

## Synchronization in the molting and spawning activity of northern krill (*Meganyctiphanes norvegica*) and its effect on recruitment

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### Abstract

The molting, spawning, and recruitment of northern krill (*Meganyctiphanes norvegica*) were analyzed over an annual cycle (1999–2000) in the Clyde Sea (west coast of Scotland). Results supported the hypothesis of a functional relationship between egg production and molt development for the duration of the reproductive season (March to August), with one reproductive cycle being made up of two molt cycles. Females remained in reproductive condition throughout the reproductive season, and the timing of their spawning and molting was synchronized at the population level throughout this period. A semiempirical model predicted that the krill population produced an egg pulse every 20 to 26 d (depending on temperature), and three cohorts were evident in net samples taken later in the year. The likely date on which the first cohort was spawned was around 26 d after the main phytoplankton bloom, suggesting that the bloom triggered egg development in all adult females. Such a synchronized spawning period was observed directly in adult females 26 d after a bloom in March 2000. A total of three cohorts over the 6-month reproductive season is less than the maximum of seven that would be possible if spawning occurred at a periodicity of between 20 and 26 d, suggesting that larval recruitment was not always successful. Analysis showed that successful recruitment was only achieved when chlorophyll *a* levels were adequate during both the period of egg maturation in the ovary and the subsequent development of larvae, especially the furcilia stages.

The reproductive cycles of euphausiids are known to be adapted to local conditions. The length and timing of the spawning season varies interspecifically, from the apparently continuous breeding of *Euphausia hanseni* in the subtropical Benguela upwelling system to the seasonally distinct breeding episodes of *Euphausia superba* in the Antarctic (Siegel 2000). Intraspecific variation is also evident in widely distributed species, such as northern krill (*Meganyctiphanes norvegica*), that have short reproductive seasons in Mediterranean waters (e.g., the Ligurian Sea) but longer reproductive seasons in temperate boreal regions (e.g., the Clyde Sea and the Kattegat). A common pattern throughout the range of this species is the coincidence of reproductive scheduling with periods of optimal trophic conditions (Cuzin-Roudy and Buchholz 1999). The abundance of food items in boreal North Atlantic areas is generally high from early spring to late summer, facilitating a reproductive season that lasts from March to October. In the Mediterranean, the large blooms of

phytoplankton and zooplankton during early spring quickly die away by late spring and reproductive activity in northern krill is rarely seen outside the period of February to May (Cuzin-Roudy 1993).

Despite these differences, incubation experiments have shown that the reproductive cycle of individual females is the same throughout the wide geographic range of this species (Cuzin-Roudy and Buchholz 1999). The timing of one reproductive cycle is tightly linked with two successive molt cycles, a “vitellogenic molt cycle” and a “spawning molt cycle.” Female krill release a mature egg batch in one to three spawns during the premolt phase of the spawning molt cycle. The first spawn takes place at *apolysis* (between C late and D<sub>0</sub> molt stages), when the epidermis retracts from the old cuticle and has regained activity. The second and third spawns take place during D<sub>0</sub> and D<sub>1</sub>, when the reorganized epidermis starts to secrete the new cuticle. Vitellogenesis starts for a new egg batch as soon as egg release has been completed, several days before molting (*ecdysis*). Lipid yolk accumulation in the new batch will go on through a complete vitellogenic molt cycle and the first part of the next spawning molt cycle.

In a study of northern krill over a 3-week summer period in the Kattegat, Tarling et al. (1999) found that the population was undergoing a synchronized molting event. Given the interdependence of ovarian and molt development, such a pattern implies that spawning must also have taken place in a synchronized manner at the population level. Females continue with successive reproductive cycles throughout the reproductive season (Cuzin-Roudy 2000), so, if such synchrony persisted over this entire period, one would expect

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to see pulses of eggs in the water column at time points separated by the period of two molt cycles, which would be between 14 and 26 d, depending on temperature (Cuzin-Roudy and Buchholz 1999). This would mean that, in the Clyde Sea and Kattegat, up to seven reproductive cycles may be completed by the end of the reproductive season.

Mauchline (1960), Boysen and Buchholz (1984), and Labat and Cuzin-Roudy (1996) examined the population dynamics of northern krill in the Clyde Sea, Kattegat, and Ligurian Sea, respectively. Only a single juvenile cohort was identified in the Ligurian Sea, while up to three were evident in the Clyde Sea and Kattegat studies. This is much less than the seven spawning periods that are possible based on the above assumptions. The difference could be the result of two alternative scenarios: first, that synchrony does not remain apparent throughout the reproductive period and cohorts become merged, or, second, that environmental factors impinge to make some cohorts succeed and others fail. The first scenario is likely in the Ligurian Sea since the intermolt periods were short and the spawning periods close together. The second scenario has been observed in *E. pacifica* off the Californian coast (Rumsey and Franks 1999), where prevailing conditions had a strong influence on the mortality of early furcilia stages and determined the eventual strength of a recruiting cohort.

This study will address the influences of both egg development and larval mortality on the population dynamics of northern krill in the Clyde Sea. The site is particularly suited to population dynamic studies since it is mostly landlocked and experiences limited advective exchange with Atlantic waters to the west (Edwards et al. 1986), thus minimizing the confounding influences of immigration and emigration. *M. norvegica* is found in the deeper regions, especially the Arran Deep, which reaches depths of between 140 and 200 m. The Clyde Sea exhibits many of the physical and biological features that characterize North Atlantic waters (Jones et al. 1995), and it contains the majority of the zooplankton species found within the North Atlantic biome (Colebrook 1978; Adams 1986). Zooplankton studies of the Clyde Sea are therefore likely to reflect patterns that occur throughout the North Atlantic and its periphery. The primary aims of this study are to investigate molting and spawning at the population level, to assess the degree of synchrony, and to determine whether or not spawning was pulsed over time. The secondary aim will be to examine recruitment through relating the strength of cohorts to the trophic conditions experienced by reproducing adults and their larvae. The approach will be a step toward predicting success or failure in krill recruitment.

## Methods

**Sampling**—All sampling was carried out in the vicinity of a mooring located at Inchmarnock Water (55.80°N, 5.20°W), which lies at the northern end of a trench between 140 and 160 m deep (Fig. 1). Seven net sampling campaigns were carried out between the period June 1999 to May 2000 (Table 1) on board R/V *Calanus*. During each campaign, numerous visits to the site were time tabled such that, by the

end of the 5-d period, samples were taken at all phases of the day/night cycle. This approach was necessary because the ship was not able to remain at sea more than 12 h out of every 24 h. The ship's winch was used to operate a 1 m<sup>2</sup> multiple open/closing net system (MOCNESS; Biological Environmental Sampling Systems; see Wiebe et al. 1985), which was lowered to 130 m at 0.5 m s<sup>-1</sup> and subsequently raised to the surface at 0.2 m s<sup>-1</sup>. The net collected samples in a depth-discrete fashion (see Tarling et al. 2002 for details), but these were subsequently pooled for the present analyses. A failure in the conducting cable in August 1999 and December 1999 disabled the capability to locate the depth of the net on line, so the net was deployed in a depth-blind manner, where 150 m of warp was paid out at 0.5 m s<sup>-1</sup> and recovered at 0.2 m s<sup>-1</sup>. Subsequent calibration hauls, carried out at the same ship's speed and with a depth/time recorder (VEMCO TDX) attached to the MOCNESS frame, estimated the maximum depth of the net to have been 60 m. Tarling et al. (2002) showed that the modal depth of the population was around 80 m during the daytime, rising to around 30 m at night. The population was scattered over a depth range of ±20 m through the diel cycle. When the MOCNESS was fully operational, we assumed that the entire population was sampled because the net covered the entire vertical range of the population. Although it is likely that capture efficiency altered between night and day, the relative proportion of different size classes of juveniles (10–25 mm) caught by the net was unlikely to be different, so all catches were considered. When the MOCNESS achieved a maximum depth of only 60 m as a result of malfunctions, only nighttime samples were considered when assessing the length–frequency of the population because it was only during the night that the entire juvenile population was sampled by the net.

Temperature and salinity profiles were taken with a Neil Brown conductivity temperature depth (CTD) recorder in the June and August 1999 campaigns and with a SeaBird CTD in all other campaigns. The SeaBird instrument also collected fluorescence profiles. All net samples were fixed in 10% formalin and subsequently preserved in 70% ethanol.

**Home laboratory analysis**—Length–frequency analysis on adult and juvenile specimens of *M. norvegica* was carried out approximately 6 months after capture. Body length was measured to the nearest millimeter from the front of the eye to the tip of the telson. Molt staging was adapted from Buchholz (1991) and Cuzin-Roudy and Buchholz (1999) and simplified because of tissue disturbance caused by formalin. The simplified classification scheme was “postmolt” for stage B; “intermolt” for stages C and D<sub>0</sub>; “pre-molt” for stages D<sub>1</sub>, D<sub>2</sub>, and most of D<sub>3</sub>; and “molting” for late D<sub>3</sub>, E, and A. Sexual development stages (SDSs) were assessed from the structure of the ovary and the degree of oocyte development using the squash technique devised by Cuzin-Roudy and Amsler (1991) for Antarctic krill and following Cuzin-Roudy and Buchholz (1999) for SDS definition in *M. norvegica*. The total number of eggs released by a female during one reproductive cycle was measured as the number of mature oocytes (NMO) present in the fully developed ovary of females in SDS 4 (Cuzin-Roudy 2000).

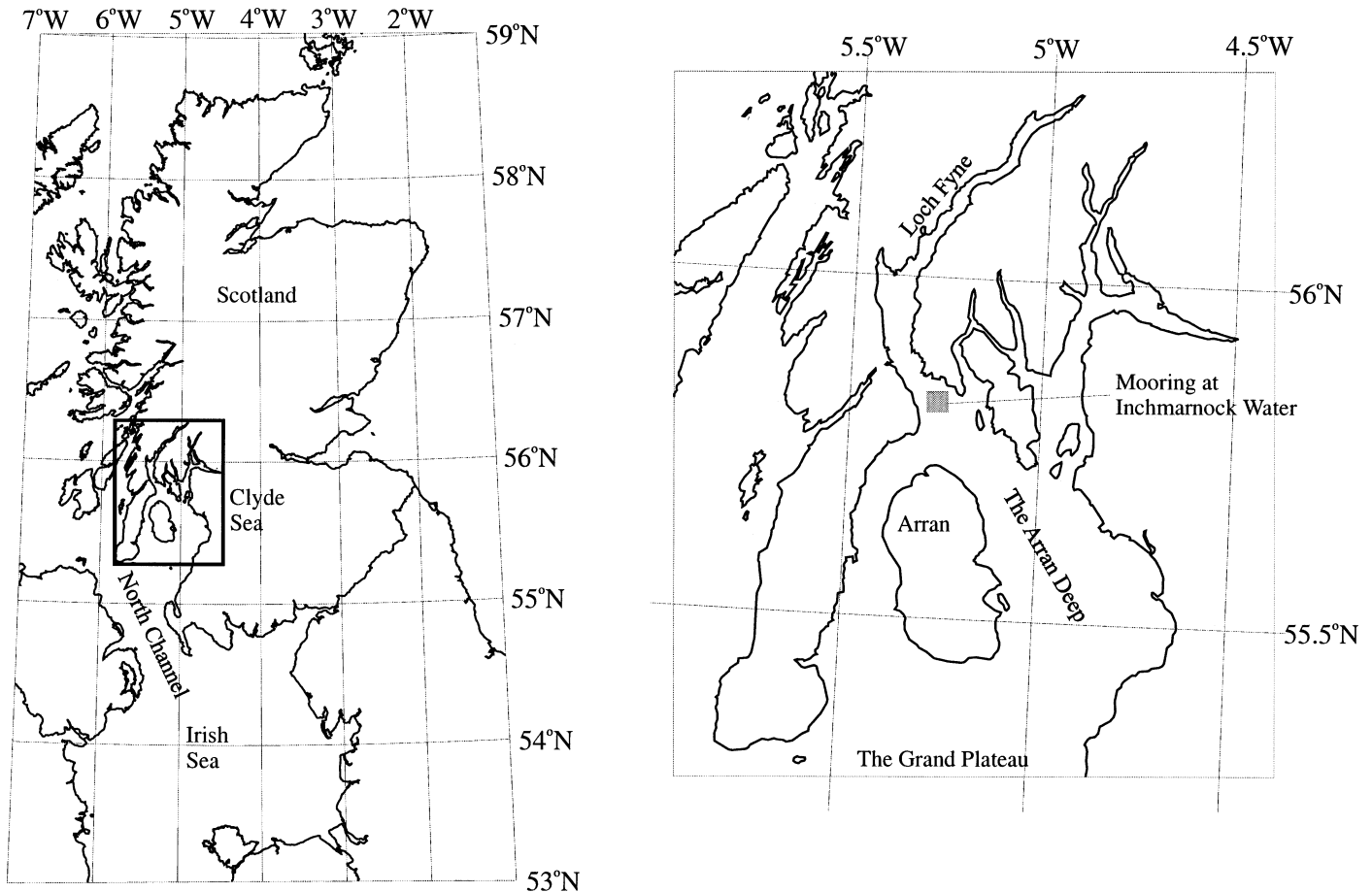


Fig. 1. The sampling area.

**Chlorophyll data**—A time series of Chlorophyll *a* (Chl *a*) concentrations was derived from the sea viewing wide field of view sensor (SeaWiFS) ocean color satellite. Values were taken from nine pixels in the vicinity of the mooring in Inchmarnock Water and integrated into 6-d averages between 28 January 1999 and 16 November 2000. The values were converted to Chl *a* biomass ( $\text{mg m}^{-3}$ ) using the bright pixel atmospheric correction algorithm developed by Plymouth Marine Laboratory (Moore et al. 1999) and the NASA OC2V2 chlorophyll algorithm (O'Reilly et al. 1998).

**Analysis of sample data**—Molt and sexual development stages: Cuzin-Roudy and Buchholz (1999) determined the relative duration of each ovarian development stage and molt stage in the reproductive cycle through incubation experiments. In a situation where there is no temporal synchrony in the molting behavior of a population, the relative proportion of individuals within each molt and reproductive stage should be equivalent to the relative stage durations. According to Cuzin-Roudy and Buchholz (1999; their table 5), the relative proportion of time spent, and hence the relative pro-

Table 1. Cruise data from the Clyde Sea campaigns.

Campaign	Dates	Depth range (m)	No. net hauls		No. krill caught	% juveniles	Average no. krill per haul ( $\pm$ SD)	
			Night	Day			Night	Day
Jun 99	28 Jun–2 Jul	0–130	6	7	1,611	37	187 $\pm$ 88	70 $\pm$ 19
Aug 99	9–16 Aug	0–60	4	3	2,966	76	286 $\pm$ 154	186 $\pm$ 166
Oct 99	4–8 Oct	0–130	6	4	6,676	77	769 $\pm$ 155	515 $\pm$ 134
Dec 99	29 Nov–3 Dec	0–60	1	1	311	70	287	24
Jan 00	18 Jan–20 Jan	0–130	4	4	488	51	92 $\pm$ 56	44 $\pm$ 35
Mar 00	6 Mar–8 Mar	0–130	2	7	280	4	162 $\pm$ 216	67 $\pm$ 64
May 00	8–12 May; 23–31 May	0–130	8	4	237	1	22 $\pm$ 14	12 $\pm$ 8

portion of individuals within each molt phase was 15% post-molt, 31% intermolt, 43% premolt, and 11% molting. For the sexual development stages, the proportions were 38% SDS 3 (vitellogenesis), 4% SDS 4 (first spawn), 27% SDS 5<sub>1</sub> (second and third spawn), and 31% SDS 5<sub>2</sub> (postspawn). When not in reproductive condition, females may be found to have a resting ovary (SDS 1 or 10, for small and large females, respectively), to be in the first phase of yolk accumulation (previtellogenesis: SDS 2), or to be in oosorption (SDS 6). Two  $\chi^2$  goodness of fit tests were carried out to examine whether there was a significant difference between the observed and expected proportions of, first, the molt phases of females and, second, the respective sexual development stages (SDSs).

In some campaigns, there was a significant male to female bias of up to 4:1, which made it difficult to obtain enough females for statistical tests without pooling samples from both day and night. This does not bias the observed relative proportions of stages, since the majority lasted for days rather than hours. The exceptions are SDS 4 and molting, which last for less than 12 h and 6 h, respectively (Cuzin-Roudy et al. 1999), meaning that their proportions could differ according to day-to-night catch ratios. Nevertheless, the fact that the durations of these stages was relatively short also means that they were unlikely to cause a type II statistical error, i.e., failing to detect synchrony when it was apparent. This is because even if no individuals of these stages were found, it would not be significant because numbers were expected to be low. A large proportion of individuals in these stages, by contrast, can only be the result of synchrony. The analysis was carried out for all campaigns apart from mid-winter, when numbers were insufficient to achieve an acceptable level of robustness.

**Intermolt period (IMP) and temperature:** The expected IMP for the Clyde population during the reproductive season was estimated from the relationship established for IMP with in situ temperature by Cuzin-Roudy and Buchholz (1999):

$$\text{IMP (d)} = 19.11 - 0.843 \text{ Temp}^\circ\text{C} \quad (1)$$

The temperature parameter in this equation was estimated through averaging the product of the vertical distribution of krill over a diel cycle and the temperature/depth profile of the water column. This gave the following values: June 1999, 10°C; August 1999, 11°C; March 2000, 7°C; May 2000, 8°C. As a result, IMP was estimated to range from 13 d in March to 10 d in August. Equation 1 does not hold outside of the reproductive season (October to February).

**Length frequency:** Length–frequency analysis focused on the juvenile part of the population to determine the timing and extent of recruitment. Overlapping length–frequency distributions were segregated using component fitting software (MIX 3.1; MacDonald and Green 1988). The method finds the best fit to the length–frequency distribution through iterating between a series of component types (normal, log-normal, exponential, and gamma). The user must identify the expected number of components within the distribution before initializing the fitting routines. A quasi-Newton algorithm performed the fitting procedures without any con-

straints being placed on the proportions, the mean length, and the variance expected within each component.

**Back calculation of spawning period:** A back calculation was made from the first appearance of a juvenile cohort in the samples to the likely spawning period of that cohort. Likely development rates were extrapolated from data provided by Mauchline (1977; his table 3) on the larval and early juvenile stages of *M. norvegica* in the Clyde Sea (Loch Fyne) during spring. The development of the first larval stages (egg to furcilia I) was calculated to take 29 d. These calculations assumed that spawning took place on 1 April and development occurred over the late spring and early summer. Developmental rates for cohorts spawned at different times of year are likely to be altered by the ambient temperature. This was accommodated for by applying a developmental rate  $Q_{10}$  value of 2.81, provided by Ross (1981) for *Euphausia pacifica* that were incubated at 8°C and 12°C. All further development followed a linear function fitted to the Mauchline (1977) data set.

$$\text{length (mm)} = 0.2090 \text{ age (d)} - 3.691;$$

$$R^2 = 0.998 \quad (2)$$

## Results

**Environmental parameters**—The water column was well mixed for the majority of the winter and spring, with temperatures between 7°C and 8°C (Fig. 2). A thermocline developed during the late summer, reaching to around 20 m at its maximum. Above the thermocline, temperatures warmed to around 15°C by August, while below the thermocline the increase was more limited. Salinity at the surface was on average 1.5 below that in the deeper strata, most likely as a result of the freshwater runoff from the surrounding catchments (Fig. 2). The salinity of the deeper strata was characteristically between 33.0 and 33.5, with values tending to be lower during the winter months when the water column was mixed. Fluorescence profiles (Fig. 2) showed that most Chl *a* occurred within the top 30 m, being more restricted to the surface earlier in the productive season. During the spring bloom in March 2000, the highest Chl *a* levels were measured in the top 5 m, whereas in May 2000 the maximum had deepened to around 15 m. Chl *a* levels were negligible between October and January.

There were several blooms in surface Chl *a* measured by SeaWiFS in both 1999 and 2000 (Fig. 3). In 1999, a bloom started in early February and persisted until early March, with maximum levels (18 mg m<sup>-3</sup>) being reached toward the end of this period (25 February). Two further blooms occurred in early May and mid-July, reaching 10 mg m<sup>-3</sup> and 8 mg m<sup>-3</sup>, respectively. At the intervening periods, Chl *a* levels varied between 0 and 6 mg m<sup>-3</sup>. In 2000, the spring bloom started at a similar time to that in 1999 but was comparatively weaker and did not persist to the same extent. A larger bloom occurred later on in the spring and also in mid-July. Chl *a* biomass levels through the rest of the year were similar to that in 1999.

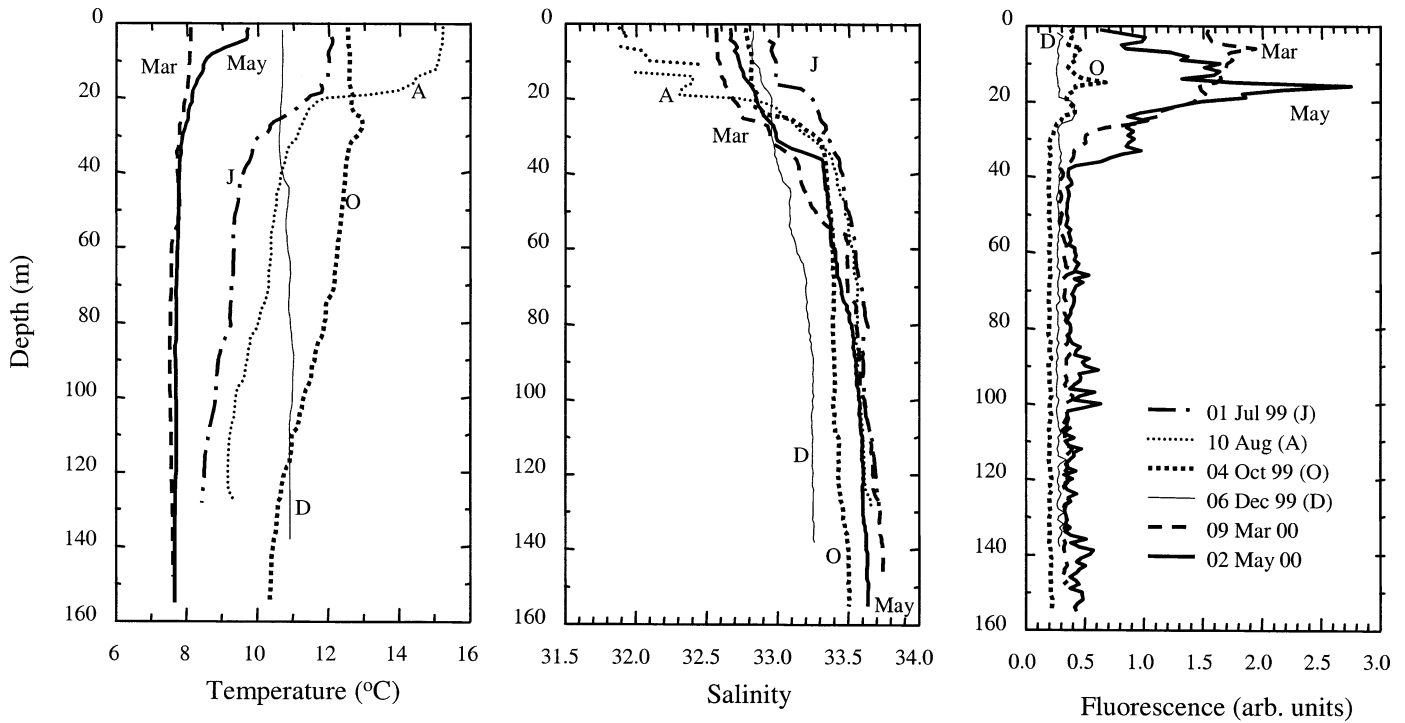


Fig. 2. Temperature, salinity, and fluorescence profiles of the Clyde Sea during sampling campaigns in 1999 and 2000.

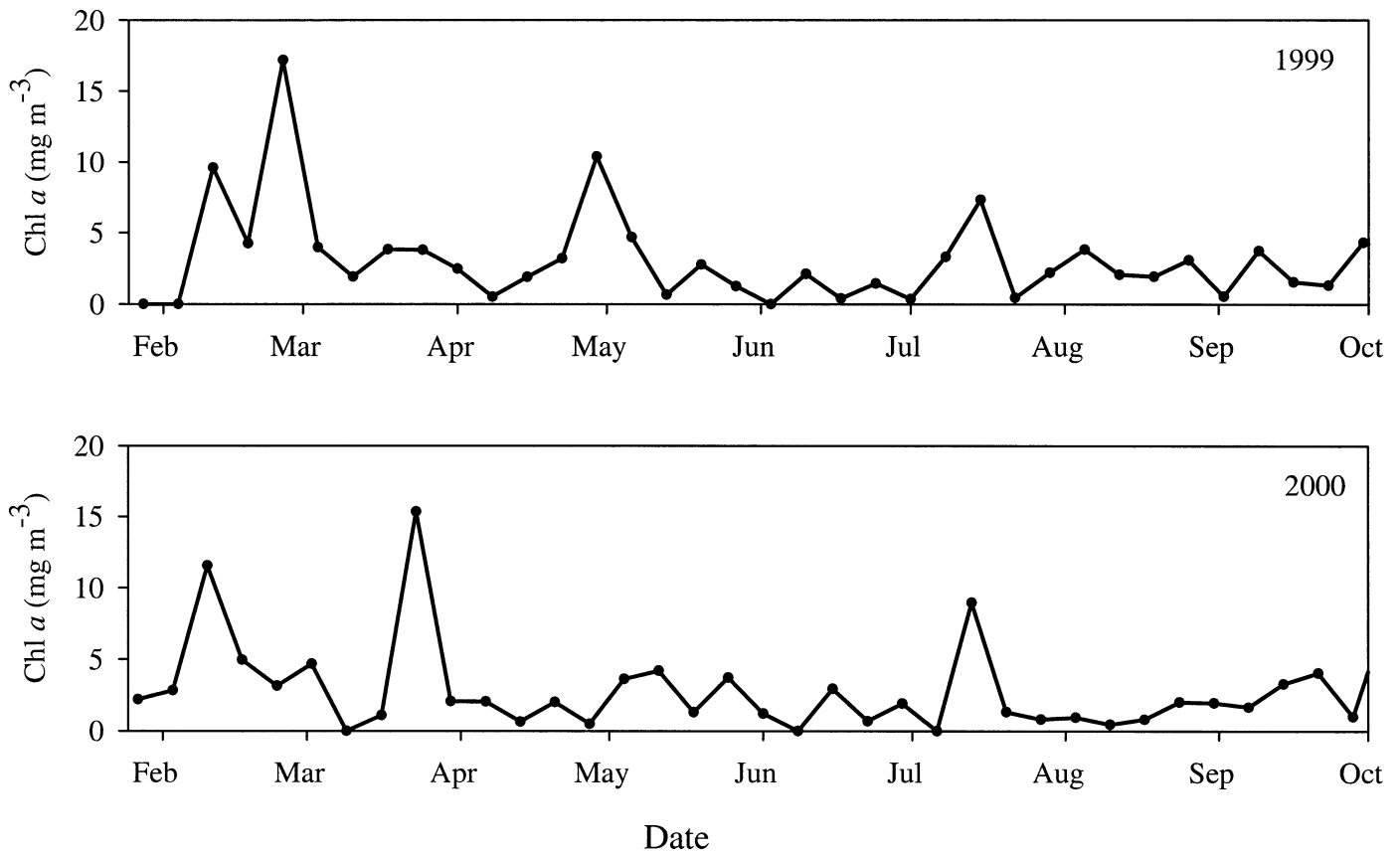


Fig. 3. SeaWiFS time series for nine pixels in the vicinity of the Clyde Sea mooring in 1999 and 2000.

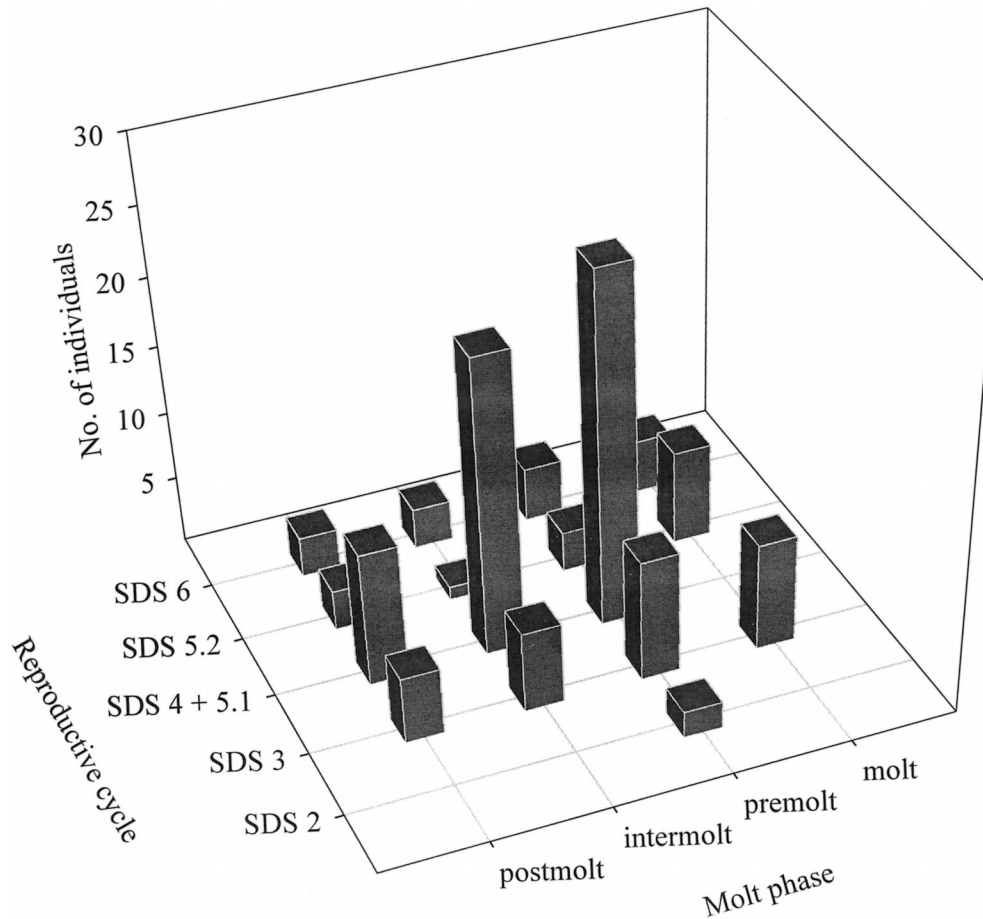


Fig. 4. General distribution of female krill ( $N = 116$ ) scored for molt phases and reproductive stages (SDS 2 to 6, see *Materials and methods* for definition) during the reproductive season. Samples from June 1999, August 1999, March 2000, and May 2000 have been pooled.

*Female molt and reproductive patterns*—Figure 4 shows the distribution of all adult females from samples taken in June 1999, August 1999, March 2000, and May 2000. Ready-to-spawn females (SDS 4 and 5<sub>1</sub>) were mostly either in intermolt or premolt and never in molting condition. Females with vitellogenic ovaries (SDS 3) could be found in every molt stage, as were females with an ovary in oosorption (SDS 6). Taken over the whole reproductive season, 15% of all the females were in molting condition, while 51% were spawning. According to Cuzin-Roudy and Buchholz (1999), the spawning period (SDS 4 and 5<sub>1</sub>) should only comprise 31% of the reproductive cycle of an individual female. In a situation where females spawn every other molt cycle, this means that only 15.5% should be in spawning condition at any one time in a randomly distributed population. The observed percentage of 51% indicates, first, that female spawning periods must have been synchronized and, second, that some of the campaigns coincided serendipitously with these events.

All adult females were engaged in ovarian development as early as March in 2000, irrespective of their body size or whether they had overwintered once or twice (Table 2). The proportion of the female population that was in reproductive condition, i.e., either carrying out vitellogenesis (SDS 3) or

spawning (SDS 4 and 5<sub>1</sub>), varied through the course of the reproductive season (Table 2; right). In June 1999, all females were reproducing, with 79% of those being in spawning condition and the remaining 21% in vitellogenesis or postspawn (SDS 5<sub>2</sub>). Such a significantly high percentage of spawning krill ( $\chi^2$ ;  $p < 0.01$ ) indicates that the campaign had been carried out while a synchronized spawning event was taking place. In August 1999, 40% of the population were spawning, with a significant fraction carrying out their first spawn (SDS 4), as indicated by the large batches of mature oocytes in the ovaries (95% confidence interval for NMO = 560–1,393). Another 50% were in vitellogenesis or postspawn. The remaining 10% of the females were not in reproductive condition, either because the ovary was in oosorption (SDS 6) or because the females were young and in the process of developing their ovaries for the first time (SDS 2). By October 1999, the entire adult population was in reproductive rest, with large adults containing regressed ovaries (SDS 10) as a result of oosorption, while young females had yet to start ovarian development (SDS 1). Almost all females had resumed vitellogenesis and spawning by March 2000, with only 3% still in previtellogenesis (SDS 2). Nevertheless, the presence of females with ovaries in oosorption during spring (20% in March 2000, 14% in May

Table 2. Samples analysis of molt and reproductive development in female krill. The samples of a given campaign have been pooled. BL, body length; M, molting stages; *N*, number of krill; Pr, premolt; Im, intermolt; Pt, postmolt; SDI, population sexual development index; SDS, individual sexual development stage.

Sampling campaign	BL (mm) (95% CI)	<i>N</i> krill	Molt phase (%)				$\chi^2$ (0.05, 2)	SDS (%)						SDI	$\chi^2$ (0.05, 2)		
			Pt	Im	Pr	M		1	2	3	4	5 <sub>1</sub>	5 <sub>2</sub>			6	10
Jun 99	32.7–34.8	54	11	43	46	0	8.96*	0	0	13	29	50	8	0	0	4.5	52.32*
Aug 99	31.5–35.1	20	9	48	29	14	4.74	0	5	25	25	15	25	5	0	4.2	28.10*
Oct 99	30.7–34.1	24	58	29	13	0	33.77*	63	0	0	0	0	0	8	29	1.4	n/a
Mar 00	23.7–28.0	36	28	25	33	14	4.71	0	2	25	25	28	0	20	0	4.4	67.86*
May 00	28.6–30.9	36	20	17	31	32	20.48*	0	0	31	9	26	20	14	0	4.5	4.27

\*Significantly different from a random distribution among stages.

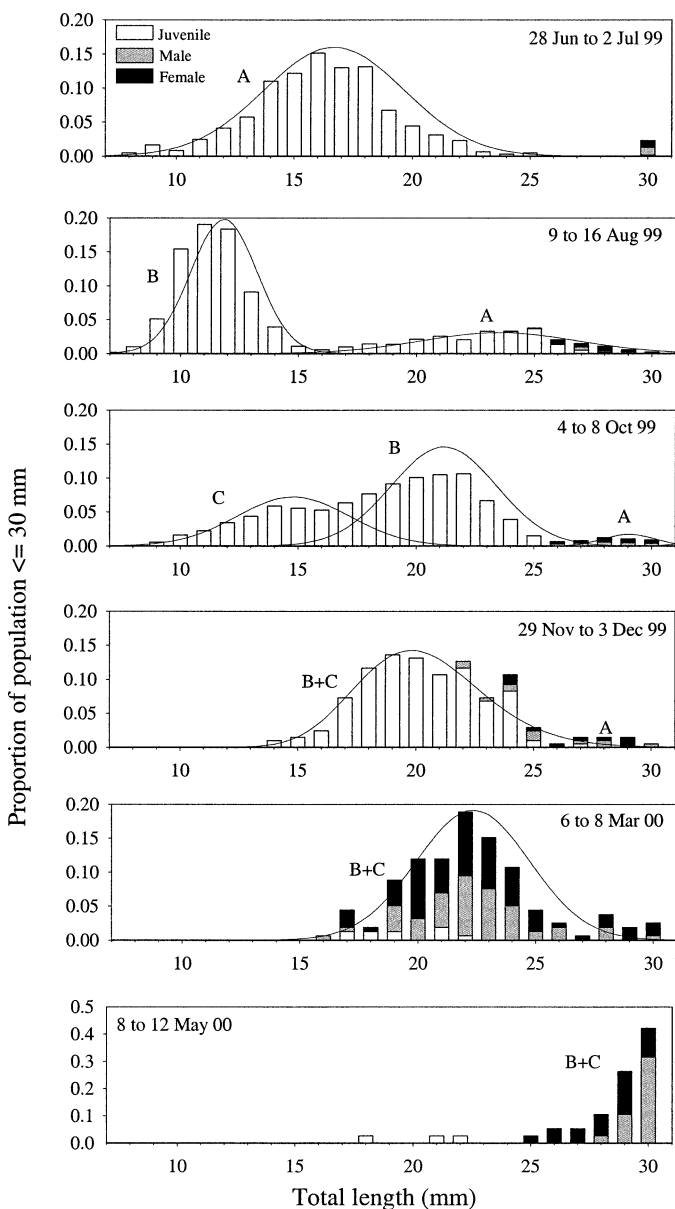


Fig. 5. Length–frequency plots of juvenile krill from each campaign. The juvenile modes A, B, and C were fitted according to the methods outlined in the text.

2000) indicated that a fraction of females did not succeed in maintaining vitellogenesis during this period. The sexual development index (SDI; Table 2), which is the average SDS of the population, was between four and five in June 1999, August 1999, March 2000, and May 2000, indicating that most females were actively reproducing from the spring to late summer.

The distributions of the molt stages in June 1999, October 1999, and May 2000 were significantly different than expected, showing that synchrony was evident at the population level. In the instance of May 2000, the respective reproductive stage distribution did not show a significant difference. However, the functional relationship between the molt and reproductive cycle means that only one of these needs to show a significant difference to indicate population level synchrony (the absence of synchrony in the other being a type II statistical error resulting from the division of stages being too coarse). The distributions of molt stages in August 1999 and March 2000 were not significantly different than expected. However, by the same reasoning as above, the fact that synchrony was evident in the reproductive stages during both campaigns means that the population was synchronized at those times. The only instance where individuals were analyzed outside of the reproductive season was October 1999, where the molt stage distribution was significantly different than expected. This indicates that population level synchrony may persist in the molt cycle even when the functional relationship with the reproductive cycle is no longer present.

*Length–frequency analysis*—Several juvenile cohorts were evident through the course of the year (Fig. 5). The first (cohort A) was identified in the June 1999 campaign with a modal length of 17 mm but with a relatively wide spread (10 to 25 mm). This cohort reached a modal length of 24 mm by August 1999 and 29 mm by October 1999. Cohort B was first identified in August 1999, with a modal length of 12 mm and a much narrower spread than cohort A. The cohort numerically dominated the population through the late summer and autumn, and its growth was more rapid than the first cohort, reaching 21 mm by October 1999. Cohort C was numerically smaller than cohort B but achieved an even faster rate of growth, such that it merged with cohort B by the end of November 1999. As with all the other cohorts, little growth in cohorts B and C occurred through the winter up to March 2000. Growth was rapid the following

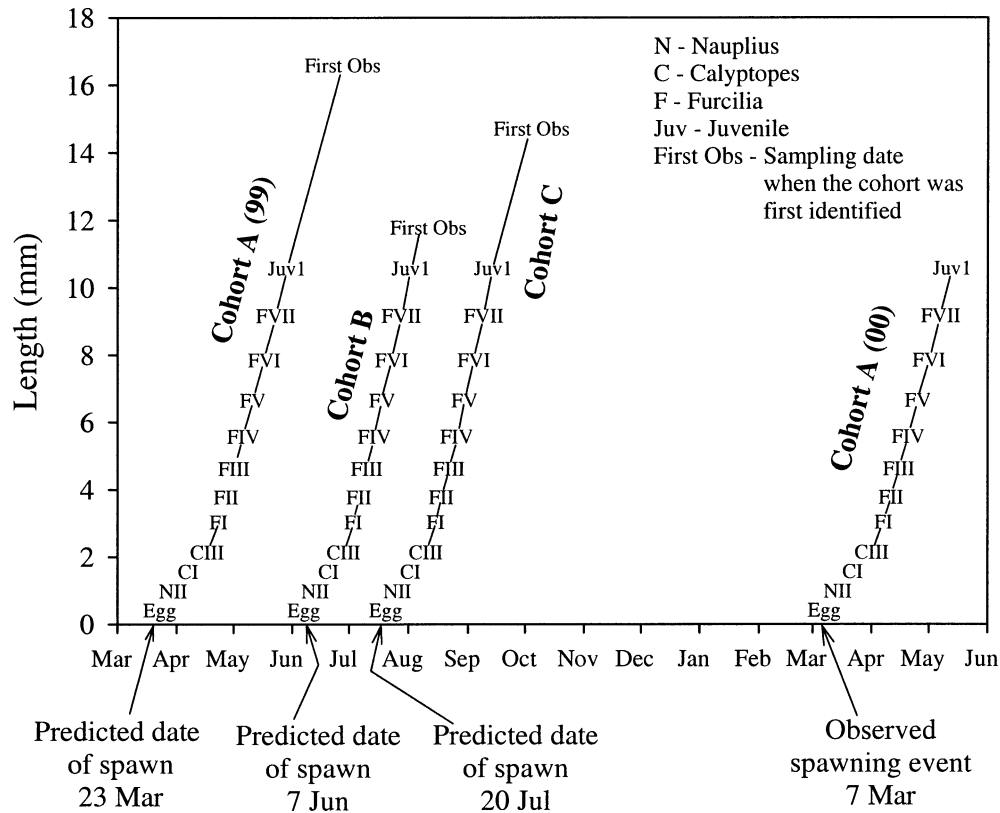


Fig. 6. The growth trajectory and developmental sequence of juvenile cohorts identified from modal analysis. Trajectories were tracked backward from the first observations (First Obs) in the modal analysis to the spawn period (Egg). The rate of development was calculated according to the methods outlined in the text.

year between March and May 2000, with the modal length increasing by 10 mm as juveniles developed into adults. A new juvenile cohort was not found in May 2000, indicating that the equivalent of cohort A did not recruit successfully the following year.

*Back calculation of spawning periods*—The development rates for *M. norvegica* larvae provided by Mauchline (1977) were based on a spring cohort, equivalent to cohort A in the present study. Surface temperature over the period of development of cohort A was 11.4°C. In the two months preceding the first observations of cohorts B and C, the average surface temperature was 13.9°C and 13.8°C, respectively. To accommodate this temperature difference, the developmental rate from nauplius I (NI) to juvenile I (JI) was adjusted as follows:

Development rate for cohort A (NI to JI)	68 d
Using $Q_{10}$ of 2.81	
Developmental rate ( $x$ ) at 10°C higher	$68 \text{ d}/x = 2.81$
	$x = 24 \text{ d}$
Reduction in days for increase of 10°C	$68 \text{ d} - 24 \text{ d} = 44 \text{ d}$
For cohort B	
Increase of 2.5°C relative to cohort A	25% of 44 d = 11 d
Developmental rate for cohort B (NI to JI)	$68 \text{ d} - 11 \text{ d} = 57 \text{ d}$
For cohort C	
Increase of 2.4°C relative to cohort A	24% of 44 d = 11 d
Developmental rate for cohort C (NI to JI)	$68 \text{ d} - 11 \text{ d} = 57 \text{ d}$

Beyond juvenile 1, development occurred according to Eq. 2, which was temperature adjusted in a similar manner to the above. The proportional stage duration remained the same as that provided by Mauchline (1977).

The results of the back calculation are presented in Fig. 6. The likely spawning period for cohort A was around 23 March 1999; cohort B, 7 June 1999; and cohort C, 20 July 1999. Furcilia I peaked in the water column around 23 April for cohort A, 3 July for cohort B, and 15 August for cohort C. Given the significantly high level of spawning activity during the March 2000 campaign, a forward calculation was carried out to predict the modal length of the resulting cohort during a subsequent campaign, 2 months later. Assuming that March 7 was the spawning peak, the cohort would have reached a length of 11 mm by the start of the May 2000 campaign on 8 May 2000.

*Reproductive phase model*—Chl *a* levels rose from the start of February in 1999 and late January in 2000 (Fig. 3), which would probably have initiated previtellogenesis in the ovaries, as this first phase of glycoprotein yolk accumulation in the oocytes must prepare them for cyclical vitellogenesis of successive egg batches. After this, in 1999, a major peak in Chl *a* occurred around 26 February, 26 d before cohort A was spawned. In 2000, the equivalent phytoplankton bloom was almost 3 weeks earlier (~7 February) and a major spawning event was observed during a campaign carried

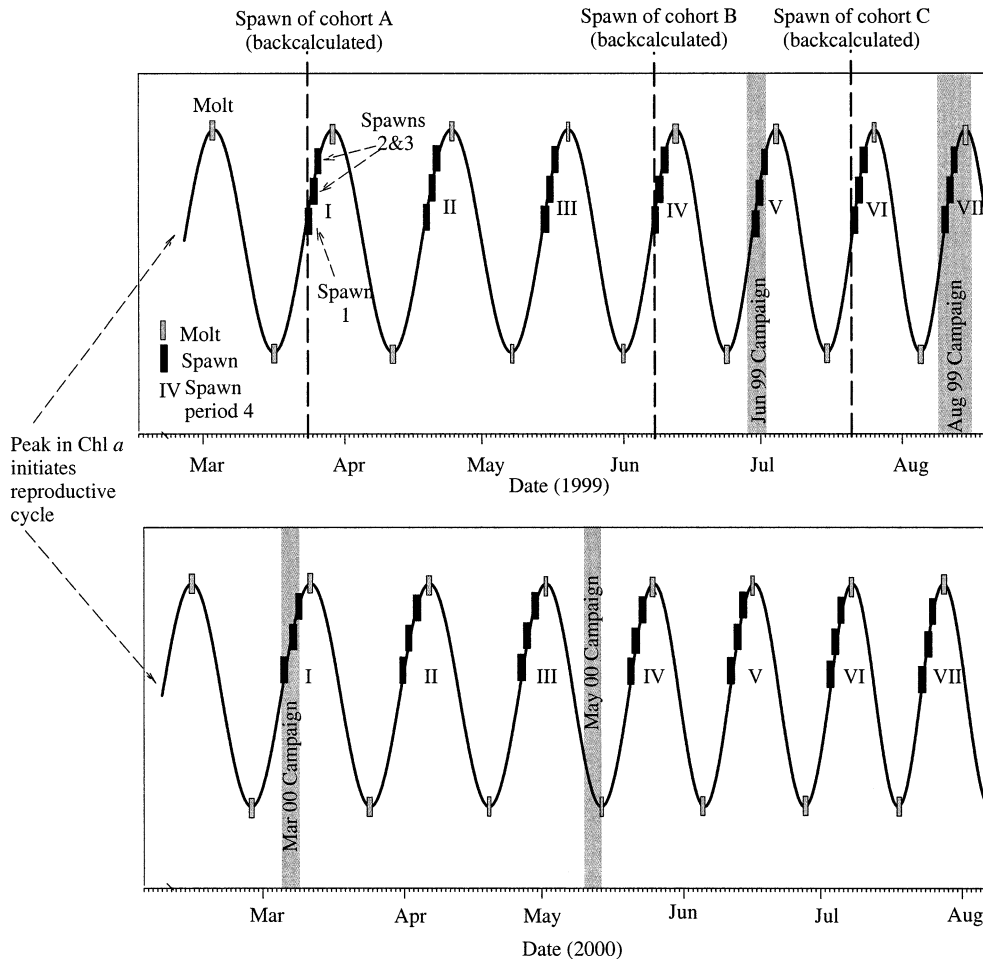


Fig. 7. The predicted periodicity of the reproductive cycle during 1999 (upper) and 2000 (lower). The model assumes that the Chl *a* peak initiates reproduction on 25 February 1999 and 7 February 2000 and that the periodicity of the cycle decreases from 26 d to 20 d as temperatures warm through the year. A full reproductive cycle consists of two molts and one spawning period, itself consisting of up to three spawns. Vitellogenesis takes place between spawning periods. The dates on which the three cohorts identified from back calculation were spawned are superposed as dashed lines.

out 26 d later, on March 4 (Table 2). The delay of 26 d corresponds well with the predicted period of a full reproductive cycle at that time of year ( $2 \times \text{IMP}$  of 13 d = 26 d). The correspondence suggests that reproductive activity started in females in a synchronized manner in response to an enhancement of the phytoplankton food supply. The females developed an egg batch over 26 d, i.e., two molt cycles.

Population level synchrony in the reproductive cycles of adult females continued throughout the reproductive season. It follows that, throughout the reproductive season, some of the time windows in which females became ready to spawn should correspond to the back-calculated birth dates of cohorts. To verify this, it was necessary, first, to calculate the period of the reproductive cycle as it varied with temperature over the reproductive season. Depth-averaged temperature ranged from 7°C to 11°C through the year, which, according to Eq. 1, resulted in IMPs of between 13 and 10 d, respec-

tively. A reproductive cycle was initiated 2 d after the peak in Chl *a* (thus allowing for energetic assimilation) and continued with a period corresponding to the predicted IMP through the course of the reproductive season (Fig. 7). It can be seen that a total of seven spawning periods were predicted before the end of August, with the interspawn period decreasing through the course of the reproductive season from 26 d to 20 d.

The model predicts that the female population would have been actively spawning during both the June 1999 and August 1999 campaigns. The predictions correspond well with observations (Table 2). In June 1999, the majority of females were midway through the spawning phase, with over 50% in SDS 5<sub>1</sub> and a further 37% in the other spawning stage (SDS 4) or postspawn (SDS 5<sub>2</sub>). In August 1999, active spawning was being carried out by 40% of the population, while a further 25% were recently postspawn. Egg batch size was within the range observed for different populations, in-

cluding the Clyde Sea population in early July 1996 (Cuzin-Roudy 2000). A relatively larger fraction was in the vitellogenesis stage (SDS 3) in August compared to June, but it is to be noted that the duration of the August 1999 campaign was relatively longer and covered a larger fraction of the reproductive cycle. The good match between the model and observations is a further indication that the reproductive cycles of females remained synchronized through the course of the reproductive season. It also gives confidence to further predictions on the timing of other spawning periods.

The spawning periods predicted by the reproductive phase model (Fig. 7) matched those of the cohort back-calculation method throughout the reproductive season. In the case of cohort B, for instance, females were predicted to be in ready-to-spawn condition between 7 and 12 June, while the back-calculation method estimated a spawning period around 8 June. Similarly, for cohort C, the reproductive phase method predicted females to be ready to spawn between 20 and 25 July, while back calculations estimated that the cohort was spawned around 20 July. The model also shows that not every reproductive event resulted in successful recruitment. This indeed corresponds with observations, since spawning was observed directly during spawn periods V and VII (i.e., the June 1999 and August 1999 campaigns) and in March 2000, but successful cohorts did not result. The model predicts that the same must have occurred during spawning periods II and III.

Figure 8 shows the Chl *a* environment that would have been experienced by each female reproductive cycle or subsequent larval development stage predicted by the reproductive phase model. At first glance there seems to be little to distinguish the Chl *a* environment that resulted in successful recruitment from that which resulted in failure. In general, successful cohorts arose from situations where the Chl *a* environment experienced by the females prior to spawning was higher than a threshold of around  $1 \text{ mg m}^{-3}$ . However, high Chl *a* levels were present prior to certain spawning periods that did not produce successful cohorts (e.g., spawn period III). Chl *a* levels were also generally high during periods of larval development, especially the early furcilia stages, in those cohorts that were successful. However, the larvae resulting from spawn period V also experienced better than average levels of Chl *a* without achieving success. This indicates that there is more than one critical phase in the production of a successful cohort.

The sequence of events resulting in successful recruitment was investigated by comparing the Chl *a* concentrations experienced by successful cohorts with those that failed (Table 3). First, a comparison of just the three successful cohorts was carried out to find the minimum Chl *a* concentrations experienced by each stage (both vitellogenesis and subsequent larval development stages were grouped to increase statistical robustness). Then, these minima were compared to the unsuccessful cohorts to see whether any of their stages experienced concentrations that were below these thresholds. Assuming that the minima represent the necessary concentration to avoid failure, stages that fell below these minima show where failure probably occurred. The analysis showed that the unsuccessful cohorts experienced below-threshold Chl *a* concentrations during at least one stage of reproduc-

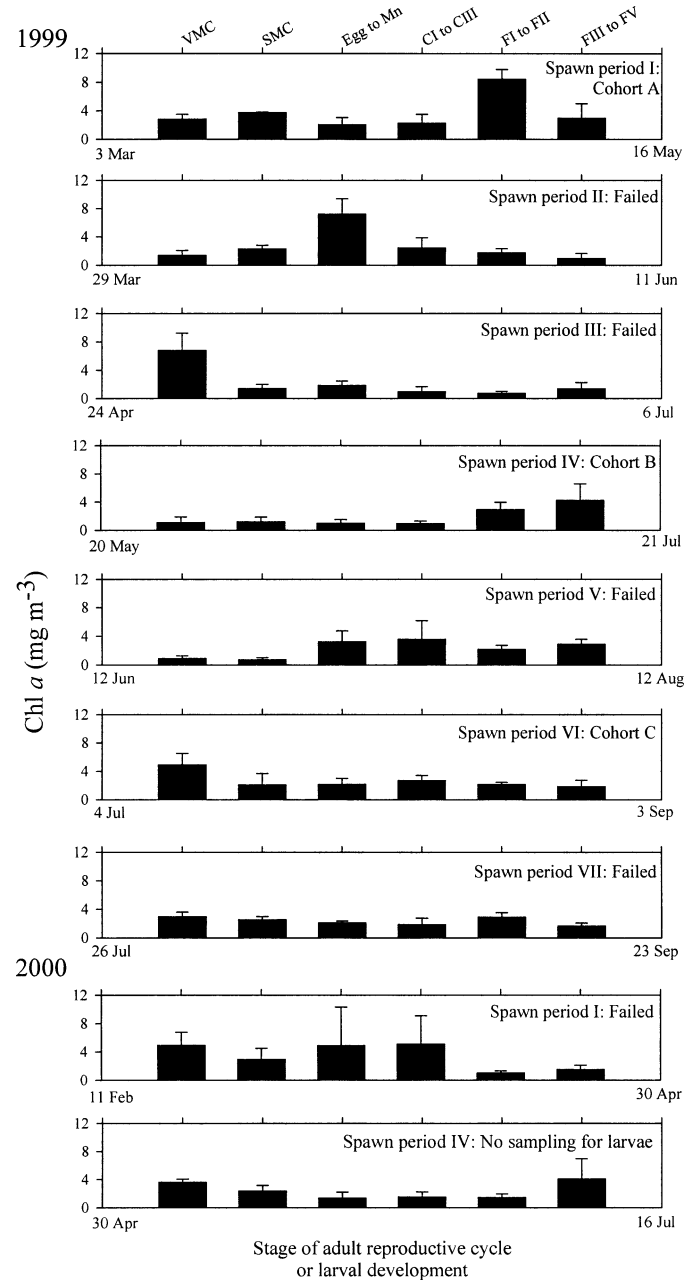


Fig. 8. Average surface Chl *a* experienced by the reproductive stages of females and the developmental stages of their offspring between dates predicted by the reproductive phase model (see text for further details). Error bars denote standard deviation; VMC refers to the first (vitellogenic) molt cycle in the reproductive cycle; and SMC refers to the second (spawning) molt cycle up to the point of spawning; Mn = metanauplius; CI to CIII = calyptopes stages I to III; F = furcilia.

tion or larval development. For instance, although females experienced higher than minimum concentrations of Chl *a* during spawn periods II, III, and VII in 1999 and I in 2000, their furcilia all experienced concentrations that were below the minimum experienced by any successful cohort. These unsuccessful cohorts probably experienced high mortality through starvation at the furcilia stages. By contrast, star-

Table 3. The Chl *a* experienced by reproductive stages of females and the developmental stages of their offspring. The first row of data is the minimum Chl *a* experienced by any of the three successful cohorts (I, IV, and VI). Plus sign denotes where Chl *a* was higher than this minimum; minus sign denotes where Chl *a* was lower;  $\langle \rangle$  denotes where the minimum Chl *a* value occurred in successful cohorts;  $\sim$  denotes where value in an unsuccessful cohort was the same as  $\langle \rangle$ ; CI to CII; calyptopes stages I to III; F, furcilia; Mn, metanauplius; VMC refers to the first (vitellogenic) molt cycle and SMC to the second (spawning) molt cycle of the reproductive cycle; asterisk identifies events that produced successful cohorts.

Developmental stage	VMC	SMC	Egg to Mn	CI to CIII	FI to FII	FIII to FV
Min. Chl <i>a</i>	1.12 mg m <sup>-3</sup>	1.21 mg m <sup>-3</sup>	1.00 mg m <sup>-3</sup>	0.97 mg m <sup>-3</sup>	2.19 mg m <sup>-3</sup>	1.89 mg m <sup>-3</sup>
Spawns 1999						
Period I*	+	+	+	+	+	+
Period II	+	+	+	+	-	-
Period III	+	+	+	+	-	-
Period IV*	$\langle \rangle$	$\langle \rangle$	$\langle \rangle$	$\langle \rangle$	+	+
Period V	-	-	+	+	$\sim$	+
Period VI*	+	+	+	+	$\langle \rangle$	$\langle \rangle$
Period VII	+	+	+	+	+	-
Spawns 2000						
Period I	+	+	+	+	-	-

vation would have been unlikely in the furcilia arising from the unsuccessful spawn period V because the Chl *a* measurements were above the minimum experienced by any successful cohort. However, concentrations prior to spawning were low, suggesting that failure occurred during vitellogenesis. Therefore, there appears to be a sequence of criteria that must be met in order for a cohort to recruit successfully into the subadult population.

## Discussion

This is the first study of euphausiids to have documented a population level temporal synchronization in molt and ovarian development over the whole reproductive season. The molt and spawning stages of some samples of *E. superba* have been found to be relatively homogenous (Buchholz et al. 1996), and some swarms have been observed to spawn in synchrony (Nicol 1984). However, it remains unclear whether *E. superba* swarms sort themselves according to reproductive stage or, as in the present example, remain as temporally synchronized reproductive units over extended periods. Results from campaigns within the reproductive season of *M. norvegica* in the Clyde Sea showed that spawning occurred in late intermolt and early premolt and never in coincidence with actual molt (Fig. 4), which agrees with the model put forward by Cuzin-Roudy and Buchholz (1999; their fig. 4) of the functional relationship between ovarian and molt development. Most Malacostracan crustaceans release their eggs at molting (ecdysis), with the exception of some dendrobranchiate shrimps (peneoids, some sergestoids) and Euphausiacea (Nelson 1991). These latter groups exhibit an alternative reproductive pattern, in which spawning occurs at intermolt and early premolt (as described for *Penaeus indicus*) and not at molting. They possess a fat body that is involved in yolk accumulation and have a capacity for oosorption when resources are limited. Eggs are released freely into the water column, and the resulting planktonic larvae

undergo a relatively long period of development. The combination of this reproductive pattern with such flexible physiology allows krill to cope with the variability of the pelagic environment over their multiyear life cycles.

The initiation of the reproductive season appeared to be triggered by phytoplankton blooms in both 1999 and 2000. This has also been suggested in a number of other studies on euphausiids, especially those occurring in high latitudes (Einarsson 1945; Berkes 1976; Falk-Petersen and Hopkins 1981; Asthorsson 1990; Dalpadado and Skjoldal 1991; Gislason and Astthorsson 1995). The delay of just under a month between the major spring bloom peak and the spawning of the first cohort in 1999 and in 2000 indicates that the krill went through a full reproductive cycle before spawning. Astthorsson and Gislason (1997) investigated the correspondence between Chl *a* and recruitment of *Thysanoessa raschii* and *T. inermis* in sub-Arctic waters north of Iceland. A peak in Chl *a* occurred in late April and was followed by a peak in egg abundance approximately 1 month later (late May). The spawning period corresponded to subsequent pulses of calyptopes and furcilia. The delay of approximately a month between the bloom and the appearance of eggs in the water column suggests that euphausiids in this study also went through a full reproductive cycle before spawning.

Although *M. norvegica* is generally considered as carnivorous (Falk-Petersen et al. 2000), Virtue et al. (2000) detected relatively high levels of a diatom fatty acid marker in the triacylglycerol fatty acids of the Clyde Sea krill in summer. Lass et al. (2001) also found high levels of phytol, diatom fatty acid, and sterol markers in stomach content extracts that coincided with very high chlorophyll levels in the water column of the Clyde Sea during early July 1996, when females were producing eggs (Cuzin-Roudy 2000). This suggests that phytoplankton blooms are necessary for the maintenance of yolk accumulation in successive egg batches during the whole reproductive season, which fits with the observation, in the present study, that successful cohorts

were spawned at the next reproductive cycle following a bloom. Furthermore, in instances where phytoplankton levels had not peaked recently (e.g., May 2000), oosorption was observed in the ovaries, indicating that some females needed to recover resources from the energy-rich ovaries to meet metabolic demands. Euphausiid eggs must contain all the necessary resources for the larva to pass through nonfeeding stages after hatching, so it is likely that vitellogenesis only occurs when resources are optimal and eggs can be conditioned appropriately.

The presence of ready-to-spawn females in the Clyde Sea during March, May, June, and August samples indicates that reproduction in *M. norvegica* in the Clyde Sea took place continuously over a period lasting at least 6 months. In 1957, Mauchline (1960) noticed reproductive activity in this region only in the early summer. The difference illustrates the degree of interannual variability in female reproductive activity, which must, in part, be related to variability in their trophic environment. In *Euphausia pacifica*, for example, increases in phytoplankton have been shown to be associated with the timing of egg release throughout its range (Brinton 1976; Ross et al. 1982). The spawning intensity in *Nyctiphanes australis* was shown by Ritz and Hosie (1982) to be related to optimum food supply. However, phytoplankton may not be the only cue. In *Euphausia lucens*, a major spawning event took place prior to the onset of the upwelling that causes the spring phytoplankton bloom (Barange and Stuart 1991). In that instance, the animals relied on stored lipid reserves to develop the oocytes.

The condition of the female is not the sole factor affecting the success of cohorts, as was observed by the failure of the cohort spawned in March 2000, following a phytoplankton bloom in February. The strength of a larval cohort showed a distinct correspondence to the level of Chl *a* during the period of early furcilia stage development. The early furcilia stages of each of the three successful cohorts in 1999 developed at the start of or within phytoplankton blooms, whereas some cohorts that were unsuccessful experienced low or decreasing levels of Chl *a* during the furcilia stages (e.g., spawn periods II, III, and VII). Feeding conditions during the calyptopis stages appear to have less influence on the success of a cohort, since phytoplankton levels varied greatly between successful and unsuccessful cohorts and were indeed extremely high during the calyptopis stages of the unsuccessful cohort spawned in March 2000. Rumsey and Franks (1999) found that variability in the duration of the furcilia stage 1 and 2 in *E. pacifica* was responsible for the high mortality in larval development and hence overall recruitment success. The reasons for this could be that the pleopods and gills develop during this stage together with higher oxygen consumption and growth rates. These higher energy requirements may reduce the carrying capacity of the environment with respect to the density of larvae that can be maintained when resources are limited. The fact that mortality may be particularly high in larval stages that occur some time after initial spawning means that the abundance and condition of eggs and the consequent success of the cohort may show little relationship. Such a lack of correspondence has been noted in other species, such as *Thysanoessa spinifera* (Tanasichuk 1998a) and *Euphausia pacifica*

(Brinton 1976). However, it is likely that there is a selective pressure to optimize the spawning strategy to maximize the potential for subsequent recruitment success. In *Euphausia superba*, for example, Hofmann et al. (1992) suggested that there was an offshore migration of gravid females that exploit a deep temperature inversion in order to optimize the early larval developmental regime. The spawning of *E. lucens* before the onset of the phytoplankton bloom (Barange and Stuart 1991) is a strategy that ensures larvae hatch during a period of high food supply.

In order for *M. norvegica* to produce a successful cohort, two conditions must be met. First, a phytoplankton bloom precedes a synchronized spawning period, allowing females to build up enough resources to invest in vitellogenesis. Second, phytoplankton levels are sufficiently high during the critical early furcilia stages of development to meet their metabolic demands. The requirement to match the development of critical larval stages with appropriate feeding conditions, such as phytoplankton blooms, makes the risk that any one cohort might fail particularly high. This is especially so in the Clyde Sea, where the timing of phytoplankton blooms is notably variable, as is evidenced by the 3-week difference between the principal spring blooms in 1999 and 2000. Producing pulses of eggs intermittently over an extended reproductive period is a strategy that evens out the risks of any one cohort failing. Such a strategy also appears to be employed by *Euphausia pacifica*, where four pulses have been observed in a single year off California (Brinton 1976) and six off British Columbia (Tanasichuk 1998b).

Pulsing spawning periods is a risky strategy with high rewards, since, if it is timed correctly, the numbers of individuals that will benefit will be many orders of magnitude higher. Reproductive synchrony of individuals at the population level has other benefits, especially in terms of minimizing predation on vulnerable larvae (Ims 1990). A sudden mass appearance of prey in a vulnerable stage may satiate the predator population and thereby reduce the fraction of the prey population taken by predators (Reaka 1976). The synchronized behavior of spawning females may minimize predation on adults in a similar fashion.

It is difficult to determine a process by which pelagic animals such as krill may maintain reproductive synchronization over extended periods at the population level. External *zeitgebers* are unlikely since the length of molt and reproductive cycles does not seem to conform to any lunar or solar cycle. Chemical induced signals (Oh and Hartnoll 2000) or communication through photophores (Fregin and Wiese 2002) might play a coordinating role in species with a swarming behavior like krill, but direct evidence of their influence on physiological cycles is still lacking. It is also possible that there is no signaling between individuals but, instead, each individual is constrained in the same way by environmental variables. Temperature has a strong influence on molt rate, which in turn dictates the periodicity of reproductive cycles. If the females start the reproductive cycles together, such constraints may reduce individual variability in the timing of all subsequent molt and reproduction events.

Overall, this study has shown for the first time that spawning activity in northern krill starts at the same time for all the adult females in response to the early spring phytoplank-

ton bloom and remains synchronized for the entire reproductive season. The consequences are that egg release is pulsed and up to seven cohorts may potentially be produced in any one year. The eventual recruitment strength of each cohort depends both on adequate conditioning of the female prior to the spawn and suitable trophic conditions during larval development, especially during the furcilia stages. It is believed that this model is applicable throughout the distributional range of this species and is also appropriate with respect to other euphausiid species that experience seasonal and/or variable trophic conditions.

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