Vertical distributions and susceptibilities to vertebrate predation of the marine copepods *Metridia lucens* and *Calanus pacificus*

**Abstract** We present results of a 2-yr field study of the vertical distributions and diel vertical migrations (DVM) of *Metridia lucens* Boeck in Dabob Bay, Washington, and compare them to previous findings for co-occurring *Calanus pacificus* Brodsky. *M. lucens* was found deeper than *C. pacificus*, both day and night, and always exhibited DVM behavior, whereas *C. pacificus* exhibited more variable migration behavior, occasionally occurring in the surface layer in the daytime. These results led us to test the hypothesis that *M. lucens* exhibits greater avoidance of the well-lit surface layer than *C. pacificus* because the former is more susceptible to predation by planktivorous fish. A 2-yr field study of the diet and ambient prey fields of planktivorous fish in Dabob Bay indicated that 31 of 39 species/size classes of fish exhibited greater electivity for *C. pacificus* than *M. lucens*. A series of laboratory experiments corroborated these findings by showing juvenile Pacific herring to exhibit a highly statistically significant preference for *C. pacificus* over *M. lucens*. On the basis of both studies we reject the hypothesis that *M. lucens* is more susceptible to visual predation than *C. pacificus* and we conclude that the deeper distribution and greater avoidance of surface waters of *M. lucens* must be due to some other factor.

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**References**


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dominant components of the epipelagic zoo- 
plankton community of temperate seas. These 
two similarly sized copepods (seasonal range 
of mean total lengths: adult female *M. Zucens*, 
2.59-2.90 mm; *C. pacificus*, 3.03-3.49 mm) 
were widely discussed in much of the quali- 
tative, descriptive zooplankton literature of the 
late 19th and early 20th centuries. Yet only a 
handful of quantitative studies have been pub- 
lished on the comparative ecology of these two 
genera, with only a few recent studies address- 
ing these two species (Marlowe and Miller 1975 
and Smith et al. 1989 on vertical distributions; 
Mackas and Burns 1986 on feeding; Dagg et 
al. 1989 on vertical distributions and feeding).

The present study was stimulated by the 
paucity of information on comparative ecol- 
ogies of these two copepod species in general, 
as well as the specific observation of Dagg et 
al. (1989) that in Dabob Bay, Washington, *M. 
lucens* exhibited greater avoidance of the well- 
lit surface layer than *C. pacijicus* and that this 
may be because the former is more susceptible 
to predation by visual predators. Because in- 
vertebrate visual predators do not occur in the 
surface layer during the day in Dabob Bay (e.g. 
juvenile and adult euphausiids, Bollens et al. 
1992), planktivorous fish must be the domi- 
nant visual predators in this system. Thus the 
purpose of the present paper is twofold: first, 
to present results of a detailed 2-yd field study 
of the vertical distributions and diel vertical 
migrations of *M. lucens* and compare these to 
previously published results for *C. pacificus* 
(Bollens and Frost 1989), and second, as a test 
of the hypothesis of Dagg et al. (1989), to 
compare the relative susceptibilities of the two 
copepods to vertebrate predation by presenting 
results of both field and experimental studies 
of the feeding selectivity of planktivorous fish.

Vertical distribution and diel migrations of 
copepods were determined from samples col- 
clected at a central, deep (193 m) station in 
Dabob Bay (47°45'N, 122°50'W) on eight 
cruises between April 1985 and October 1986. 
The bay exhibits very weak circulation as a 
result of a sill at the basin's mouth and very 
low freshwater input, which in turn allows for 
repeated sampling of the same population of 
zooplankton over the course of at least several 
days (Frost 1988 and references therein). Sam- 
ping and sample analysis of vertical distri- 
bution and abundance of copepods are de- 
scribed in detail by Frost (1988), but briefly, 
a 1 x 1 m, 333-μm mesh multiple-net vertical 
sampler was used to sample six discrete depth 
strata (175-125, 125-75, 75-50, 50-25, 25-10, 
10-0 m on all cruises except April 1985, 
when 25-10- and 10-0-m strata were com- 
bined). Duplicate series of samples were col-
lected near noon and midnight on each of two 
consecutive days during each cruise. Methods 
described by Frost (1988) were used to deter-
mine abundances of adult female *M. lucens* 
and *C. pacificus* in each sample. Weighted mean 
depth was calculated for each daytime and 
nighttime series of samples as

\[
WMD = \frac{\left(\sum n_{d}\Delta d \cdot d\right)}{\sum n_{d} \Delta d}
\]

where \(n_{d}\) is abundance (No. m\(^{-3}\)) in sampling 
depth interval \(\Delta d\) whose midpoint is \(d\) (\(d_1 = 
5.0, d_2 = 17.5, d_3 = 37.5, d_4 = 62.5, d_5 = 100.0,\) 
and \(d_6 = 150.0 \text{ m})\). Additionally, a single night-
time series of samples of the upper 50 m of 
the water column from each date was analyzed 
for total species composition and abundance 
of zooplankton.

Sampling of pelagic fish and analysis of 
stomach contents are described in detail by 
Bollens and Frost (1989). Briefly, juvenile and 
adult planktivorous fish were collected from 
the upper 50 m of the water column at night 
with two trawl types—a midwater trawl with 
mouth area of 81.0 m\(^2\) (9.0 x 9.0 m) and stretch 
mesh ranging from 8.9 cm nearest the mouth 
to 1.3 cm in the cod end, and a surface tow 
et with mouth area 18.3 m\(^2\) (3.0 x 6.1 m) 
and mesh size grading from 8.9 cm nearest the 
mouth to 0.6 cm at the cod end. Two or three 
tows were made with each net on each cruise. 
Upon retrieval of the net, fish were injected in 
the gut cavity with a small volume of For- 
malin, preserved in buffered Formalin-sea- 
water solution, and returned to the laboratory 
for analysis of stomach contents. For each spe-
cies of fish, several different size classes were 
established (≤49, 50-74, 75-99, 100-149, 
≥150 mm for salmonids; 50-74 and 75-99 
classes combined for nonsalmonids), and 5-14 
individual stomachs were analyzed from 
each species/size class. Prey were identified to 
the lowest possible taxon with a dissecting mi-
roscope, and data from the 5-14 stomachs of 
each species/size class were subsequently 
pooled. Only those species/size classes con-
taining adult *M. lucens* and (or) *C. pacificus* in their diet were used in the present analysis.

Ivlev's electivity index (Ivlev 1961) was calculated as a measure of the selectivity of juvenile and adult planktivorous fishes for *C. pacificus* and *M. lucens* in the upper 50 m of the water column at night, where

\[ E_i = \frac{(r_i - p_i)}{(r_i + p_i)}. \]

*E*, the electivity of the predator for prey type *i*, *r*, the proportion (by number) of prey type *i* in the diet (ration), and *p*, the proportion (by number) of prey type *i* in the environment.

This index takes a value of zero for random feeding and deviates symmetrically between plus one and minus one as a prey item is preferred or avoided, respectively (Lechowicz 1982). While of limited utility in quantifying the magnitude of preference between different prey types, this index has been recommended as appropriate for simple rank-order comparisons of electivities (Lechowicz 1982). We therefore focus on the relative difference between *E*, values of *C. pacificus* and *M. lucens* for each species/size class of predator.

The experimental determination of feeding selectivities of Pacific herring (*Clupea harengus pallasi*) was as follows. Zooplankton were collected in the central, deep part of the bay on the nights of 18 April 1991, 10 March 1992, and 27 March 1992 with vertical hauls (175–0 m) of a plankton net (1-m diam, 500-μm mesh) fitted with a closed cod end. Zooplankton were transferred to 4-liter jars filled with seawater pumped from a depth of 30 m and transported in coolers to the laboratory in Seattle, where they were stored in an 8°C cold room. Shortly after collection of zooplankton, juvenile Pacific herring (*C. h. pallasi*) ~12 cm long were obtained from a local bait dealer and placed in 40-liter (26 x 50 x 31 cm deep) aerated aquaria with blackened sides (to prevent fish from bumping the sides) in the 8°C cold room. These fish were presented a mixture of live zooplankton later that day and actively fed and produced fecal material.

Preliminary observations in the laboratory provided us with several pieces of information that guided our subsequent experiments. First, the herring would only be induced to feed on adult female *C. pacificus* and *M. lucens* if placed under direct incandescent light and first presented with a mixture of live zooplankton. Second, adult female *C. pacificus* and *M. lucens* tended to aggregate near the bottom of the aquaria, although *C. pacificus* had a broader distribution throughout the water column that included the occasional individual in the surface. Third, the herring made most of their strikes from below. Fourth, fish placed in the aquaria in 1991 (but not in 1992) were much more likely to feed in pairs than if held singly.

We undertook 17 experiments on the feeding selectivity of juvenile herring: five on 20 April 1991, four on 22 March 1992, four on 2 April 1992, and four on 11 April 1992. Based on our preliminary observations, we established the following protocol. Several herring were held in a 40-liter aquarium and fed a small volume of mixed live zooplankton. A second 40-liter aquarium containing ~20 liters (i.e. ~16 cm deep) of filtered (206 μm) seawater and known numbers of adult female *C. pacificus* and adult female *M. lucens* (80 of each species in the 1st experiment in April 1991, 50 of each species in subsequent experiments) was held nearby. When the fish were observed to begin feeding on the mixed zooplankton in the first aquarium, one (1992) or two (1991) herring were immediately transferred by dip net to the second aquarium containing the copepods. The herring were allowed to feed on the copepods until ~10–20 strikes were made, after which time the fish were removed from the aquarium. The water and remaining copepods were then drained through a sieve and the remaining copepods enumerated. Missing copepods were presumed eaten by fish. This experiment was repeated five times in April 1991 and four times in March 1992, with new fish taken from the mixed zooplankton aquarium and used for each new experiment.

The same protocol was undertaken during eight additional experiments in April 1992, but with one major change: copepods were gently mixed during the experiments by nearly continuously forcing additional seawater to the bottom of the aquaria via plastic tubing. Visual observations of copepods in fishless tanks mixed in this manner indicated that the two species of copepods did not vertically segregate or stratify themselves during mixing.

Daytime vertical distributions of adult female *M. lucens* varied only slightly between
dates and were concentrated between 75 and 125 m on all dates except October, when they were concentrated between 75 and 175 m (Fig. 1). Nighttime vertical distributions were slightly more variable, with peak abundances fluctuating throughout the upper 50 m of the water column (Fig. 1). On all dates, *M. lucens* undertook pronounced diel vertical migration, as evidenced by the highly statistically significant differences between mean daytime and mean nighttime weighted mean depths (WMD) for each date (*P* < 0.01, *t*-test, 6 df); however, the presence of substantial numbers of adult female *M. lucens* at depth both day and night during October suggests that some fraction of the population was not migrating at this time.

These distributions differed considerably from those determined for *C. pacificus* from the same sets of samples (Fig. 2; see also Figure 2 of Bollens and Frost 1989). During the day *M. lucens* was deeper than *C. pacificus* (Fig. 2) by an average of 23 m (although this difference reduces to 18 m if the outlier of April 1985 is excluded from the comparison), with mean daytime WMD differences between species statistically significant on seven of eight dates (*P* < 0.05, *t*-test, 6 df). Similarly, a trend toward greater depth of *M. lucens* was evident in the nighttime data (mean difference, 16 m), although nighttime differences between species were more variable (Fig. 2). Specifically, mean nighttime WMD of *M. lucens* was significantly greater than that of *C. pacificus* on four dates (April and August 1985, June and October 1986); only in May 1986 was mean nighttime WMD of *M. lucens* significantly less than *C. pacificus* (*P* < 0.05, *t*-test, 6 df). The large fraction of *M. lucens* females apparently staying at depth in October introduces a bias into the comparisons of mean depths of *M. lucens* and *C. pacificus* at this time, since *C. pacificus* females showed no decrease in migratory activity. Nevertheless, in general *M. lucens* tended to be more deeply distributed, both day and night, than *C. pacificus* and always avoided the surface layer in the daytime, whereas the migratory behavior of *C. pacificus* was more variable.

Of the 39 species/size classes of planktivorous fish sampled for stomach contents over the course of the field study, negative electivity (i.e. avoidance) of one or both of the copepod species was common (Table 1). However, in comparing selection between copepod species, 31 of 39 species/size classes of planktivorous fish showed greater electivity for *C. pacificus* than *M. lucens* (Table 1).

Results from the 17 feeding experiments varied considerably (Table 2). When presented with equal proportions of adult female *C. pacificus* and adult female *M. lucens* as potential prey, juvenile Pacific herring selected between the two prey types in a proportion that was statistically significantly different from unity in 8 of 17 experiments (Table 2, *P* < 0.05, binomial). In all but one of these cases (exp. 3) *C. pacificus* was preferentially selected over *M. lucens* (Table 2). When data from these experiments are pooled, either by considering the nonmixed (1–9) and mixed (10–17) experiments separately or collectively, juvenile Pacific herring exhibit a highly statistically significant preference for adult female *C. pacificus* over adult female *M. lucens* (Table 2, *P* < 0.001, binomial).

Differences in the vertical distributions and DVM behaviors of these copepod species have been noted previously. Perhaps the first to do so was Esterly (1912) who sampled the California Current and found *C. finmarchicus* (=*pacificus*) to be maximally abundant between 90 and 135 m during the day and 18 and 55 m at night, whereas *M. lucens* was maximally abundant between 180 and 360 m during the day and 13 and 180 m at night. With regard to migration behavior, Esterly (1912) concluded that for *Calanus* "differences between day and night (stratified) hauls . . . are not great . . . but . . . they are suggestive . . . that *Calanus* performs diurnal migrations" (p. 288), whereas for *Metridia* he made the more
Fig. 2. Mean daytime (open) and nighttime (closed) weighted mean depths of adult females of Metridia lucens (squares) and Calanus pacificus (diamonds) in 1985 and 1986. Symbols are means (±1 SE) of four weighted mean depths determined from replicate series of daytime or nighttime samples collected on each cruise. Day and night mean depths were compared between species by t-test (6 df) on each date: ***, P < 0.001; **, P < 0.01; *, P < 0.05; for all other pairs, mean depths between species not significantly different (P > 0.05).

More recently, Marlowe and Miller (1975) found adult female M. pacifica (=lucens) during summer in the Gulf of Alaska to migrate from at least 300 m during the day to the upper 100 m at night, whereas adult female C. pacificus was nonmigratory, remaining in the upper 50 m both day and night. Similar migratory patterns during summer in the Gulf of Alaska were reported by Frost and McCrone (1974) for M. pacifica (=lucens) and Frost (1988) for C. pacificus. Likewise, Smith et al. (1989) sampled zooplankton on one spring date in the California Current and reported C. pacificus to be nonmigratory (upper 50 m day and night) and M. pacifica (=lucens) to be largely migratory (several hundred meters in the day to the surface 50 m at night). These previous studies, while more limited in their seasonal and interannual coverage, corroborate our own findings: diel vertical migration behavior of M. lucens seems more consistent and invariant, effectively excluding this species from the surface layer during the day, whereas the migration behavior of C. pacificus is more variable and can include daytime residence in surface waters. The one caveat to our findings of invariant migration behavior in M. lucens is the suggestion in our October data that some fraction of the population remains at depth (cf. Hirakawa 1991).

These distributional differences have also been noted for other species within these genera. For instance, Clarke (1933) noted that while adult female C. finmarchicus and M. lucens sampled at a shallow station in the Gulf of Maine were both migratory, C. finmarchicus exhibited depths of maximum abundance of
Table 1. Ration (r), availability (p), and electivity (E) of various species and size classes of zooplanktivorous fish for adult female *Calanus pacificus* and *M. lucens*. All nonzero values have been rounded to two decimal places.

| Date              | Size class (mm) | Calanus |  | *M. lucens* |  |
|-------------------|-----------------|---------|  |------------|  |
|                   | r   | p   | E   | r   | p   | E   |
| June/July 1985    |     |     |     |     |     |     |
| *Gasterosteus aculeatus* | 50–99 | 0.16 | 0.02 | 0.80 | 0   | 0.16 | -1.00 |
| *Merluccius productus* | ≤49  | 0.18 | 0.02 | 0.82 | 0   | 0.16 | -1.00 |
| *Oncorhynchus keta* | 50–74 | 0.06 | 0.02 | 0.56 | 0   | 0.16 | -1.00 |
| *Oncorhynchus tshawytscha* | 75–99 | 0.28 | 0.02 | 0.88 | 0   | 0.16 | -1.00 |
|                    | 100–149 | 0.00 | 0.02 | -0.68 | 0   | 0.16 | -1.00 |
| *Oncorhynchus tshawytscha* | 75–99 | 0.80 | 0.02 | 0.96 | 0   | 0.16 | -1.00 |
|                    | 100–149 | 0.47 | 0.02 | 0.93 | 0   | 0.16 | -1.00 |
| August 1985        |     |     |     |     |     |     |
| *Clupea harengus pallasi* | 100–149 | 0.01 | 0.06 | -0.69 | 0.02 | 0.61 | -0.94 |
| *G. aculeatus*     | 50–99 | 0.00 | 0.06 | -0.94 | 0   | 0.61 | -1.00 |
| *M. productus*    | ≤49  | 0.08 | 0.06 | 0.17 | 0.69 | 0.61 | 0.06 |
|                   | 50–99 | 0.06 | 0.06 | 0.07 | 0.54 | 0.61 | -0.06 |
| *O. keta*         | ≥150 | 0.05 | 0.06 | -0.02 | 0   | 0.61 | -1.00 |
| *O. tshawytscha*  | 100–149 | 0.03 | 0.06 | -0.23 | 0.01 | 0.61 | -0.97 |
| *Porichthys notatus* | 75–99 | 0   | 0.06 | -1.00 | 0.06 | 0.61 | -0.83 |
| October 1985       |     |     |     |     |     |     |
| *M. productus*    | ≥150 | 0.00 | 0.08 | -0.93 | 0   | 0.17 | -1.00 |
| April/May 1986    |     |     |     |     |     |     |
| *Ammodites hexapterus* | 50–99 | 0.04 | 0.04 | -0.02 | 0   | 0.09 | -1.00 |
| *C. h. pallasi*   | ≤49  | 0.01 | 0.04 | -0.48 | 0   | 0.09 | -1.00 |
| *O. keta*         | 50–74 | 0.00 | 0.04 | -0.87 | 0   | 0.09 | -1.00 |
|                   | 75–99 | 0.01 | 0.04 | -0.73 | 0   | 0.09 | -1.00 |
| June 1986         |     |     |     |     |     |     |
| *C. h. pallasi*   | ≥150 | 0   | 0.00 | -1.00 | 0.02 | 0.02 | -0.09 |
| *O. keta*         | 75–99 | 0.00 | 0.00 | -0.89 | 0   | 0.02 | -1.00 |
|                    | 100–149 | 0.00 | 0.00 | -0.74 | 0   | 0.02 | -1.00 |
| *Oncorhynchus kisutch* | 100–149 | 0.00 | 0.00 | -0.05 | 0   | 0.02 | -1.00 |
| August 1986       |     |     |     |     |     |     |
| *C. h. pallasi*   | 50–99 | 0.10 | 0.03 | 0.53 | 0   | 0.34 | -1.00 |
| *G. aculeatus*    | 50–99 | 0.04 | 0.03 | 0.14 | 0.02 | 0.34 | -0.90 |
| *M. productus*   | ≤49  | 0.02 | 0.03 | -0.19 | 0.88 | 0.34 | 0.44 |
|                   | 50–99 | 0.09 | 0.03 | 0.51 | 0.61 | 0.34 | 0.28 |
| *O. keta*         | 100–149 | 0.06 | 0.03 | 0.30 | 0.00 | 0.34 | -0.99 |
| *O. tshawytscha*  | 100–149 | 0.03 | 0.03 | -0.03 | 0   | 0.34 | -1.00 |
| October 1986      |     |     |     |     |     |     |
| *C. h. pallasi*   | 50–99 | 0.40 | 0.07 | 0.69 | 0.19 | 0.18 | 0.02 |
|                   | 100–149 | 0.00 | 0.07 | -0.93 | 0.01 | 0.18 | -0.87 |
| *G. aculeatus*    | 50–99 | 0.05 | 0.07 | -0.21 | 0.17 | 0.18 | -0.02 |
| *M. productus*   | 50–99 | 0.00 | 0.07 | -0.97 | 0.00 | 0.18 | -1.00 |
| *O. keta*         | 50–99 | 0.04 | 0.07 | -0.31 | 0.04 | 0.18 | -0.65 |
| *O. tshawytscha*  | ≥150 | 0   | 0.07 | -1.00 | 0.01 | 0.18 | -0.94 |
|                   | ≥150 | 0   | 0.07 | -1.00 | 0.00 | 0.18 | -0.97 |

30 m during the day and 6 m at night, whereas the more deeply distributed *M. lucens* exhibited maxima at 54 m during the day and 18–30 m at night. Yet at two other stations in the Gulf of Maine, Clarke (1933) reported *C. finmarchicus* to be "distributed irregularly, apparently undergoing no definite migration." The following year Clarke (1934) sampled at
Table 2. Numbers and proportions of adult female *Calanus pacificus* and *Metridia lucens* consumed by *Calanus harengus pallasi*, ratio of proportions, and probability (P) of ratio differing from 1.0 by chance as determined by binomial distribution for each experiment and nonmixed (1-9), mixed (10-17), and total experiments combined.

<table>
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<th>Date</th>
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<tr>
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</tbody>
</table>

As an additional point, fine-scale timing of DVM in *M. lucens* and *C. pacificus* was investigated on one of our sampling dates (August 1986) by Dagg et al. (1989) who collected closely temporally spaced (~every 30 min) samples and found that while both *M. lucens* and *C. pacificus* were migratory on this date, the timing of *M. lucens'* migration was much more tightly coupled to sunset and sunrise; *M. lucens* arrived in the surface layer later and left earlier than *C. pacificus*. These observations were similar to those made by Clarke (1934) who noted that *Metridia* was more sensitive to light than *Calanus*, arriving at the surface later than *Calanus* and leaving the surface earlier at both stations. Dagg et al. (1989) suggested that the greater activity of *M. lucens* may make this species more conspicuous and attractive to visual predators, and thus its migratory behavior may be more tightly constrained by predation than that of *C. pacificus*. While our distributional data confirm that *M. lucens* avoids the surface layer more strongly than *C. pacificus*, our field and laboratory results on the feeding of planktivorous fish, discussed below, do not support the hypothesis by Dagg et al. that this is due to the greater susceptibility of *M. lucens* to visual predators. The different patterns of timing of diel migration in the two species could simply be due to their different responses to the diel cycle of light (Forward 1988).

The high negative selectivity for both *C. pacificus* and *M. lucens* exhibited by the planktivorous fish caught in our field study was due to the fact that many of these fish fed largely on other, larger organisms such as euphausiids.
and amphipods (Bollens unpubl.), with copepods being of only minor importance in their diet and certainly proportionately less abundant in their diet than in the environment. But again, the point most relevant to the current discussion is the relative electivity of the fish between the two copepod species.

We offer three explanations for the generally greater electivity of zooplanktivorous fish, in both our field and laboratory studies, for C. pacificus over M. lucens. The first and most obvious explanation is the larger body size of C. pacificus. A vast literature exists that points to larger body size as an important factor increasing susceptibility of zooplankton to visual predators (e.g. Galbraith 1967; Zaret 1980; Eggers 1982), and this factor alone may account for the greater selection of C. pacificus compared with M. lucens.

A second possible explanation of our field and experimental results relates to the differing activity levels between the two copepods. Metridia is well known to be more active than Calanus (e.g. Mackas and Burns 1986; Wong 1988; Dagg et al. 1989) and high activity level may be beneficial to planktonic prey if it translates into improved escape ability from attacking predators (e.g. Drenner et al. 1978). However, many studies have shown that motion in planktonic prey can actually increase susceptibility to visual predators, presumably by making the prey more conspicuous to predators (e.g. Zaret 1972, 1980), and it was exactly these results that led Dagg et al. (1989) to suggest that the greater activity level of M. lucens should make the vertical migration behavior of this species more constrained by visual predators than that of C. pacificus.

Finally, potential bias due to our sampling plan-protocol must be considered yet another possible explanation of our results. With respect to our field study, although both our trawling and hydroacoustic observations (Bollens and Frost 1989) indicated fish were concentrated in the upper 50 m of the water column at night, these fish may have been feeding most actively closer to the surface. If so, the generally greater depth distribution of M. lucens at night (Fig. 2) would make this copepod less “available” to the fish than C. pacificus, irrespective of numerical abundances, and thus our use of 50–0 m plankton hauls to establish proportions of prey type in the environment (p.) would introduce a bias into our calculations of electivity indices.

Indeed, it was exactly this potential bias in the field study that led us to the laboratory experiments, in which we tried to eliminate distributional differences between the two copepod species by the use of experimental containers shallow enough (15 cm deep) to effectively make the two copepods equally available to the fish. However, as noted above, the two copepods seemed to segregate vertically even in the shallow confines of the aquaria. We attempted to mitigate this by providing near continuous gentle mixing during experiments 10–17. Thus the results of the experimental study corroborate those of our field study, i.e. that planktivorous fish preferentially select C. pacificus over M. lucens.

Our field data show two differences between the migration behavior of M. lucens and C. pacificus. M. lucens was more deeply distributed, both day and night, than C. pacificus, and always exhibited DVM behavior (i.e. never occurred in the surface layer in the daytime), whereas C. pacificus exhibited more variable migration behavior, occasionally occurring in the surface layer in the daytime. The most obvious and straightforward explanation of these observations is an interspecific difference in susceptibility to predation. To the degree that DVM is considered to be a predator avoidance tactic, our field results showing M. lucens more deeply distributed and more strongly migratory than C. pacificus tend to support Dagg et al.’s (1989) hypothesis that M. lucens should be more constrained by predators, whereas our field and laboratory experiments on the feeding selectivity of planktivorous fish directly contradict it. How do we reconcile these results?

It must be kept in mind that although these two suspension-feeding copepod species are superficially similar, they differ in several ways other than their migration behavior. M. lucens is luminescent while C. pacificus is not (Clarke et al. 1962). M. lucens is generally classified as an omnivore while C. pacificus is thought to be more herbivorous (Arashkevich 1969). M. lucens may be less fecund than C. pacificus. Thus, although predation pressure is probably the primary force for DVM, these other aspects of the species’ biology may affect the specific details of their migration behaviors.
For example, at the population level, both fecundity and mortality would need to be considered in determining a species' susceptibility to predation. Limited experimental data on *M. lucens* (Batchelder and Miller 1989; Hirakawa 1991) suggest that its egg production rate is lower than that of *C. pacificus* (Runge 1984). If *C. pacificus* is much more fecund than *M. lucens*, then it could experience greater mortality than *M. lucens* but still have the same population growth rate. That is, the higher fecundity of *C. pacificus* would allow this copepod to have less than perfect predator avoidance behavior (i.e. nonmigratory and remaining in the surface day and night), whereas the less fecund *M. lucens* would have to maintain exceptionally effective avoidance behavior (e.g. by remaining migratory at all times and avoiding the surface layer except under conditions of total darkness). To help sort this out, we recommend that further studies on the feeding and fecundity of *M. lucens* be done and compared with those of *C. pacificus*.

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**Notes**

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**References**


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Notes

Lack of endogenous rhythmicity in Daphnia diel vertical migration

Abstract—A population of Daphnia galeata × hyalina was induced to perform diel vertical migration (DVM) by the addition of fish-kairomones to a large plankton tower. Vertical profiles of zooplankton abundance were measured every 12 h. When the tower was covered to shield the water column from the light, DVM ceased, and vertical distributions were not statistically different from the night profiles that had been observed before the tank was covered. This result suggests that endogenous rhythms do not trigger DVM, but that a change in light intensity must occur.

The ultimate causes of zooplankton diel vertical migration (DVM) have received much attention since the phenomenon was discovered (see Lampert 1989, 1993). The predator avoidance hypothesis (Kozhov 1963; Zaret and Suffern 1976) has gained recent strong support from studies showing that DVM can be induced by chemical exudates from predators (Dodson 1988; Neill 1990; Dawidowicz and Loose 1992; Loose 1993).

However, the proximate causes triggering migration every morning and evening have received less attention, and the question of endogenous vs. environmental control remains unanswered. Early work of Ringelberg (1964) showed that a phototactic reaction is provoked by relative changes in light intensity that cross a certain threshold. This phototactic response was later shown to be enhanced by exudates from predators (Ringelberg 1991a, b; De Meester 1993). This proximate mechanism requires a change in light intensity for migration to occur (Ringelberg 1993). Another mechanism could be endogenous rhythms that provide a regular internal trigger on a diel basis without external stimuli being active. A signal by an internal clock would then cause the animals to migrate. These rhythms have indeed been found in the phototactic responses (Rimet 1960; Ringelberg and Servaas 1971) and in the vertical distribution of Daphnia in small-scale laboratory columns (Harris 1963; Young and Watt 1993). A large-scale experiment with marine zooplankton revealed endogenous rhythms in some taxa and environmental control in others (Enright and Hamner 1967).

Previous research has not directly tested whether an internal clock governs DVM in Daphnia or whether a relative change in light intensity is necessary. I performed a simple large-scale experiment to test the hypothesis that DVM in Daphnia is controlled by an endogenous rhythm.

The experiment was conducted in one of the plankton towers at the Max Planck Institute for Limnology in Plön. A detailed description of the plankton towers is given by Lampert and Loose (1992). The tower (stainless steel, 11.2 m high, 85.8-cm diam) was filled with 10-

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