Phenology in *Calanus finmarchicus*; hypotheses about control mechanisms

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ABSTRACT: *Calanus finmarchicus* (Gunnerus) stratify narrowly near 500 m depth during their fifth copepodite resting phase in North Atlantic Slope Water off southern New England, USA. They probably achieve this by migration to a specific, daytime isolume. Photoperiod information provided by light intensity at depth could serve as a cue for termination of the resting phase. Population data on tooth formation and gonad growth show that the resting stock prepares for termination in late winter and matures in February–March. Photoperiods are lengthening throughout that seasonal interval, and might cue arousal. An endogenous, 'long-range' timer that cues arousal after an interval of rest is another possible mechanism.

INTRODUCTION

Phenological features, particularly resting stages, do not receive sufficient attention in marine pelagic ecology, which tends to be distracted by trophic dynamics. Phenology is much more amenable to rapid evolution than are the acceptable temperature and nutritional ranges of a species. If temperature varies widely in a copepod's habitat, it is far easier for selection to adjust the time for taking refuge from conditions too warm or too cold (a matter of a few gene changes) than it is to adjust the whole metabolism and stay active, which requires gene changes in almost the entire metabolic machinery (Hochochka & Somero 1984). Equally, a species can more rapidly adjust to a change in the timing of predatory activity by changing its rest timing, than it can by enhancing escape behavior, population dynamical parameters, or other strategies. Thus, it is to be expected that species will achieve local adaptation over broad geographic ranges primarily by adjusting their phenology. This is fully established for insects (Tauber et al. 1986). Some work has been done on such evolution to maintain appropriate temperature ranges in marine copepods that produce resting eggs (Marcus 1984, Uye 1986), and changes of timing to escape from predators have been fully established in limnetic cyclopoids (Nilssen 1980) and diaptomids (Hairston 1987, Hairston & Olds 1987).

Another way of expressing the importance of resting stages is to say that they allow the animal to focus its 'reproductive potential' at the times of year when it will be most productive of surviving offspring. 'Reproductive value' (sensu Fisher 1930) often can be protected best by going to a dark hiding place for a portion of the life cycle. Many species do this (Tauber et al. 1986). Theoretical analysis (Caswell 1982) suggests that long-term payoffs are to be expected for such life history strategies. Models of copepod population processes would be much more satisfying if we had a clear understanding of the basic biology of resting phases. As shown below, resting phase mechanisms can be expected to be regionally and habitat specific. They are key enabling features in regional adaptive complexes, differing according to varying habitat demands.

Phenology in calanoid copepods

Life histories of mid- and high latitude, marine, calanoid copepods often include a resting phase. *Acartia*, *Tortanus*, and several other heterarthrandrid genera produce diapause eggs. In the Calanidae and related families (all among the amphascandrids) there is a quiescent phase, or possibly a true diapause (Elgmork & Nilssen 1978), at one or more of the copepodite stages. There has been research on both types of rest-

ing stage, and for resting eggs this has included some work on the events in the habitat that trigger diapause egg production (Johnson 1979, Marcus 1982, Sullivan & McManus 1986) and on conditions allowing hatching of such eggs (Uye & Fleminger 1976). Much less has been done with copepodite resting stages. Conover (1988) has reviewed work on the family Calanidae. Field studies show the seasonal timing of the resting phase and the range of the accompanying ontogenetic vertical migrations. However, there is little work on the mechanics of dormant phase onset or termination comparable to that for species with diapausing eggs.

A start on experimental work with *Calanus finmarchicus* was made by Grigg & Bardwell (1982). We want to amplify the implications of their results here. There is some work on freshwater Cyclopoida, which also have copepodite resting stages. In particular, Watson & Smallman (1971a, b) have shown that photoperiod, interacting with temperature, controls onset and termination of a diapause phase in several species of *Diacyclops*. We propose that in *Calanus finmarchicus*, as in *Diacyclops*, termination of the resting phase could occur in response to changing photoperiod. We argue that photoperiod information is available to the animals, despite the depth in the ocean at which the resting phase is spent. Other hypotheses are also open, particularly the possibility that an endogenous, long-range timer (Saunders 1982) cues arousal after an interval of months regardless of external factors.

Knowledge of resting phases gives us strong insights about what matters to animals in their commerce with their habitat. As a means for escape from harsh circumstances, resting phases, often spent in refugia, are essential to survival. We must understand them to interpret ecological relationships and evolutionary history. Mechanisms of the resting phase probably differ among the Calanidae dominant in different regions (reviewed in the 'Discussion'). Thus, these are key adaptive variations for survival in habitats with different challenges.

Phenology in *Calanus*

The 'classical' phenological sequence in *Calanus* is that of *Calanus finmarchicus* as originally demonstrated in the Clyde Sea by Marshall et al. (1934) and in the Gulf of Maine by Bigelow (1926) and Fish (1936). Arctic data are provided by Tande (1982). In summer or early autumn individuals reaching the fifth copepodite stage (C5) load their oil sacs with lipids (known to be wax esters) and descend to depths greater than 200 m (Williams & Conway 1988; present data), unless stopped by the bottom (Herman et al. in press) or an anoxic layer (Alldredge et al. 1984). Resting animals have empty guts with reduced epithelia (Hallberg & Hirche 1980) and negligible or strongly reduced digestive enzyme activity (Tande & Slagstad 1982, Hirche 1983, 1989). They move very little, exhibiting no hop-sink behavior. In some localities they have been reported unresponsive to poking (Hirche 1983), but we have observed that resting C5's in the Firth of Clyde and Gulf of Maine are always very responsive and will make strong escape jumps. Observations of feeding and substantial respiratory activity (Marshall & Orr 1958, Butler et al. 1970, Corner et al. 1974) are all from specimens collected well above the usual depth zone for the resting phase, or the individuals used may have been disturbed from their rest during experimental measurements (see below). In winter, 1 to 3 mo after the solstice, the resting C5's molt, mature, and mate. The females move to surface layers, feed, and spawn. Development follows and *C. finmarchicus* completes 1, 2, or more generations before a late spring or summer generation re-enters dormancy. *C. helgolandicus* completes up to 5 generations from February to August (Williams 1985).

Dormancy induction and termination in *Calanus finmarchicus*

We can find no reports of experimental studies of the factors inducing the resting phase. For dormancy termination, the arousal phase, experiments by Grigg & Bardwell (1982) suggest for *Calanus finmarchicus* and *C. helgolandicus* that there is a direct effect of light. They demonstrated that any time in the resting season *C. finmarchicus* are collected, sorted and held in dim, blue light they will begin the terminal molt after a 10 d lag (Fig. 1). In one tiny experiment some members of a group held in the dark did not molt for about 30 d (Table 1). These chance data suggest that light stimulates dormancy termination. It remains to protect the C5's from exposure to light before holding begins and to hold them under various illumination regimes.

Some similar experiments on maturation molts have been done by Hirche (1989). In June and August in the Fram Strait and Greenland Sea he sorted groups of C5 of *Calanus finmarchicus* from collections taken above 100 m, a horizon in which digestive enzyme activity was higher than for C5 from 200 to 500 m. The groups were held in the dark apart from checking for molts at regular intervals by sieving. There was typically a 20 to 30 d interval before substantial molting, which then proceeded rapidly. It is not clear that these specimens from above 100 m were resting, so it is uncertain whether the observed molts involved arousal from the rest phase.

In the field *Calanus finmarchicus*, *C. helgolandicus*,

and *C. pacificus* (at various sites) all appear to mature over a rather brief interval centered on February. Since they remain at depth until they mature (or mature very shortly after rising), it is not clear how they could receive a dose of light in mid-winter comparable to that in Grigg & Bardwell's (1982) laboratory treatment. We now show some new data on the depth distribution of the resting phase off New England. Coupling these data to (1) morphological evidence on the timing of premolt development and (2) a consideration of light intensity cycling at mid-depth allows us to argue that arousal could be induced by lengthening photoperiod. Other mechanisms are also feasible, including an endogenous, long-range interval timer.

METHODS

Vertically stratified net collections were made in the upper 800 to 1000 m of the North Atlantic Slope Water during darkness at roughly monthly intervals from 29 April 1981 until 15 March 1982, with additional samples in May and June of 1982 (Table 2). Station locations were generally south of New England, USA, and were selected with the aid of satellite sea surface temperature images so as to avoid warm-core rings from the Gulf Stream. For all dates the 10 °C isotherm was above 200 m, an indicator of slope water proper. The sampler was the MOCNESS multiple net system (Wiebe et al. 1985). Hauls were subsampled by splitter, and abundances were estimated separately for females, males, fifth copepodites (C5's), and fourth copepodites (C4's)

Table 1 *Calanus finmarchicus*. Experimental results from Grigg & Bardwell (1982). Numbers of adults and C5 individuals recovered from experimental containers after an incubation period at the habitat temperature. All but one batch (marked*) were held in continuous light. Other details in Grigg & Bardwell (1982)

Date	Duration (d)	Food	Initial no. C5	Males	Females	C5
14 Nov	26	Absent	55	12	41	2
		Present	72	17	54	1
11 Dec	29	Absent	58	6	52	0
		Present	59	11	48	0
11 Dec	29	Absent	20	7	13	0
		Absent*	35	7	22	6[a]
16 Jan	23	Absent	58	13	44	1
		Present	60	17	42	1

[a] The reduced fraction maturing in this group held in darkness is a key observation. It is not statistically significant. However, it is reasonable to suppose that fully eliminating illumination would increase the fraction not molting
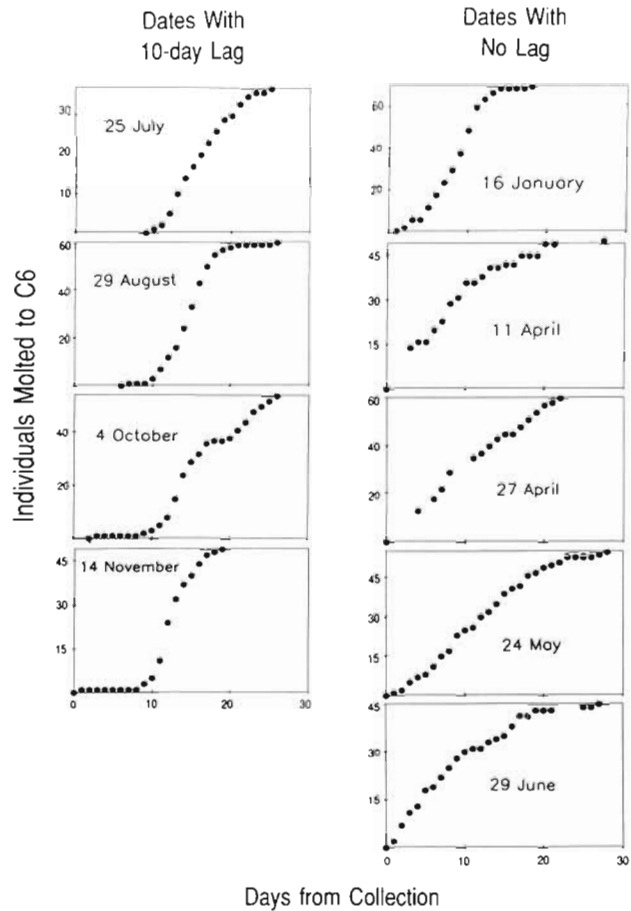

Fig. 1 *Calanus finmarchicus*. Cumulative fraction of individual C5 molted to C6 at progressively later times following collection and distribution into containers held at constant, low illumination. Note particularly the 10 d lag to first molting from 25 July through 14 November. Redrawn from Grigg & Bardwell (1982) by combining males and females, fed and unfed groups for each date. See the original for experimental details

of *Calanus finmarchicus*. Since the resting phase occurs during C5, this is sufficient detail for determination of its timing and vertical location.

Fifty to 60 specimens of C5 were sorted for morphological examination from the single sample at the abundance peak for each sampling date. Since during the resting phase at depth the C5's were mostly captured in a single MOCNESS sampling horizon, these samples represent the status of the stock. For spring months when C5 were abundant both at the resting depth and near the surface, specimens were examined from both peaks. We dissected and examined the mandibular gnathobases to determine the development phase of new teeth (Miller & Nielsen 1988). Since teeth are the part of the copepod exoskeleton requiring most time to form, their state of development in the C5 gives an early indication of forthcoming ecdysis. Moreover, as reported by Miller & Terazaki (1989) for *Neocalanus*

Table 2. Station locations of MOCNESS hauls and depth intervals sampled in the North Atlantic Slope Water time series study. MOCNESS tows taken April through August were sampled in 100 m intervals from 8 to 800 m except for MOC-1-134 that sampled 800 to 600 m, 100 m intervals from 600 to 100 m, 100 to 50 m and 50 m to the surface. The remaining 9-net tows, October through March, were sampled in 150 m intervals from 1000 to 400 m and in 100 m intervals from 400 m to the surface. One net in each 9-net tow was open while shooting the net. The three 20-net tows fished from 1000 to 200 m in 100 m intervals and from 200 m to 0 m in 25 m intervals. Two nets were used to balance the system during the tow, one while shooting and the other while hauling

Date	Tow no.	Lat.	Long.	No. of nets
29 Apr 1981	MOC-1-133	39° 48'N	69° 57'W	9
13 May	MOC-1-134	39° 47'N	69° 58'W	9
29 May	MOC-1-135	39° 37'N	71° 00'W	9
29 Jun	MOC-1-136	39° 40'N	70° 58'W	9
28 Jul	MOC-1-137	39° 45'N	71° 00'W	9
19 Aug	MOC-1-138	39° 45'N	71° 00'W	9
3 Oct	MOC-1D-145	40° 15'N	65° 57'W	20
27 Oct	MOC-1-148	39° 39'N	71° 00'W	9
23 Nov	MOC-1-149	39° 34'N	71° 02'W	9
13 Dec	MOC-1-151	39° 11'N	70° 02'W	9
5 Jan 1982	MOC-1-152	39° 41'N	71° 07'W	9
8 Feb	MOC-1-153	39° 38'N	69° 40'W	9
15 Mar	MOC-1-158	39° 57'N	68° 34'W	9
2 May	MOC-1D-175	39° 28'N	70° 57'W	20
16 Jun	MOC-1D-177	39° 56'N	71° 32'W	20

spp., the resting phase retains the so-called 'postmolt' facies until termination of diapause. This is, then, an independent indication of the resting state in individuals living at great depth.

We classified the jaws of individuals according to the tooth development phases defined in Table 3. Postmolt and 'Late Postmolt' phases are not sharply distinct and could perhaps have been combined. However, there are distinctions among samples in the proportions of these phases, so we have retained them. The samples of 50 to 60 are small, which was necessary to make the large number of inter-sample comparisons possible. Sample size was adequate to show statistically significant and reasonably interpreted differences between dates.

We measured and determined the sex of developing gonads when they were visible without staining. The smallest anlagen require staining to be seen and measured, as was done by Tande & Hopkins (1981). For the 8 February and 15 March samples, in which the gonads were large and obviously maturing, we made prosome length measurements, gonad measurements, and gonad sex evaluations in samples of 300 individuals. Prosome length was measured to check the observation by Grigg et al. (1985) that male C5 are on average

Table 3. *Calanus finmarchicus*. Definitions of molt cycle phases based on status of the hemocoele and of tooth development in the mandibular gnathobase. These vary slightly from Table 1 in Miller & Nielsen (1988), which includes micrographs of gnathobases in these stages

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Postmolt:	The hemocoele extends into the expanded, distal part of the gnathobase. It is seen as a large empty space between the epidermal tissue and the anterior exoskeleton
Late Postmolt:	The hemocoele is still visible in the gnathobase, but it only extends into the isthmus portion
Intermolt:	No sign either of hemocoele or of differentiation in the cytoplasm at the distal ends of the epidermal cells within the gnathobase. No apolysis space evident
Premolt:	Showing any of several phases of new tooth development. This includes apolysis, presence of tooth molds in the ends of the epidermal cells, and full development of teeth ready for ecdysis
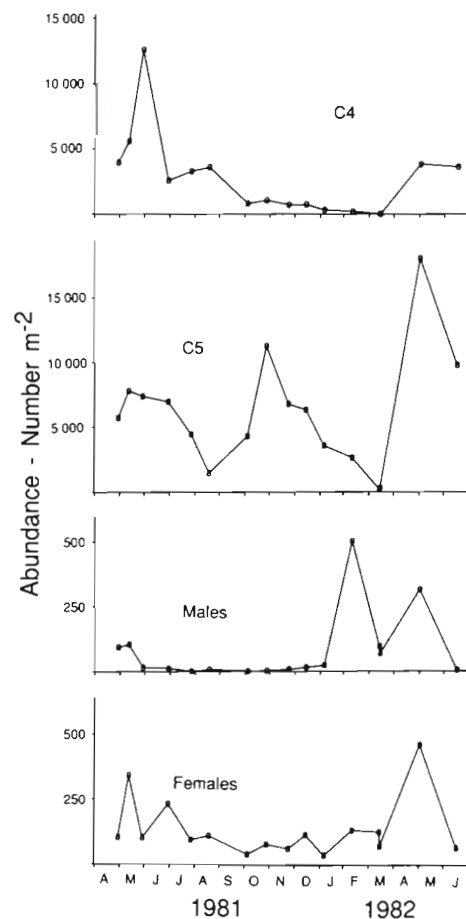
Fig. 2. *Calanus finmarchicus*. Integrated (0 to 800 m, or 0 to 1000 m) abundance estimates for several life stages derived from MOCNESS samples collected over the continental slope southeast of Cape Cod (Massachusetts, USA)

larger than female C5. Testes are distinguished by fine granular texture, and a single duct emerging at the anterior end of the gonad then bending left and posteriorly (see Tande & Hopkins 1981 for figures). Ovaries close to maturation have paired anterior diverticulae and (usually) oviducts visible along the sides of the thorax. Ovaries at an earlier stage have a coarsely granular texture. Many gonads, even those over 0.5 mm long, were not yet distinguishable as to sex.

RESULTS

Abundance and depth distribution

Abundance of the life cycle stages of *Calanus finmarchicus* oscillated seasonally during the study (Fig. 2). Fourth copepodites were most abundant in May–June, and present in smaller numbers through August. Fifth copepodites were usually present in excess of 4000 m^{-2}. There was an unexplained dip during August. From autumn through March there was steady decline in the stock, which mostly was at depth in the resting phase (see below). The decline must have been due to a combination of dispersal into offshore waters, mortality, and molting to C6. The final decline in February and March can be attributed to molting to the C6, since the stocks of first males (8 February) and then females (late April–May of both years) peaked then. The 15 March 1982 sample was taken close to Gulf Stream warm-core ring 82-B, so that abundance may have been lower than for Slope Water generally.

Abundance of adults was low from summer through mid-winter (Fig. 2). The C5 had an essentially inverse pattern, being the dominant stage in summer and autumn. In Slope Waters, as elsewhere, the C5 clearly is a resting phase. They molt to C6 in February–March, and the resulting adults reproduce. Development of their offspring occurs in late winter to spring with return to C5 by May–June.

From May through February the C5 stayed remarkably close to 500 m (Fig. 3). Typically there was a very strong mode, well over half the population, in the single sample that included 500 m. Several vertical profiles (Fig. 4) illustrate the narrow stratification of the population, especially during the later parts of the rest phase. Given the 100 to 150 m thickness of the sampling strata, the centering of the population may well have been even more pronounced than our data can show. During the period when most individuals are resting as C5, there were always some younger copepodites and some females present. These also centered between 400 and 600 m (Fig. 3). Occupation of near-surface layers was restricted to March through May for all stages. Accurate distribution patterns were

difficult to determine for males because of their low abundance. However, when they were numerous in February and March 1982, they too clustered around 500 m. In April 1982, the center of the male population was shallower.

Development

Fifth copepodites from shallow, spring samples had greater proportions of 'Late' Postmolt and Intermolt
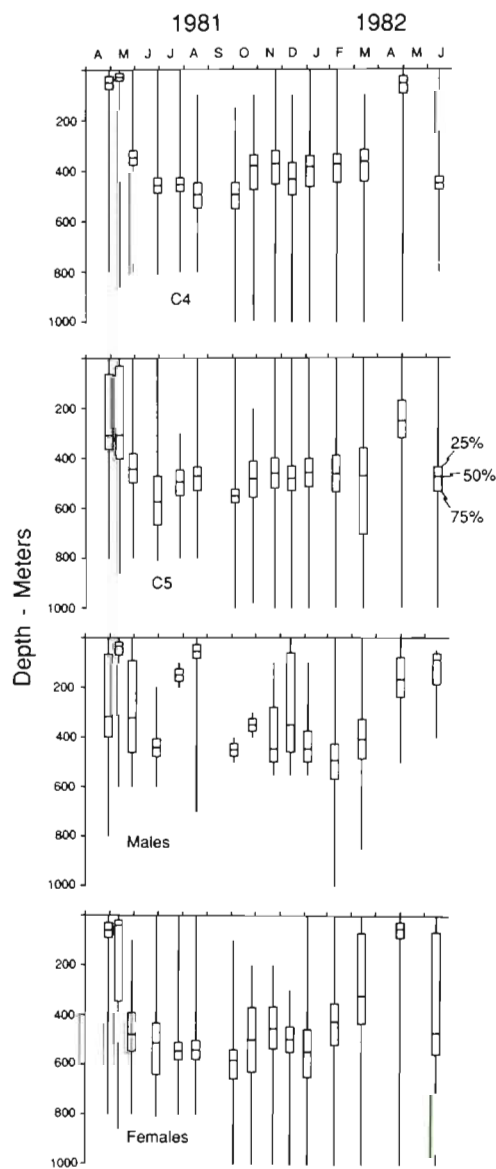

Fig. 3. *Calanus finmarchicus*. Vertical distributions of life stages. For each date in 1981–1982 the vertical lines represent the range of all captures. The boxes extend from the depth below which 25 % of the population was found to that above which 75 % was found. The crossbar in the box is at the median population depth

individuals than those from deep samples, except for November, February and March (Table 4). Since jaws of C5 from around 500 m in mid-summer so strongly
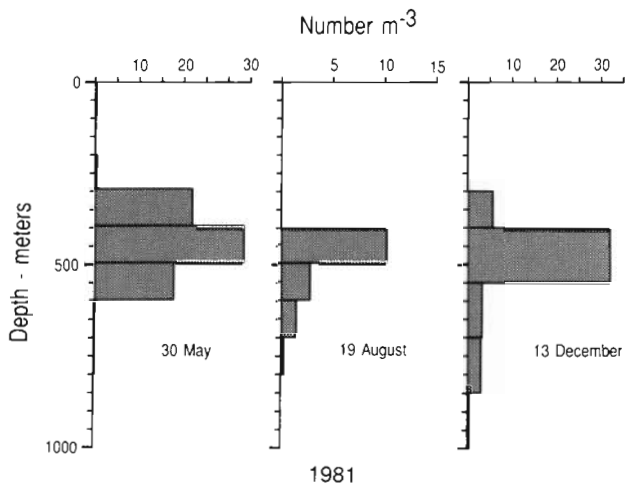

Fig. 4. *Calanus finmarchicus.* Three examples of data derived from MOCNESS samples showing the depth distribution of resting phase copepods. There is consistently a very strong mode in one sample

retain the Postmolt facies, we suspect that the substantial fraction of near-surface C5's with Late Postmolt and Intermolt facies in late April or May were proceeding with development. There is no sign in the present data set that spawning by these adults produces another, complete generation.

Gnathobases of C5 from the deep samples of summer were nearly all in Postmolt or 'Late' Postmolt phase. This agrees with Miller & Terazaki's (1989) observations for *Neocalanus* spp. Samples for late autumn and winter did not progress monotonically from lesser to greater fractions developing teeth. The 400 to 550 m samples for 23 November and 13 December show progress in proportions with late postmolt and intermolt facies, but that for 5 January has proportions like the mid-summer samples. The gonad data (see below) suggest that the November specimens were more advanced than either the December or January ones. There is surely local variability in such development, and we make no claim to be repeatedly sampling exactly the same population. We can only look for general trends. Both February and March samples showed by far the highest proportions of premolt indi-

Table 4. *Calanus finmarchicus.* Jaw development phase determinations for C5 from the Slope Water sample series

Date	Depth (m)	No. of specimens with jaws in given phases:				
		Postmolt	'Late' Postmolt	Intermolt	Premolt	Total
Shallow samples						
29 Apr 1981	0–100 m	13	18	28	0	59
12–13 May	0–50	13	31	16	0	60
29 May	0–100	1	1	1	1[a]	4
2 May 1982	0–75	24	22	14	2[b]	62
29 Jun	50–75	9	0	1	0	10
Deep samples						
29 Apr 1981	400–500	40	13	1	1[b]	55
12–13 May	400–500	41	13	1	0	55
29 May	400–500	51	9	0	0	60
29 Jun	500–600	53	0	0	0	53
28 July	400–500	47	5	0	0	52
19 Aug	400–500	46	8	1	0	55
3 Oct	500–600	58	2	0	0	60
27 Oct	400–550	51	9	0	0	60
23 Nov	400–550	40	19	0	2[c]	61
13 Dec	400–550	21	3	36	0	60
5 Jan 1982	400–550	53	6	1	0	60
8 Feb	400–550	16	17	9	13[d]	55
15 Mar	400–550	31	3	10	11[e]	55
2 May	400–500	54	4	0	0	58
29 Jun	400–500	50	2	0	0	52

[a] 0.43 mm ovary
[b] No gonads visible
[c] Both with gonad > 0.5 mm; both identifiable as testes
[d] 10 with gonad > 0.5 mm; 7 identifiable as testis
[e] 8 with gonad > 0.5 mm; 6 identifiable as testis, 1 as ovary

Table 5. *Calanus finmarchicus*. Gonad size in C5 from the Slope Water sample series. Gonads were first visible in the sample of 23 November. There were again none on 13 December January, February, and March samples had increasing proportions of large gonads and gonads identifiable as testis or ovary

Date	No gonad	< 0.2 mm	0.2–0.3	0.3–0.4	0.4–0.5	> 0.5 mm
Smaller samples from all dates with significant number of visible gonads:						
27 Oct 1981	60	0	0	0	0	0
23 Nov	4	9	15	15	15	3
13 Dec	60	0	0	0	0	0
5 Jan 1982	9	4	10	13	16	7
8 Feb	2	5	6	9	12	19
15 Mar	4	7	6	13	7	14

Date	No gonad	< 0.2 mm	0.2–0.3	0.3–0.4	0.4–0.5	> 0.5 mm
Larger samples from 8 Feb and 15 Mar 1982:						
8 Feb 1982	11	30	28	49	58	117
Percent	4	10	10	17	20	40
15 Mar 1982	33	43	38	64	43	67
Percent	12	15	13	22	15	23

Gonads < 0.3 mm were all undifferentiated. Some gonads in larger categories are distinguishable as testes or ovaries:

Date	Status	0.3–0.4	0.4–0.5	> 0.5 mm
8 Feb 1982	Testis	2	14	51
	Ovary	8	21	44
	Undiff.	39	23	22
15 Mar 1982	Testis	4	11	21
	Ovary	8	14	38
	Undiff.	52	25	8

Gonads > 0.5 mm showed a significant contingency between sex and date: χ^2 (2 df) = 6.29; p < 0.05

viduals[*]. Thus the tooth development data are consistent with strong onset of arousal from the C5 resting phase in February. Observed tooth development does not, however, suggest that arousal is sharply simultaneous for stocks distributed in the Slope Water off southern New England.

None of the deep samples from spring through 27 October had any specimens with visible gonads (Table 5). Gonads first appeared in the 23 November sample, but none were seen in the 13 December sample. Gonads exceeding 0.5 mm were first seen in the 5 January sample and were found in an increasing proportion of individuals on 8 February and 15 March. More convincingly than jaw development, gonad

growth and differentiation suggest that arousal from the resting phase and maturation begins in mid-winter (January) and occurs for much of the population in February–March.

Most of the gonads larger than 0.4 mm on both 8 February and 15 March could be distinguished as to sex (Table 5, lower part). For those over 0.5 mm, there was a significant contingency of observed sex with the month: February had more males, March more females. This agrees with a general trend in the Calanidae for males to appear first in seasonally breeding species.

There was a strong tendency in February and March for testes to occur mostly in individuals from the upper portion of the size range. Individuals with ovaries were found all across the size range, but they were mostly of modal size and smaller (Fig. 5).

DISCUSSION

Depth distribution

Our data show the resting stock as consistently centered near 500 m. There are few published accounts of the

[*] All of the pairwise sample comparisons characterized as different here were found to be statistically significant at p = 0.001 by Chi-square test for H_0: both samples were from the same multinomial distribution. There are 306 pairwise comparisons for n ≥ 52. Thus, only 306 × p = 0.3 are expected to be significant at this level by chance. Moreover, all of the observed differences make good biological sense and agree with everything known about the resting phase and development of *Calanus finmarchicus*
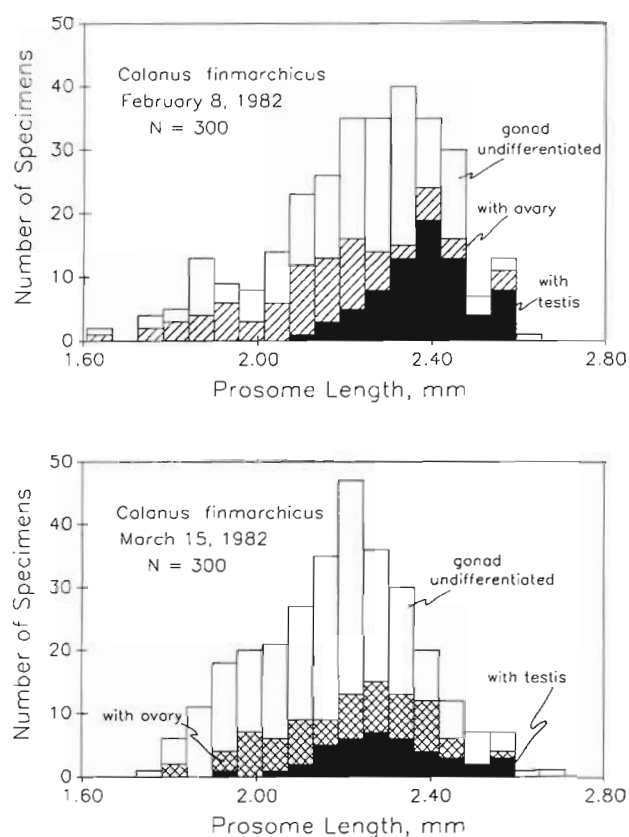
Fig. 5. *Calanus finmarchicus.* Histograms of body size of C5 sorted from the 400 to 500 m samples of 8 February and 15 March 1982. Individuals with gonads identifiable as testes are indicated in black; those with ovaries are indicated by diagonal hatching. Males are derived mostly from larger specimens; females are developed from the whole distribution but are more strongly represented among modal and smaller specimens

vertical distribution of *Calanus finmarchicus* in oceanic waters. Williams & Conway (1988, Fig. 4) show a seasonal sequence of distributions from LHPR (Longhurst-Hardy plankton recorder) sampling that reached 1000 m at continental slope stations southwest of the British Isles. Profiles from the resting phase of the life cycle (January, July, September, and December) all showed maximum peaks of fifth copepodites at or near 500 to 600 m. This resembles our result. However, in at least the September profile, a substantial fraction of the total population scattered downward from the 500 m mode to at least 1000 m. Data covering 0 to 500 m from 4 yr of spring-summer sampling at Weather Station 'I' (59° N, 19° W) (Williams 1988) showed late season accumulation of *C. finmarchicus* between 400 and 500 m. The bulk of the stock could have been deeper. A pair of day-night LHPR profiles from 'I' in late March 1975 showed an abundant stock extending from 350 m down to the limits of sampling at 650 m (day) and 550 m (night). Williams's data overall suggest that farther to the east the resting

stock may reside somewhat deeper than we observed over the New England continental slope.

Generations per year

Our sample series from Slope Water off southern New England shows only one successful generation during the year, that from eggs spawned by females that matured in the winter of 1980/81. However, the tooth development data for near-surface samples (Table 4) suggest that at least a fraction of the population did not enter the resting phase but molted immediately to C6. Sherman (1980) found that *Calanus finmarchicus* are abundant considerably longer each year in the colder waters of the Gulf of Maine than in Slope Waters off southern New England. He found termination of high surface abundance off southern New England exactly when we did. However, persistence of high abundance through September in the Gulf of Maine suggests a complete second generation. Our development data suggest that both strategies are attempted off southern New England, but the second generation simply fails.

Gonad development and sexual size dimorphism

Our data on gonad size in C5 from near 500 m differ from those of Tande & Hopkins (1981) for *Calanus finmarchicus* collected in Balsfjorden. Their population showed a majority of 'P1' and 'P2' individuals from June onward, categories for which the gonad was smaller than we could see (less than 0.2 mm; we did not use their staining technique). However, the appearance of a large fraction of definite males among the C5 occurred both in their location and ours in January/early February, and female C5 predominated after that.

It has been recognized previously for eastern Atlantic populations (Grigg et al. 1981, 1985, 1987, 1989) that males of *Calanus finmarchicus* mostly derive from the upper end of the size range of C5's, females from the lower. Our data (Fig. 5) demonstrate that this is also true for western Atlantic populations.

The arousal mechanism

Facts we have established constrain hypotheses about termination of the C5 resting phase of *Calanus finmarchicus.* Those facts are: (1) Arousal can be stimulated at any time during the resting phase with molting after a 10 d lag (Fig. 1). The most likely stimulus, based on the experiments available, is a change in the intensity or timing of illumination (Grigg & Bardwell 1982).
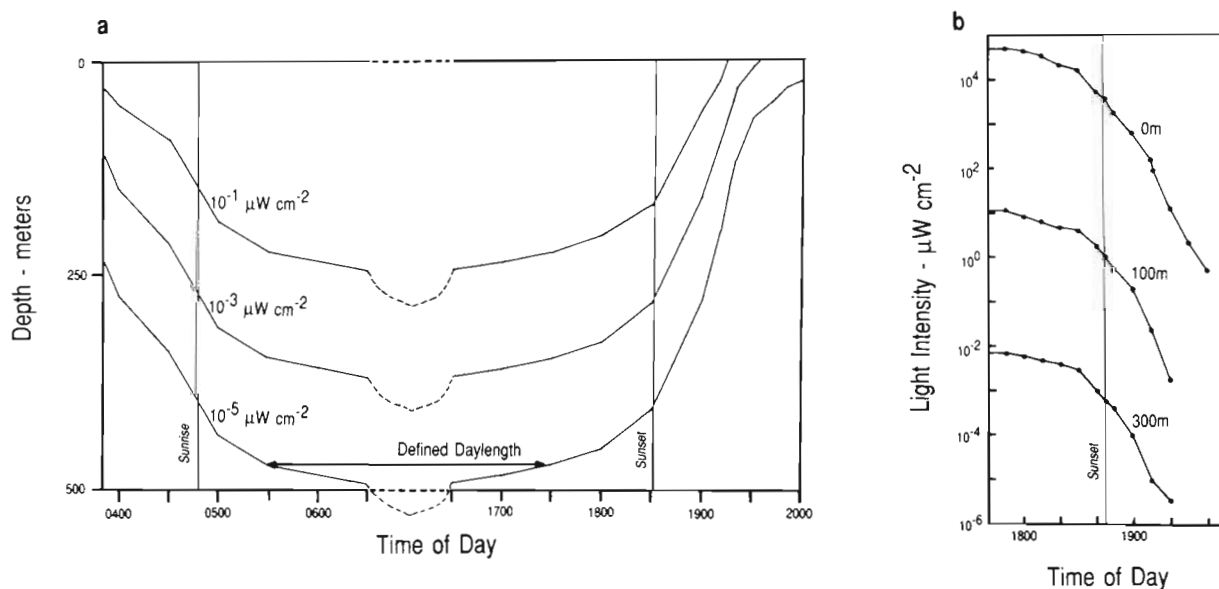
Fig. 6. (a) Position of several isolumes with respect to time of day. An arbitrarily defined daylength is shown. For progressively lower intensities at progressively greater depths, the defined daylength is the same. Curves were calculated from a time series of near-surface, downwelling irradiance and profiles of transmissivity. Redrawn from Clarke & Backus (1964). (b) Time series of downward irradiance measures obtained at progressively greater depths during the sunset interval. Irradiance changes in the same temporal pattern at all depths, demonstrating that 'defined submarine daylengths' [see (a)] are the same at all depths. Redrawn from Clarke & Kelly (1965)

(2) In deep water off New England the resting C5 stay very close to 500 m (Figs. 3 & 4). (3) Gnathobase (Table 4) and gonad development data (Table 5) show that arousal in the field occurs principally in February–March with a tendency for males to precede females. That agrees with previous data, particularly observations of a population in Balsfjorden at 70° N (Tande 1982).

If we seek a single hypothesis, the facts suggest that arousal in the field at depth is cued by increasing photoperiod in late winter. We will develop that possibility first, then show an alternate possibility.

Maintenance of narrow layering in depth implies that the resting C5 stock has an environmental cue to depth, and that they adjust their positions at least intermittently. Light is the obvious cue; it is by no means utterly dark at 500 m. Fig. 6a is redrawn from Clarke & Backus (1964). It shows August illumination of about 10^{-5} µW cm^{-2} at 500 m, which Clarke (1971) indicates is about the limit inducing phototaxis in Crustacea. Stearns & Forward (1984) found phototaxis in *Acartia tonsa* at intensities down to 2.8×10^{11} photons m^{-2} s^{-1}, which is ca 5.6×10^{-5} µW cm^{-2}. The more oceanic *Calanus finmarchicus* is almost certainly at least this sensitive.

Probably 500 m is not an accidental level; intensities have been measured at 500 m as high as 10^{-3} µW cm^{-2} (Clarke & Kelly 1965), well above the limit of light-sensing capability for small curstaceans. Fig. 6a also

shows that deep-sea daylength, defined by progressively lower intensities at greater depths, is roughly constant with depth. Direct measurements by Clarke & Kelly (1965; Fig. 6b here) accord with the calculations of Clarke & Backus, demonstrating that isolumes only move sharply close to sunset (and presumably sunrise). Thus, it is expected that daylength (as defined in Fig. 6a) will be a roughly constant fraction of daylength at the surface (Table 6).

Daylength at 500 m (duration of $> 10^{-5}$ µW cm^{-2}) will be about 80 to 100 min less than the sunrise–sunset interval, but it will have the same proportional seasonal change to act as a seasonal cue. In terms of fractional increase per day, change of daylength accelerates markedly in February, and could be an arousal signal

Table 6. Daylength at 40°N (Slope Water area) in late winter

	Sunrise-sunset (h)	% Change from solstice
Winter solstice	9.32	–
1 Jan	9.40	0.9
15 Jan	9.63	3.3
1 Feb	10.17	9.1
15 Feb	10.75	15.3
1 Mar	11.27	20.9
15 Mar	11.92	27.9
Spring equinox	12.18	30.7

for dormant C5's of *Calanus finmarchicus*. This scheme also could explain the Grigg & Bardwell (1982) result; if the resting C5's are moved to the surface, they are suddenly subject to longer daylengths and termination is initiated. In fact, even night illuminance close to the surface usually exceeds 10^{-5} μW cm^{-2}, so photoperiod automatically would increase in the field. This would have survival value. If a C5 is moved by water circulation into surface layers at a time other than the usual maturation season, its best strategy may well be to return to the active phase, to mature, and to reproduce.

This scheme, like the others to follow, must be able to produce the observed similarity of arousal times over the entire range from our site at roughly 40°N to at least 70°N, the latitude of Balsfjorden (Tande 1982), where the sun is below the horizon from 20 November to 20 January. We are uncertain about this. The arousal in Balsfjorden must be rapid after 20 January to give the timing shown by Tande (1982), which is not different from that we observed at 40°N. The apparent change in daylength will be much greater farther to the north, and the early post-dark rate of change greater, simply because the total change from continuous dark to the equinox is 12 h instead of the 2.9 at 40°N. This is surely an adequate signal, but it seems likely to be available only very close to actual maturation, compared to lower latitudes. Again, phenological features are the traits most amenable to evolution for regional or latitudinal adaptation. Tande et al. (1985) consider a population found even farther north, in the Arctic sector of the Barents Sea, as likely to be expatriates in waters unsuitably cold for sustaining the full life cycle.

Another, more complex, possible scheme is that the arousal mechanism has 2 parts. First, any marked increase in illumination (either intensity or duration) would trigger arousal. The survival value of this would be as explained above. Second, an endogenous, long-range timer could trigger arousal and maturation at depth. This would explain the rough synchrony of arousal in the field. An endogenous, interval timer is more strongly suggested by data for other Calanidae, which we review below. A problem with the notion of an endogenous timer is that actual demonstrations of long-range timers are few in zoology as a whole, and none seem very reliable. A timer that measures a large fraction of a year was claimed by Blake (1958) for *Anthrenus verbasci* (L.), a beetle whose larvae develop in birds' nests. However, the diapause duration of *A. verbasci* is affected by photoperiod in several ways (Blake 1960, 1963), and Tauber et al. (1986) report that Blake's observations have not been duplicated when an attempt was made. Similar claims of long-term activity cycles (which recur with modified period when free-running under constant conditions) have been made for various mites (reviewed by Saunders 1982),

but again Tauber et al. (1986) recommend cautious interpretation ('further study').

A final possibility is that there is no termination cue and no particularly sophisticated timer. According to Tauber et al. (1986): 'for most temperate-zone species [of insects] that undergo an overwintering diapause and in which the conditions influencing diapause maintenance have been examined throughout the winter and spring, no specific diapause-terminating stimulus has been identified. Rather, sometime during winter, the insects cease to respond to diapause-*maintaining* factors, and diapause ends gradually and spontaneously sometime during late fall or early winter' [italics ours].

That is not to say no well-studied animals have specific cues for diapause termination – many do. However, some factor related to the season and detectable at 500 m, such as shortening (or simply short) photoperiods could maintain the rest phase in *Calanus finmarchicus*. It would end a variable, probably temperature-dependent, interval after the winter solstice.

Experimental examination of these possibilities should be straightforward, although not easily achieved given the inaccessible habitat of the resting phase and the difficulties of both long term maintenance and continuous rearing for *Calanus finmarchicus* (Marcus & Alatalo 1989). Miller & Grigg (in press) report an initial examination of photoperiod effects, but more experimentation is required.

Arousal mechanisms in other Calanidae

The range of circumstances surrounding arousal in other Calanidae suggests that either a long-range timer or a direct response to strong illumination is probably the dominant arousal mechanism in other species. For example, *Neocalanus plumchrus* matures and spawns at depth without ascending to the surface or needing to feed. In coastal habitats where it has been studied (Fulton 1973, Georgia Strait; Miller & Terazaki 1989, Sea of Japan), it matures mostly in January and early February. In the more oceanic Gulf of Alaska, it matures over a wide range of dates from August through January (Miller & Clemons 1989). The resting C5's live at depths between 400 and 2000 m in the oceanic part of the range. At the deeper levels they would receive no cues from seasonal light variation. There is probably an interval timer of some sort. The difference in its setting between coastal and oceanic habitats may depend upon the nutrition available during growth. That would be decidedly less in the open sea (Dagg & Walser 1987).

Neocalanus flemingeri rests in the Gulf of Alaska as mated females with small, inactive ovaries. It under-

goes ovarian ripening in December and spawns during January (Miller & Clemons 1989). This, too, could depend upon an interval timer by the same argument as for *N. plumchrus*. There is not likely to be enough light to provide seasonal cues at all of the depths inhabited, and the depth range for the resting phase (400 to 2000 m) is so great that light could not provide a consistent cue throughout. Other seasonal cues operating in mid-winter at these depths are hard to imagine. Every physical variable is either extremely constant or varies with a nonseasonal period.

Conover (1965, 1988) showed that C5's of *Calanus hyperboreus* from the arctic (and western subarctic Atlantic) would molt to C6 in the laboratory during the fall-winter season regardless of the season of collection. It is hard to see how they could receive much daylength information under sea ice at great depths. Conover simply held some C5's in coolers until they matured. He specifically invokes an interval timer in describing his results: 'Apparently C5 *C. hyperboreus* can remember the correct month in which to molt for up to 305 days of laboratory captivity. . . .' Fulton (1973) cited a similar result from experiments with *Neocalanus plumchrus*.

In contrast, we suspect that the tropical species *Calanoides carinatus* has a purely light-stimulated arousal mechanism. It has somewhat different arousal times on the Atlantic and Indian sides of Africa, and perhaps to the north and south of the equator. In the Gulf of Guinea along the Ivory Coast (Binet & Suisse de Sainte Claire 1975, Binet 1979, Mensah 1974a, b) there is a period of upwelling from June through September (much the strongest in July) which brings the resting C5's to the surface in the region of the shelf (Liberia, Ivory Coast, Ghana). They mature and spawn, and the offspring carry through 4 to 6 full life cycles with 9 to 23 d development time (typically 16 d). The final generation of September–October returns as C5's to deep water offshore of the continental slope. Sea surface temperatures during this 'cool' season activity are around 20 °C, contrasting with warm season temperatures around 26 °C.

Off east Africa the *Calanoides carinatus* growing season presumably corresponds to the period of the southwest monsoon which is from late April–early May until October (Smith 1982, 1984). There has never been a study comparable to Binet's to show how close the correspondence is to the whole period of monsoonal upwelling, since there has not been late season sampling. There are only small seasonal variations in daylength and irradiance throughout the range, so that photoperiod arousal cues probably could not be received at depth. An a priori guess is that light is a direct stimulus; when the C5's are moved near the surface layer by feeder flows to the upwelling, they mature, initiate

feeding, and spawn. Warming is another potential cue, since the rising layers are heated by mixing and insolation. The mechanism should be amenable to a direct experimental evaluation, provided that C5's can be collected alive and relatively uninjured from depth.

Correlation of arousal mechanisms and habitat

This contrast between the likely arousal mechanisms in the Calanidae of different regions has a clear correlation to the relationships of the animals to their habitats. In mid- and high latitude systems the animals need to anticipate the season of maximum production, which is predictable in time. Moreover, production variations are roughly contemporary over large parts of the range, certainly throughout the region underlain by deep water containing resting populations. So, they rise (literally) for work on the schedule proved successful by their ancestors. They either do this by responding to an internal 'alarm clock', or by responding to seasonally appropriate daylengths. In the tropical regions where upwelling sites are the only suitable near-surface habitats, the upwelling schedule varies from site to site. Moreover, upwelling conditions (cool, high productivity) are not established directly above the deep water containing the resting populations. The best strategy would be to stay in the resting phase until the feeder flow carries them to an upwelling site, then complete development in response to increased light or temperature.

Calanus finmarchicus, C. helgolandicus and their relatives appear to retain mechanisms allowing for both contingencies. If moved to the surface at a seasonally inopportune time, the best strategy is to wake up, to resume responding to things like fish attacks, and to prepare for feeding and reproduction. However, the best time for arousal remains early winter, and individuals still resting will contribute most to future generations by reactivation at that time, a time indicated by photoperiod or by an internal timer.

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