A high-frequency time series at Ocean Weather Ship Station M (Norwegian Sea): population dynamics of *Calanus finmarchicus*

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ABSTRACT: Between the end of March and mid-June 1997, net samples in the upper 100 m were taken almost daily on Weathership M (Norwegian Sea) to determine the abundance and stage composition of *Calanus finmarchicus*. Biomass showed high day-to-day variability with several peaks, ranging from 0.05 to 6.3 g C m^{-2}, with an average of 0.84 g C m^{-2}. Consequently, stage abundances were also highly variable, but stage composition was consistent. Although population egg production was almost constant throughout the study period, a clear cohort was formed. During the pre-bloom period, nauplii and Copepodite Stage I (CI) were frequently abundant, but further stage development proceeded only during the short bloom. At the end of the bloom, no young nauplii continued to grow, but older stages did. Some specimens had reached CV at the end of the investigation period. The extended seasonal presence of some stages made estimates of stage duration and production difficult. Three different numerical methods were applied to estimate productivity and production. All methods resulted in similar estimates of productivity, 0.031 to 0.055 d^{-1}, corresponding to a production of 30 to 56 mg C m^{-2} d^{-1}. These rates are considerably lower than optimum rates measured in the laboratory, suggesting strong food limitation of growth during most of the observation period.

KEY WORDS: Population dynamics · *Calanus finmarchicus* · Norwegian Sea · Food limitation

INTRODUCTION

The copepod *Calanus finmarchicus* is a key species in the pelagic system of the North Atlantic, coupling primary production and zooplanktivorous fish (Runge 1988). A strong interannual variability in its abundance has been described recently by Planque & Fromentin (1996), and Fromentin & Planque (1996) have demonstrated correspondences between its oceanic abundance and the North Atlantic Oscillation (NAO). The oceanic stocks are of vital importance for the shelf seas (Steele 1998). Thus, Marshall & Orr (1955) recognized the dependence of the abundance of *C. finmarchicus* in the North Sea on immigration from the North Atlantic. Similar immigration takes place on the Norwegian shelf (e.g. Slagstad & Tande 1996) and

Georges Bank (Miller et al. 1991), where *C. finmarchicus* supports local fish stocks.

Despite considerable efforts to understand the life cycle and production of this species, little is known about the population dynamics and the factors controlling it in the open ocean. This is, however, a prerequisite to understanding the effect of climatological changes on the production of this species and the system it inhabits. So far, time series of abundance data, with reasonable temporal resolution, from the open North Atlantic are only available from Ocean Weather Ship Stations 'Mike' (Østvedt 1955) and 'India' (Williams 1988, Irigoien 2000). In addition, the Continuous Plankton Recorder dataset has been analyzed for seasonal abundance (e.g. Colebrook 1982). Most studies have concentrated on fjords (Tande 1982, Aksnes & Magnesen 1983, Diel & Tande 1992), coastal areas and shallow seas (Fransz & van Arkel 1980, Williams & Lindley 1980, Fransz & Diel 1985, Diel & Klein Breteler

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1986, Durbin et al. 1995, Gaard 1996, Gislason & Astthorson 1996).

From these studies and laboratory observations a concept evolved describing *Calanus finmarchicus* as a conservative spawner, which spawns only after serving its basic metabolic needs (Runge 1985). The need for high food densities in order to start producing eggs (60 µg C l^{-1}) and to achieve maximum rates (200 to 300 µg C l^{-1}, Runge 1985) seemed to imply a close link between production of the spring generation and the spring bloom (Marshall & Orr 1955, Cushing 1959, Diel & Tande 1992, Plourde & Runge 1993). This view was supported by the high threshold concentration for ingestion that was measured by Gamble (1978) and Daro (1980) and was later applied in models (Carlotti & Radach 1996, Carlotti & Hirche 1997).

In contrast to this concept, the presence of spawning females and young stages of *Calanus finmarchicus* before the spring bloom indicated the onset of reproduction before the phytoplankton bloom (Østvedt 1955, Melle & Skjoldal 1987). The importance of pre-bloom spawning at Ocean Weather Ship Station 'Mike' (Station M) in the Norwegian Sea (66°N, 2°E) was recently reported by Niehoff et al. (1999). Although egg production was strongly food-limited, approximately half of the egg production of the population was deposited before the onset of the bloom at the beginning of May. The question arose whether the offspring were able to develop and whether growth, as well as egg production, was food-limited. Based on laboratory experiments with small calanoids (Uye 1982, Kiørbœ et al. 1985, Fryd et al. 1991), it has been suggested that somatic production of young stages would equal specific egg production of the female also in *C. finmarchicus* (Laabir et al. 1995, Hirche 1996). In this case, egg production could be used as a measure of secondary production.

This study describes the development of the spring generation of *Calanus finmarchicus* at Station M in relation to food concentration. The high sampling frequency allowed us to study the dynamic relationship between phytoplankton development and the production of *C. finmarchicus*. We applied and compared different methods to estimate production based on population structure and egg production. Recent information from laboratory rearings (Campbell et al. in press) and the equations from Huntley & Lopez (1992) have also been compared. Furthermore, we used the 1948/1949 dataset from the same location (Østvedt 1955) for interannual comparison.

MATERIALS AND METHODS

Sampling. The time series at Station M was obtained from 22 March to 9 June 1997. Details on the ship's drift and the hydrography, phytoplankton concentrations and reproductive biology at the site are published in Irigoien et al. (1998) and Niehoff et al. (1999). During the investigation period of 80 d, vertical hauls with a WP2 net (mesh size 50 µm) from the upper 100 m were taken at 0.3 m s^{-1} on 65 days at around 10:00 h. The hauls were fixed in 4% formalin buffered with hexamethylentetramin, for determination of abundance. A sampling efficiency of 100% was assumed as, due to the low phytoplankton concentrations, no clogging was expected or observed.

Counting and species identification. The 4 species *Calanus finmarchicus*, *C. helgolandicus*, *C. glacialis* and *C. hyperboreus* are all found at this site (A. Bucklin et al. unpubl.). During the present study, prosome length from the tip of the cephalosome to the distal lateral end of the last thoracic segment was measured from 50 CV and adult females per sample using a video image digitizing system with a resolution of 25 µm. According to body size and curvature of the fifth swimming leg there were no *C. helgolandicus* or *C. glacialis* of these stages in the samples. Therefore no nauplii or young copepodites of these species were expected either. The co-occurring *C. hyperboreus* are easily distinguished by their much larger size (Hirche et al. 1994). Eggs were identified by their size. Nauplii were sorted according to size and morphological characteristics; for separation from *Pseudocalanus* spp. and *C. hyperboreus* the characters described by Østvedt (1955) were used. NI and NII and NIV to NVI were pooled. All adults and CV were counted; for the younger stages the sample was split down to 1/128 if necessary. At least 100 specimens of each stage were counted when possible.

Dry weight and carbon content. For the analysis of dry weight, every week, groups of 10 adult females and 10 CV, respectively, were sorted alive on preweighed aluminum dishes from WP2 samples, rinsed briefly in distilled water and frozen (–25°C). Later they were dried at 60°C for 48 h and measured on a Sartorius microbalance. For conversion to carbon content a factor of 0.5 was applied to measurements of dry weight.

Productivity calculation. Somatic production and productivity were estimated by 3 different methods: (1) the increment summation method, (2) a mortality model, and (3) from egg production rates.

Increment summation method: Somatic production and productivity were computed with 2 different approaches according to Rigler & Downing (1984) and Crisp (1984). Method 1 computes production from stage to stage, either by (Method 1A) daily increment in biomass:

$$P_{i,i+1} = (M_{i+1} - M_i) \times (X_i/D_i + X_{i+1}/D_{i+1})/2$$

Table 1. Production calculation by increment summation. Method 1A: increment in biomass. Method 1B: loss of biomass. Method 2: production within stage 1. Minimum and maximum body mass computed by: $M_{2,min} = (M_1 + M_2)/2$; $M_{2,max} = M_{3,min}$

Stage	Mean abundance X (m^{-2})	Duration D (days)	X / D	Body mass (µg C)			Production (mg C m^{-2} d^{-1})		
				Mean	Minimum	Maximum	Method 1A	Method 1B	Method 2
Eggs	47 744	2[a]	23 872	0.23	0.00	0.23			(5.49)
NI/NII	3 806	5[a]	761	0.19[b]	0.19[b]	0.25	−0.49	4.85	0.04
NIII	10 753	13	827	0.30	0.25	0.50	0.09	−0.02	0.21
NIV/NVI	15 585	9	1 732	0.70	0.50	1.55	0.51	−0.45	1.82
CI	7 170	6	1 195	2.40	1.55	4.00	2.49	0.83	2.93
CII	6 241	7	892	5.60	4.00	8.45	3.34	1.21	3.97
CIII	6 645	9	738	11.30	8.45	20.15	4.65	1.29	8.64
CIV	6 627	12	552	29.00	20.15	55.00	11.42	3.75	22.01
CV	2 939	12[a]	245	91.00[c]	60.00	101.90	24.71	18.44	10.26
Adults	3 632	24[a]	151	112.80[c]	101.90	144.25[c]	4.32	9.54	6.14
				Residual biomass[d]			−	17.07	−
				$\sum$ production			51.03	56.52	56.28
				Mean biomass			1022.42	1022.42	1022.42
				P/B ratio (d^{-1})			0.050	0.055	0.055

[a]Taken from literature; [b]Mean body mass of NI/NII; [c]Measured during the present study; [d]Biomass of remaining adults

or by (Method 1B) daily loss of biomass:

$$P_{i,i+1} = (X_i/D_i - X_{i+1}/D_{i+1}) \times (M_i + M_{i+1})/2$$

If the population is in a steady state, both approaches will result in the same population production figure.

Method 2 computes daily production P within each stage:

$$P_i = (M_{i,max} - M_{i,min}) X_i/D_i$$

where X_i, M_i, $M_{i,max}$ and $M_{i,min}$ are average abundance, mean, maximum and minimum body mass in Stage i, respectively, and D_i is the duration of the stage in days. Stage duration was inferred from the development of stages over the sampling period (NIII, NIV/NVI, CI to CIV) using data from the literature or the steepest-increase method (Table 1): (1) The 3 d moving average (MA3) of the abundance of each stage was computed. (2) All MA3s were converted into a percentage of the sum of all stages at the corresponding day, and a 3 d weighed average (WA3) was computed for each stage. (3) The steepest increase in the WA3 of a particular stage was defined as the start of this stage's lifespan and as the end of the previous stage's lifespan.

For comparison purposes, stage duration was also calculated using the median development time method (Landry 1983). Abundances were smoothed with a 4-point running mean filter, and proportions of individuals who had completed a given molt were calculated (see Fig. 4a). A linear regression was fit only to the linear portions of these curves (Fig. 4b). Stage duration was then depicted as the distance between successive stages at 50% frequency.

Mean biomass per day was computed from average abundance and mean body mass per stage during the investigation period. Body mass for the developmental stages was taken from the literature (Table 2) or from dry weight measurements converted to carbon (Table 3).

Mortality model: Mortality rate Z was estimated by the single negative exponential mortality model,

$$N_t = N_o e^{-Zt} <=> \ln(N_t) = \ln(N_o) - Z t$$

where N is abundance and t is age, i.e. by a linear regression of the ln-transformed abundance data

Table 2. Carbon content (µg) of developmental stages of *Calanus finmarchicus* used in calculations of biomass and production. N: nauplius; C: copepodite; AF: adult females; AM: adult males

Eggs	0.23	Ohman & Runge (1994)
NI/NNII	0.19	Estimated
NIII	0.30[b]	Carlotti et al. (1993)
NIV/NVI	0.70[b]	Carlotti et al. (1993)
CI	2.4	Hirche (unpubl.)
CII	5.6	Hirche (unpubl.)
CIII	11.3	Hirche (unpubl.)
CIV	29	Hirche (unpubl.)
CV	65–137[a]	Present study
AF	92–130[a]	Present study
AM	90–153[a]	Present study

[a]Calculated from data presented in Table 3, assuming C = 50% dry weight
[b]Mean of all available data in Carlotti et al. (1993, their Fig. 1), assuming C = 50% dry weight

(X_i/D_i) versus the cumulative stage duration (D_i). In steady state populations, mortality rate Z approximates the production-to-biomass ratio (Allen 1971, Brey 1999) and hence is an additional proxy for somatic productivity.

Egg production rates: Specific egg production rate (SEPR) has been suggested as a measure of population growth for *Calanus* spp. (Laabir et al. 1995, Hirche 1996), assuming the SEPR to be equivalent to somatic growth. Daily SEPR was calculated using mean daily egg production at Station M from Niehoff et al. (1999), an egg weight of 0.23 µg C (Ohman & Runge 1994) and female carbon content converted from weekly dry weight measurements (Table 3). Daily secondary production of the population was computed by multiplying daily SEPR with population biomass.

Other growth rates: For comparison, growth rate was calculated according to Huntley & Lopez (1992) from the relationship:

$$g = 0.0445 \, e^{0.111T}$$

where T is temperature. Growth rate was also calculated by Campbell et al. (in press) for developmental times obtained under optimum food conditions. Developmental time (D) from egg to CVI was calculated from their Belehradek equation:

$$D = a \, (T + 9.11)^{-2.05}$$

Growth rate was then calculated from D using the equation from Huntley & Lopez (1992):

$$g = 0.025 + (4.327/D)$$

RESULTS

Hydrography and phytoplankton

Environmental conditions are only briefly described here; details are presented in Irigoien et al. (1998) and Meyer-Harms et al. (1999). Station M is situated on the slope of the Norwegian Shelf in the North Atlantic Current. In the study area, the surface water is of Atlantic origin (Hopkins 1991). According to temperature and salinity measurements (Irigoien et al. 1998), the Atlantic layer mostly extends to 300–400 m depth and does not rise above 150 m depth. Samples for the present study were therefore taken in Atlantic water throughout the investigation period. Intermediate water of Atlantic and Polar origin (temperature <3°C, salinity <35 psu) underlies the Atlantic water in depths between 150 and 700 m; the deep water in this region is formed by Polar water (see Hopkins 1991).

Three periods of phytoplankton development were distinguished at Station M (Irigoien et al. 1998, Niehoff

Table 3. Dry weights (µg) of CV, adult females (AF), and males (AM) of *Calanus finmarchicus* from Weathership M. Averages of 2 parallel samples

Date	CV	AF	AM
23 Mar	No data	235	–
30 Mar	180	210	305
6 Apr	185	275	245
13 Apr	175	210	220
24 Apr	130	185	180
1 May	130	200	265
8 May	145	190	230
12 May	165	215	210
17 May	215	235	185
27 May	275	260	–
2 Jun	200	235	–
8 Jun	205	220	–

et al. 1999). During the pre-bloom (22 March to 10 May), the upper 200 m were well mixed, with temperatures between 5 and 6°C. The chlorophyll *a* concentration was very low at <0.5 µg l^{-1} (<40 mg m^{-2} integrated total chlorophyll *a* for the upper 100 m). During this period, small algae (<5 µm), e.g. green algae (approx. 40%), haptophytes (approx. 30%) and cryptophytes (approx. 25%), were dominating the phytoplankton community (Irigoien et al. 1998). The warming of the surface water led to stratification at 30 to 50 m depth, and subsequently (11 to 29 May) a phytoplankton bloom developed, with a maximum chlorophyll *a* concentration of 3 µg l^{-1} (133 mg m^{-2} integrated total chlorophyll *a* for the upper 100 m). The cell size distribution of the algae shifted to larger cells; dominant taxa during the bloom were diatoms (approx. 30%), cryptophytes (approx. 30%) and dinoflagellates (approx. 15%). By the end of May, the chlorophyll *a* concentration decreased and did not exceed 1.5 µg l^{-1} (60 mg m^{-2} integrated total chlorophyll *a* for the upper 100 m) during the post-bloom (30 May to 9 June). During this period, haptophytes and cryptophytes were dominant again, shifting the cell size distribution back to smaller cells.

Biomass and abundance

During the period of investigation, the seasonal ontogenetic migration was almost completed (W. Melle et al. unpubl.) and most of the *Calanus finmarchicus* population was found in the upper strata during the whole investigation period. Only females were abundant below 100 m, in varying numbers during part of the study period (Niehoff et al. 1999), but they were not considered here. Biomass of the *C. finmarchicus* population in the upper 100 m is presented in Fig. 1b.
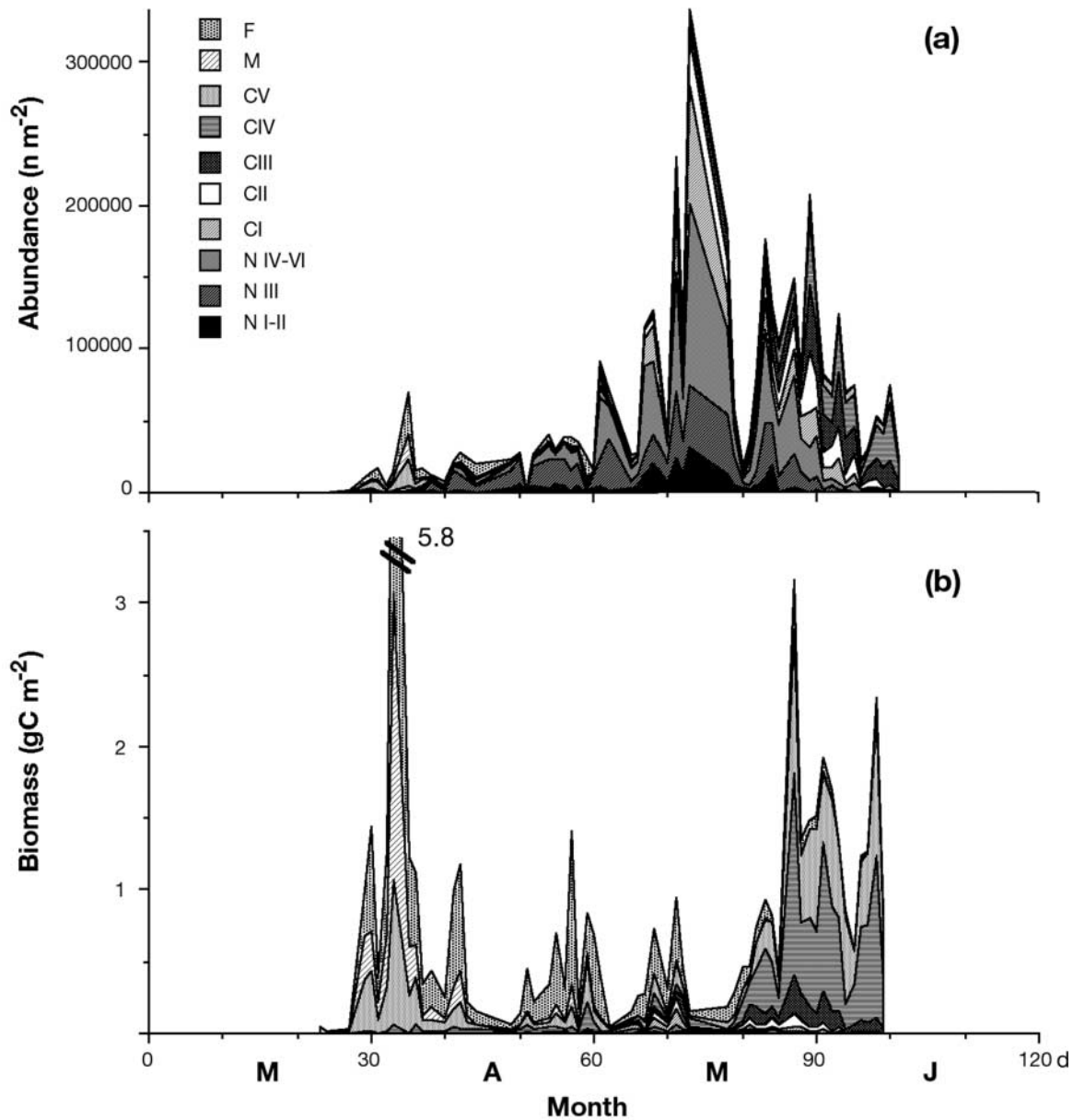
Fig. 1. Abundance (a) and biomass (b) of *Calanus finmarchicus* at Station M between March and June 1997

Details on the vertical distribution of adult females were described by Niehoff et al. (1999). Abundance was highly variable (Fig. 1a), ranging from 950 to 335 000 ind. m^{-2}, including all stages except eggs. The outstanding peak in abundance of CV, adult males and adult females on 4 April (Fig. 2) co-occurred with an intrusion of colder (Irigoien et al. 1998) and saltier (Klenke 1998) water recorded mostly below 200 m and lasted only 1 d. Highest numbers were recorded in mid-May during an outburst of naupliar development. Weekly biomass of adult females, males and CV is presented in Table 3. Biomass showed considerable

variability, with several peaks, ranging from 0.05 to 6.3 g C m^{-2} (Fig. 1b), and an average of 0.84 g C m^{-2}. As expected, biomass was proportional to the presence of older stages.

Despite high variability of total abundance, stage composition was consistent (Fig. 2). The population stage distribution shifted through time towards older stages, suggesting an actively developing cohort of the spring generation (G$_1$) during the study period. Distinct cohort development is clearly apparent in the cumulative portion of all stages (Fig. 3). Nauplii were present from the beginning of the investigation but at
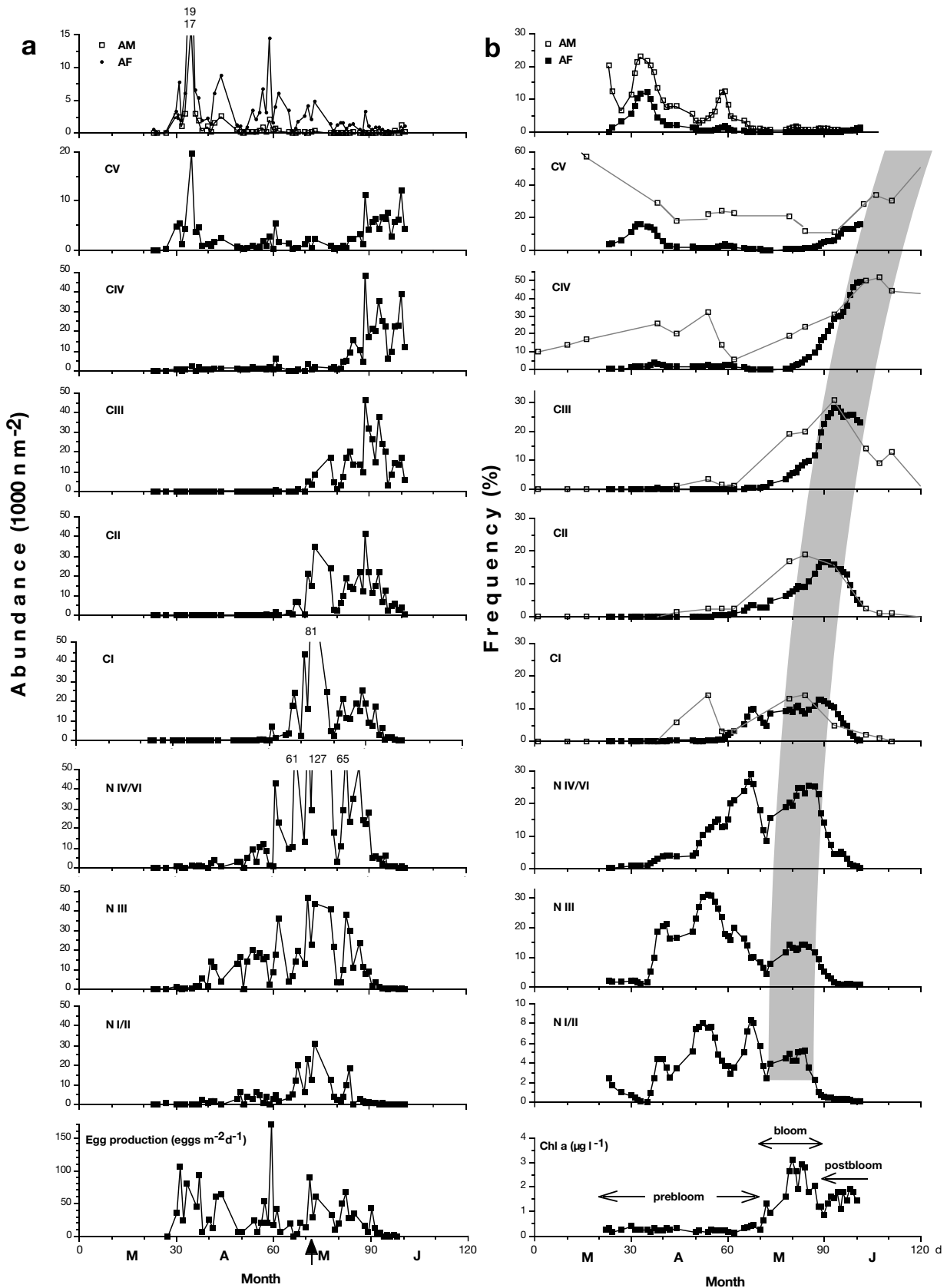
Fig. 2. Absolute (a) and relative (b) stage composition of *Calanus finmarchicus* at Station M between March and June 1997. Shaded line: suggested cohort development. For comparison, open squares in (b) CI to CV show the stage composition from 1948 (Østvedt 1955, from his Fig. 11)
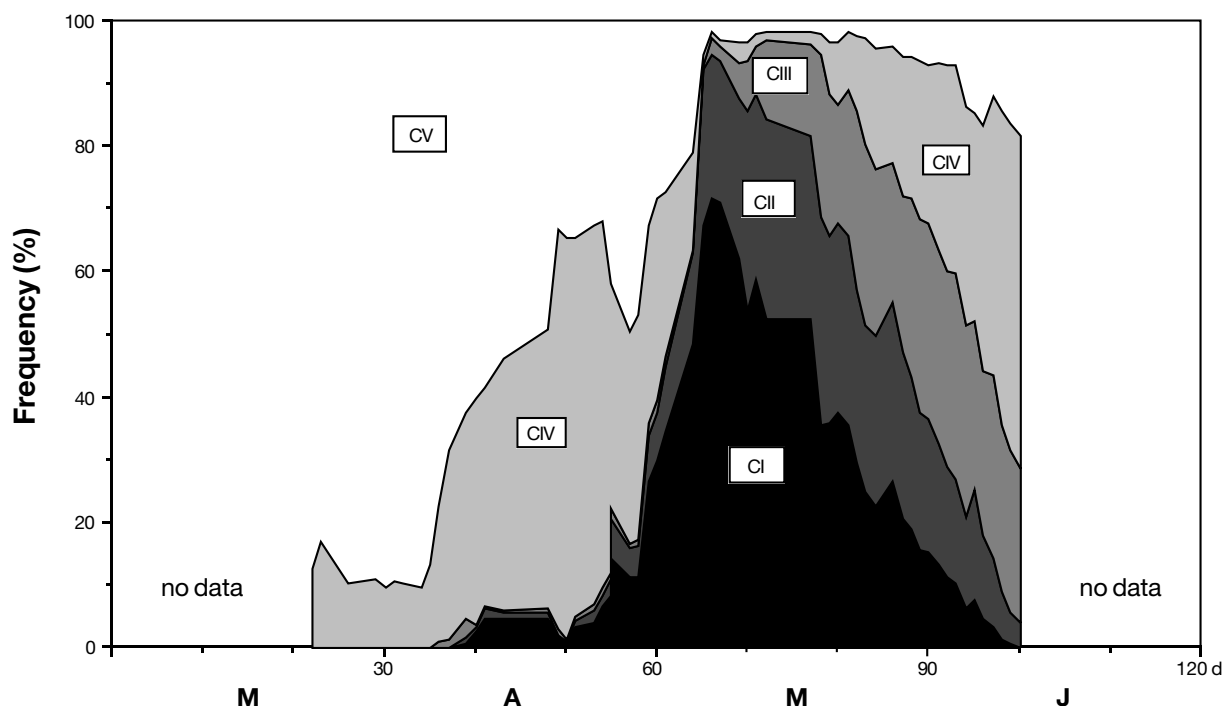
Fig. 3. Cumulative stage distribution of CI to CV of *Calanus finmarchicus* from Station M. Data were smoothed by a 3-point running average

very low numbers (<100 ind. m^{-2}; Fig. 2a). NIII was the most frequent of the naupliar groups counted, while the numbers of NI/NII were extremely low, despite continuous and rather steady population egg production rates (Fig. 2a). The portion of nauplii, especially stages NI/NII to NIII, increased strongly from the beginning of April, while NIV to NVI peaked approximately 1 mo later, in mid-May (Fig. 2b). After a steep decrease, also noted in Stages CI to CIII (Fig. 2a), another peak developed at the end of May. Thereafter the naupliar stages disappeared (<1%) successively on 28 May (NI/NII), 3 June (NIII) and 7 June (NIV to NVI) despite ongoing egg production. Taking 2 d for egg development into account, no offspring were found from eggs deposited after 26 May.

Young copepodites were first observed on 10 April, however at very low concentrations. A first increase of CI to CIII was observed at the beginning of May (Fig. 2). While there was considerable variability in day-to-day abundance, the relative stage composition shows a clear successive development within the copepodite stages, with the succession expressed both in the first appearance and maximum (Figs 2 & 3). The relative stage composition (Fig. 2b) shows that CI and CII had completed most of their development by the end of the study, while CIII had just reached its maximum portion. CIV and CV present in March and April were overwintering stages of the G_0 generation. They had

maxima in the beginning of April and disappeared thereafter (Fig. 3). New CIV of the G_1 generation seemed to be very close to their maximum, and the portion of new CV was still increasing at the end of the study period. There was no indication yet for an occurrence of G_1 adults. The overwintering adults had maxima at the beginning of April and May. Their absolute numbers decreased steadily from a median of 3480 m^{-2} in April to ca 500 in June. The sex ratio (males:females) decreased from 0.5 in April to <0.05 in June.

For comparison of stage development and food concentration, chlorophyll *a* concentration at the surface and phases of phytoplankton development were added to Fig. 2b. Population egg production rate from Niehoff et al. (1999) is also shown (Fig. 2a). To evaluate the role of the pre-bloom period for population development, Table 4 shows estimates for the presence of the stages of the G_1 generation before and after the beginning of the bloom. 10 May was defined as the beginning of the bloom. Accordingly, eggs and nauplii were present much longer during the pre-bloom phase. In contrast, copepodites were present long after 10 May. While CI still spent approximately one-third of its presence in the pre-bloom period, the later copepodite stages hardly showed up before the bloom (CII, CIII) or at the end of the bloom (CIV, CV). Minimum stage durations taken from laboratory rearing at optimal feeding conditions (Campbell et al. in press) and calculated for

Table 4. Occurrence (days) of eggs and developmental stages of *Calanus finmarchicus* before and after beginning of the bloom (10 May). Stage durations calculated from Campbell et al. (in press) for 7°C

Stage	Presence	Before bloom	After bloom	Stage duration
Eggs	62	41	21	2
NI/NII	55	36	19	3.3
NIII	54	35	19	4.7
NIV/NVI	54	31	23	7.8
CI	42	13	29	3.2
CII	40	9	31	3.8
CIII	32	1	31	4.8
CIV (G_1)	20	0	20	7.3

7°C, i.e. the mean temperature between beginning of April and mid-June at Station M, were added to Table 4. They show that presence, especially of the younger stages, was a manifold of stage duration.

Stage duration

Stage duration was computed using 2 methods. In Method 1 the steepest increase in MA3 (3 d weighed average, see 'Methods') was used. The times required for development of 3 groups of nauplii and CI to CIV are listed in Table 1.

The median development time method (Method 2, see 'Methods') provided a time series of the proportion of completed molts (Fig. 4); however, difficulties were encountered in calculating stage duration for nauplii due to their extended presence. Thus, only the linear portions of the time series curves were used for stage duration calculations (Fig. 4a, b, Table 5). For NIII and NIV/VI, 2 linear portions were chosen (Fig. 4b), but only the shorter durations are shown in Table 5. Comparison of the different methods shows similar stage durations for the 2 naupliar stages (Table 5), but half the durations for CI to CIII, respectively. For CIV, Method 2, in contrast, gives more than twice the duration as Method 1. This may be due to the fact that CIV still made up only a small portion of the population.

Another, more subjective approach is to follow the peaks of cohorts. The eye-fit trajectory from the latest peaks in the composition of the naupliar stages in Fig. 2b clearly indicates a homogenous cohort developing from NI/NII to CIV. The approximate developmental time for this cohort is 22 d. This is similar to the minimum development time of 24.6 d calculated for NII (our youngest nauplii, NI and NII, are pooled) until CIV from Campbell et al. (in press) at 7.5°C, the mean seawater temperature in the upper 100 m during this growth period.

Productivity and mortality

The increment summation method estimated daily production to be 51.03 mg C m^{-2} d^{-1} (Method 1A), 56.52 mg C m^{-2} d^{-1} (Method 1B) and 56.28 mg C m^{-2} d^{-1} (Method 2) during the 80 d observation period (Table 1). Correspondingly, productivity amounted to 0.050 and 0.055 d^{-1}, respectively.

Daily mortality rate Z was estimated to be 0.035 d^{-1} by the single negative exponential model (Fig. 5). Excluding data refering to stages NI/NII and NIII from the regression resulted in an estimate of $Z = 0.048$ d^{-1}.

Daily carbon-specific egg production rates are presented in Fig. 6. Mean rates were calculated for the pre-bloom (0.02 d^{-1}), bloom (0.066 d^{-1}) and post-bloom (0.0073 d^{-1}) period as defined by Irigoien et al. (1998; see also Fig. 2b). The overall mean of specific egg productivity was 0.031 d^{-1}. Production from SEPR is 30 mg C m^{-2} d^{-1}.

For comparison, productivity was computed according to Huntley & Lopez (1992) from growth rates (their Fig. 2) and from developmental times provided by Campbell et al. (in press), using the mean temperatures in the upper 50 m. The resulting productivity is very similar between these authors, but considerably higher than our field data for SEPR and population development (Fig. 6). Secondary production, as calculated from specific egg production, was 1.84 g C m^{-2}; the production of eggs accounted for 0.5 g, or 27%.

DISCUSSION

Population dynamics

Stage duration

Our data show a high degree of mesoscale variability in zooplankton distribution, expressed in considerable changes of biomass and abundance over time. This could reflect methodological problems such as clogging of the nets, or indicate different populations drifting by Station M. The strong variability in abundance and biomass during the very low phytoplankton concentrations of the pre-bloom period (Fig. 1) makes clogging unlikely. The hydrographic data showed the presence of Atlantic water in the upper water layer over the entire study period (Irigoien et al. 1998). One month back-tracking of particles collected at Station M in mid-May using a circulation model driven by the actual meteorological data for our study period shows the most distant origin of particles to be approximately 100 km to the south, in the Norwegian Basin (D. Slagstad pers. comm.). Furthermore, drifter trajectories (Poulain & Warn-Varnas 1996) and hydrodynamic

Table 5. Comparison of stage durations of *Calanus finmarchicus* from different areas. MTD: median development time method; SI: steepest increase method (see 'Materials and methods' for explanation)

| Origin	NIII	NIV/NVI	CI	CII	CIII	CIV	T (°C)	Reference
Norwegian Sea	13.0	9.0	6.0	7.0	9.0	12.0	6−8	Present study, SI
Norwegian Sea	12.6	14.6	2.6	3.4	5.9	26.3	6−8	Present study, MTD
Gulf of Maine					4.0	6.6/24.8[a]	6.0	Durbin et al. (1995)
Nova Scotia					5.0	5.5	7.0	Runge et al. (1985)
Northern Norway			2.4	4.6	5.8	19.0	6.0	Tande (1988)
laboratory	4.7	7.8	3.2	3.8	4.8	7.3	7.0	Campbell et al. (in press)
laboratory	7.2	9.3	6.8	5.4	6.4	7.6	7.7	Thompson (1982)
laboratory				4.0	5.2	5.0	8.2	Corkett et al. (1986)

[a]Post-bloom value
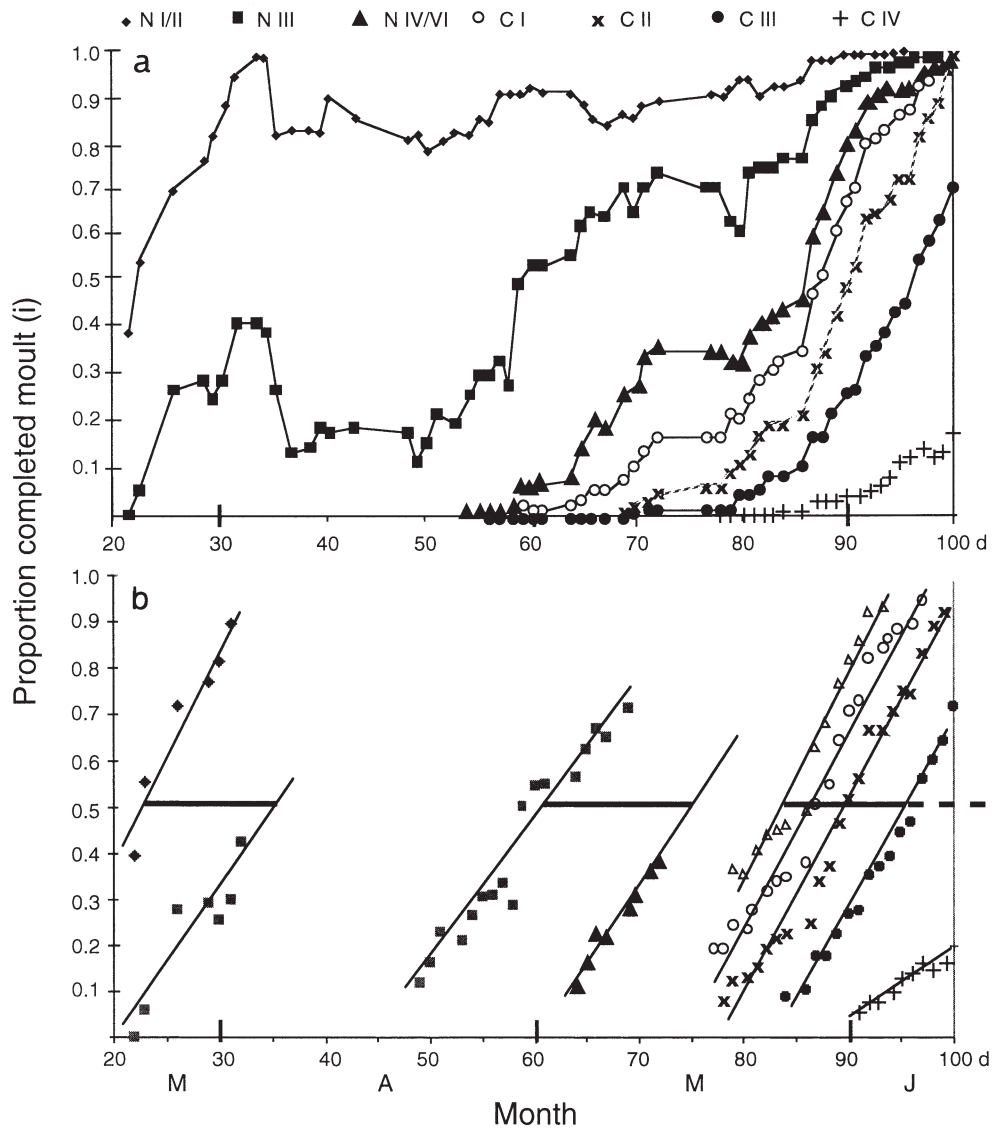
Fig. 4. Calculation of median development time. (a) Time series of the proportion of completed molts filtered with a 4-point running mean. (b) Linear regressions of linear periods in (a). Bars denote the stage durations used in calculations for Table 5
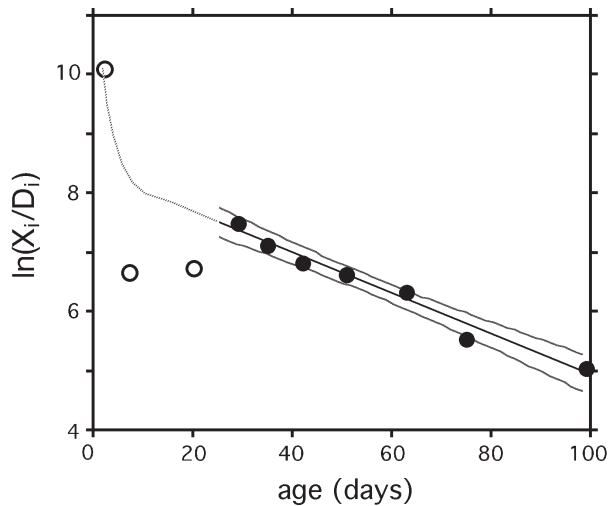
Fig. 5. Mortality of *Calanus finmarchicus* at Station M estimated by the single negative exponential model. Data are taken from Table 1: $\ln(X_i/D_i) = 8.289 - 0.035 \ln(\text{cumulative } D_i)$; $r^2 = 0.614$. With eggs and stages NI/NII and NIII (circles) excluded from the regression (stippled line indicates presumed mortality from eggs to NIII): $\ln(X_i/D_i) = 9.254 - 0.048 \ln(\text{cumulative } D_i)$; $r^2 = 0.891$

models (Bryant et al. 1998) indicate relatively low current velocities upstream of Station M. We thus assume that during the study period only the population of the southeastern Norwegian Basin was collected, which, due to similar environmental conditions, should develop synchronously. This is supported by observations during transects from the shelf to the open Norwegian Sea, south of Station M in April (Niehoff & Hirche 2000). There was a strong gradient in reproductive

variables between shelf and open ocean stations, while between-station variability was low at most open ocean stations. However, food maxima at 2 offshore stations caused significantly higher egg production rates. The significance of such local maxima on basin-wide variability of population development certainly deserves more attention.

The variability of abundances made application of population dynamics statistics on stage duration, growth and mortality very difficult. The long duration of the spawning period and, consequently, the extremely long lasting occurrence of some of the developmental stages (Table 4) added further difficulties. The assumptions of constant growth rate and stage duration needed for several models (Aksnes et al. 1997) were impossible to verify from the extended presence of all stages observed here. In contrary, our data suggest a wide range of stage durations, with our numbers probably representing the upper (pre-bloom, Table 5) and lower end (bloom) of the range. The development time of the cohort identified during the bloom is in good agreement with most laboratory observations (Thompson 1982, Table 5 in Tande 1988, Campbell et al. in press). On the other hand, our pre-bloom values from 2 different approaches (Tables 1 & 5) are among the lowest ever recorded. These observations clearly indicate food limitation in *Calanus finmarchicus*, not only for egg production (Niehoff et al. 1999), but also for juvenile growth during most of the period studied. This is decided in contrast to the concept of Huntley & Lopez (1992) of non-limited growth in the ocean. Similar, Durbin et al. (1995) observed a much longer duration of CIV during a post-bloom (24.8 d) versus a bloom situation (6.6 d) in the Gulf of
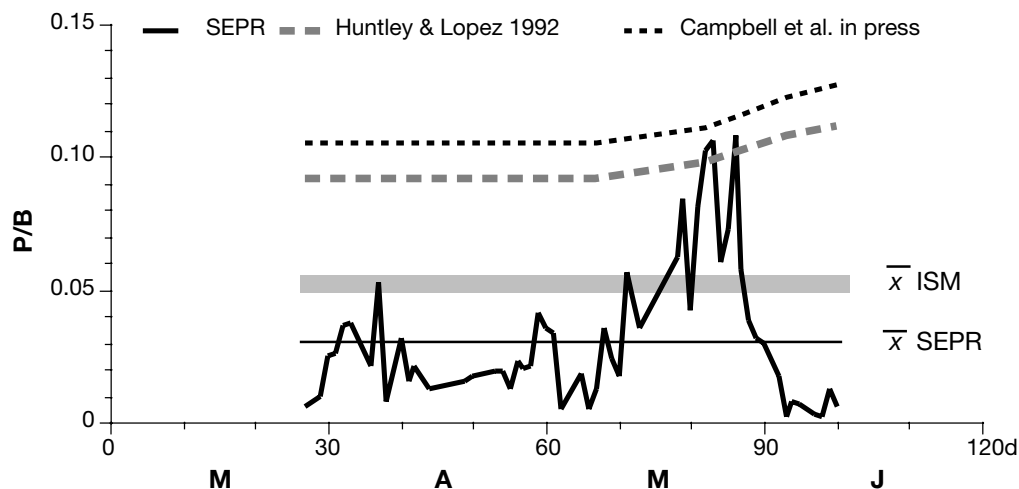

Fig. 6. Comparison of different measures of productivity of *Calanus finmarchicus* at Station M between March and June 1997. SEPR: specific egg production rate (egg-carbon female-carbon^{-1}), $\bar{x}$ SEPR: mean SEPR; $\bar{x}$ ISM: mean by increment summation method

Maine. Increased stage durations due to unfavorable conditions were reported also from *in situ* molting experiments in the North Sea by Diel & Klein Breteler (1986) and Fransz & Diel (1985). In the laboratory, sub-optimal food conditions have recently been shown to increase the development times among nauplii and copepodites considerably (Campbell et al. in press). Measurement of molting rates in other copepods have also shown food limitation (Burkhill & Kendall 1982, Klein Breteler et al. 1982, Huntley & Boyd 1984, Runge et al. 1985, Kimmerer & McKinnon 1987, Berggreen et al. 1988). In contrast, McLaren (1978) and McLaren et al. (1989) concluded, based on cohort analysis, that juveniles in coastal environments completed their development at the same rate as in the laboratory under conditions of unlimited food. Similar arguments were made by Davis (1984).

Productivity and production

Three different, although not fully independent, numerical methods were applied to estimate productivity and production. Increment summation and mortality rate depend on vertical life tables (sensu Aksnes et al. 1997), whereas the egg production rate method is a rather empirical approach. All methods result in similar estimates of productivity, 0.032 to 0.055 d^{-1}, corresponding to a production of 30 to 56 mg C m^{-2} d^{-1}. The very similar results obtained by Method 1A and 1B (Table 1) indicate that the population can be considered to be in a steady state, i.e. there is no detectable bias in our data owing to potential vertical migration in or out of the upper 100 m layer investigated. This seems to validate our results; however, the critical point in increment summation and mortality modeling is stage duration. If we use optimal stage duration data (Campbell et al. in press), which in the field probably only applied to the bloom phase, instead of data from the beginning of the investigation (Table 1), production values increase by 15 to 18%, depending on the method applied. This difference indicates that it is rather unlikely that we overestimated production owing to incorrect determination of stage duration. Including the deep living females found during the beginning of the investigation would alter the production by only a few percentage points, as the total contribution of adults is only ca 6% (see Table 1).

Mean specific egg production was lower by 38 to 45% as compared to productivity calculated with the increment summation method (Fig. 6). Using a structural female weight of 80 µg C (Carlotti & Hirche 1997) rather than total weight, as advocated by McLaren & Leonard (1995), would increase mean specific egg production by only 0.001. Unfortunately a detailed com-

parison of SEPR and juvenile growth was not possible here, as the stage duration estimates did not have sufficient resolution to resolve different food situations. Future studies should therefore apply direct stage duration measurements to correlate both growth measurements. This is especially important during the pre-bloom phase and during the post-bloom, when egg production was apparently limited (Niehoff et al. 1999) but growth of older stages was not affected.

Comparison of our productivity measurements at Station M with laboratory experiments under optimal conditions (Huntley & Lopez 1992, Campbell et al. in press) clearly shows that both unlimited growth and egg production (Fig. 6) took place only during the bloom. For the whole investigation period, the laboratory rates would overestimate productivity by a factor of 2.5 to 4. Only very few field measurements are available for secondary production in areas dominated by *Calanus finmarchicus*. On the Fladen Ground (59° N, 1° E) Fransz & van Arkel (1980) estimated the production of *C. finmarchicus* during the period examined in the FLEX project, before and after the exponential growth of the population, as 20 mg C m^{-2} d^{-1}. Williams & Lindley (1980) computed, from stage durations and weight differences during the same project, 490 to 910 mg C m^{-2} d^{-1} for the exponential growth phase in May, at a very similar temperature regime (6 to 9°C), but Fransz & Diel (1985) found only an average of 44 mg C m^{-2} d^{-1} in the same area 7 yr later. In the Skagerrak total production of the copepod populations consisting mainly of small calanoids ranged from 30 to 80 mg C m^{-2} d^{-1}, with an average of 46 mg C m^{-2} d^{-1}. Egg production accounted for 25% of total production (Peterson et al. 1991), which fits our data (27%) well.

Mortality

Data on growth and reproduction of copepods may be obtained more readily than on mortality. It is therefore often difficult to decide whether population growth is controlled by food limitation or by predation. At Station M an enormous loss was observed between eggs and young naupliar stages (Fig. 5). High mortality rates were also observed in other copepod species, but no data are available for *Calanus finmarchicus*. For *Acartia clausi*, Landry (1978) found only ca 20% survival, and Uye (1982) found ca 7.5%. Kiørbœ et al. (1988) reported egg mortalities in the order of 99% in a Swedish fjord. Mortalities around 50% were observed by Beckman & Peterson (1986) for *A. tonsa*, by Daan (1986) for *Temora longicornis*, and by Ianora et al. (1992) for *Centropages typicus*.

As eggs, NI and NII are not dependent on food, loss rates are due either to endogenous mortality or preda-

tion. Direct experimental estimates of endogenous egg mortality in *Calanus helgolandicus* (Laabir et al. 1995) showed high seasonal variability and an annual mean of 30%, while during the diatom bloom up to 75% of the eggs were not vital. At Station M, however, diatoms contributed only 8 and 14% to total phytoplankton during the pre- and post-bloom, respectively, and up to 47% during the short bloom (Meyer-Harms et al. 1999).

Previous reports attributed *in situ* copepod mortality during the early life stages mainly to predation (Landry 1978, Ohman 1986, Kiørboe & Nielsen 1994, Liang et al. 1994, Peterson & Kimmerer 1994, Ohman & Wood 1996). Egg cannibalism by *Calanus finmarchicus* was frequently observed in the laboratory (Marshall & Orr 1955). Copepod eggs are a preferred food source for many species of fish larvae (Runge 1988), but also many other types of predator (e.g. Daan 1986). Interestingly, at Station M most of these predators are only found after June (Østvedt 1955).

In contrast to egg mortality, our mean daily mortality estimates (Z = 3.5 to 4.8%) are lower than those of studies on *Calanus finmarchicus* from 2 Norwegian fjords. In the Korsfjord, Matthews et al. (1978) estimated a daily mortality rate of 10% for CIII to CVI. Similarly, in Lindåspollene Aksnes & Magnesen (1983) observed daily mortality >10% when the younger stages were present, and <1% when CV was dominant.

Life history

Our analysis of the stage distribution of *Calanus finmarchicus* on Weathership M confirms the importance of the pre-bloom period that was demonstrated in a previous publication on the reproductive physiology of this species (Niehoff et al. 1999). This is in contrast to the classical concept of a close link between the reproduction and growth of *C. finmarchicus* and the spring bloom, which is based on the high food requirements of egg production and juvenile growth (Cushing 1959). Our data show that *C. finmarchicus* does not only spawn half of its eggs long before the bloom, but many of these eggs also develop into feeding naupliar stages and some CI and CII, which seem to accumulate in expectance of the phytoplankton bloom. In contrast to the younger stages, the development of CI to CIII was centered in the bloom phase, and, consequently, the older CIV and CV developed during the post-bloom phase. Thus, the bloom formed a bottleneck for further development of the copepodite stages. It is not clear whether this is due to different feeding mechanisms or food requirements of the young copepodite stages as compared to nauplii and females. In laboratory studies

all stages of *C. finmarchicus* grew equally well at concentrations of 0.25 µg C l⁻¹ (Campbell et al. in press), which is close to our pre-bloom concentrations (Irigoien et al. 1998). The main differences between the pre-bloom and bloom conditions were the larger cell size, the presence of ciliates, no matter how low the concentrations, and the increased portion of diatoms during the bloom (Irigoien et al. 1998, Meyer-Harms et al. 1999). Marshall & Orr (1956) observed no differences in the feeding behavior between younger and older stages of *C. finmarchicus*, although there was a tendency for the setules to be closer in the younger stages.

A remarkably similar population development was observed by Østvedt (1955, his Fig. 11) some 50 yr ago at the same location. In Fig. 2b his stage composition for the year 1948 was added for comparison. He also mentioned considerable numbers of nauplii in April, May and June, from which he concluded the beginning of spawning in the first days of April. Similar to our observations, a first peak in CI was not followed by CII before the bloom, which he related to unfavorable conditions for this part of the brood.

The main benefit of the strategy observed here is probably to spread risk of mortality and to have as many offspring as possible ready to utilize the short window of growth provided by the bloom. The strategy includes an early ascent from diapause, which allows utilization of early blooms in fjords (Tande 1982, Aksnes & Magnesen 1983, Diel & Tande 1992), on shelves (Niehoff & Hirche 2000) and in shelf seas (Williams & Lindley 1980), as well as along longitudinal gradients in ocean basins such as the Norwegian Sea (Braarud et al. 1958). Early spring spawning helps to cope with predation stress on females due to increased predation by a number of fish species, as suggested by S. Kaartvedt (unpubl.). Predation may have caused the marked decrease in female number, as in laboratory studies they are long-lived and capable of spawning for several months (Hirche 1990, Niehoff & Hirche unpubl. data). Consequently, an earlier bloom would lead to an increased population egg production rate due to a higher abundance of females. Two week shifts of the timing of the bloom were obtained by Henderson & Steele (1995) and Radach et al. (1998) from models forced with meteorological data for the North Sea. Even more important for a sustained population development may be a longer period of food conditions, which allows successful transition from nauplii to copepodite stages. To better understand the limiting factors and realistically predict production, more studies are needed on the nutritional requirements of developmental stages at low food concentrations and on the causes of mortality, especially in young stages.

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