	226	1083	187.00	165.72	3.25	17.97
100	500	29-May-86	4960	2256	1444	992	356.00	232.03	56.63	76.95
500	1000	29-May-86	3335	2030	0	722	450.00	189.17	11.39	249.12
0	30	04-Jun-86	5376	4992	32	352	492.98	484.61	1.33	7.04
30	100	04-Jun-86	3808	1676	232	1900	211.86	168.73	6.74	36.39
100	250	04-Jun-86	4976	2352	432	2192	400.26	261.32	21.92	117.03
250	500	04-Jun-86	4240	1232	2352	656	345.08	123.49	114.80	106.79
500	1000	04-Jun-86	1764	1008	156	600	633.33	255.57	32.13	345.62
0	30	24-Jun-86	9456	9072	144	240	917.08	887.55	8.43	21.09
30	100	24-Jun-86	2060	804	396	860	191.57	66.26	37.43	87.88
100	250	24-Jun-86	5008	1296	1840	1872	520.53	207.60	101.80	211.14
250	500	24-Jun-86	4104	1840	920	1344	392.59	217.02	42.00	133.57
500	1000	24-Jun-86	8832	7312	688	832	1707.98	1011.78	62.07	634.13
0	30	24-Jun-86	9940	9820	40	80	957.45	953.16	2.04	2.25
30	100	24-Jun-86	4360	3413	107	840	433.72	344.95	7.88	80.89
100	250	24-Jun-86	3588	1152	732	1704	266.25	129.84	33.45	102.96
250	500	24-Jun-86	6556	3048	1192	2316	1053.20	578.98	52.31	421.91
500	1000	24-Jun-86	8392	6760	628	1004	1345.83	934.14	39.10	372.59
0	30	30-Jun-86	864	400	244	220	83.71	47.76	10.94	25.00
30	100	30-Jun-86	4912	2548	1048	1316	584.77	302.09	42.82	239.86
100	250	30-Jun-86	2744	852	884	1008	187.47	81.06	32.90	73.52
250	500	30-Jun-86	1424	416	420	588	72.57	31.38	10.70	30.49
500	1000	30-Jun-86	13968	13848	0	120	886.29	863.04	0.00	23.25
0	30	30-Jun-86	7236	6108	568	560	1154.85	746.19	63.74	344.92
30	100	30-Jun-86	6368	3256	960	2152	884.29	556.22	58.54	269.53
100	250	30-Jun-86	2800	916	600	1284	395.95	292.55	26.05	77.25
250	500	30-Jun-86	1716	524	432	760	87.48	41.27	19.07	27.14
500	1000	30-Jun-86	10140	10080	0	60	999.15	992.68	0.00	6.47
0	100	09-Feb-87	1243	472	108	670	36.15	21.95	4.50	9.70
100	250	09-Feb-87	3344	1552	624	1168	203.70	106.48	52.69	44.53
250	500	09-Feb-87	8980	6080	1240	1660	888.39	541.38	76.00	271.01
500	750	09-Feb-87	38840	33820	1020	4000	2255.24	2107.54	126.20	21.50
750	1000	09-Feb-87	31712	31228	208	276	2325.30	2083.15	21.40	220.75
1000	1200	09-Feb-87	30064	27604	2404	56	2014.95	1877.40	125.86	11.69
0	100	09-Feb-87	21480	20160	1160	160	844.23	117.91	7.21	719.12
100	250	09-Feb-87	616	412	156	48	56.63	29.64	9.28	17.70
250	500	09-Feb-87	3188	1904	932	352	455.15	127.49	250.61	77.06
500	750	09-Feb-87	19280	17720	1000	560	1814.20	1523.49	28.40	262.32
750	900	09-Feb-87	5340	4296	968	76	732.76	407.98	288.89	35.89
0	1200	16-Feb-87	67640	59160	6080	2400	6600.50	4620.44	871.08	1396.11
0	30	30-Jul-87	35680	35280	120	280	1783.33	1774.30	5.09	3.94
30	100	30-Jul-87	1744	556	856	332	107.00	51.30	26.32	29.39
100	250	30-Jul-87	1436	796	392	248	131.48	41.76	14.53	75.18
250	500	30-Jul-87	7348	6380	636	332	1640.25	1368.32	195.76	76.17
500	1000	30-Jul-87	19040	17240	1320	480	2131.43	1839.72	101.40	190.30
0	30	01-Nov-87	2060	588	28	1444	31.116	21.064	1.456	8.596
30	100	01-Nov-87	992	260	92	640	58.21	23.70	2.99	31.52
100	250	01-Nov-87	3012	1032	292	1688	194.08	51.82	7.21	135.04

Appendix 4. (continued)

Depth interval			----------N/m2----------				----------mg C/m2----------			
Upper	Lower	Date	Total	Hrb	Omn	Crn	Total	Hrb	Omn	Crn
50	100	13-Aug-88	3700	2608	132	960	254.81	158.04	13.91	82.86
100	200	13-Aug-88	1952	1040	224	688	126.79	50.42	19.99	56.38
200	300	13-Aug-88	1364	1132	64	168	96.45	59.29	10.41	26.75
300	500	13-Aug-88	4752	3960	304	488	578.51	291.18	15.01	362.32
500	600	13-Aug-88	9536	95	0	0	774.56	141.89	4.60	139.78
600	800	13-Aug-88	23028	22560	280	188	2682.94	1325.93	18.24	1338.77
800	1000	13-Aug-88	9436	8288	640	508	1189.01	853.14	105.60	230.27
1000	1200	13-Aug-88	2396	1480	816	100	1017.41	826.91	132.68	57.83
0	25	21-Aug-88	340896	340896	0	0	284.90	284.90	0.00	0.00
25	50	21-Aug-88	3896	3036	24	836	71.42	46.82	4.95	19.65
50	100	21-Aug-88	5964	5384	304	276	98.25	15.82	13.53	68.90
100	150	21-Aug-88	1056	692	108	256	118.99	65.12	4.60	49.28
150	200	21-Aug-88	912	484	172	256	78.72	37.91	17.87	22.94
200	250	21-Aug-88	1384	440	20	924	51.22	9.52	1.96	39.74
250	300	21-Aug-88	1528	1008	28	492	104.79	29.83	5.27	69.70
300	400	21-Aug-88	1756	1472	44	240	79.93	38.66	3.29	37.98
400	500	21-Aug-88	11739	5489	199	6051	884.95	361.81	46.83	476.31
500	700	21-Aug-88	19312	15344	352	3616	1610.57	795.83	144.84	669.90
700	900	21-Aug-88	40024	36588	308	3128	2880.28	1844.85	150.14	885.29
900	1100	21-Aug-88	15332	13376	1364	592	924.38	709.46	86.72	128.20
1100	1300	21-Aug-88	3464	2668	648	148	967.70	776.21	90.45	101.04
0	25	21-Aug-88	152612	152560	0	52	198.38	193.12	0.00	5.25
25	50	21-Aug-88	18968	18848	4	116	94.56	82.92	0.23	11.42
50	100	21-Aug-88	2252	1692	132	428	141.72	22.56	6.41	112.75
100	150	21-Aug-88	1120	660	68	344	23.05	7.52	4.74	8.39
150	200	21-Aug-88	992	556	112	324	44.92	10.15	6.48	28.29
200	250	21-Aug-88	1644	996	12	636	27.79	16.81	0.44	10.55
250	300	21-Aug-88	804	788	16	0	17.69	12.44	5.25	0.00
300	400	21-Aug-88	1780	1488	80	212	192.33	98.72	42.09	51.52
400	600	21-Aug-88	21980	17144	744	4092	1117.40	860.49	29.92	226.99
600	800	21-Aug-88	19732	19080	480	172	1717.43	1203.98	109.44	404.02
800	976	21-Aug-88	22696	21420	680	596	1252.53	1134.89	34.84	82.80
976	1200	21-Aug-88	6848	4728	1512	608	1482.43	900.13	104.82	477.48
0	50	30-Aug-88	105810	105510	140	160	325.74	275.32	10.29	40.13
50	100	30-Aug-88	1164	428	8	728	45.16	39.18	0.28	5.69
100	250	30-Aug-88	2048	1096	112	840	141.62	27.67	66.14	47.81
250	500	30-Aug-88	7338	4432	308	2598	766.23	235.51	63.22	467.50
500	1200	30-Aug-88	48960	42460	2040	4460	6020.09	2902.24	396.24	2721.62
0	50	31-Aug-88	34320	27740	0	6580	235.38	222.04	0.00	13.33
50	100	31-Aug-88	836	368	8	460	18.50	7.38	0.21	10.91
100	150	31-Aug-88	1200	588	52	560	62.06	48.36	6.64	7.06
150	200	31-Aug-88	3472	2600	212	660	183.26	154.92	10.18	18.16
200	250	31-Aug-88	4308	2790	138	1380	262.42	143.15	17.61	101.65

Appendix 5. Metazooplankton groups comprising 5 % or more of total metazooplankton number per sample.

Depth	Date	Code #	Sex	Size range (mm) Upper	Lower	Percent
100	13-May-86	1	1	3.4	3.2	32.9
100	13-May-86	1	1	3.6	3.6	32.4
100	13-May-86	1	1	4	3.8	14.6
1000	13-May-86	6	1	4.2	4	13.9
1000	13-May-86	1	1	4	3.8	5.2
1000	13-May-86	1	1	3.2	3.2	14.4
1000	13-May-86	1	1	3.6	3.6	11
1000	13-May-86	1	1	3.4	3.4	14
1000	13-May-86	25	3	2	1.6	10.9
30	27-May-86	1	1	3.6	3.4	37.1
30	27-May-86	1	1	3.2	2.9	29.5
30	27-May-86	1	1	3.8	3.8	15
30	27-May-86	1	1	4	4	10.6
100	27-May-86	1	1	3.4	2.9	36.8
100	27-May-86	1	1	3.6	3.4	29.7
100	27-May-86	1	1	4	3.8	17.2
1000	27-May-86	1	1	3.6	3.6	26.7
1000	27-May-86	1	1	4	3.8	12.9
1000	27-May-86	1	1	3.2	3.2	8.3
1000	27-May-86	1	1	3.4	3.4	22.6
1000	27-May-86	6	1	4.2	4	11.5
30	29-May-86	1	1	3.2	3.2	14.1
30	29-May-86	1	1	3.4	3.4	29.4
30	29-May-86	1	1	3.6	3.6	21.2
30	29-May-86	1	1	4	3.8	14.1
100	29-May-86	1	1	3.2	3.2	24.3
100	29-May-86	1	1	3.6	3.6	12.8
100	29-May-86	1	1	3.4	3.4	23.6
100	29-May-86	15	1	1.2	1.2	12.8
100	29-May-86	1	1	4	3.8	8.1
500	29-May-86	1	1	3.2	3.2	16.3
500	29-May-86	1	1	3.6	3.6	12.7
500	29-May-86	1	1	3.4	3.4	22.2
500	29-May-86	15	1	1.2	1.2	12.7
500	29-May-86	1	1	4	3.8	6
1000	29-May-86	15	1	1.2	1.2	9.7
1000	29-May-86	1	1	3.6	3.6	10.7
1000	29-May-86	1	1	3.4	3.4	20.4
1000	29-May-86	1	1	3.2	3.2	20.1
1000	29-May-86	1	1	4	3.8	7.8
30	04-Jun-86	1	1	3.2	3.2	17.6
30	04-Jun-86	1	1	3.4	3.4	25.3
30	04-Jun-86	1	1	3.6	3.6	23.5
30	04-Jun-86	1	1	4	3.8	16.4
100	04-Jun-86	1	1	3.2	3.2	13.4
100	04-Jun-86	15	1	1.2	1.2	43.3
100	04-Jun-86	1	1	3.4	3.4	14.4
100	04-Jun-86	1	1	3.6	3.6	8.3
250	04-Jun-86	1	1	3.2	3.2	13.2
250	04-Jun-86	1	1	3.6	3.6	9.3
250	04-Jun-86	1	1	3.4	3.4	12.5
250	04-Jun-86	15	1	1.1	1.1	34.1
250	04-Jun-86	1	1	4	3.8	10
500	04-Jun-86	1	1	3.4	3.4	6.8
500	04-Jun-86	1	1	3.2	3.2	13.2
500	04-Jun-86	6	1	4.2	4	38.1

Appendix 5. (continued)

Depth	Date	Code #	Sex	Size range (mm) Upper	Lower	Percent
1000	04-Jun-86	87	3	3.6	3.2	11.3
1000	04-Jun-86	82	3	4	4	9.1
1000	04-Jun-86	87	3	2.4	2.4	14.7
1000	04-Jun-86	1	1	3.2	3.2	6.3
1000	04-Jun-86	82	3	25	25	7.9
30	24-Jun-86	1	1	3.2	3.2	10.2
30	24-Jun-86	1	1	3.6	3.6	29.2
30	24-Jun-86	3	3	2.4	2.4	7.4
30	24-Jun-86	1	1	3.6	3.6	25.5
30	24-Jun-86	1	1	3.2	3.2	12.9
30	24-Jun-86	1	1	4	3.8	22.2
30	24-Jun-86	1	1	3.4	3.4	28.6
30	24-Jun-86	1	1	3.4	3.4	33.8
30	24-Jun-86	3	3	2.4	2.4	6.6
30	24-Jun-86	1	1	4	3.8	11.9
100	24-Jun-86	1	1	3.2	3.2	8.3
100	24-Jun-86	1	1	4	3.8	11
100	24-Jun-86	80	3	4	4	5
100	24-Jun-86	1	1	3.2	3.2	16.2
100	24-Jun-86	82	3	4	4	15.1
100	24-Jun-86	1	1	3.4	3.4	8.5
100	24-Jun-86	6	1	4.2	4.2	6.2
100	24-Jun-86	1	1	3.6	3.6	5
100	24-Jun-86	82	3	5.6	5.6	5.5
100	24-Jun-86	15	1	1.1	1.1	7.6
100	24-Jun-86	82	3	8	8	10.3
100	24-Jun-86	1	1	3.6	3.6	18.3
100	24-Jun-86	26	3	2.4	2.4	6.2
100	24-Jun-86	1	1	4	3.8	5.2
100	24-Jun-86	1	1	3.4	3.4	30
250	24-Jun-86	15	1	1.1	1.1	29.7
250	24-Jun-86	1	1	3.6	3.6	11.3
250	24-Jun-86	25	3	2	2	5.1
250	24-Jun-86	1	1	4	3.8	7.4
250	24-Jun-86	8	1	3	2.8	5.1
250	24-Jun-86	6	1	4.2	4	24.3
250	24-Jun-86	1	1	3.4	3.4	8.3
250	24-Jun-86	6	1	4.2	4	8.2
250	24-Jun-86	25	3	2	2	5.2
250	24-Jun-86	1	1	3.4	3.4	5.9
250	24-Jun-86	1	1	3.2	3.2	8.6
250	24-Jun-86	15	1	1.1	1.1	24
500	24-Jun-86	82	3	5.6	5.6	11
500	24-Jun-86	15	1	1.1	1.1	16.6
500	24-Jun-86	1	1	3.2	3.2	6.2
500	24-Jun-86	82	3	4	4	9.4
500	24-Jun-86	15	1	1.1	1.1	15.9
500	24-Jun-86	6	1	4.2	4	11.1
500	24-Jun-86	1	1	3.4	3.4	17.2
500	24-Jun-86	6	1	4.2	4	5.5
500	24-Jun-86	1	1	3.6	3.6	15
500	24-Jun-86	8	1	3.2	3.2	6.3
500	24-Jun-86	1	1	3.4	3.4	13.8
500	24-Jun-86	1	1	4	3.8	5.7
500	24-Jun-86	1	1	3.6	3.6	14.8
500	24-Jun-86	1	1	3.2	3.2	5.4
1000	24-Jun-86	87	3	3.2	3.2	6.4
1000	24-Jun-86	1	1	3.6	3.6	8.3
1000	24-Jun-86	1	1	3.2	3.2	31.7
1000	24-Jun-86	82	3	4	4	5.2

Appendix 5. (continued)

Depth	Date	Code #	Sex	Size range (mm) Upper	Lower	Percent
1000	24-Jun-86	1	1	3.4	3.4	25.5
1000	24-Jun-86	1	1	3.4	3.4	23.9
1000	24-Jun-86	1	1	3.6	3.6	7.4
1000	24-Jun-86	1	1	3.2	3.2	35
30	30-Jun-86	1	1	3.4	3.4	13
30	30-Jun-86	6	2	3.6	3.4	12
30	30-Jun-86	1	1	3.2	3.2	33.7
30	30-Jun-86	6	1	4.2	4	8.8
30	30-Jun-86	1	1	3.2	2.4	24.5
30	30-Jun-86	1	1	3.4	3.4	30.4
30	30-Jun-86	1	1	3.6	3.6	5.8
30	30-Jun-86	15	1	1.1	1.1	14.8
100	30-Jun-86	82	3	4	4	6.3
100	30-Jun-86	1	1	3.4	3.4	13.8
100	30-Jun-86	15	1	1.1	1.1	17
100	30-Jun-86	1	1	3.2	3.2	27.9
100	30-Jun-86	6	1	4.2	4	7.7
100	30-Jun-86	1	1	3.4	3.4	15
100	30-Jun-86	6	2	3.2	3.2	5.7
100	30-Jun-86	1	1	3.2	3.2	28.3
100	30-Jun-86	15	1	1.1	1.1	13.8
250	30-Jun-86	8	2	2.8	2.6	7
250	30-Jun-86	1	1	3.6	3.6	6.3
250	30-Jun-86	15	1	1.1	1.1	32.6
250	30-Jun-86	6	1	4.2	4	7.9
250	30-Jun-86	1	1	3.2	3.2	17.1
250	30-Jun-86	6	1	4.2	4	8.7
250	30-Jun-86	1	1	3.4	3.4	9.8
250	30-Jun-86	1	1	3.4	3.4	10.4
250	30-Jun-86	1	1	3.2	3.2	8.5
250	30-Jun-86	15	1	1.1	1.1	20.8
500	30-Jun-86	8	2	2.8	2.6	5.6
500	30-Jun-86	1	1	3.4	3.4	5.1
500	30-Jun-86	1	1	3.6	3.6	6.8
500	30-Jun-86	1	1	3.2	3.2	7.7
500	30-Jun-86	15	1	1.1	1.1	25
500	30-Jun-86	1	1	3.2	3.2	8.4
500	30-Jun-86	11	1	2.6	2.6	8.4
500	30-Jun-86	8	2	2.8	2.6	11.5
500	30-Jun-86	6	1	4.2	4	5.1
500	30-Jun-86	15	1	1.1	1.1	33.6
500	30-Jun-86	11	1	2.6	2.4	10.1
1000	30-Jun-86	1	1	3.4	3.4	26.2
1000	30-Jun-86	3	3	2.4	2.4	8.1
1000	30-Jun-86	3	3	2.4	2	62
1000	30-Jun-86	3	3	1.6	1.6	13.7
1000	30-Jun-86	1	1	3.2	3.2	10.7
1000	30-Jun-86	1	1	3.4	3.4	6.5
1000	30-Jun-86	1	1	3.2	3	56
100	09-Feb-87	3	1	3.2	3.2	17.1
100	09-Feb-87	3	1	2.8	2.8	19.6
100	09-Feb-87	30	1	1.2	1.2	10.3
100	09-Feb-87	3	1	3	3	15.8
100	09-Feb-87	3	1	2.4	2.4	12.3
100	09-Feb-87	15	1	1.1	1.1	49.5
100	09-Feb-87	3	1	2.6	2.4	7.7
100	09-Feb-87	3	1	2.6	2.6	10.4
100	09-Feb-87	3	3	2.2	2.2	7.3

Appendix 5. (continued)

Depth	Date	Code #	Sex	Size range (mm) Upper	Lower	Percent
100	09-Feb-87	3	1	3.2	3	13.2
250	09-Feb-87	3	1	2.8	2.8	14.9
250	09-Feb-87	15	1	1.1	1.1	28.7
250	09-Feb-87	30	1	1.2	1.2	6.9
250	09-Feb-87	3	1	3.2	3	16.7
250	09-Feb-87	3	1	2.4	2.4	13.6
250	09-Feb-87	3	1	3.2	3.2	15.6
250	09-Feb-87	3	1	2.6	2.4	9.8
250	09-Feb-87	3	1	2.6	2.6	8.4
250	09-Feb-87	12	1	1.8	1.8	14.3
250	09-Feb-87	6	1	4.2	4	9.1
500	09-Feb-87	3	1	2.4	2.4	7.2
500	09-Feb-87	3	1	3.2	3.2	13.7
500	09-Feb-87	15	1	1.1	1.1	9.8
500	09-Feb-87	3	1	3.4	3	27.2
500	09-Feb-87	3	1	2.8	2.8	11
500	09-Feb-87	6	1	4.2	4.2	6.6
500	09-Feb-87	3	1	3	3	9.3
500	09-Feb-87	3	1	2.8	2.4	28.5
500	09-Feb-87	3	1	2.6	2.6	7.4
500	09-Feb-87	6	1	4.2	4	8.9
750	09-Feb-87	15	1	1.1	1.1	9.8
750	09-Feb-87	3	1	3	3	14.1
750	09-Feb-87	3	1	2.2	2.2	6.4
750	09-Feb-87	3	1	3.2	3.2	18.5
750	09-Feb-87	3	1	2.6	2.6	11.6
750	09-Feb-87	3	1	3.4	3	43.8
750	09-Feb-87	3	1	2.89	2.8	19.7
750	09-Feb-87	3	1	2.8	2.4	32.4
750	09-Feb-87	3	1	2.4	2.4	10.8
750	09-Feb-87	3	1	4	3.6	8.8
900	09-Feb-87	3	1	2.4	2.4	23.4
900	09-Feb-87	6	1	4.2	4.2	7.4
900	09-Feb-87	3	1	2.2	2.2	9.4
900	09-Feb-87	3	1	3.2	3.2	9.2
900	09-Feb-87	3	1	3	3	7.6
900	09-Feb-87	3	1	2.8	2.8	12.4
900	09-Feb-87	3	1	2.6	2.6	5.5
1000	09-Feb-87	3	1	2.8	2.4	44.8
1000	09-Feb-87	3	1	3.4	3	41
1000	09-Feb-87	3	1	4	3.6	7.6
1200	09-Feb-87	3	1	2.8	2.4	40.6
1200	09-Feb-87	3	1	3.4	3	39.2
1200	09-Feb-87	6	1	4.2	4	5.3
1200	16-Feb-87	3	1	2.6	2.6	11.8
1200	16-Feb-87	3	1	3	3	8.9
1200	16-Feb-87	3	1	2.4	2.4	13.7
1200	16-Feb-87	3	1	2.8	2.8	17.9
1200	16-Feb-87	3	1	2.2	2.2	14
1200	16-Feb-87	3	1	3.2	3.2	10.4
2000	16-Feb-87	3	1	2.4	2.4	23.4
2000	16-Feb-87	3	1	2.2	2.2	26.1
2000	16-Feb-87	35	1	4.2	4.2	8.5
2400	16-Feb-87	3	1	2.7	2.7	7.8
2400	16-Feb-87	3	1	3	3	5.7
2400	16-Feb-87	3	1	2.5	2.5	20.8
2400	16-Feb-87	3	1	2.9	2.9	6.8

Appendix 5. (continued)

Depth	Date	Code #	Sex	Size range (mm) Upper	Lower	Percent
2400	16-Feb-87	3	1	2.2	2.2	14.6
2400	16-Feb-87	3	1	3.3	3.3	7.3
2800	16-Feb-87	6	1	4.2	4.2	8.3
2800	16-Feb-87	61	3	3.8	3.8	8.3
2800	16-Feb-87	61	1	4.2	4.2	8.3
2800	16-Feb-87	3	1	3	3	41.7
2800	16-Feb-87	48	1	2.5	2.5	8.3
2800	16-Feb-87	25	3	2.1	2.1	8.3
2800	16-Feb-87	1	1	4	4	16.7
30	30-Jul-87	3	1	2.4	2	22.5
30	30-Jul-87	3	1	2.8	2.6	22.3
30	30-Jul-87	3	1	3.2	3	44.1
100	30-Jul-87	1	1	3.8	3.4	8.5
100	30-Jul-87	6	1	4.4	4	6.9
100	30-Jul-87	8	1	3.2	2.8	33.3
100	30-Jul-87	92	3	3.8	2.8	5.5
100	30-Jul-87	3	1	3.2	3	6.4
100	30-Jul-87	82	3	10	5.1	6.4
250	30-Jul-87	3	1	2.8	2.6	22.8
250	30-Jul-87	3	1	2.4	2.2	6.7
250	30-Jul-87	8	1	3.2	2.8	18.7
250	30-Jul-87	3	1	3.2	3	22.3
500	30-Jul-87	3	1	2.4	2.2	28.3
500	30-Jul-87	3	1	2.8	2.6	34.4
500	30-Jul-87	3	1	3.2	3	20.8
1000	30-Jul-87	3	1	3.2	3	35.5
1000	30-Jul-87	3	1	2.8	2.6	19.7
1000	30-Jul-87	3	1	2.4	2.2	14.7
1000	30-Jul-87	3	1	3.6	3.4	13.9
30	01-Nov-87	3	1	2.8	2.4	6.8
30	01-Nov-87	75	3	1	0.8	5.4
30	01-Nov-87	15	1	1.1	1.1	66.8
30	01-Nov-87	3	1	3.4	3	10.3
100	01-Nov-87	3	1	3.4	3	6
100	01-Nov-87	62	3	1.1	1.1	6
100	01-Nov-87	3	1	2.8	2.4	7.3
100	01-Nov-87	15	3	1.2	1.2	57.3
250	01-Nov-87	3	1	2.8	2.4	12.6
250	01-Nov-87	15	3	1.2	1.2	49
250	01-Nov-87	3	1	3.4	3	14.5
50	13-Aug-88	75	3	1	0.48	26.9
50	13-Aug-88	75	3	0.48	0.32	64.3
100	13-Aug-88	82	3	15	15	5.9
100	13-Aug-88	3	1	3.1	2.9	6.9
100	13-Aug-88	82	3	10	10	7.8
100	13-Aug-88	75	3	1	0.48	6.6
100	13-Aug-88	1	1	4	3.7	15
100	13-Aug-88	82	3	8	8	8.3
100	13-Aug-88	1	1	3.6	3.2	16.3
100	13-Aug-88	75	3	0.48	0.32	6.9
200	13-Aug-88	82	3	4	4	15
200	13-Aug-88	3	1	2.8	2.4	12.9
200	13-Aug-88	3	1	3.1	2.9	12.5
200	13-Aug-88	82	3	8	8	12.3
200	13-Aug-88	3	1	3.3	3.2	7.6
300	13-Aug-88	3	1	3.3	3.2	13.5
300	13-Aug-88	3	1	2.8	2.4	25.5

Appendix 5. (continued)

Depth	Date	Code #	Sex	Size range (mm) Upper	Lower	Percent
300	13-Aug-88	3	1	3.6	3.4	5.3
300	13-Aug-88	3	1	3.1	2.9	29.9
500	13-Aug-88	3	1	3.1	2.9	41.9
500	13-Aug-88	3	1	3.3	3.2	12.8
500	13-Aug-88	3	1	2.8	2.4	24.9
600	13-Aug-88	3	1	3.6	3.4	15.4
600	13-Aug-88	3	1	3.3	3.2	33.9
600	13-Aug-88	3	1	2.8	2.4	14.3
600	13-Aug-88	3	1	3.1	2.9	31.4
800	13-Aug-88	3	1	3.6	3.4	9.7
800	13-Aug-88	3	1	2.8	2.4	15.3
800	13-Aug-88	3	1	3.3	3.2	29.5
800	13-Aug-88	3	1	3.1	2.9	38.2
1000	13-Aug-88	3	1	3.3	3.2	25.4
1000	13-Aug-88	3	1	2.8	2.4	11.4
1000	13-Aug-88	3	1	3.1	2.9	31.8
1000	13-Aug-88	1	1	4	3.7	5.9
1200	13-Aug-88	3	1	3.3	3.2	5.8
1200	13-Aug-88	6	2	3.2	3.2	9
1200	13-Aug-88	3	1	3.1	2.9	23.4
1200	13-Aug-88	34	1	5.6	5.6	6
1200	13-Aug-88	34	1	9.6	9.6	9.8
1200	13-Aug-88	6	1	4.2	4	21.2
1200	13-Aug-88	3	1	2.8	2.4	9
25	21-Aug-88	75	3	0.48	0.32	37.9
25	21-Aug-88	75	3	0.48	0.32	31.1
25	21-Aug-88	75	3	1	0.48	60.1
25	21-Aug-88	75	3	1	0.48	64.1
50	21-Aug-88	75	3	0.48	0.32	22.3
50	21-Aug-88	75	3	1	0.48	41.8
50	21-Aug-88	75	3	0.48	0.32	47.6
50	21-Aug-88	15	1	1.3	1.1	18.5
50	21-Aug-88	75	3	1	0.48	31.7
100	21-Aug-88	75	3	1	0.48	26.6
100	21-Aug-88	75	3	1	0.48	48.6
100	21-Aug-88	75	3	0.48	0.32	29.8
100	21-Aug-88	3	1	3.1	2.9	6
100	21-Aug-88	82	3	12	12	9.8
100	21-Aug-88	82	3	16	16	7.3
100	21-Aug-88	75	3	1.3	1	7.4
100	21-Aug-88	75	3	0.48	0.32	21.8
150	21-Aug-88	6	1	4.2	4	5
150	21-Aug-88	75	3	1	0.48	23.5
150	21-Aug-88	82	3	12	8	15.2
150	21-Aug-88	75	3	1	0.48	10.7
150	21-Aug-88	3	1	3.1	2.9	6.4
150	21-Aug-88	75	3	0.48	0.32	19.3
150	21-Aug-88	15	1	1.3	1.1	21.8
150	21-Aug-88	75	3	1.3	1	5.7
150	21-Aug-88	6	2	3.6	3.2	6.4
150	21-Aug-88	75	3	0.48	0.32	35
200	21-Aug-88	15	1	1.3	1.1	11.8
200	21-Aug-88	3	1	3.1	2.9	6
200	21-Aug-88	15	1	1.3	1.1	16.9
200	21-Aug-88	6	1	4.2	4	11
200	21-Aug-88	75	3	1	0.48	26.8
200	21-Aug-88	3	1	3.3	3.2	10.1

Appendix 5. (continued)

Depth	Date	Code #	Sex	Size range (mm) Upper	Lower	Percent
200	21-Aug-88	75	3	1	0.48	16.1
200	21-Aug-88	82	3	8	8	8.3
200	21-Aug-88	3	1	3.1	2.9	7.9
200	21-Aug-88	3	1	3.3	3.2	7
200	21-Aug-88	75	3	0.48	0.32	16.9
250	21-Aug-88	75	3	0.48	0.32	9.5
250	21-Aug-88	3	1	3.3	3.2	5.5
250	21-Aug-88	3	1	3.1	2.9	7.3
250	21-Aug-88	75	3	1	0.48	6.9
250	21-Aug-88	15	1	1.3	1.1	58.7
250	21-Aug-88	75	3	1	0.48	7.8
250	21-Aug-88	75	3	0.48	0.32	34.3
250	21-Aug-88	15	1	1.3	1.1	38
300	21-Aug-88	3	1	3.1	2.9	15.9
300	21-Aug-88	75	3	0.48	0.32	39.8
300	21-Aug-88	75	3	1	0.48	28.8
300	21-Aug-88	15	1	1.3	1.1	27.7
300	21-Aug-88	3	1	3.4	3.2	7.5
300	21-Aug-88	75	3	0.48	0.32	13.9
300	21-Aug-88	75	3	1	0.48	28.9
400	21-Aug-88	75	3	0.48	0.32	21.6
400	21-Aug-88	3	1	3.1	2.9	30.8
400	21-Aug-88	3	1	3.3	3.2	6.8
400	21-Aug-88	3	1	3.1	2.9	8.9
400	21-Aug-88	75	3	1	0.48	30.5
400	21-Aug-88	15	1	1.3	1.1	10.3
400	21-Aug-88	3	1	3.4	3.2	9.4
400	21-Aug-88	3	1	2.8	2.4	14.6
400	21-Aug-88	75	3	0.48	0.32	18
400	21-Aug-88	15	1	1.3	1.1	10
500	21-Aug-88	3	1	3.3	3.2	23.3
500	21-Aug-88	3	1	3.1	2.9	14
500	21-Aug-88	3	1	3.6	3.4	6.1
500	21-Aug-88	15	1	1.3	1.1	45.5
600	21-Aug-88	15	1	1.3	1.1	16.7
600	21-Aug-88	3	1	2.8	2.4	7.1
600	21-Aug-88	3	1	3.1	2.9	49.3
600	21-Aug-88	3	1	3.3	3.2	16.9
700	21-Aug-88	15	1	1.3	1.1	17.6
700	21-Aug-88	3	1	3.1	2.9	27.1
700	21-Aug-88	3	1	3.3	3.1	35.6
700	21-Aug-88	3	1	3.6	3.4	9.3
800	21-Aug-88	3	1	3.6	3.4	6.1
800	21-Aug-88	3	1	3.3	3.2	15.4
800	21-Aug-88	3	1	3.1	2.9	56.6
800	21-Aug-88	3	1	2.8	2.4	12.2
900	21-Aug-88	3	1	3.1	2.9	31.4
900	21-Aug-88	3	1	3.6	3.4	14.8
900	21-Aug-88	3	1	3.3	3.2	36.1
900	21-Aug-88	15	1	1.3	1.1	6
976	21-Aug-88	3	1	2.8	2.4	15.9
976	21-Aug-88	3	1	3.6	3.4	8.5
976	21-Aug-88	3	1	3.1	2.9	49.5
976	21-Aug-88	3	1	3.3	3.2	17.8
1100	21-Aug-88	3	1	2.8	2.4	7.8
1100	21-Aug-88	6	1	4.2	4	6.3
1100	21-Aug-88	3	1	3.6	3.4	11

Appendix 5. (continued)

Depth	Date	Code #	Sex	Size range (mm) Upper	Lower	Percent
1100	21-Aug-88	3	1	3.3	3.2	32.6
1100	21-Aug-88	3	1	3.1	2.9	27.1
1200	21-Aug-88	3	1	3.1	2.9	24.8
1200	21-Aug-88	6	2	3.2	3	8.8
1200	21-Aug-88	6	1	4.2	4	10.8
1200	21-Aug-88	3	1	3.6	3.4	6.4
1200	21-Aug-88	3	1	2.8	2.4	6.4
1200	21-Aug-88	15	1	1.3	1.1	5.8
1200	21-Aug-88	30	1	1.2	1.2	10.2
1200	21-Aug-88	3	1	3.3	3.2	10.2
1300	21-Aug-88	6	1	4.2	4	9.8
1300	21-Aug-88	3	1	3.1	2.9	31.2
1300	21-Aug-88	34	1	11	10	8.7
1300	21-Aug-88	8	1	3.6	3.6	5.2
1300	21-Aug-88	3	1	3.3	3.2	17.3
1300	21-Aug-88	3	1	2.8	2.4	8.1
50	30-Aug-88	75	3	1.5	1.5	5.3
50	30-Aug-88	75	3	1.3	1	18.2
50	30-Aug-88	75	3	1	0.48	69.3
100	30-Aug-88	75	3	1	0.48	11.3
100	30-Aug-88	75	3	1.3	1	11.3
100	30-Aug-88	15	1	1.3	1.1	60.1
250	30-Aug-88	75	3	1.3	1	10.4
250	30-Aug-88	82	3	12	12	6.1
250	30-Aug-88	3	1	3.1	2.9	7.4
250	30-Aug-88	15	1	1.3	1.1	26.2
250	30-Aug-88	75	3	1	0.48	21.7
500	30-Aug-88	3	1	3.3	3.2	23.8
500	30-Aug-88	3	1	3.1	2.9	21
500	30-Aug-88	3	1	3.6	3.4	8
500	30-Aug-88	15	1	1.3	1.1	30.1
1200	30-Aug-88	3	1	3.6	3.4	13.2
1200	30-Aug-88	3	1	3.3	3.2	30.3
1200	30-Aug-88	15	1	1.3	1.1	7.9
1200	30-Aug-88	3	1	3.1	2.9	36.9
50	31-Aug-88	75	3	1.3	1	33.9
50	31-Aug-88	15	1	1.3	1.1	19.1
50	31-Aug-88	75	3	1	0.48	33
100	31-Aug-88	75	3	1	0.48	9.1
100	31-Aug-88	3	1	3.3	3.2	5.3
100	31-Aug-88	15	1	1.3	1.1	52.6
100	31-Aug-88	75	3	1.3	1	9.1
150	31-Aug-88	75	3	1	0.48	13.7
150	31-Aug-88	15	1	1.3	1.1	41.3
150	31-Aug-88	75	3	1.3	1	22
200	31-Aug-88	3	1	3.6	3.4	9.9
200	31-Aug-88	3	1	3.3	3.2	26.6
200	31-Aug-88	3	1	3.1	2.9	28.6
200	31-Aug-88	15	1	1.3	1.1	16.5
250	31-Aug-88	15	1	1.3	1.1	26.9
250	31-Aug-88	3	1	3.3	3.1	19.3
250	31-Aug-88	3	1	3.1	2.9	24.8
250	31-Aug-88	3	1	3.6	3.4	8.8

Appendix 6. Metazooplankton groups comprising 5 % or more of total metazooplankton POC per sample.

Depth	Date	Code #	Sex	Size range (mm) Upper	Lower	Percent
100	13-May-86	1	1	4	3.8	14.7
100	13-May-86	35	1	6	5.6	6.1
100	13-May-86	1	1	3.4	3.2	33
100	13-May-86	1	1	3.6	3.6	32.5
100	13-May-86	34	1	8.4	8.2	7.7
1000	13-May-86	1	1	3.2	3.2	10
1000	13-May-86	34	1	6	6	8.2
1000	13-May-86	1	1	3.4	3.4	9.7
1000	13-May-86	6	1	4.2	4	5.3
1000	13-May-86	1	1	3.6	3.6	7.7
1000	13-May-86	82	3	30	30	27.2
30	27-May-86	1	1	3.2	2.9	30.8
30	27-May-86	1	1	3.6	3.4	38.8
30	27-May-86	1	1	3.8	3.8	15.6
30	27-May-86	1	1	4	4	11.1
100	27-May-86	1	1	3.4	2.9	40.7
100	27-May-86	1	1	3.6	3.4	32.9
100	27-May-86	1	1	4	3.8	19
1000	27-May-86	1	1	3.2	3.2	9.5
1000	27-May-86	1	1	4	3.8	14.7
1000	27-May-86	1	1	3.6	3.6	30.5
1000	27-May-86	1	1	3.4	3.4	25.7
1000	27-May-86	6	1	4.2	4	7.3
30	29-May-86	1	1	4	3.8	13.4
30	29-May-86	1	1	3.4	3.4	27.9
30	29-May-86	1	1	3.6	3.6	20.1
30	29-May-86	35	1	6	6	18.5
30	29-May-86	1	1	3.2	3.2	13.4
100	29-May-86	1	1	3.6	3.6	16.3
100	29-May-86	1	1	3.4	3.4	30
100	29-May-86	1	1	3.2	3.2	30.9
100	29-May-86	1	1	4	3.8	10.3
500	29-May-86	1	1	3.4	3.4	30.8
500	29-May-86	1	1	3.2	3.2	22.6
500	29-May-86	1	1	3.6	3.6	17.6
500	29-May-86	1	1	4	3.8	8.3
1000	29-May-86	1	1	3.4	3.4	22.3
1000	29-May-86	34	1	7.7	7.7	5.6
1000	29-May-86	1	1	3.2	3.2	22
1000	29-May-86	1	1	4	3.8	8.5
1000	29-May-86	1	1	3.6	3.6	11.7
1000	29-May-86	82	3	30	30	8.2
30	04-Jun-86	1	1	3.6	3.6	26.4
30	04-Jun-86	1	1	3.4	3.4	28.4
30	04-Jun-86	1	1	3.2	3.2	19.7
30	04-Jun-86	1	1	4	3.8	18.4
100	04-Jun-86	1	1	3.4	3.4	26.6
100	04-Jun-86	1	1	3.2	3.2	24.9
100	04-Jun-86	1	1	3.6	3.6	15.4
100	04-Jun-86	1	1	4	3.8	8.4
250	04-Jun-86	1	1	3.4	3.4	16.1
250	04-Jun-86	82	3	20	20	12.6
250	04-Jun-86	34	1	8.8	8.8	6.5
250	04-Jun-86	1	1	3.6	3.6	11.9
250	04-Jun-86	17	1	8	8	6.5
250	04-Jun-86	1	1	4	3.8	12.8
250	04-Jun-86	1	1	3.2	3.2	16.9
500	04-Jun-86	1	1	3.2	3.2	16.7

Appendix 6. (continued)

Depth	Date	Code #	Sex	Size range (mm) Upper	Lower	Percent
500	04-Jun-86	1	1	3.4	3.4	8.6
500	04-Jun-86	6	1	4.2	4	26.7
500	04-Jun-86	82	3	20	20	11.7
1000	04-Jun-86	17	1	8	8	10.2
1000	04-Jun-86	87	3	3.6	3.2	10
1000	04-Jun-86	34	1	8	8	10.3
1000	04-Jun-86	34	1	7.2	7.2	7.2
1000	04-Jun-86	20	1	11	11	5.4
1000	04-Jun-86	82	3	25	25	29
30	24-Jun-86	1	1	3.4	3.4	36.1
30	24-Jun-86	1	1	3.6	3.6	27.1
30	24-Jun-86	1	1	3.2	3.2	13.8
30	24-Jun-86	1	1	4	3.8	12.7
30	24-Jun-86	1	1	3.4	3.4	30.4
30	24-Jun-86	1	1	3.2	3.2	10.8
30	24-Jun-86	1	1	3.6	3.6	31.2
30	24-Jun-86	1	1	4	3.8	23.5
100	24-Jun-86	1	1	3.2	3.2	9.2
100	24-Jun-86	80	3	4	4	10.9
100	24-Jun-86	1	1	3.6	3.6	5.6
100	24-Jun-86	82	3	20	20	5.8
100	24-Jun-86	1	1	3.6	3.6	19
100	24-Jun-86	26	3	4	4	5.8
100	24-Jun-86	1	1	3.4	3.4	9.5
100	24-Jun-86	1	1	4	3.8	5.8
100	24-Jun-86	1	1	3.4	3.4	31
100	24-Jun-86	82	3	20	20	10.5
100	24-Jun-86	26	3	2.4	2.4	15.4
100	24-Jun-86	1	1	4	3.8	11.4
100	24-Jun-86	1	1	3.2	3.2	16.8
250	24-Jun-86	1	1	3.4	3.4	8.2
250	24-Jun-86	81	3	11.5	11.5	7.1
250	24-Jun-86	82	3	25	25	11.8
250	24-Jun-86	1	1	3.6	3.6	15.6
250	24-Jun-86	1	1	4	3.8	10.2
250	24-Jun-86	26	3	3	3	7.6
250	24-Jun-86	6	1	4.2	4	6.3
250	24-Jun-86	1	1	3.4	3.4	8.2
250	24-Jun-86	1	1	3.2	3.2	8.5
250	24-Jun-86	82	3	25	25	20.2
250	24-Jun-86	6	1	4.2	4	13.3
500	24-Jun-86	6	1	4.2	4	6.6
500	24-Jun-86	1	1	3.2	3.2	6.7
500	24-Jun-86	82	3	65	65	11.7
500	24-Jun-86	1	1	3.4	3.4	11
500	24-Jun-86	82	3	28	28	15.9
500	24-Jun-86	1	1	3.6	3.6	9.5
500	24-Jun-86	17	1	8.5	8.5	6.6
500	24-Jun-86	1	1	3.4	3.4	14.9
500	24-Jun-86	81	3	25	25	22.5
500	24-Jun-86	1	1	3.6	3.6	16.2
500	24-Jun-86	82	3	25	25	18.7
1000	24-Jun-86	34	1	9	8	6.1
1000	24-Jun-86	82	3	30	30	20.7
1000	24-Jun-86	82	3	30	30	18
1000	24-Jun-86	1	1	3.4	3.4	16.4
1000	24-Jun-86	87	3	3.2	3.2	12.7

Appendix 6. (continued)

Depth	Date	Code #	Sex	Size range (mm) Upper	Lower	Percent
1000	24-Jun-86	1	1	3.4	3.4	12.7
1000	24-Jun-86	1	1	3.2	3.2	18.6
1000	24-Jun-86	1	1	3.2	3.2	20.4
1000	24-Jun-86	34	1	9	9	9.7
1000	24-Jun-86	1	1	3.6	3.6	5.4
30	30-Jun-86	1	1	3.2	3.2	21.8
30	30-Jun-86	34	1	8	8	7.8
30	30-Jun-86	34	1	9	9	5.6
30	30-Jun-86	1	1	3.2	2.4	26.1
30	30-Jun-86	6	1	4.2	4	5.2
30	30-Jun-86	82	3	25	25	12.6
30	30-Jun-86	35	3	5.6	4.8	5.6
30	30-Jun-86	1	1	3.4	3.4	19.6
30	30-Jun-86	1	1	3.4	3.4	13.8
30	30-Jun-86	6	2	3.6	3.4	5.6
30	30-Jun-86	82	3	30	30	18.3
100	30-Jun-86	1	1	3.4	3.4	10.3
100	30-Jun-86	81	3	22	22	9.5
100	30-Jun-86	1	1	3.2	3.2	24.1
100	30-Jun-86	81	3	27	27	22.1
100	30-Jun-86	1	1	3.4	3.4	13
100	30-Jun-86	82	3	30	30	19.7
100	30-Jun-86	82	3	20	20	5.6
100	30-Jun-86	17	1	9	9	11
100	30-Jun-86	1	1	3.2	3.2	21
100	30-Jun-86	82	3	30	30	9.8
250	30-Jun-86	82	3	20	20	9.4
250	30-Jun-86	82	3	25	25	8.4
250	30-Jun-86	1	1	3.6	3.6	9.4
250	30-Jun-86	82	3	25	25	8
250	30-Jun-86	1	1	3.2	3.2	12.5
250	30-Jun-86	1	1	3.4	3.4	7.6
250	30-Jun-86	1	1	3.4	3.4	14.7
250	30-Jun-86	6	1	4.2	4	7.3
250	30-Jun-86	26	3	3	3	5.4
250	30-Jun-86	81	3	35	35	50.6
250	30-Jun-86	1	1	3.2	3.2	12.7
250	30-Jun-86	26	3	4	4	5.4
500	30-Jun-86	26	3	4	4	14.7
500	30-Jun-86	80	3	5	4	6.4
500	30-Jun-86	26	2	5.6	5.6	8.6
500	30-Jun-86	8	2	2.8	2.6	5.9
500	30-Jun-86	82	3	14	14	8.5
500	30-Jun-86	1	1	3.2	3.2	17
500	30-Jun-86	82	3	25	25	7.2
500	30-Jun-86	1	1	3.6	3.6	13.7
500	30-Jun-86	1	1	3.4	3.4	8
500	30-Jun-86	1	1	4	3.8	5.2
500	30-Jun-86	26	3	3	3	5.3
500	30-Jun-86	1	1	3.2	3.2	15.5
500	30-Jun-86	6	1	4.2	4	5.7
500	30-Jun-86	26	3	4	4	8.9
500	30-Jun-86	1	1	3.4	3.4	10.2
500	30-Jun-86	1	1	3.6	3.6	7.4
1000	30-Jun-86	3	3	1.6	1.6	10.8
1000	30-Jun-86	1	1	3.4	3.4	10.6
1000	30-Jun-86	1	1	3.4	3.4	27.4

Appendix 6. (continued)

Depth	Date	Code #	Sex	Size range (mm) Upper	Lower	Percent
1000	30-Jun-86	1	1	3.2	3.2	17.3
1000	30-Jun-86	3	3	2.4	2	48.9
1000	30-Jun-86	1	1	3.2	3	58.6
1000	30-Jun-86	1	1	3.6	3.6	7
100	09-Feb-87	3	1	2.6	2.4	13.3
100	09-Feb-87	82	3	18	18	9.8
100	09-Feb-87	81	3	7	7	6.4
100	09-Feb-87	3	1	3.2	3	22.7
100	09-Feb-87	6	1	4.2	4	7.6
100	09-Feb-87	82	3	111	111	85.2
100	09-Feb-87	19	3	5.6	5.6	11.5
250	09-Feb-87	3	1	2.4	2.4	7.4
250	09-Feb-87	3	1	2.8	2.8	8.1
250	09-Feb-87	3	1	3.2	3	13.7
250	09-Feb-87	80	3	10	10	10.6
250	09-Feb-87	3	1	3.2	3.2	8.5
250	09-Feb-87	82	3	15	15	6.9
250	09-Feb-87	6	1	4.2	4	8.5
250	09-Feb-87	82	3	25	25	9.3
250	09-Feb-87	24	1	5.8	5.8	7.3
250	09-Feb-87	34	1	8.5	8.5	6.4
250	09-Feb-87	81	3	9	9	9.1
250	09-Feb-87	82	3	18.3	18.3	6.6
250	09-Feb-87	80	3	12	12	11.8
250	09-Feb-87	3	1	2.6	2.4	8.1
250	09-Feb-87	34	1	8.3	8.3	11.5
500	09-Feb-87	80	3	10	501	21.5
500	09-Feb-87	34	1	6.6	6.6	7.3
500	09-Feb-87	80	3	25	20.1	12.3
500	09-Feb-87	6	1	4.2	4	5.1
500	09-Feb-87	80	3	15	10.1	9.2
500	09-Feb-87	3	1	3.4	3	13.7
500	09-Feb-87	17	1	8	8	14.5
500	09-Feb-87	81	3	10	10	7
500	09-Feb-87	81	3	16	16	12.9
500	09-Feb-87	3	1	2.8	2.4	14.4
750	09-Feb-87	23	1	8	7	7.1
750	09-Feb-87	3	1	3	3	7.5
750	09-Feb-87	3	1	2.8	2.4	27.9
750	09-Feb-87	3	1	2.89	2.8	10.5
750	09-Feb-87	87	3	3.6	2.2	17.9
750	09-Feb-87	3	1	2.4	2.4	5.7
750	09-Feb-87	3	1	3.2	3.2	9.8
750	09-Feb-87	81	3	12	10	13.4
750	09-Feb-87	81	3	11	11	18
750	09-Feb-87	3	1	2.6	2.6	6.2
750	09-Feb-87	3	1	3.4	3	37.7
750	09-Feb-87	3	1	4	3.6	7.5
900	09-Feb-87	80	3	26.6	26.6	7.6
900	09-Feb-87	35	1	5.8	5.8	8
900	09-Feb-87	80	3	10	10	15.6
900	09-Feb-87	3	1	2.4	2.4	8.5
1000	09-Feb-87	3	1	3.4	3	28
1000	09-Feb-87	3	1	2.8	2.4	30.5
1000	09-Feb-87	3	1	4	3.6	5.2
1000	09-Feb-87	81	3	12	12	22.2
1200	09-Feb-87	35	1	5.6	5.6	8.5

Appendix 6. (continued)

Depth	Date	Code #	Sex	Size range (mm) Upper	Lower	Percent
1200	09-Feb-87	34	1	8.4	8.4	16.1
1200	09-Feb-87	3	1	2.8	2.4	30.3
1200	09-Feb-87	3	1	3.4	3	29.3
1200	16-Feb-87	3	1	2.2	2.2	6.9
1200	16-Feb-87	3	1	3.2	3.2	5.1
1200	16-Feb-87	80	3	19.2	19.2	6.1
1200	16-Feb-87	3	1	2.8	2.8	8.8
1200	16-Feb-87	3	1	2.4	2.4	6.7
1200	16-Feb-87	82	3	25	20.1	7.6
1200	16-Feb-87	87	3	1	1	9.5
1200	16-Feb-87	3	1	2.6	2.6	5.8
2000	16-Feb-87	35	1	4.2	4.2	7.2
2000	16-Feb-87	34	1	7.5	7.5	16.6
2000	16-Feb-87	35	1	6	6	7
2000	16-Feb-87	76	3	18.3	18.3	7.9
2000	16-Feb-87	35	1	5.8	5.8	11.9
2000	16-Feb-87	34	1	8.3	8.3	6
2400	16-Feb-87	3	1	2.5	2.5	7.1
2400	16-Feb-87	17	1	8.3	8.3	5.7
2400	16-Feb-87	7	3	2.1	2.1	5.8
2400	16-Feb-87	80	3	15	15	12.4
2400	16-Feb-87	34	1	7.5	7.5	5.8
2400	16-Feb-87	80	3	15	15	12.4
2400	16-Feb-87	48	1	3.7	3.7	10
2800	16-Feb-87	6	1	4.2	4.2	7.9
2800	16-Feb-87	48	1	2.5	2.5	19.3
2800	16-Feb-87	3	1	3	3	34.5
2800	16-Feb-87	1	1	4	4	28.4
30	30-Jul-87	1	1	3.8	3.4	5.8
30	30-Jul-87	3	1	3.2	3	44.1
30	30-Jul-87	3	1	2.8	2.6	22.3
30	30-Jul-87	3	1	2.4	2	22.5
100	30-Jul-87	81	3	10.4	8.3	19.3
100	30-Jul-87	3	1	3.2	3	5.2
100	30-Jul-87	24	1	4.2	4	19.4
100	30-Jul-87	1	1	3.8	3.4	14.2
100	30-Jul-87	6	1	4.4	4	6.4
100	30-Jul-87	8	1	3.2	2.8	14.1
250	30-Jul-87	26	3	2.8	2.4	22.1
250	30-Jul-87	3	1	2.8	2.6	12.5
250	30-Jul-87	8	1	3.2	2.8	5.3
250	30-Jul-87	3	1	3.2	3	12.2
250	30-Jul-87	26	3	2	1.8	25.3
500	30-Jul-87	87	3	2.2	1.1	52.9
500	30-Jul-87	3	1	2.8	2.6	7.7
500	30-Jul-87	81	3	15	10	6.3
500	30-Jul-87	80	3	6.8	5.2	9.6
500	30-Jul-87	3	1	2.4	2.2	6.3
1000	30-Jul-87	17	1	8.2	8.2	6.1
1000	30-Jul-87	87	3	2	1.1	16.9
1000	30-Jul-87	3	1	3.2	3	15.9
1000	30-Jul-87	3	1	3.6	3.4	6.2
1000	30-Jul-87	3	1	2.8	2.6	8.8
1000	30-Jul-87	87	3	3.6	2.4	24.4
1000	30-Jul-87	3	1	2.4	2.2	6.6
30	01-Nov-87	3	1	2.8	2.4	22.5
30	01-Nov-87	47	1	4	4	5.1

Appendix 6. (continued)

Depth	Date	Code #	Sex	Size range (mm) Upper	Lower	Percent
30	01-Nov-87	3	1	3.4	3	34.1
30	01-Nov-87	82	3	10	10	5.7
30	01-Nov-87	26	3	5.6	5.6	6.7
100	01-Nov-87	3	1	2.8	2.4	6.2
100	01-Nov-87	82	3	20	10	15.1
100	01-Nov-87	81	3	10	10	21.4
100	01-Nov-87	82	3	30	20	36.1
100	01-Nov-87	3	1	3.4	3	5.2
250	01-Nov-87	82	3	30	20	43.3
250	01-Nov-87	26	3	6	5	15
250	01-Nov-87	3	1	2.8	2.4	9.8
250	01-Nov-87	3	1	3.4	3	11.2
250	01-Nov-87	26	3	2	2	8.6
50	13-Aug-88	3	1	2.8	2.4	16.9
50	13-Aug-88	3	1	3.3	3.2	8.5
50	13-Aug-88	3	1	3.1	2.9	60.3
100	13-Aug-88	82	3	15	15	21
100	13-Aug-88	1	1	3.6	3.2	24.4
100	13-Aug-88	3	1	3.1	2.9	5
100	13-Aug-88	82	3	10	10	7.2
100	13-Aug-88	1	1	4	3.7	22.5
200	13-Aug-88	80	3	7	7	9.5
200	13-Aug-88	3	1	2.8	2.4	9.9
200	13-Aug-88	82	3	30	30	22.7
200	13-Aug-88	3	1	3.3	3.2	5.8
200	13-Aug-88	82	3	8	8	5.8
200	13-Aug-88	82	3	16	16	14.2
200	13-Aug-88	3	1	3.1	2.9	9.6
300	13-Aug-88	3	1	2.8	2.4	18
300	13-Aug-88	3	1	3.3	3.2	9.5
300	13-Aug-88	3	1	3.1	2.9	21.2
300	13-Aug-88	80	3	8	8	8.3
300	13-Aug-88	26	3	4.2	4	17.3
500	13-Aug-88	3	1	2.8	2.4	10.2
500	13-Aug-88	3	1	3.3	3.2	5.3
500	13-Aug-88	3	1	3.1	2.9	17.2
500	13-Aug-88	82	3	32	32	49.2
500	13-Aug-88	82	3	16	16	6.2
600	13-Aug-88	3	1	3.1	2.9	16.6
600	13-Aug-88	3	1	3.6	3.4	8.1
600	13-Aug-88	17	1	10	10	6.2
600	13-Aug-88	81	3	30	30	9.7
600	13-Aug-88	3	1	2.8	2.4	7.5
600	13-Aug-88	3	1	3.3	3.2	17.9
600	13-Aug-88	82	3	30	30	27.6
800	13-Aug-88	3	1	3.1	2.9	16.4
800	13-Aug-88	3	1	2.8	2.4	6.6
800	13-Aug-88	82	3	80	80	27.3
800	13-Aug-88	3	1	3.3	3.2	12.7
800	13-Aug-88	82	3	40	30	20.2
1000	13-Aug-88	3	1	3.3	3.2	10.1
1000	13-Aug-88	82	3	30	30	11.3
1000	13-Aug-88	80	3	8	8	6.7
1000	13-Aug-88	3	1	3.1	2.9	12.6
1000	13-Aug-88	35	3	5.6	5.6	31.7
1000	13-Aug-88	82	3	18	18	6
1200	13-Aug-88	34	1	5.6	5.6	23

Appendix 6. (continued)

Depth	Date	Code #	Sex	Size range (mm) Upper	Lower	Percent
1200	13-Aug-88	80	3	8	8	8.6
1200	13-Aug-88	34	1	8	8	15.3
1200	13-Aug-88	34	1	9.6	9.6	37.7
25	21-Aug-88	3	1	2.8	2.4	7
25	21-Aug-88	3	1	3.3	3.2	7.9
25	21-Aug-88	75	3	1	0.48	32.5
25	21-Aug-88	1	1	3.5	3.2	16.8
25	21-Aug-88	75	3	1.3	1	7.1
25	21-Aug-88	1	1	3.5	3.2	9
25	21-Aug-88	3	1	3.1	2.9	6.7
25	21-Aug-88	1	1	4	3.6	12.3
25	21-Aug-88	75	3	1	0.48	19.6
25	21-Aug-88	3	1	3.3	3.1	12.6
25	21-Aug-88	3	1	3.1	2.9	22.6
25	21-Aug-88	1	1	4	3.6	21.7
50	21-Aug-88	3	1	3.3	3.2	5.9
50	21-Aug-88	82	3	12	12	6.5
50	21-Aug-88	1	1	3.2	3.5	21.8
50	21-Aug-88	3	1	3.6	3.4	5.7
50	21-Aug-88	80	3	8	8	5.6
50	21-Aug-88	1	1	4	3.6	19.6
50	21-Aug-88	3	1	3.1	2.9	10.1
50	21-Aug-88	1	1	4	3.6	16.2
50	21-Aug-88	1	1	3.5	3.2	24.2
50	21-Aug-88	3	1	3.1	2.9	10.8
50	21-Aug-88	3	1	3.3	3.4	14.6
50	21-Aug-88	26	3	4.8	3.6	14.6
100	21-Aug-88	82	3	25	20	41.5
100	21-Aug-88	6	1	4.2	4	5.3
100	21-Aug-88	26	3	6.4	5.6	21.2
100	21-Aug-88	82	3	16	16	34.8
100	21-Aug-88	82	3	30	30	20.3
100	21-Aug-88	6	2	3.2	3.2	7.3
100	21-Aug-88	82	3	12	12	18.1
150	21-Aug-88	26	1	9.4	9.4	5.2
150	21-Aug-88	60	1	6.4	5.6	6.3
150	21-Aug-88	82	3	20	16	13.4
150	21-Aug-88	26	3	4.8	4.8	7
150	21-Aug-88	81	3	16	16	19.3
150	21-Aug-88	6	1	4.2	4	13.8
150	21-Aug-88	82	3	12	12	20.2
150	21-Aug-88	3	1	3.4	3.2	6.9
150	21-Aug-88	26	1	7	7	7
150	21-Aug-88	66	2	3.2	3	10.4
150	21-Aug-88	82	3	12	8	8.6
150	21-Aug-88	82	3	16	16	10.5
150	21-Aug-88	81	3	11	11	27.3
150	21-Aug-88	3	1	3.1	2.9	15.6
200	21-Aug-88	3	1	3.1	2.9	6.7
200	21-Aug-88	26	1	9	8	5.3
200	21-Aug-88	82	3	16	16	21.5
200	21-Aug-88	26	3	5.6	4	10.6
200	21-Aug-88	81	3	16	16	29.1
200	21-Aug-88	6	1	4.2	4	7.2
200	21-Aug-88	82	3	12	12	12.5
200	21-Aug-88	6	1	4.2	4	6.1
200	21-Aug-88	76	3	9	9	20.4

Appendix 6. (continued)

Depth	Date	Code #	Sex	Size range (mm) Upper	Lower	Percent
200	21-Aug-88	55	1	4	4	5.5
200	21-Aug-88	80	3	12	12	7.6
200	21-Aug-88	82	3	16	16	6.1
200	21-Aug-88	81	3	10	10	7.9
200	21-Aug-88	3	1	3.3	3.2	11.1
250	21-Aug-88	85	3	6	6	5.4
250	21-Aug-88	85	3	10	10	22.4
250	21-Aug-88	3	1	3.4	3.2	13.7
250	21-Aug-88	26	3	5.6	5.6	7.5
250	21-Aug-88	3	1	3.1	2.9	21.6
250	21-Aug-88	26	3	2.4	1.6	20.3
250	21-Aug-88	82	3	16	16	9.4
250	21-Aug-88	82	3	30	30	37.4
250	21-Aug-88	3	1	3.3	3.2	7.4
250	21-Aug-88	3	1	2.8	2.4	10.8
300	21-Aug-88	3	1	3.4	3.2	17
300	21-Aug-88	80	3	8	8	22.6
300	21-Aug-88	82	3	30	30	64
300	21-Aug-88	87	3	3.2	3.2	7.2
300	21-Aug-88	3	1	3.6	3.4	5.7
300	21-Aug-88	87	3	2.4	1.6	11.5
300	21-Aug-88	3	1	3.1	2.9	36.2
400	21-Aug-88	87	3	3	2.4	16.6
400	21-Aug-88	81	3	13	13	6.7
400	21-Aug-88	81	3	12	12	12.9
400	21-Aug-88	3	1	2.8	2.4	6.8
400	21-Aug-88	80	3	8	8	8.3
400	21-Aug-88	82	3	30	30	36
400	21-Aug-88	80	3	6	6	12.5
400	21-Aug-88	82	3	20	20	9.4
400	21-Aug-88	3	1	3.3	3.2	7.5
400	21-Aug-88	82	3	40	40	12.9
400	21-Aug-88	3	1	3.1	2.9	9.8
400	21-Aug-88	82	3	30	30	10
400	21-Aug-88	3	1	3.1	2.9	14.2
500	21-Aug-88	82	3	30	30	33.6
500	21-Aug-88	82	3	20	20	12.5
500	21-Aug-88	3	1	3.3	3.2	15.4
500	21-Aug-88	3	1	3.1	2.9	9.3
600	21-Aug-88	3	1	3.3	3.2	16.6
600	21-Aug-88	3	1	3.1	2.9	48.5
600	21-Aug-88	82	3	30	30	5.1
600	21-Aug-88	17	1	10	10	5.8
600	21-Aug-88	82	3	20	20	8.6
600	21-Aug-88	3	1	2.8	2.4	7
700	21-Aug-88	3	1	3.3	3.1	21.4
700	21-Aug-88	82	3	40	30	36.6
700	21-Aug-88	80	3	11	7	7.9
700	21-Aug-88	3	1	3.1	2.9	16.3
700	21-Aug-88	3	1	3.6	3.4	5.6
800	21-Aug-88	82	3	40	30	20.4
800	21-Aug-88	3	1	3.1	2.9	32.5
800	21-Aug-88	3	1	2.8	2.4	7
800	21-Aug-88	3	1	3.3	3.2	8.9
800	21-Aug-88	87	3	3.2	3.2	13.3
900	21-Aug-88	82	3	30	30	14.3
900	21-Aug-88	82	3	40	40	12

Appendix 6. (continued)

Depth	Date	Code #	Sex	Size range (mm) Upper	Lower	Percent
900	21-Aug-88	3	1	3.1	2.9	21.8
900	21-Aug-88	3	1	3.3	3.2	25.1
900	21-Aug-88	3	1	3.6	3.4	10.3
976	21-Aug-88	3	1	2.8	2.4	14.4
976	21-Aug-88	3	1	3.6	3.4	7.7
976	21-Aug-88	3	1	3.1	2.9	44.9
976	21-Aug-88	3	1	3.3	3.2	16.1
1100	21-Aug-88	3	1	3.3	3.2	27
1100	21-Aug-88	3	1	2.8	2.4	6.5
1100	21-Aug-88	82	3	30	30	7.3
1100	21-Aug-88	3	1	3.6	3.4	9.1
1100	21-Aug-88	6	1	4.2	4	5.9
1100	21-Aug-88	3	1	3.1	2.9	22.5
1200	21-Aug-88	3	1	3.1	2.9	5.7
1200	21-Aug-88	35	1	7.2	7.2	6.9
1200	21-Aug-88	1	3	6.4	4.8	11.6
1200	21-Aug-88	82	3	90	90	24.3
1200	21-Aug-88	34	1	10	10	28.5
1300	21-Aug-88	82	3	40	30	6.6
1300	21-Aug-88	3	1	3.1	2.9	5.6
1300	21-Aug-88	35	1	8	6	14.2
1300	21-Aug-88	34	1	11	10	50.4
50	30-Aug-88	1	1	3.5	3.2	19.9
50	30-Aug-88	1	1	4	3.6	14.2
50	30-Aug-88	3	1	3.1	2.9	5.5
50	30-Aug-88	75	3	1.3	1	9.4
50	30-Aug-88	75	3	1.5	1.5	6.1
50	30-Aug-88	81	3	6	6	7
50	30-Aug-88	26	1	8	7	11.2
50	30-Aug-88	75	3	1	0.48	9.5
100	30-Aug-88	81	3	16	16	50.8
100	30-Aug-88	81	3	12	12	22.9
250	30-Aug-88	82	3	12	12	10.2
250	30-Aug-88	3	1	3.1	2.9	5.4
250	30-Aug-88	80	3	7	5	38.1
250	30-Aug-88	26	1	5	4	8.8
250	30-Aug-88	82	3	16	16	9.4
250	30-Aug-88	87	3	2	1.6	5.1
500	30-Aug-88	3	1	3.3	3.2	11.4
500	30-Aug-88	82	3	40	30	22.9
500	30-Aug-88	80	3	8	6	6.3
500	30-Aug-88	17	1	10	10	8.4
500	30-Aug-88	3	1	3.1	2.9	10
500	30-Aug-88	82	3	75	75	25.7
1200	30-Aug-88	3	1	3.1	2.9	15
1200	30-Aug-88	34	1	11	11	6.5
1200	30-Aug-88	3	1	3.6	3.4	5.3
1200	30-Aug-88	3	1	3.3	3.2	12.3
1200	30-Aug-88	82	3	50	40	37
50	31-Aug-88	1	1	4	3.6	24.5
50	31-Aug-88	3	1	3.1	2.9	17.4
50	31-Aug-88	3	1	3.6	3.4	5.1
50	31-Aug-88	3	1	3.3	3.2	15.7
50	31-Aug-88	1	1	3.5	3.2	14
50	31-Aug-88	75	3	1.3	1	7.9
100	31-Aug-88	26	3	4.4	3.6	56.2
100	31-Aug-88	1	1	4	3.6	8.9

Appendix 6. (continued)

Depth	Date	Code #	Sex	Size range (mm) Upper	Lower	Percent
100	31-Aug-88	3	1	3.3	3.2	11.9
100	31-Aug-88	3	1	3.1	2.9	5.4
150	31-Aug-88	82	3	12	12	5.3
150	31-Aug-88	80	3	6	6	6.4
150	31-Aug-88	81	3	20	20	68.5
200	31-Aug-88	3	1	3.3	3.2	25.2
200	31-Aug-88	3	1	3.6	3.4	9.4
200	31-Aug-88	3	1	3.1	2.9	27.1
200	31-Aug-88	81	3	16	16	12.5
200	31-Aug-88	81	3	8	8	5.5
250	31-Aug-88	3	1	3.3	3.1	15.8
250	31-Aug-88	26	3	6	5	7.9
250	31-Aug-88	82	3	30	30	7.3
250	31-Aug-88	3	1	3.6	3.4	7.2
250	31-Aug-88	3	1	3.1	2.9	20.4
250	31-Aug-88	35	1	8	7	6.5
250	31-Aug-88	82	3	20	20	7.7

Appendix 7. Distribution of *Calanus finmarchicus* numbers and POC: totals, adult females and CV copepodites

Date	Depth interval		Total	C. fin.	Adult females		Copepodites	
	Upper	Lower	N/m2	mgC/m2	N/m2	mgC/m2	N/m2	mgC/m2
13-May-86	0	100	16647	1647.78	15113	1557.00	451	22.56
13-May-86	100	1000	1714	131.03	767	79.00	587	29.35
27-May-86	0	30	19849	2010.96	19173	1974.78	496	24.81
27-May-86	30	100						
27-May-86	100	1000						
29-May-86	0	30	3158	318.67	3023	311.32	90	4.51
29-May-86	30	100	1624	165.44	1579	162.60	0	0.00
29-May-86	100	500	2211	216.98	1986	204.56	135	6.75
29-May-86	500	1000	1939	189.55	1714	176.54	90	4.50
04-Jun-86	0	30	4960	484.58	4448	458.14	448	22.40
04-Jun-86	30	100	1624	163.92	1548	159.44	24	1.20
04-Jun-86	100	250	2288	233.33	2240	230.72	32	1.60
04-Jun-86	250	500	1024	103.78	992	102.18	32	1.60
04-Jun-86	500	1000	316	30.64	280	28.84	36	1.80
24-Jun-86	0	30	9072	887.55	8176	842.13	848	42.40
24-Jun-86	30	100	672	63.90	560	57.68	64	3.20
24-Jun-86	100	250	1120	113.87	1088	112.06	16	0.80
24-Jun-86	250	500	1696	171.08	1624	167.27	56	2.80
24-Jun-86	500	1000	6368	638.10	6032	621.30	336	16.80
24-Jun-86	0	30	9820	953.16	8720	898.16	1100	55.00
24-Jun-86	30	100	3387	343.88	3293	339.21	93	4.67
24-Jun-86	100	250	1036	104.32	988	101.76	36	1.80
24-Jun-86	250	500	2928	296.28	2824	290.87	88	4.40
24-Jun-86	500	1000	5820	594.68	5720	589.16	60	3.00
30-Jun-86	0	30	372	36.62	340	35.02	32	1.60
30-Jun-86	30	100	2480	241.02	2208	227.42	272	13.60
30-Jun-86	100	250	812	80.24	748	77.04	64	3.20
30-Jun-86	250	500	340	30.83	260	26.78	76	3.80
30-Jun-86	500	1000	13824	862.92	3240	333.72	10584	529.20
30-Jun-86	0	30	5260	534.36	5120	527.36	140	7.00
30-Jun-86	30	100	3060	310.94	2980	306.94	80	4.00
30-Jun-86	100	250	804	82.65	800	82.40	0	0.00
30-Jun-86	250	500	432	40.68	360	37.08	72	3.60
30-Jun-86	500	1000	10060	969.40	8800	906.40	1260	63.00
09-Feb-87	0	100	312	18	36	4	260	13.00
09-Feb-87	100	250	1128	65.92	160	16.48	888	44.40
09-Feb-87	250	500	5660	283.00	0	0.00	5660	283.00
09-Feb-87	500	750	33200	1670.60	200	20.60	33000	1650.00
09-Feb-87	750	1000	30400	1541.20	400	41.20	30000	1500.00
09-Feb-87	1000	1200	26800	1350.60	200	20.60	26600	1330.00
09-Feb-87	0	100	19960	1048.88	960	98.88	19000	950.00
09-Feb-87	100	250	384	19.62	8	0.82	376	18.80
09-Feb-87	250	500	1844	95.38	60	6.18	1784	89.20
09-Feb-87	500	750	17160	891.92	640	65.92	16520	826.00
09-Feb-87	750	900	3928	210.39	264	27.19	3664	183.20

Appendix 7. (continued)

Date	Depth interval		Total	C. fin.	Adult females		Copepodites	
	Upper	Lower	N/m2	mgC/m2	N/m2	mgC/m2	N/m2	mgC/m2
16-Feb-87	0	1200	56440	3000	3320	342	53000	2650.00
16-Feb-87	1200	2000	2504	140	276	28	2228	111.40
16-Feb-87	2000	2400	568	30	24	2	544	27.20
16-Feb-87	2400	2800	28	2	8	1	20	1.00
30-Jul-87	0	30	34280	1773.36	1120	115.36	33160	1658.00
30-Jul-87	30	100	372	26.44	148	15.24	224	11.20
30-Jul-87	100	250	768	39.25	16	1.65	752	37.60
30-Jul-87	250	500	6296	317.34	48	4.94	6248	312.40
30-Jul-87	500	1000	16240	826.84	280	28.84	15960	798.00
13-Aug-88	0	50	15520	812.04	680	70.04	14840	742.00
13-Aug-88	50	100	1808	151.88	1160	119.48	648	32.40
13-Aug-88	100	200	748	39.31	36	3.71	712	35.60
13-Aug-88	200	300	1060	55.54	48	4.94	1012	50.60
13-Aug-88	300	500	3920	198.12	40	4.12	3880	194.00
13-Aug-88	400	600	13720	694.48	160	16.48	13560	678.00
13-Aug-88	600	800	22160	1150.40	800	82.40	21360	1068.00
13-Aug-88	800	1000	7680	426.40	800	82.40	6880	344.00
13-Aug-88	1000	1200	992	49.60	0	0.00	992	49.60
21-Aug-88	0	25	2232	156.54	848	87.34	1384	69.20
21-Aug-88	25	50	2256	142.48	560	57.68	1696	84.80
21-Aug-88	50	100	552	42.49	280	28.84	268	13.40
21-Aug-88	100	150	1032	71.74	380	39.14	652	32.60
21-Aug-88	150	200	312	16.87	24	2.47	288	14.40
21-Aug-88	200	250	212	13.57	56	5.77	156	7.80
21-Aug-88	250	300	128	6.40	0	0.00	128	6.40
21-Aug-88	300	400	140	8.06	20	2.06	120	6.00
21-Aug-88	400	500	180	9.00	0	0.00	180	9.00
21-Aug-88	500	700	164	8.25	0	0.00	160	8.00
21-Aug-88	700	900	172	8.81	4	0.41	168	8.40
21-Aug-88	900	1100	296	16.12	24	2.47	268	13.40
21-Aug-88	1100	1300	220	11.00	0	0.00	220	11.00
21-Aug-88	0	25	272	15.51	36	3.71	236	11.80
21-Aug-88	25	50	1032	52.45	16	1.65	1016	50.80
21-Aug-88	50	100	452	25.78	60	6.18	392	19.60
21-Aug-88	100	150	5253	262.67	0	0.00	5253	262.67
21-Aug-88	150	200	16360	818.00	0	0.00	16360	818.00
21-Aug-88	200	250	14800	744.24	80	8.24	14720	736.00
21-Aug-88	250	300	17920	902.36	120	12.36	17800	890.00
21-Aug-88	300	400	34840	1773.80	600	61.80	34240	1712.00
21-Aug-88	400	600	20880	1048.24	80	8.24	20800	1040.00
21-Aug-88	600	800	12280	626.72	240	24.72	12040	602.00
21-Aug-88	800	976	3360	172.24	80	8.24	3280	164.00
21-Aug-88	976	1200	2140	109.12	40	4.12	2100	105.00
30-Aug-88	0	50	1970	155.74	1080	111.24	890	44.50
30-Aug-88	50	100	56	3.22	8	0.82	48	2.40
30-Aug-88	100	250	288	14.82	8	0.82	280	14.00
30-Aug-88	250	500	4260	218.83	110	11.33	4150	207.50
30-Aug-88	500	1200	41720	2117.80	600	61.80	41120	2056.00
31-Aug-88	0	50	2880	190.64	880	90.64	2000	100.00
31-Aug-88	50	100	112	6.66	20	2.06	92	4.60
31-Aug-88	100	150	92	4.81	4	0.41	88	4.40
31-Aug-88	150	200	2412	120.60	0	0.00	2412	120.60
31-Aug-88	200	250	2440	123.06	20	2.06	2420	121.00
01-Nov-87	0	30	400	20.42	8	0.82	392	19.60
01-Nov-87	30	100	140	7.26	4	0.41	132	6.60
01-Nov-87	100	250	924	46.93	0	0.00	868	43.40

Appendix 8. Distribution of *Limacina retroversa* numbers and POC according to shell length

Date	Depth interval (m)		Limacina retroversa					
			.32 -.48 mm		.48 - 1.00mm		> 1.00 mm	
	Upper	Lower	N/m2	mgC/m2	N/m2	mgC/m2	N/m2	mgC/m2
13-May-86	0	100	0	0.00	0	0.00	0	0.00
13-May-86	100	1000	0	0.00	0	0.00	0	0.00
27-May-86	0	30	0	0.00	0	0.00	0	0.00
27-May-86	30	100	0	0.00	0	0.00	0	0.00
27-May-86	100	1000	0	0.00	0	0.00	0	0.00
29-May-86	0	30	0	0.00	0	0.00	0	0.00
29-May-86	30	100	0	0.00	0	0.00	0	0.00
29-May-86	100	500	0	0.00	0	0.00	0	0.00
29-May-86	500	1000	0	0.00	0	0.00	0	0.00
04-Jun-86	0	30	0	0.00	0	0.00	0	0.00
04-Jun-86	30	100	0	0.00	0	0.00	0	0.00
04-Jun-86	100	250	0	0.00	0	0.00	0	0.00
04-Jun-86	250	500	0	0.00	0	0.00	0	0.00
04-Jun-86	500	1000	0	0.00	0	0.00	0	0.00
24-Jun-86	0	30	0	0.00	0	0.00	0	0.00
24-Jun-86	30	100	0	0.00	0	0.00	4	0.01
24-Jun-86	100	250	0	0.00	0	0.00	0	0.00
24-Jun-86	250	500	0	0.00	0	0.00	0	0.00
24-Jun-86	500	1000	0	0.00	0	0.00	0	0.00
24-Jun-86	0	30	0	0.00	0	0.00	0	0.00
24-Jun-86	30	100	0	0.00	0	0.00	0	0.00
24-Jun-86	100	250	0	0.00	0	0.00	0	0.00
24-Jun-86	250	500	0	0.00	0	0.00	0	0.00
24-Jun-86	500	1000	0	0.00	0	0.00	0	0.00
30-Jun-86	0	30	0	0.00	0	0.00	0	0.00
30-Jun-86	30	100	0	0.00	0	0.00	0	0.00
30-Jun-86	100	250	0	0.00	0	0.00	0	0.00
30-Jun-86	250	500	0	0.00	0	0.00	4	0.02
30-Jun-86	500	1000	0	0.00	0	0.00	0	0.00
30-Jun-86	0	30	0	0.00	0	0.00	0	0.00
30-Jun-86	30	100	0	0.00	0	0.00	0	0.00
30-Jun-86	100	250	0	0.00	0	0.00	0	0.00
30-Jun-86	250	500	0	0.00	0	0.00	4	0.01
30-Jun-86	500	1000	0	0.00	0	0.00	0	0.00
09-Feb-87	0	100	0	0.00	0	0.00	0	0.00
09-Feb-87	100	250	0	0.00	0	0.00	0	0.00
09-Feb-87	250	500	0	0.00	0	0.00	0	0.00
09-Feb-87	500	750	0	0.00	0	0.00	0	0.00
09-Feb-87	750	1000	0	0.00	0	0.00	0	0.00
09-Feb-87	1000	1200	0	0.00	0	0.00	0	0.00
09-Feb-87	0	100	0	0.00	40	0.02	0	0.00
09-Feb-87	100	250	0	0.00	4	0.00	0	0.00
09-Feb-87	250	500	0	0.00	8	0.01	0	0.00
09-Feb-87	500	750	0	0.00	0	0.00	0	0.00
09-Feb-87	750	900	0	0.00	0	0.00	0	0.00
16-Feb-87	0	1200	0	0.00	240	0.19	0	0.00
16-Feb-87	1200	2000	0	0.00	0	0.00	0	0.00
16-Feb-87	2000	2400	0	0.00	16	0.01	0	0.00
16-Feb-87	2400	2800	0	0.00	0	0.00	0	0.00

Appendix 8. (continued)

Date	Depth interval (m)		Limacina retroversa					
			.32 -.48 mm		.48 - 1.00mm		> 1.00 mm	
	Upper	Lower	N/m2	mgC/m2	N/m2	mgC/m2	N/m2	mgC/m2
30-Jul-87	0	30	720	0.07	0	0.00	120	0.35
30-Jul-87	30	100	0	0.00	0	0.00	0	0.00
30-Jul-87	100	250	0	0.00	0	0.00	0	0.00
30-Jul-87	250	500	0	0.00	0	0.00	0	0.00
30-Jul-87	500	1000	0	0.00	0	0.00	0	0.00
13-Aug-88	0	50	228120	39.32	5760	9.17	680	4.21
13-Aug-88	50	100	500	0.12	0	0.00	56	0.23
13-Aug-88	100	200	0	0.00	0	0.00	12	0.02
13-Aug-88	200	300	0	0.00	0	0.00	0	0.00
13-Aug-88	300	500	0	0.00	0	0.00	0	0.00
13-Aug-88	400	600	0	0.00	0	0.00	0	0.00
13-Aug-88	600	800	0	0.00	0	0.00	0	0.00
13-Aug-88	800	1000	0	0.00	0	0.00	0	0.00
13-Aug-88	1000	1200	0	0.00	0	0.00	0	0.00
20-Aug-88	0	25	40	0.01	0	0.00	4	0.01
20-Aug-88	25	50	102480	26.08	5280	8.41	1280	5.98
20-Aug-88	50	100	468	0.03	452	0.72	16	0.06
20-Aug-88	100	150	1320	0.37	0	0.00	68	0.32
20-Aug-88	0	25	336	0.05	20	0.03	0	0.00
20-Aug-88	25	50	180160	39.53	11000	17.52	2120	12.35
20-Aug-88	50	100	5072	1.16	336	0.54	480	3.97
20-Aug-88	100	150	1012	0.15	108	0.17	200	1.53
21-Aug-88	0	25	324360	99.80	12640	20.13	1640	6.38
21-Aug-88	25	50	2104	0.58	68	0.11	280	2.44
21-Aug-88	50	100	4672	1.35	444	0.71	56	0.20
21-Aug-88	100	150	452	0.12	60	0.10	12	0.17
21-Aug-88	150	200	264	0.11	32	0.05	0	0.00
21-Aug-88	200	250	228	0.05	12	0.02	0	0.00
21-Aug-88	250	300	652	0.20	64	0.10	4	0.01
21-Aug-88	300	400	916	0.25	32	0.05	4	0.01
21-Aug-88	400	500	0	0.00	0	0.00	0	0.00
21-Aug-88	500	700	40	0.02	0	0.00	0	0.00
21-Aug-88	700	900	0	0.00	0	0.00	0	0.00
21-Aug-88	900	1100	160	0.07	0	0.00	0	0.00
21-Aug-88	1100	1300	0	0.00	0	0.00	0	0.00
21-Aug-88	0	25	149520	42.78	416	0.66	352	2.12
21-Aug-88	25	50	16960	3.97	148	0.24	692	5.95
21-Aug-88	50	100	1092	0.29	72	0.12	172	2.25
21-Aug-88	100	150	512	0.08	0	0.00	0	0.00
21-Aug-88	150	200	328	0.08	16	0.02	4	0.01
21-Aug-88	200	250	692	0.09	0	0.00	0	0.00
21-Aug-88	250	300	552	0.12	0	0.00	4	0.01
21-Aug-88	300	400	408	1.06	0	0.00	0	0.00
21-Aug-88	400	600	0	0.00	0	0.00	0	0.00
21-Aug-88	600	800	160	0.03	0	0.00	0	0.00
21-Aug-88	800	976	120	0.01	0	0.00	0	0.00
21-Aug-88	976	1200	0	0.00	0	0.00	0	0.00
23-Aug-88	0	25	99280	27.97	9520	15.16	400	2.43
23-Aug-88	25	50	6980	2.91	1220	1.94	2220	30.32
23-Aug-88	50	100	868	0.31	112	0.18	252	2.44
23-Aug-88	100	150	384	0.12	16	0.03	0	0.00
30-Aug-88	0	50	77080	31.35	19240	30.64	7160	34.87
30-Aug-88	50	100	156	0.06	132	0.21	20	0.11
30-Aug-88	100	250	504	0.19	212	0.34	52	0.27
30-Aug-88	250	500	80	0.03	0	0.00	40	0.23
30-Aug-88	500	1200	0	0.00	0	0.00	0	0.00
31-Aug-88	0	50	11420	4.82	11640	18.54	1560	6.92
31-Aug-88	50	100	96	0.03	76	0.12	68	0.50
31-Aug-88	100	150	172	0.07	264	0.42	40	0.18
31-Aug-88	150	200	44	0.02	72	0.12	12	0.04
31-Aug-88	200	250	60	0.02	90	0.14	0	0.00
01-Nov-87	0	30	0	0.00	140	0.09	12	0.03
01-Nov-87	30	100	0	0.00	0	0.00	0	0.00
01-Nov-87	100	250	0	0.00	0	0.00	32	0.06