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Rearing cohorts of *Calanus finmarchicus* (Gunnerus) in mesocosms

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Cohort development and nutritional conditions of *Calanus finmarchicus* were studied in experimental seawater mesocosms in a Norwegian fjord. Artificially added cohorts developed from early naupliar stages to copepodite stage IV in 41–43 days at ambient temperature increasing from 4.3 to 6.8°C. A natural stock of *C. finmarchicus*, initially dominated by early copepodite stages, developed to CV, males and females. Total storage lipid increased exponentially until CV. Individual body carbon weight increased sigmoidally with age. Relationship of body carbon weight (W, µg) to prosome length (L, µm) determined for copepodites and adults ($W = 2.6 \times 10^{-10} L^{3.45}$, $r^2 = 0.92$) showed a higher weight than from *in situ* studies. This investigation demonstrates (i) that cohorts of *C. finmarchicus* can be reared successfully in mesocosms, (ii) a good nutritional state of copepods in terms of body carbon content and lipid reserves, and (iii) that part of the final CV moulted to both males and females.

Key words: body carbon, *Calanus finmarchicus*, cohort, development, lipid.

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Introduction

Precise measurement of the abundance, biomass, and developmental stage composition of copepod populations at frequent intervals permits estimates of growth rates as inputs to understanding population dynamics. It is obviously difficult to carry out effective time-series analyses on natural populations of copepods in the ocean. Estimates by *in situ* sampling are biased directly by advection (Kiørboe, 1993), indirectly by the phenotypic variability within a population (Båmstedt, 1988) and the patchy distribution of individuals in the water column, either horizontally or vertically (Conover, 1988; Backhaus *et al.*, 1994; Falkenhaug *et al.*, 1997). In addition to these obstacles, direct assessment of *in situ* growth and development rates of marine copepod populations is labour-intensive. Hence, knowledge of the development times of the different juvenile stages of the genus *Calanus* stems primarily from laboratory rearing experiments (Mullin and Brooks, 1970; Paffenhöfer, 1970; Fernández, 1979; Vidal, 1980a, b; Landry, 1983; Corkett *et al.*, 1986; Peterson, 1986; Tande, 1988; Pedersen and Tande, 1992) or laboratory data in combination with *in situ* sampling data (e.g. McLaren *et al.*, 1989) or shipboard incubations (Diel and Klein Breteler, 1986). However, laboratory-based determinations of growth and development rates may not necessarily serve as reliable predictors during natural conditions where, for example, the size spectra and nutritional adequacy of the diet will be more complex.

Life history studies of copepods in mesocosms may alleviate some of the disadvantages of laboratory experiments because of more realistic simulation of natural conditions of temperature, light, and food. In addition, the advective effect is eliminated. These advantages might provide better time-series data. Copepods can be stocked at natural densities, probably providing a more accurate *in situ* description of population growth and

individual behavioural response than in comparable experiments conducted in small laboratory containers. Furthermore, when newly hatched eggs are put into mesocosms, the feeding history effects on further population development can be observed (Huntley, 1988; Harris, 1996). However, there are also shortcomings of mesocosm studies, e.g. true replication cannot be achieved in detailed analyses of phytoplankton and zooplankton population samples, and the spatial and temporal heterogeneity in the enclosed water column will often affect sampling (Gamble, 1990), even if this heterogeneity is reduced compared with oceanic situations.

Here we present results from the first mesocosm rearing study of *Calanus finmarchicus* within the framework of the Trans-Atlantic Study of *Calanus finmarchicus* project. The experiment was carried out in large enclosures that allowed frequent zooplankton sampling over a period of six weeks. The copepod diet was a natural phytoplankton and protist community maintained by additions of inorganic nutrients. We report several life-history parameters for *C. finmarchicus*, including stage development time, length–weight relationship, copepod nutritional condition in terms of body carbon weight and total storage lipid content, and aspects of the feeding biology of *Calanus*.

Materials and methods

A mesocosm experiment was carried out at the Marine Biological Field Station, Espegrend, University of Bergen, Norway, from 9 March to 9 May 1996. The experiment included two mesocosms constructed of polyethylene (90% penetration for PAR), with a volume enclosed of approximately 18.5 m^3 (diameter 2 m, depth 7 m; Figure 1). The mesocosms were installed at a raft with a small floating laboratory in an inlet of the Raunefjord (60°17′N 05°10′E). They were filled on 9 March, two weeks before the cohorts were added. During the filling of the mesocosms, a natural stock of mesozooplankton, mostly dominated by late nauplii and copepodites of *C. finmarchicus*, entered. Owing to a development stage difference between the natural *Calanus* stock in the fjord, the development and growth of the artificially added cohorts of *C. finmarchicus* could be distinguished and followed easily. The development stages of *C. finmarchicus* were distinguished on the basis of their dimensions, as documented by Ogilvie (1953), Marshal and Orr (1972), and Unstad and Tande (1991). Euphausids were never observed, and medusae, ctenophores, and chaetognaths were only sometimes caught during the routine plankton sampling, suggesting a generally low abundance of potential predators in the mesocosms. An airlift system kept the water mass inside the mesocosms in circulation. In order to maintain phytoplankton production, nitrate, silicate, and phosphate were added directly at regular intervals.

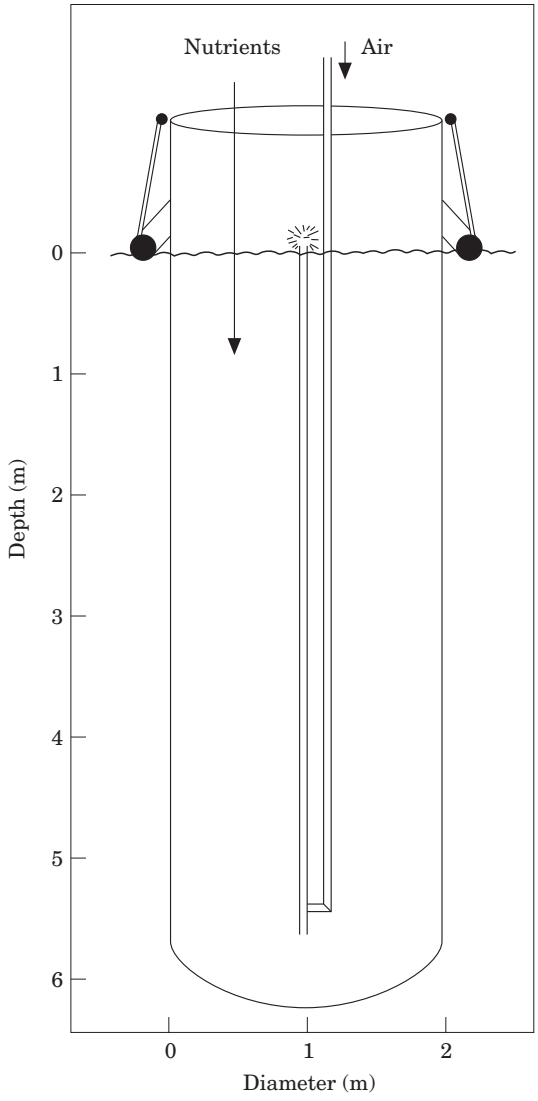

Figure 1. Schematic presentation of the mesocosm set-up with airlift.

Collecting females and eggs

Females were collected in Raunefjord using a plankton net of 90 cm diameter, 500-µm mesh size, and an Isaacs-Kidd pelagic fish larva trawl of 1 m^2 opening and 600-µm mesh, both fitted with a non-filtering 15-l plastic codend. Hauls covered the depth strata 0–120 m. The net was retrieved at low speed and the contents of the codend were gently emptied into a darkened container with 30 l of surface water. Sampling was usually initiated in the morning and again in the afternoon, but the

abundance of females in the fjord was low. Therefore, sampling went on for several days to capture sufficient females. The copepods were transported to the laboratory within 2–3 h of capture and brought to a walk-in cold room at 4–5°C. The total >500-µm contents of the codend were diluted with seawater in 90-l containers, excluding any settled material.

The animals were fed cultures of a mixture of three diatom species (*Thalassiosira anguste-lineata*, *Skeletonema costatum*, and *Chaetoceros calcitrans* f. *pumilus*) at excess food concentration. Every day, the eggs produced were sampled and suspended in 5-l glass beakers with gentle aeration. Numbers of nauplii were recorded daily, allowing an estimate of total numbers and developmental stage composition. Because of relatively low daily egg production, the cohorts were initiated at different times in mesocosms A and B. Approximately 25 000 nauplii, representing the age composition 3–10 d, were added into mesocosm A on 25 March. Mesocosm B received 5000 nauplii (5–9 d) on 2 April, 13 000 nauplii (3–5 d) on 4 April and 6000 nauplii (2–7 d) on 7 April.

Plant pigment, particulate material, nanoplankton, and microplankton

Water was sampled every second day, starting on 23 March. Temperature and salinity were taken with a YSI Model 33 (Yellow Springs Instruments). Samples from the mesocosms representing 0, 1, 2, 3, 4, and 5 m depths were taken with a 3-l heart-valve water sampler, and all water samples were pooled in a container prior to subsampling. Samples of 1–2 l for determination of particulate organic carbon and nitrogen (POC and PON) were filtered through a precombusted Whatman GF/C (47 mm) filter. The filters were immediately frozen and later analysed in an Eager 2000 (CE instruments) analyser. Samples of 1–2 l for determination of total plant pigment were spectrophotometrically determined in ethanol extract on a Novaspec II Spectrophotometer, following the method of Jespersen and Christoffersen (1987). To analyse the quantitative aspects of food particle size in the mesocosms, total plant pigment of <10 µm particles was measured. This was done by gentle inverted filtration through a 10-µm Nitex screen.

Enumeration and identification of diatoms, dinoflagellates, and ciliates from mesocosm A were done by the Utermöhl (1931) technique on 2% acid Lugol preserved samples. Cell volume was calculated using simple geometric formulae and carbon was calculated by multiplying cell volume by a conversion factor of 0.13 pgC μm^{-3} for thecate dinoflagellates (Smetacek, 1975) and 0.11 pgC μm^{-3} for diatoms (Strathmann, 1967), athecate dinoflagellates, and ciliates (Smetacek, 1975). Estimates of diatom cell volume followed the method described by Strathmann (1967), using a constant thickness of 1 µm of plasma, and 90% of the vacuole volume was subtracted from the plasma volume.

Copepod stage, size, and biochemical composition

Throughout the experiment, the cohort was sampled every fourth day with a plankton net of 100-µm mesh (mouth diameter 25 cm, filtering cone 50 cm long). The net was hauled vertically from 5 m up the centre of the mesocosm by hand. Assuming 100% filtration efficiency, a net sample represented 226 l of water. The contents of the codend were preserved in 5% buffered formalin. Nauplii and copepodites were staged and counted, and total body length and carapace length of nauplii (n=40) and prosome length of copepodites (n=40) were measured using a stereomicroscope. Copepods were separated into two groups: animals belonging to the artificially added cohort, and animals originating from the natural stock. The different cohorts were generally not difficult to distinguish visually. However, at the end of the experimental period, late copepodite stages dominated both the natural stock and the artificial cohort, so separation of the two cohorts was not possible.

Individual copepods for carbon analysis were sorted from freshly collected material with a fine-pointed forceps, rinsed in 0.2 µm filtered seawater, placed in precombusted aluminium boats, dried at 60°C overnight, and stored at −18°C for later measurement. Individual measurements were made on stages CIII–CVI. Measurements on stages CI–CII were made on 2–3 individuals and those on nauplius stages NIV–NVI on 5–10 individuals, from which a mean carbon value for the group was calculated. Carbon content was determined with a IRGA infra-red gas analyser ADC 225 MK3.

Individual copepods for lipid analysis were placed in glass vials containing chloroform:methanol (2:1 v/v), purged with nitrogen gas and stored in liquid nitrogen. Hexadecane-3-one (ketone) was used as internal standard, and lipids were analysed by Thin Layer Chromatography/Flame Ionization Detection (TLC-FID) using an IatroscanTM MK-5. The extraction procedure and analysis were performed following standard procedures (Jónasdóttir, 1999). A standard of native wax esters extracted from *C. finmarchicus* stage V was used to calibrate the TLC-FID. Other standards for calibration were tristearine (triacylglycerol), palmitine acid (free fatty acid), cholesterol (sterol), and methyl manganate (phospholipid). Measurements on stage CI were made on 40 animals, CII–CIV on 5–20 and CV–CVI on 2–5 animals, from which a mean lipid value for the group was calculated. Wax esters (WE) and triacylglycerols (TAG) dominated the store lipid of *C. finmarchicus*.

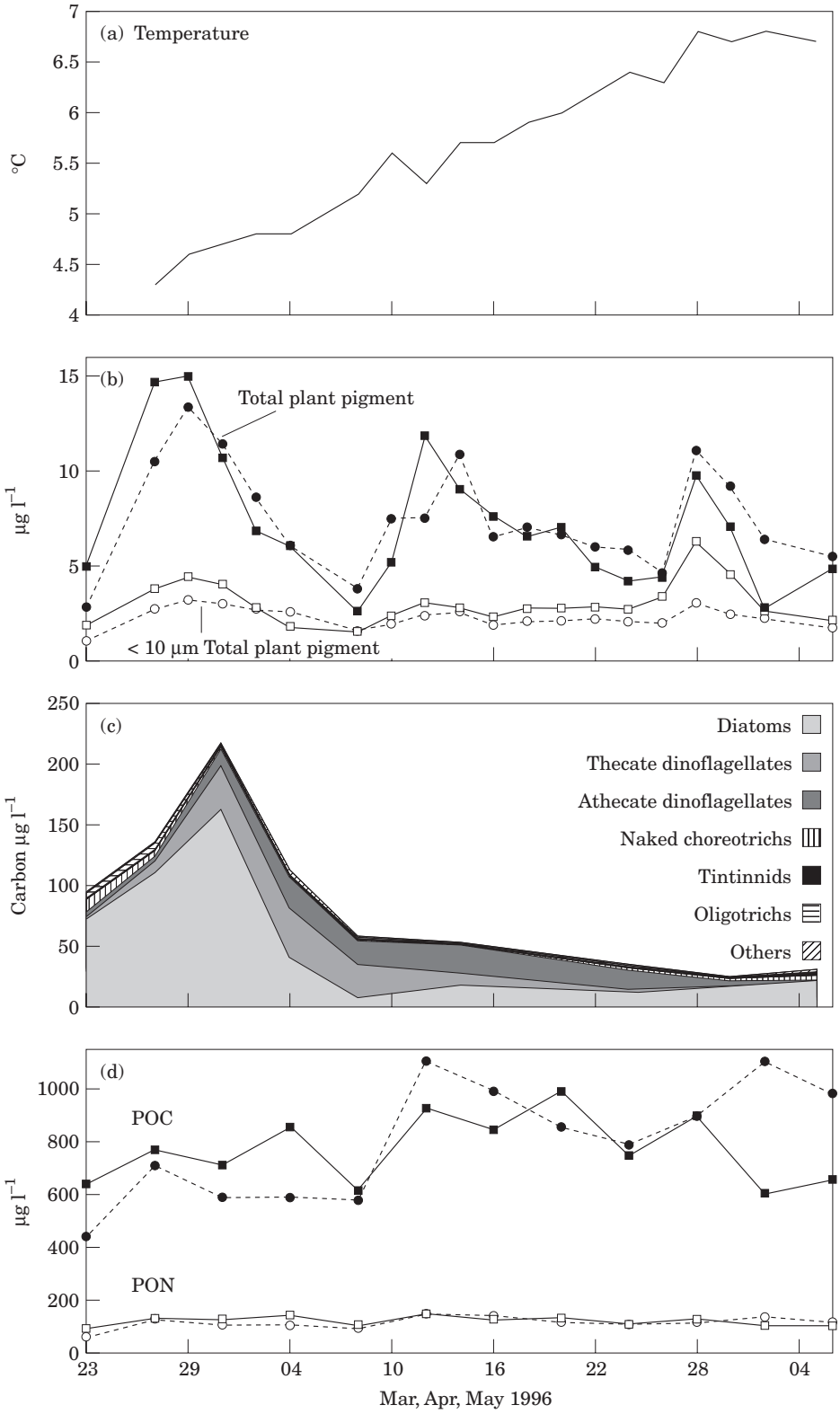

Figure 2. Development in mesocosm A (squares) and B (circles) between 23 March and 5 May 1996: (a) temperature, (b) total plant pigment and total plant pigments in <10-µm particles, (c) diatom, dinoflagellate, and ciliate biomass in mesocosm A, (d) POC and PON.

Table 1. Estimates of median development time of stage (days) for *Calanus finmarchicus* raised in mesocosms A and B at ambient temperature.

Mesocosm	Egg–NII	NIII	NIV	NV	NVI	CI	CII	CIII	CIV	Egg–NVI	Eggs–CIV	CI–CIV
A	6.3	7.0	2.2	4.2	3.1	3.8	3.9	5.1	7.5	22.8	43.1	20.3
B	9.3	4.8	3.2	2.3	2.6	3.6	3.6	4.4	7.3	22.2	41.1	18.9

Time zero = time when 50% of the eggs hatched.

Treatment of data

Stage durations were estimated on cumulative frequencies of individuals from the added cohort using the method of median development time of untransformed data described by Landry (1983) and Peterson and Painting (1990), defined as the time when 50% of the population had moulted to a specific stage. The initial time t_0 was defined as the mean time of egg collection:

$$t_0 = \Sigma N_i \times t_i / (\Sigma N_i) n$$

where N_i is the egg number released on day i, t_i is the time of day i, and n is the total number of days where eggs were collected.

Results

The temperature increased from 4.3 to 6.8°C during the experiments [Figure 2(a)]. The initial concentration of total plant pigment was 3–5 μg l^{-1} in the mesocosms. Three peaks were observed in response to nutrient additions [Figure 2(b)], the first on 29 March with a total plant pigment concentration of 13–15 μg l^{-1}, the second and third on 12 and 28 April, with maxima of 10–12 μg l^{-1}. Initially, the major proportion of the plant pigment was >10 μm, but from 22 April to 2 May the <10 μm fraction dominated in mesocosm A [Figure 2(b)], while in mesocosm B, the <10 μm proportion was between 25% and 40% of the total plant pigment concentration.

The microplankton assemblages differed in several respects during the experimental period. Diatoms dominated only during the first bloom, principally by *Skeletonema* sp. [Figure 2(c)]. Microscopic observations showed that the non-quantified haptophyte, *Phaeocystis* sp., was very abundant during the second and third blooms, both as spherical colonies (observed under dissecting microscope on non-preserved samples) and as flagellate unicells in preserved samples. Ciliates constituted 72% of the protist carbon biomass during the first bloom, but declined rapidly during the second and third blooms [Figure 2(c)]. Thecate dinoflagellates (dominant species *Protoperidinium bipes*) declined from 36.6 μgC l^{-1} on 31 March to <2 μgC l^{-1} during the third bloom. The biomass of athecate dinoflagellates (dominant taxa *Gyrodinium* spp., *Amphidinium* spp. and *Gymnodinium* spp.) peaked during the second bloom at 22.7 μgC l^{-1} and declined to 0.45 μgC l^{-1} on 5 May.

The POC in the mesocosms increased from an initial concentration of 450–650 μg l^{-1} to 750–1000 μg l^{-1} during April and May [Figure 2(d)]. PON was initially between 60 and 90 μg l^{-1}, but peaked during the second bloom with values of 120–140 μg l^{-1} [Figure 2(d)]. The C:N ratios were between 5.5 and 8.0, increasing throughout the period, suggesting an increase in the detritus pool. This is also supported by the C:total plant pigment ratio increasing from 50 during the first bloom to 150 at the end of the experimental period.

Nauplius stages I–II (75%) and III (25%) dominated the developmental stage composition of the cohort in mesocosm A on 25 March. Late nauplii and early copepodites (Figure 3) dominated the natural standing stock. In mesocosm B, nauplius stages I–II and III were equally represented on the first sampling day, 7 April. The natural standing stock in mesocosm B was represented by early copepodites (Figure 3). At the end of the experimental period, the mesocosms were emptied. Total abundance of *C. finmarchicus* was estimated to be approximately 2.3 individuals l^{-1} in mesocosm A and 1.3 individuals l^{-1} in B. Initially 1.4 nauplii l^{-1} were added to mesocosm A and 1.3 nauplii l^{-1} to B, so suggesting that the natural standing stock of *C. finmarchicus* that entered the mesosocosms during the filling was <1 individuals l^{-1}.

Development time from egg to NVI was almost equal for mesocosm A and B, with small estimated differences between instar durations (Table 1). Naupliar stage III exhibited the longest duration. Copepodite stage duration increased at each successive stage and the development time from CI to CIV was 19–20 days (Table 1).

Carapace length of naupliar stages and prosome length of copepodite stages (Table 2) were occasionally significantly different between the mesocosms. In stages CIII–CV and females, prosome length was significantly longer in mesocosm B than in mesocosm A (Table 2). A length–weight relationship based on mean length and carbon content from CI through CVI for both mesocosms was: $W = 2.6 \times 10^{-10} L^{3.45}$ ($R^2 = 0.92$), where weight (W) was in μg carbon and prosome length (L) in micrometres (Figure 4).

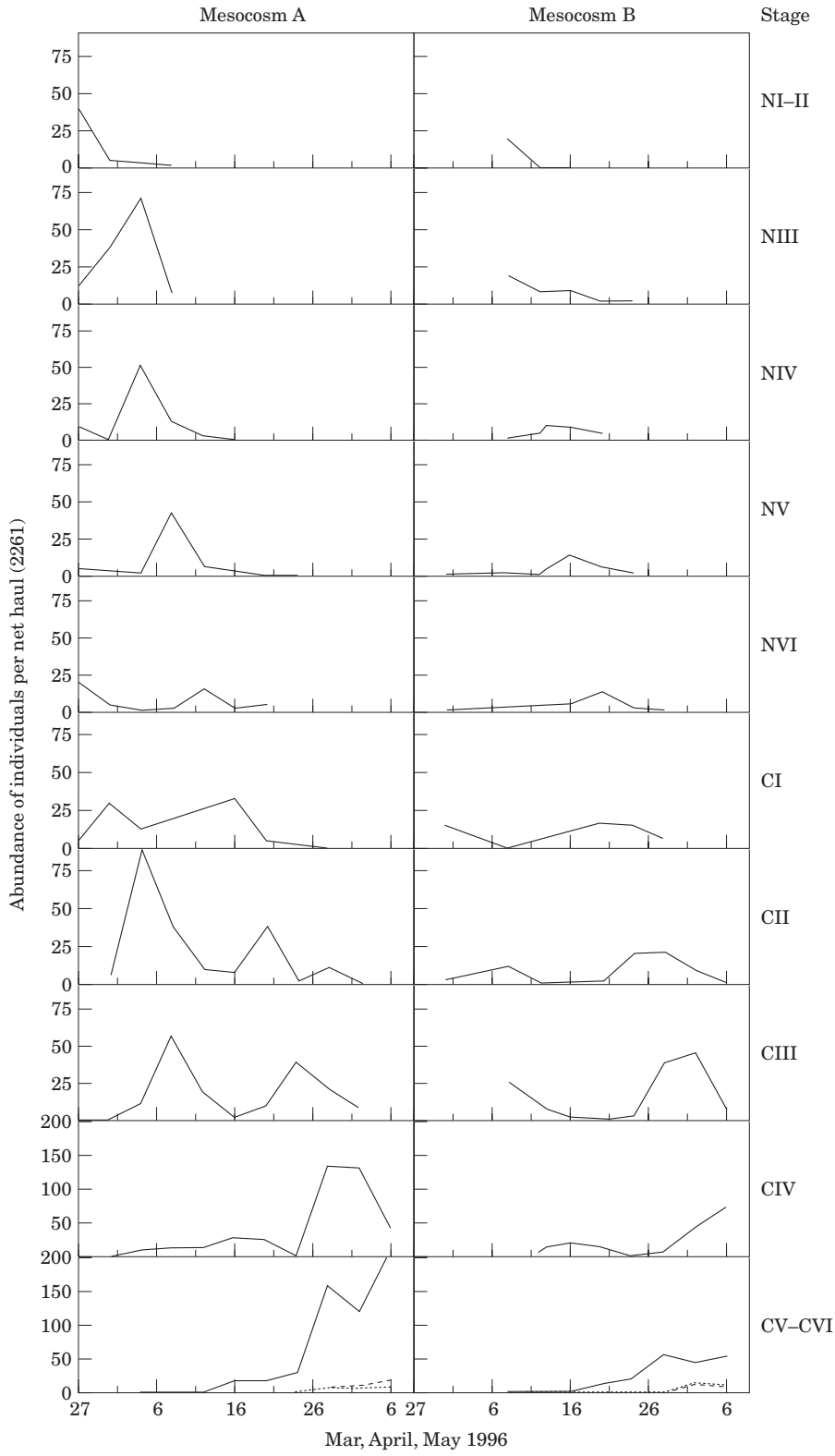

Figure 3. Abundance distributions per net tow (individuals per 226 l) of developmental stages of *Calanus finmarchicus* in mesocosms A and B. In the lower panel (CV–CVI), the dotted line represents males and the dashed line females.

Table 2. Carapace and total length (μm) of nauplii and prosome length (μm) of copepodite stages of *Calanus finmarchicus* measured in mesocosms A and B. Means ± standard deviations are given (n=40).

Parameter	NI+II	NIII	NIV	NV	NVI	CI	CII	CIII	CIV	CV	Female	Male
Mesocosm A												
Carapace	188 ± 18	240 ± 18	289 ± 14	357 ± 14	413 ± 15							
Total length		345 ± 28	439 ± 33	585 ± 31	757 ± 34							
Prosome						830 ± 34	1183 ± 31	1523 ± 40*	1995 ± 81*	2556 ± 117*	2945 ± 125*	2762 ± 114
Mesocosm B												
Carapace	190 ± 32	241 ± 21	290 ± 14	355 ± 15	413 ± 21							
Total length		357 ± 36	463 ± 29	601 ± 30	784 ± 31							
Prosome						833 ± 34	1183 ± 50	1559 ± 69	2113 ± 84	2689 ± 71	3082 ± 115	2762 ± 114

*Significant difference between the means in A and B ($p<0.05$).

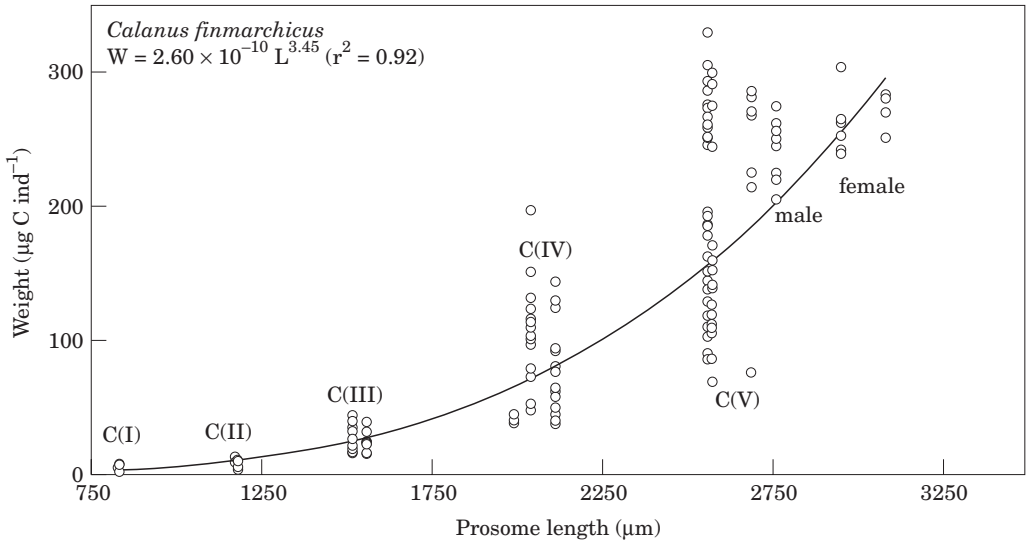

Figure 4. Length–weight relationships for *Calanus finmarchicus*. Average lengths are plotted against individual/group carbon weights.

Total storage lipid, wax ester (WE) and triacylglycerol (TAG) of copepodite stages showed exponential increase until stage CV (Figure 5). The lipid proportion in carbon equivalents (assuming that 80% of the lipids are carbon) constituted 2.2% of body carbon in stage CI and up to 17–28% in stage V and adults (Figure 5). The WE proportion was in the range 86–95% of the total storage lipid in copepodites and adults. Adults, especially males, were lower in both carbon and total storage lipid than late stage V. Late copepodites and adults taken from mesocosm B tended to have higher average carbon-weight and storage lipid content than those taken from mesocosm A, but the differences were not significant (Mann-Whitney, $p>0.05$).

During the growth of naupliar stages, the phytoplankton composition was dominated by diatoms (*Skeletonema* sp., *Nitzschia longissima*, *Thalassiosira* sp., and *Chaetoceros* cf. *decipiens*) and the protist biomass was dominated by ciliates and dinoflagellates. The ciliate biomass declined rapidly between the first and second blooms and remained relatively low (2.2–5.3 µgC l^{-1}) throughout the experimental period. During the growth of the copepodite stages (from 10 April), the diatom biomass was low (13–18 µgC l^{-1}), but the total plant pigment concentration was relatively high (5–11 µg l^{-1}). Also, thecate and athecate dinoflagellates declined from a biomass of 33.8 µgC l^{-1} in mid-April to 1.7 µgC l^{-1} at the end of the experimental period. However, the prymnesiophyte *Phaeocystis* sp. was observed as large spherical colonies in the mesocosms, indicating that *Phaeocystis* could explain the high plant pigment levels from mid-April until end of the experimental period.

Discussion

This work is the first attempt to culture *Calanus finmarchicus* cohorts in large-scale mesocosms almost simulating *in situ* growth conditions. The main goal was to evaluate how a diet of natural phytoplankton and protists, at relatively high concentration, affected cohort development and the nutritional state of the copepods under ambient temperature and light conditions. The different stages of *Calanus* spp. were assigned to species using length dimensions. This procedure will not exclude potential sibling species of *C. finmarchicus*, especially *C. glacialis* and *C. helgolandicus*, but we rate this problem as minor because *C. finmarchicus* constitutes the major biomass of *Calanus* spp. in the fjords of western Norway (Matthews *et al.*, 1978; Aksnes and Magnesen, 1983; Hirche, 1983).

Estimates of the development time from egg to CIV for individuals from the *C. finmarchicus* cohort during increasing ambient temperature [4.3–6.8°C, Figure 2(a)] were 41–43 d (Table 1). The estimated development times were consistent with data from a laboratory-reared population of *C. finmarchicus* (Corkett *et al.*, 1986). Those authors found that, at 4–7°C, the development time from hatching to CIV took approximately 32–48 d for eggs from females captured on the Scotian Shelf. Eggs from females captured from coastal areas of northern Norway showed a mean nauplii developmental time of 27 d, reared at 5°C, and 17 d for stage CI to stage CIV, reared at 6°C (Tande, 1988). Our estimates of naupliar development time were slightly shorter, around 22–23 d (Table 1).

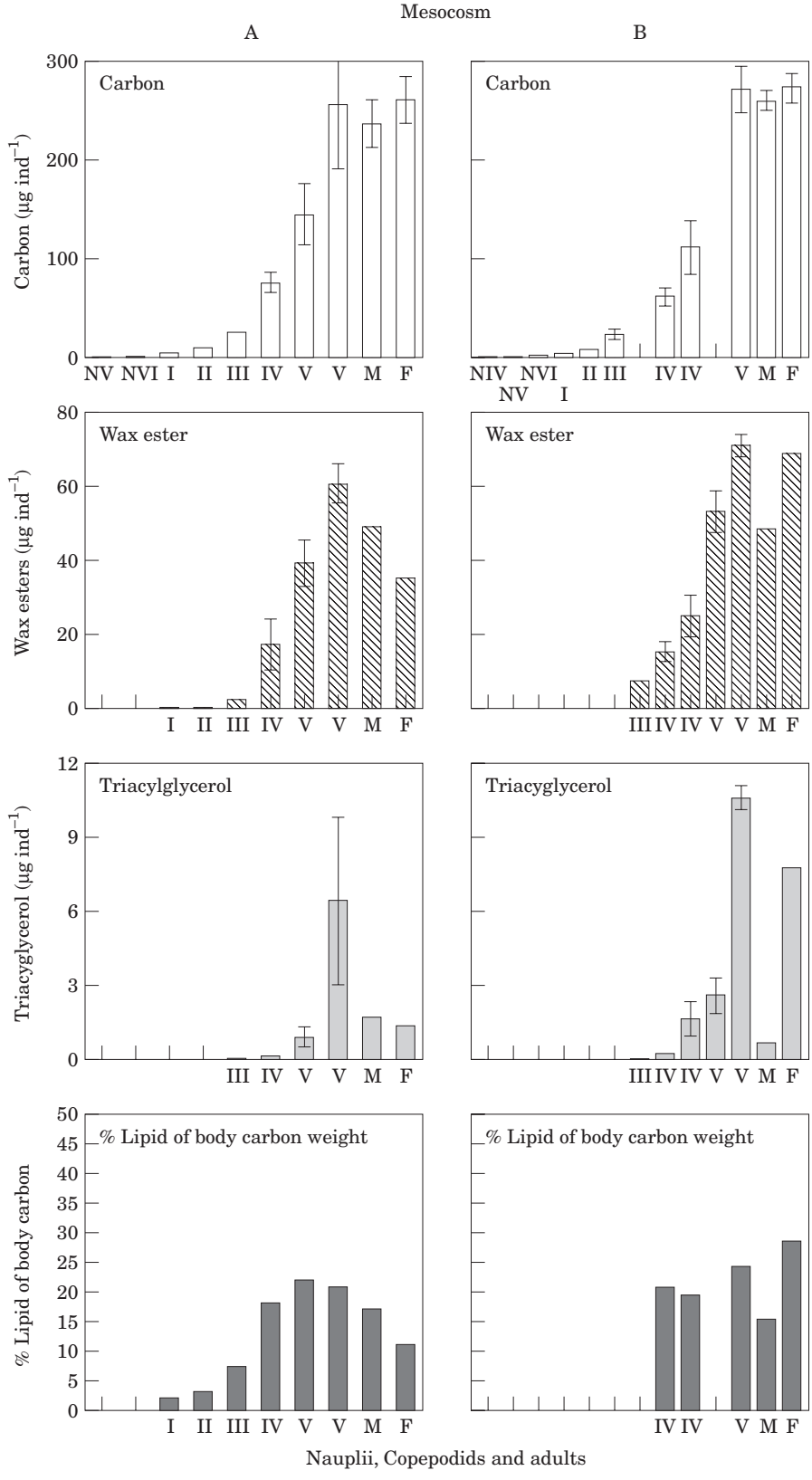

Figure 5. Mean carbon, wax ester, and triacylglycerol content in successive nauplii, copepodites, and adult stages of *Calanus finmarchicus* reared in mesocosms A and B. The carbon and total storage lipid of CIV and V represented two successive measurements, which resulted in large differences, owing to different phases of the intermoult period. Vertical lines are standard deviation.

Development of nauplii and copepodites had a characteristic pattern: the first-feeding instar, naupliar stage III, was relatively long, presumably because that stage needs time to recuperate weight lost during non-feeding instars (Marshall and Orr, 1972). Alternatively, and as pointed out by Landry (1983), NIII may be less efficient at gathering or handling food than subsequent stages. Copepodite stage duration increased with increasing stage and therefore with body size. Even though the experiments were terminated before the added cohorts reached the adult stage, the natural brood moulted to adults, and males were recruited to the adult population slightly before females (Figure 3). Some males from the freshly collected material were inactive, and a layer that had the appearance of mucus was present on the cephalosome (BHH, pers. obs.); this may indicate the onset of lysis of the body. A relatively short lifespan of *C. finmarchicus* males was suggested by Marshall and Orr (1972).

The length–weight relationships determined for copepodite stages of *C. finmarchicus* (Figure 4) were not consistent with other relationships for the species (Fransz and Van Arkel, 1980; Hirche and Mumm, 1992). Although there are great variations both in length and in dry weight of a given stage of *C. finmarchicus*, even at a single locality (see Comita *et al.*, 1966; Marshall and Orr, 1972; Båmstedt, 1988), the specific body weights of the copepods from the mesocosms were significantly higher than reported in the literature for comparable temperatures (see review by Carlotti *et al.*, 1993). However, the measured body content of carbon in stages CIV–CV, males and females, was comparable with results reported from Balsfjorden in northern Norway (Tande, 1982) and from Georges Bank (Miller *et al.*, 1998). In our study, the relatively high body carbon weight of the copepods suggests good food conditions. Factors contributing to the presence of large individuals may be (i) elimination of predation and (ii) as a result of minimal energetic cost related to diel vertical migration. Concerning (i), Ohman (1990) and Aksnes and Blindheim (1996) showed that some fish species prefer larger, more conspicuous zooplankton prey when available. Given that predation risk increases with size of the body and that predation pressure is high in a natural environment, then the size/weight distribution of surface-living populations would be biased in the direction of small animals. Off western Norway, Hirche (1983) found two *C. finmarchicus* populations in the Korsfjord, a surface population of small individuals and a deep population rich in fat and also larger than those of the surface population. Concerning (ii), vertical migration was prevented in the mesocosms because of the depth of the enclosure; therefore potential loss of the energetic cost of migration was minimized. Migration from surface water to deeper habitats reduces predation pressure (Ohman, 1990), but cooler habitats devoid of food are likely to cause a decrease in body weight and increase development time (Aksnes, 1996).

Total storage lipid (TAG+WE) in the successive copepodite stages consisted predominantly of WE with significant amounts of TAG in the late copepodite stages (Figure 5). WE proportions from stage CI to CIII were similar to values reported by Kattner and Krause (1987) for *C. finmarchicus* from different locations in the North Sea, but in late copepodite stages and in males and females the WE proportions in the present study were considerably higher.

The role of *Phaeocystis* in the diet of *Calanus* has received much attention. Some studies have demonstrated ingestion (Tande and Båmstedt, 1987; Hansen *et al.*, 1990), whereas others (Bautista *et al.*, 1992) have inferred that *Phaeocystis* was either not ingested by *Calanus* or ingested when the physiological conditions of the colonies allowed it (Estep *et al.*, 1990). In the present study, little is known about the quality of the detritus pool as a food source, and a shift toward protists and *Phaeocystis* is only a possibility. However, a dietary shift of *C. finmarchicus* from abundant, large diatoms to microzooplakton (Ohman and Runge, 1994) or *Phaeocystis* (Kattner and Krause, 1987) has been reported.

In conclusion, mesocosm rearing of *C. finmarchicus* seems to be a realistic intermediate between laboratory systems and open-sea situations. The study has revealed that *C. finmarchicus* can be reared from eggs to adults in mesocosms. The natural brood matured and eggs were produced (BHH, pers. obs.). The nutritional state of the copepods suggests that the mesocosm conditions under which the copepods were raised simulated good conditions for natural growth.

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