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# Ontogenetic and seasonal variation in the diel vertical migration of the copepods *Metridia lucens* and *Metridia longa*

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## Abstract

Plankton samples collected and analyzed by the Continuous Plankton Recorder survey were used to examine the length of time spent near the surface in the North Atlantic and the North Sea by three closely related groups of zooplankton (copepodite stages 1–4 *Metridia* spp., copepodite stages 5–6 *Metridia lucens*, and copepodite stages 5–6 *Metridia longa*). For all three groups, the mean daily length of time spent near the surface in each month of the year covaried seasonally with day length. In addition, the amount of time spent near the surface varied significantly between the three groups, being longest for the copepods of smallest body size (C1–C4 *Metridia* spp.) and shortest for the copepods of largest body size (C5–C6 *M. longa*). These results support the suggestion that diel vertical migration serves to reduce the risk of mortality from visually orienting predators.

Diel vertical migration (DVM) is a common feature in zooplankton communities. Vertical migrants are normally found deeper during the day and shallower at night. The ubiquity of DVM has provoked considerable and extended debate as to its functional significance. It has been suggested that there may be a metabolic benefit associated with movement across a thermocline (McLaren 1974), but this metabolic advantage hypothesis is now generally refuted (Lampert 1989). Alternatively, the predator-evasion hypothesis suggests that certain species of zooplankton may be readily perceived and consumed if they are near the surface during the day. Hence, there may be a selective advantage for such species to descend during the day so that they are less available to visual predators (Zaret and Suffern 1976).

There is considerable support for the predator-evasion hypothesis from both field and experimental observations. For example, DVM tends to be more marked when zooplanktivorous fish are abundant (Gliwicz 1986). Furthermore, experimental manipulations have shown rapid change in migratory behavior in previously nonmigrant populations of zooplankton when zooplanktivorous fish are introduced (Bollens and Frost 1989).

Specific a priori predictions about the migration behavior of zooplankton can be made from the predator-evasion hypothesis. When nights are brief, migrating zooplankton would be expected to restrict their near-surface foraging so that they are not near the surface during the day; similarly, when nights are longer, zooplankton would be expected to expand their near-surface foraging. The extensive epipelagic samples historically collected and an-

alyzed by the Continuous Plankton Recorder (CPR) survey have been used to examine this prediction for the copepod *Metridia lucens* (Hays et al. 1995). In accordance with the predator-evasion hypothesis, the amount of time this species spent near the surface did vary seasonally.

For planktonic Crustacea, the probability of being perceived and consumed by visual predators tends to increase with body size (Brooks and Dodson 1965). From the predator-evasion hypothesis, it may therefore be predicted that, in addition to seasonal variations, the amount of time spent near the surface should be shorter for larger species and for older (and hence larger) developmental stages. In this paper, I examine this prediction by using data from the CPR survey for different developmental stages of *Metridia longa* and *M. lucens*. These two species are frequently found in the CPR samples, so the amount of time that they spend near the surface can be calculated accurately. In addition, the two species differ markedly in body size: the typical prosome length for the adult stages is ~2.5 mm for *M. lucens* and 4.0 mm for *M. longa* (cf. Sars 1903). Hence the amount of time spent near the surface should be markedly different for the two species.

## Methods

For several decades, Continuous Plankton Recorders (CPRs) have been towed regularly from ships of opportunity in the North Sea and the North Atlantic. CPRs are towed near the surface (mean depth, 6.5 m; Hays and Warner 1993). Water entering the recorder passes through a silk mesh of 270- $\mu$ m nominal aperture. This silk mesh is preserved in Formalin; upon return of the CPR to the laboratory, the abundance of various plankton taxa is quantified. Details of the sampling protocol and analysis are given elsewhere (Warner and Hays 1994).

For the genera *Metridia*, specimens are identified as one of three groups: group 1, copepodite stages 1–4 (C1–C4) *Metridia* spp.; group 2, C5–C6 *M. lucens*; and group 3, C5–C6 *M. longa*. Both the C5–C6 *M. lucens* and *M. longa* categories consist predominantly of mature females.

## Acknowledgments

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PRIME contribution 3.

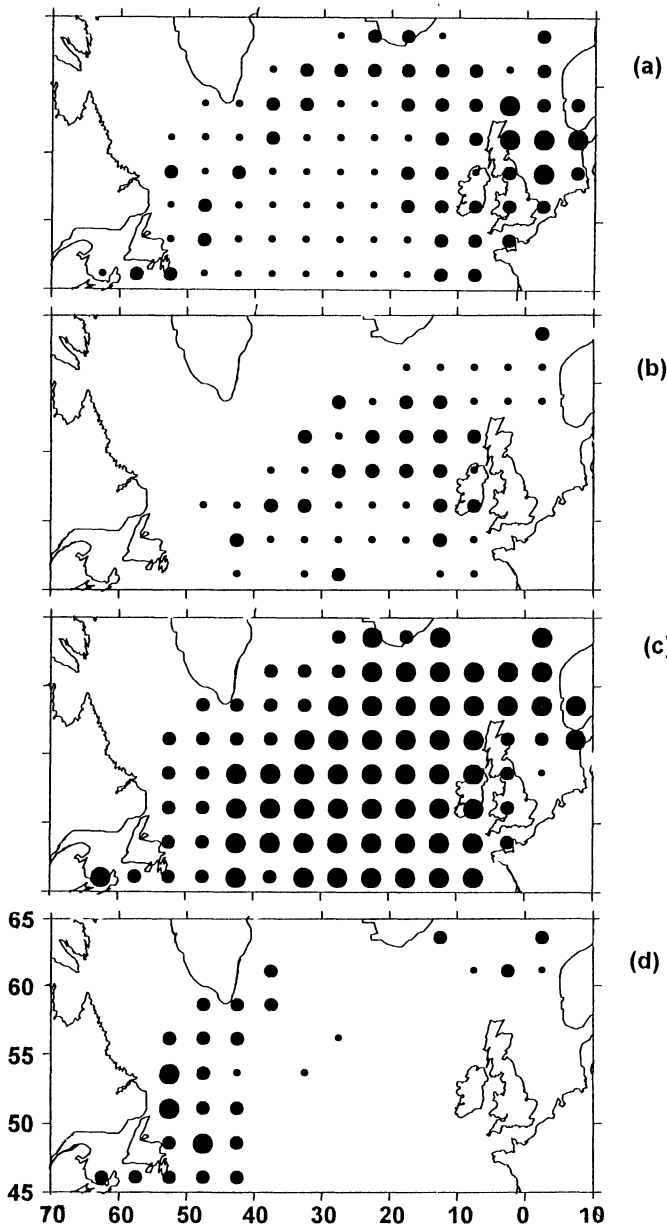


Fig. 1. For each 5°-longitude × 2.5°-latitude area in the North Atlantic and the North Sea, the number of CPR samples collected between 1948 and 1992 that have been analyzed is indicated (a); larger plot symbols represent a greater number of samples (plot symbols are 100–1,000 samples, 1,000–5,000 samples, and >5,000 samples). For these same areas, the percentage of samples that contained specimens of group 1 (b), group 2 (c), and group 3 (d) is indicated; larger plot symbols represent a greater percentage of samples (plot symbols are 1–2%, 2–10%, and >10%). Some symbols appear on land because they are plotted in the center of 5° × 2.5° areas that encompass both sea and land.

From the CPR database, the position, local time, and abundance of the three groups were extracted for every sample taken between 1948 and 1992. The time of day that each sample was collected was then expressed in relation to local midnight. Following the procedure of

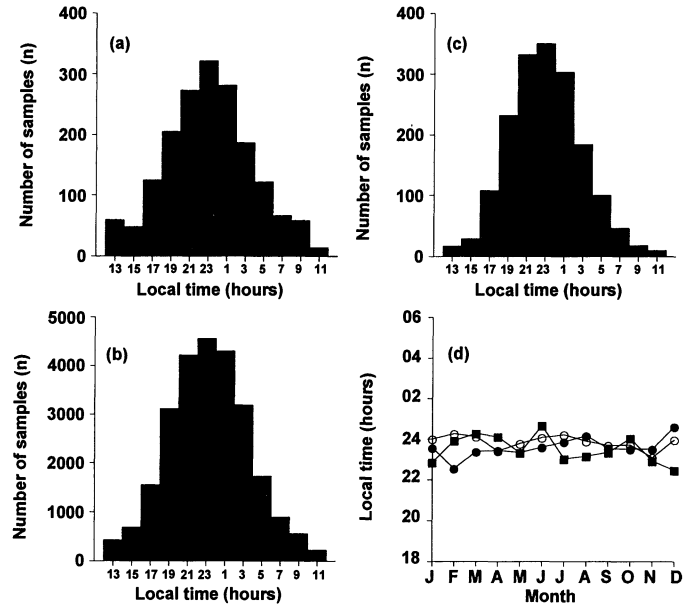


Fig. 2. Frequency histograms showing the number of samples collected in each 2-h period of the day-night in which at least one specimen was identified: a—group 1; b—group 2; c—group 3. [d.] The midpoint of the timing of occurrence in samples collected in different months of the year: ●—group 1; ○—group 2; ■—group 3.

Hays et al. (1995), I give an index of the length of time each group of copepods spent near the surface by calculating the standard deviation ( $\delta$ ) of the distribution consisting of the local time in hours since midnight that a sample was taken ( $x$ ) and the numerical abundance of specimens in those samples ( $f$ ). The standard equation for this calculation is

$$\delta^2 = \frac{1}{(\sum f) - 1} \left[ \sum (fx^2) - \frac{(\sum fx)^2}{\sum f} \right]. \quad (1)$$

The standard error (SE) of this deviation is calculated as

$$SE = \frac{\delta}{(2n)^{1/2}} \quad (2)$$

where  $n$  is the total number of specimens in the data set. Length of night (i.e. sun elevation < 0°) was calculated with Telonics satellite predictor software (Telonics Inc.).

### Results

Within the area bounded by 45°N–65°N and 70°E–10°W, 135,310 CPR samples have been analyzed from tows made between 1948 and 1992. Although the sampling intensity was highest in the North Sea, most areas within the North Atlantic have also been traversed by CPR tows (Fig. 1a). Group 1 animals were identified in 1,776 samples collected during this period, group 2 in 25,509 samples, and group 3 in 1,727 samples.

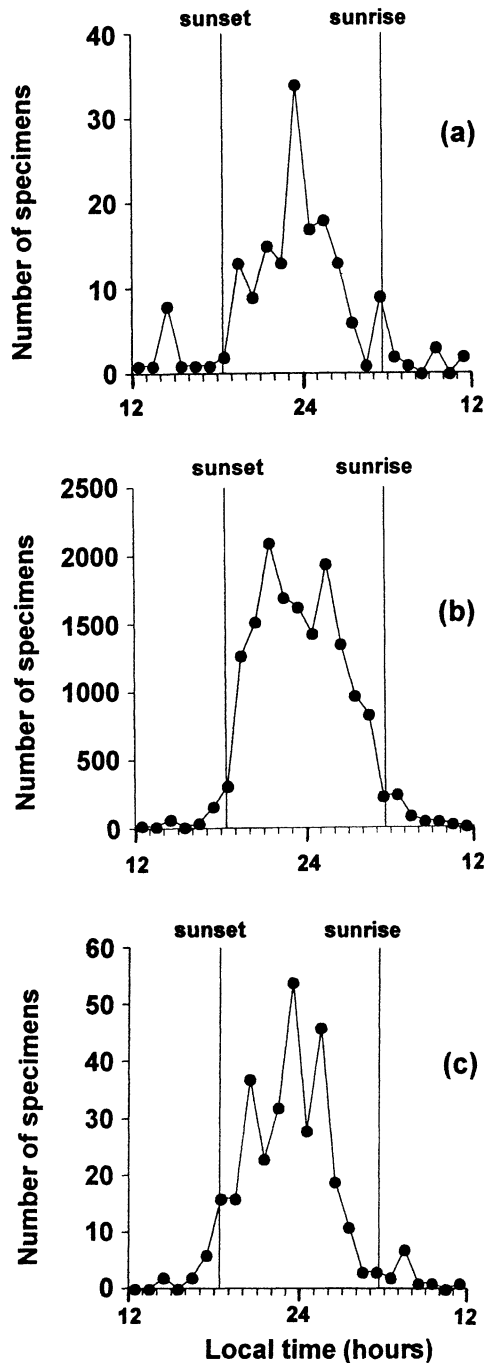


Fig. 3. The predominantly nighttime occurrence of specimens in CPR samples is illustrated by the total number of specimens collected in each hour of the day for samples taken in September: a—group 1; b—group 2; c—group 3. The times of sunset and sunrise at the mean latitude of the samples are shown.

While *M. lucens* had a widespread distribution, *M. longa* tended to be caught predominantly in the northwestern Atlantic and in the Norwegian Sea (Fig. 1c,d). The geographical distribution of group 1 (Fig. 1b) more closely matched that of group 2 than that of group 3.

All three groups occurred maximally in samples col-

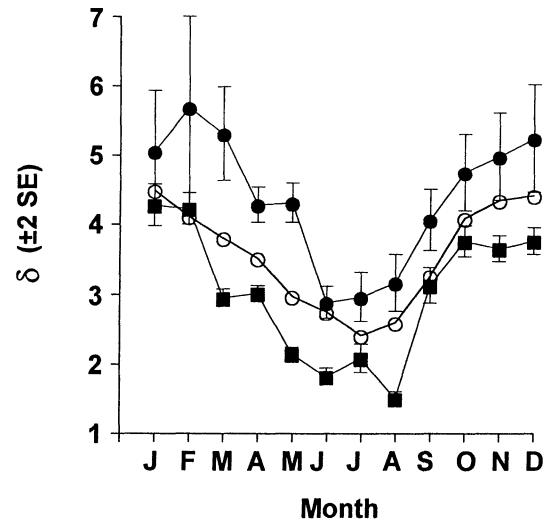


Fig. 4. The seasonal variation in the length of time spent near the surface by group 1 (●), group 2 (○), and group 3 (■). Values represent  $\delta$  (from Eq. 1)  $\pm$  1 SE (from Eq. 2). The error bars are not shown for group 2 because they are smaller than the plot symbol. For all three groups, the variation in  $\delta$  between months was closely correlated with the variation in the mean length of night in different months at 55°N ( $F_{1,10} > 40$ ,  $P < 0.001$  for all three groups,  $r^2 = 0.81$  for group 1,  $r^2 = 0.92$  for group 2, and  $r^2 = 0.84$  for group 3).

lected close to midnight, with the midpoint of timing being 2333 hours for group 1, 2347 hours for group 2, and 2337 hours for group 3 (Fig. 2a–c). There was no significant difference in these midpoints between the different groups or between different months (two-way ANOVA: for the different copepod groups,  $F_{2,22} = 1.20$ ,  $P > 0.05$ ; for different months  $F_{11,22} = 0.52$ ,  $P > 0.05$ ) (Fig. 2d). All three groups tended to be caught predominantly in samples taken at night. For example, the proportion of all specimens that were caught at night was 0.82 for group 1, 0.91 for group 2, and 0.95 for group 3 (Fig. 3).

When samples collected in different seasons were pooled, the calculated value for  $\delta$  (Eq. 1) ( $\pm$  1 SE) was 4.21 ( $\pm$  0.06) for group 1, 3.61 ( $\pm$  0.01) for group 2, and 3.25 ( $\pm$  0.02) for group 3. These three groups all showed seasonal variations in the amount of time spent near the surface which covaried with seasonal variation in night length (Fig. 4). In addition to this seasonal variation, the monthly values for  $\delta$  varied significantly between the three groups (two-way ANOVA: for the different copepod groups,  $F_{2,22} = 59.8$ ,  $P < 0.001$ ; for month  $F_{11,22} = 23.2$ ,  $P < 0.001$ ), with group 1 spending more time at the surface than was spent by either group 2 (paired *t*-test,  $t = 6.7$ ,  $P < 0.001$ ) or group 3 (paired *t*-test,  $t = 9.5$ ,  $P < 0.001$ ); similarly, group 2 spent longer at the surface than group 3 did (paired *t*-test,  $t = 5.1$ ,  $P < 0.001$ ).

## Discussion

As has been previously shown with data from the CPR survey, *M. lucens* and *M. longa* have different distribu-

tions in the North Atlantic; *M. lucens* is widespread, while *M. longa* is restricted to the areas between Newfoundland and Greenland and between Norway and Iceland (Oceanogr. Lab. 1973). The specimens identified in the CPR analysis as C1–C4 *Metridia* spp. could, in theory, be juvenile stages of either *M. lucens* or *M. longa*. However, given the far greater occurrence of *M. lucens* in the CPR samples compared to *M. longa* and the close similarity between the geographical distributions of the C1–C4 *Metridia* spp. and *M. lucens* (groups 1 and 2, Fig. 1b,c), it is likely that most of these C1–C4 specimens are *M. lucens* rather than *M. longa*. In theory, differential day-night avoidance of the CPR by different taxa could produce variations among taxa in their diel occurrence in CPR samples. Although this possibility has not been examined, such differential avoidance is unlikely given the very fast towing speeds of CPRs (mean 24 km h<sup>-1</sup>, Hays and Warner 1993).

Patterns of DVM may show great spatio-temporal variations due, for example, to variations in the abundance of both vertebrate and invertebrate planktivores (Ohman 1990). For studies made over short time and space scales, these spatio-temporal variations may obscure intertaxa differences in DVM. By pooling the extensive results from the CPR survey, this spatio-temporal variability in DVM may be masked, but the average DVM behavior for different taxa can be determined.

For a restricted area in the northeast Atlantic, samples collected with CPRs have been previously used to show that the mean daily length of time *M. lucens* spent near the surface in each month ( $\delta$  from Eq. 1) covaried seasonally with night length (Hays et al. 1995). The results presented here show that this covariation of  $\delta$  and night length applies to *M. lucens* over a wider geographical area and also applies to juvenile *Metridia* stages and to the congeneric species, *M. longa*. Thus during summer when nights are shorter, groups 1–3 all tend to spend less time near the surface than they do in winter, when nights are longer. This seasonal pattern is consistent with the predator-evasion hypothesis, which predicts that migrating zooplankton will restrict the amount of time they spend near the surface in summer so that they are not exposed to high daytime illumination levels when the risk of mortality from visual predators will be great. Furthermore, the predator-evasion hypothesis predicts that those species and developmental stages that are most susceptible to visual predation will spend the least amount of time near the surface. The differences observed between the copepod groups are consistent with this prediction, since the smallest copepods, C1–C4 *Metridia* spp. (group 1), spent the longest time near the surface, with 82% of all specimens being collected at night, while the largest copepods, C5–C6 *M. longa* (group 3), spent the shortest period of time near the surface, with 95% all specimens being collected at night.

Because the CPR only samples near the surface, the depth from which specimens have migrated cannot be determined from these samples. The shorter length of time group 3 spent near the surface could therefore be due to its residence at a greater depth during the day than

that of either group 1 or group 2; group 3 thus takes longer to reach the surface once upward movement starts. Thus, the observed differences in the length of near-surface occupation could be produced even if the different groups began their upward migration at the same time. Alternatively, the observed differences in the length of near-surface occupation could be produced by differences in the timing of vertical movements. That the patterns of occurrence were symmetrical around midnight and the midpoint in the timing of occurrence of group 3 was not significantly later than for the other groups suggests that as well as arriving latest at the surface, group 3 also departed from the surface before either group 1 or group 2. These results suggest that there may be differences between the groups in the proximal cues that initiate their vertical movements.

Factors other than body size have been implicated in the susceptibility of zooplankton to visual predation. For example, Zaret and Kerfoot (1975) suggested that pigmentation was important in determining the visibility of the cladoceran *Bosmina longirostris*, and Kerfoot et al. (1980) suggested that more streamlined zooplankton taxa may have the greater, and hence more effective, escape speed. In addition to body size, variations in body morphology and pigmentation might therefore be expected to also influence patterns of DVM; indeed, this has been shown to be the case by Hays et al. (1994). In that study, the frequency with which 41 copepod taxa were caught near the surface at night was compared with the frequency with which they were caught during the day. In contrast to the present study, the amount of time spent near the surface was not quantified due to insufficient sample sizes for some of the taxa. Hays et al. (1994) found that body size, body morphology, and pigmentation all influenced the tendency for taxa to exhibit DVM.

As the extent of the taxonomic differences in any such comparison is reduced, the intertaxa variations in body morphology and pigmentation would be expected to become smaller and hence body size would be expected to become an increasingly dominant influence on intertaxa differences in susceptibility to visual predation. Certainly, *M. lucens* and *M. longa* have extremely similar morphologies. Although pigment levels have been measured only for *M. lucens* (Fisher et al. 1964), the results presented here show that if there is a difference in the pigmentation levels for these two species, it is insufficient to obscure the predicted effect of body size on the amount of time spent near the surface.

## References

- BOLLENS, S. M., AND B. W. FROST. 1989. Predator-induced diel vertical migration in a planktonic copepod. *J. Plankton Res.* 11: 1047–1065.
- BROOKS, J. L., AND S. I. DODSON. 1965. Predation, body size, and composition of plankton. *Science* 150: 28–35.
- FISHER, L. R., S. K. KON, AND S. Y. THOMSON. 1964. Vitamin A and carotenoids in certain invertebrates. *J. Mar. Biol. Assoc. U.K.* 44: 685–692.
- GLIWICZ, M. Z. 1986. Predation and the evolution of vertical migration in zooplankton. *Nature* 320: 746–748.

- HAYS, G. C., C. A. PROCTOR, A. W. G. JOHN, AND A. J. WARNER. 1994. Interspecific differences in the diel vertical migration of marine copepods: The implications of size, color and morphology. *Limnol. Oceanogr.* **39**: 1621–1629.
- , AND A. J. WARNER. 1993. Consistency of towing speed and sampling depth for the Continuous Plankton Recorder. *J. Mar. Biol. Assoc. U.K.* **73**: 967–970.
- , ———, AND C. A. PROCTOR. 1995. Spatio-temporal patterns in the diel vertical migration of the copepod *Metridia lucens* in the northeast Atlantic derived from the Continuous Plankton Recorder survey. *Limnol. Oceanogr.* **40**: 469–475.
- KERFOOT, W. C., D. L. KELLOG, JR., AND J. R. STRICKLER. 1980. Visual observations of live zooplankton: Evasion, escape, and chemical defences. *Am. Soc. Limnol. Oceanogr. Spec. Symp.* **3**: 10–27. New England.
- LAMPERT, W. 1989. The adaptive significance of diel vertical migration of zooplankton. *Funct. Ecol.* **3**: 21–27.
- McLAREN, I. A. 1974. Demographic strategy of vertical migration by a marine copepod. *Am. Nat.* **108**: 91–102.
- OCEANOGRAPHIC LABORATORY, EDINBURGH. 1973. Continuous Plankton Records: A plankton atlas of the North Atlantic and the North Sea. *Bull. Mar. Ecol.* **7**: 1–174.
- OHMAN, M. D. 1990. The demographic benefits of diel vertical migration by zooplankton. *Ecol. Monogr.* **60**: 257–281.
- SARS, G. O. 1903. An account of the crustacea of Norway. V. 4. Copepoda Calanoida. Bergen Museum.
- WARNER, A. J., AND G. C. HAYS. 1994. Sampling by the Continuous Plankton Recorder survey. *Prog. Oceanogr.* **34**: 237–256.
- ZARET, T. M., AND W. C. KERFOOT. 1975. Fish predation on *Bosmina longirostris*: Body-size selection versus visibility selection. *Ecology* **56**: 232–237.
- , AND J. S. SUFFERN. 1976. Vertical migration in zooplankton as a predator avoidance mechanism. *Limnol. Oceanogr.* **21**: 804–813.

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