NOTE

Diel vertical migration behaviour of *Calanus hyperboreus* at temperate latitudes

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ABSTRACT Samples historically collected and analysed by the Continuous Plankton Recorder survey in the North Atlantic and adjacent seas were used to examine temporal patterns in the near-surface abundance of copepodite stages V and VI *Calanus hyperboreus* (n = a total of 32 836 samples; mean latitude of samples = 54° N, SD = 6.7°). The occurrence of CV and VI *C. hyperboreus* was largely restricted to samples collected in April, May and June. During this period there was a diel cycle in near-surface abundance which was consistent with a normal pattern of diel vertical migration. For example, CV–VI *C. hyperboreus* were 1.9 times more abundant at night than during the day, a difference which was highly significant (t-test, t_{5072} = 3.9, p < 0.001). The ratio of night:day abundance was similar in CV–VI *C. finmarchicus* (night:day abundance = 1.4), but markedly higher in CV–VI *Metridia lucens* (night:day abundance = 12.3) and CV–VI *M. longa* (night:day abundance = 15.0).

KEY WORDS: *Calanus hyperboreus* · Diel vertical migration · Atlantic · Arctic · Continuous Plankton Recorder · CPR

Diel vertical migration by zooplankton, with the 'normal' pattern (NDVM) being for populations to occur nearer the surface at night than during the day, occurs widely and has been suggested to reduce the risk of individual mortality from visually orientating predators (cf. Lampert 1989). According to this 'predator-evasion' hypothesis, zooplankton use the ocean depths as a dark, day-time refuge where their probability of being perceived and hence consumed by visual predators is lower than if they remained near the surface; then, at night, when near-surface illumination levels drop, zooplankton ascend to the surface to feed. Several lines of evidence support the predator-evasion hypothesis. For example, in natural populations, NDVM has been shown to be more pronounced when the abundance of planktivorous fish is high (Gliwicz 1986); and, in experimental enclosures, populations have been shown to switch from a non-migratory mode to a migratory mode upon the introduction of planktivorous fish (Bollens & Frost 1989). The predator-evasion hypothesis predicts that those species that are most susceptible to visual predators should exhibit the most marked NDVM. In copepods, susceptibility to visual predators is known to increase in larger and more heavily pigmented species; and, in further support of the predator-evasion hypothesis, it has recently been shown that, for 41 copepod taxa in the Northeast Atlantic, NDVM was apparently more marked in the larger and/or more heavily pigmented taxa (Hays et al. 1994).

In the Arctic during summer, however, results have been reported which appear to contradict the predator-evasion hypothesis. In particular, *Calanus hyperboreus*, which is a large copepod (e.g. mean prosome length given as 7 to 10 mm by Wilson 1932), does not appear to exhibit NDVM (cf. Kosobokova 1978, Sameoto 1984, Hansen et al. 1990). It is well known that many of the copepods that show the strongest tendencies to migrate are considerably smaller than *C. hyperboreus* (Hays et al. 1994). Therefore, if an absence of NDVM behaviour is a general trait for *C. hyperboreus*, then the predator-evasion hypothesis might need to be revised. Alternatively, the previously reported absence of NDVM behaviour in *C. hyperboreus* might simply be a consequence of the continuous daylight that exists in the Arctic during summer (Bogorov 1946).

To distinguish between these alternative possibilities, I use data historically collected by the Continuous Plankton Recorder (CPR) survey to quantify the NDVM behaviour of *Calanus hyperboreus* at temperate latitudes in the North Atlantic and adjacent seas, i.e. under conditions where there is a pronounced day/night cycle.
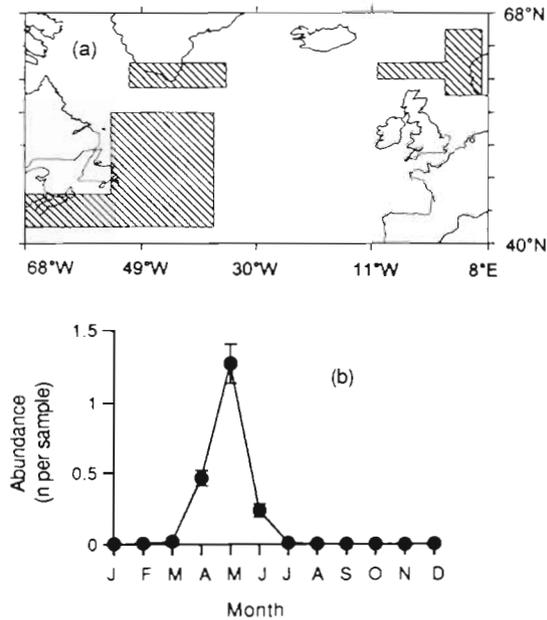
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areas, I extracted details of the position, local time and date of each sample and the abundance of CV–VI *C. hyperboreus* from the CPR data base. For comparative purposes, the abundances of CV–VI *C. finmarchicus*, CV–VI *Metridia lucens* and CV–VI *M. longa* were also extracted for these samples. The sex and/or reproductive status of the specimens sampled by the CPR was not recorded.

Times of sunset and sunrise (0° elevation of the sun) were determined using Telonics satellite predictor software (Telonics Inc., Mesa, AZ, USA).

Results. In the study areas a total of 32 836 CPR samples were collected (mean latitude 54° N, SD = 6.7°). CV–VI *Calanus hyperboreus* were identified in a total of 880 of these samples (n = 5550 specimens), with the mean latitude of these samples also being 54° N (SD 6.2°). There was a marked seasonal cycle in the abundance of CV–VI *C. hyperboreus*, with high abundance in April, May and June (Fig. 1b). Examination of the diel pattern of abundance of CV–VI *C. hyperboreus* was therefore restricted to these 3 months (n = a total of 8186 samples collected, of which *C. hyperboreus* was identified on 817 samples). There was a clear diel cycle in abundance, with higher abundance at night than
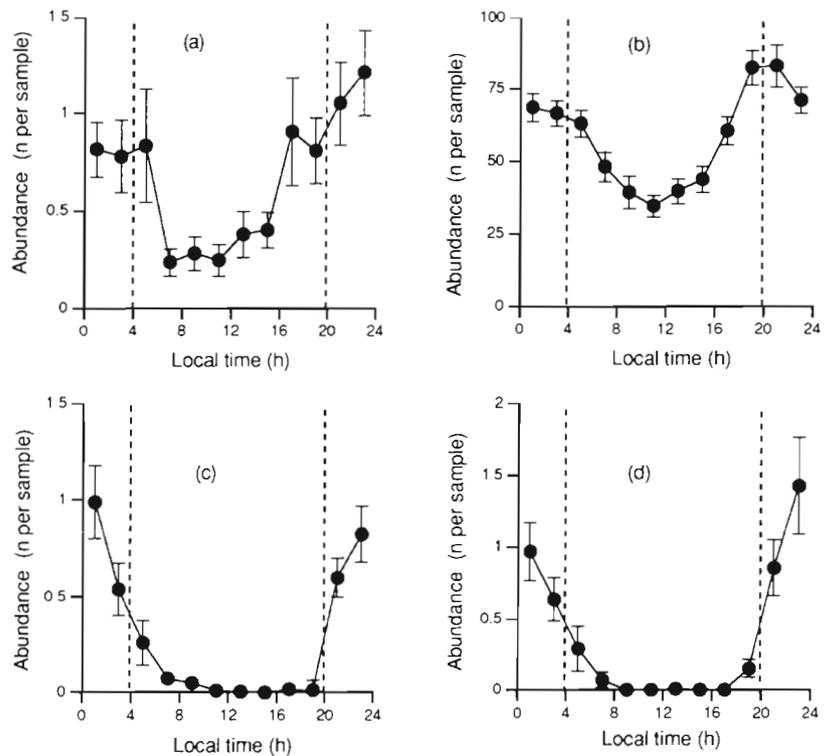

Fig. 1. (a) Areas (shaded) from which details of the temporal occurrence of copepodite stages V–VI *Calanus hyperboreus* in the CPR samples were examined. (b) Mean abundance of CV–VI *C. hyperboreus* (specimens per sample ± 1 SE) in different months

Materials and methods. Samples were collected throughout the North Atlantic and adjacent seas between 1948 and 1992 (see Warner & Hays 1994 for full details of the tow routes) using CPRs towed from ships of opportunity in near-surface waters (mean depth 6.7 m; Hays & Warner 1993). Water entering the CPR was filtered through a 270 µm mesh and the resulting samples were preserved *in situ* inside the recorder. On return of the CPRs to the laboratory, individual samples, each representing 10 nautical miles (approximately 18.5 km) of tow, were analysed using routine methods and the resulting data entered into an electronic data base (see Warner & Hays 1994 and references therein).

Previous studies have shown that, in the CPR records, copepodite stages V and VI (CV and VI) *Calanus hyperboreus* tend to be caught mainly in 3 areas: off Newfoundland, Canada, south of Greenland and in the Norwegian Sea (Oceanographic Laboratory Edinburgh 1973) (Fig. 1a); so, for these

Fig. 2. Mean abundances (± 1 SE) of CV and VI of (a) *Calanus hyperboreus*, (b) *C. finmarchicus*, (c) *Metridia lucens*, and (d) *M. longa* over 24 h. Samples collected in April, May and June from the study areas (Fig. 1a). Times of sunrise and sunset on 15 May at 54°N (the mean date and latitude of samples) are indicated by the dashed vertical lines

Table 1 *Calanus hyperboreus, C. finmarchicus, Metridia lucens,* and *M. longa.* Mean abundances (specimens per sample ± 1 SE) of copepodite stages V and VI from samples taken at night and during the day, ratios of night:day abundance, and the significance of these night/day differences (*t*-test). n = a total of 2779 night-time samples and a total of 5407 daytime samples

Species	Night abundance	Day abundance	Night:day abundance	Significance
C. hyperboreus	0.96 (± 0.096)	0.51 (± 0.061)	1.9	$t_{5072} = 3.9$, $p < 0.001$
C. finmarchicus	73.2 (± 2.8)	51.2 (± 1.7)	1.4	$t_{4984} = 6.7$, $p < 0.001$
M. lucens	0.74 (± 0.073)	0.06 (± 0.016)	12.3	$t_{3031} = 9.2$, $p < 0.001$
M. longa	0.93 (± 0.109)	0.06 (± 0.022)	15.0	$t_{3009} = 7.7$, $p < 0.001$

during the day (Fig. 2a). For example, the abundance of CV–VI *C. hyperboreus* in samples taken at night was 1.9 times the abundance in samples taken during the day, a difference which was highly significant (Table 1).

Similarly, CV–VI *Calanus finmarchicus*, CV–VI *Metridia lucens* and CV–VI *M. longa* all showed a diel cycle in near-surface abundance (Fig. 2b–d), with, for all these species, the abundance at night being significantly greater than the abundance during the day (Table 1). However, while all these species showed night/day differences in abundance, these differences were far more marked in the 2 *Metridia* species (night: day abundance = 12.3 and 15.0) than in the 2 *Calanus* species (night:day abundance = 1.9 and 1.4).

Discussion. *Calanus hyperboreus* showed a seasonal cycle of occurrence in the CPR samples that was largely restricted to 3 months of the year: April, May and June. When considering such seasonal patterns of occurrence, it must be remembered that CPRs sample at a fixed near-surface depth, and, as a consequence, seasonal variations in the vertical distribution of a species may produce seasonal variations in the observed abundance in the CPR records that do not reflect seasonal variations in the depth-integrated abundance (Rae & Fraser 1941). The restricted seasonal occurrence that was observed for *C. hyperboreus* (Fig. 1b) might, therefore, be due to a seasonally restricted occupation of near-surface waters. In support of this suggestion, Dawson (1978) found that over a 22 mo period, CV–VI *C. hyperboreus* occurred in surface samples during only a few weeks each year, while at other times they could be abundant, but only at greater depths.

The historically collected CPR records are potentially of great value for examining diel vertical migration by marine plankton due to the very large number of samples that have been collected over very broad space and time scales (Warner & Hays 1994). Traditionally NDVM has been quantified by collecting samples at several depths during both day and night and examining day/night differences in these depth distributions (cf. Frost & Bollens 1992). This method is clearly not possible with the CPR data due to the fixed near-surface sampling depth. However, diel vertical migration may still be revealed in the CPR records by day/night differences in abundance (cf. Hardy 1936, Rae & Fraser 1941). This method of inferring NDVM from the CPR records assumes that diel variation in the avoidance of CPRs by zooplankton is minimal. Increased avoidance of a variety of plankton nets during the day as compared to during the night has, however, been documented previously and occurs, for example, because in daylight an approaching net may be seen earlier, and hence avoidance behaviour initiated sooner, than in the dark (McGurk 1992). Differential day/night avoidance of the CPR has not been measured directly. However, McGurk (1992) modelled the differential day/night avoidance by herring larvae of plankton samplers towed at a variety of speeds and showed that at a towing speed of 2500 mm s^{-1} (the fastest speed examined), there was no differential day/night avoidance by herring larvae up to a size of approximately 10 mm. Since the CPR is typically towed at >6500 mm s^{-1} (Hays & Warner 1993), it can be inferred that the differential day/night avoidance by copepods is likely to be negligible.

During April, May and June at temperate latitudes, there was a clear diel cycle in the abundance of CV–VI *Calanus hyperboreus* near the surface, which is consistent with a pattern of NDVM (Fig. 1a; Table 1), i.e. a movement from greater depths during the day to shallower depths at night. The CPR results therefore suggest that the absence of NDVM reported previously in CV–VI *C. hyperboreus* under conditions of continuous daylight in the Arctic summer is not a ubiquitous trait for this species. An absence of NDVM has also been reported for other species in the Arctic in summer (Bogorov 1946), and it has been suggested that this may be due to the lack of a sufficient change in light intensity to initiate migration, i.e. to the lack of the appropriate proximal cues (Buchanan & Haney 1980). Alternatively, or additionally, the absence of NDVM in the Arctic summer may reflect the lack of appropriate ultimate cues. An axiom of the predator-evasion hypothesis is that near the surface there is a diel varia-

tion in the susceptibility of zooplankton to visual predation. However, during the Arctic summer, near-surface illumination levels may remain continuously above the threshold for visual feeding by zooplanktivores; if this is the case, then there may be no diel variation in the near-surface susceptibility of zooplankton to visual predators and hence no selective advantage for undergoing NDVM. In such cases where NDVM is not observed, it should be noted that individuals may still be migrating vertically (e.g. feeding to satiation near the surface prior to descending), but that these individual movements may not be synchronised within a population as a whole and hence cannot be detected using conventional net sampling systems (Pearre 1979).

Where they co-occurred geographically and seasonally, I compared the NDVM behaviour of CV–VI *Calanus hyperboreus* with that of CV–VI *C. finmarchicus*, since the latter is the most abundant copepod of that genus in the North Atlantic (Oceanographic Laboratory Edinburgh 1973). The tendency of these 2 species to exhibit NDVM, as quantified by the ratio of their night to day abundance, was broadly similar, but this tendency was markedly less than that of CV–VI *Metridia lucens* and CV–VI *M. longa* (Table 1). This contrast between *Calanus* spp. and *Metridia* spp. in their NDVM behaviour has been reported before and may reflect differences in their susceptibilities to visual predation caused, for example, by differences in their escape ability or visibility (Bollens et al. 1993). However, experiments to demonstrate a difference in susceptibility have produced conflicting results, with *Calanus* spp. showing the greater susceptibility in some experiments (Bollens et al. 1993) and *Metridia* spp. in others (Stuart & Huggett 1992). Although well documented, the reasons for the difference in NDVM between *Calanus* species and *Metridia* species therefore remain enigmatic.

In summary, at temperate latitudes, CV–VI *Calanus hyperboreus* exhibit a diel variation in near-surface abundance which is consistent with a pattern of NDVM and therefore suggests that the lack of NDVM reported previously in the Arctic is not a ubiquitous trait for this species.

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