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Submitted: 7 December 1992

Accepted: 10 May 1993

Revised: 18 October 1993

Limnol. Oceanogr., 38(8), 1993, 1827–1837
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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.

Acknowledgments

This research was supported by U.S. National Science Foundation grants OCE 84-08929, OCE 87-171420, and OCE 89-11536 to B. Frost, a College of Ocean and Fishery Sciences Select Program grant from the University of Washington to B. Frost and B. Miller, and a postdoctoral scholar award from the Woods Hole Oceanographic Institution to S. M. Bollens.

We thank D. Thoreson, S. Jonasdottir, C. Mobley, R. McQuin, P. Crawford, M. Landsteiner, D. Gunderson, K. Fresh, P. McAllister, R. Donnelly, and C. Simenstad for assistance in various aspects of planning and carrying out the fieldwork. Analyses of fish stomach contents by J. Cordell and zooplankton samples by G. Heron are also gratefully acknowledged.

Metridia lucens Boeck and *Calanus pacificus* Brodsky are co-occurring marine planktonic copepods belonging to genera that are often

dominant components of the epipelagic zooplankton community of temperate seas. These two similarly sized copepods (seasonal range of mean total lengths: adult female *M. lucens*, 2.59–2.90 mm; *C. pacificus*, 3.03–3.49 mm) were widely discussed in much of the qualitative, descriptive zooplankton literature of the late 19th and early 20th centuries. Yet only a handful of quantitative studies have been published on the comparative ecology of these two genera, with only a few recent studies addressing 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 ecologies 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. pacificus* and that this may be because the former is more susceptible to predation by visual predators. Because invertebrate 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 dominant visual predators in this system. Thus the purpose of the present paper is twofold: first, to present results of a detailed 2-yr 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 collected 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). Sampling and sample analysis of vertical distribution and abundance of copepods are de-

scribed in detail by Frost (1988), but briefly, a 1 × 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 combined). Duplicate series of samples were collected near noon and midnight on each of two consecutive days during each cruise. Methods described by Frost (1988) were used to determine 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

$$\text{WMD} = (\sum n_{\Delta d} \Delta d d_i) / \sum n_{\Delta d} \Delta d$$

where $n_{\Delta d}$ is abundance (No. m⁻³) in sampling depth interval Δd whose midpoint is d_i ($d_1 = 5.0$, $d_2 = 17.5$, $d_3 = 37.5$, $d_4 = 62.5$, $d_5 = 100.0$, and $d_6 = 150.0$ m). Additionally, a single nighttime 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 m² (9.0 × 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 net with mouth area 18.3 m² (3.0 × 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 Formalin, preserved in buffered Formalin-seawater solution, and returned to the laboratory for analysis of stomach contents. For each species 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 microscope, 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

$$E_i = (r_i - p_i)/(r_i + p_i).$$

E_i is the electivity of the predator for prey type i , r_i the proportion (by number) of prey type i in the diet (ration), and p_i 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_i 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 pallasii*) 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- μ m 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. pallasii*) ~12 cm long were obtained from a local bait dealer and placed in 40-liter (26 × 50 × 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 pre-

sented 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 μ m) 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

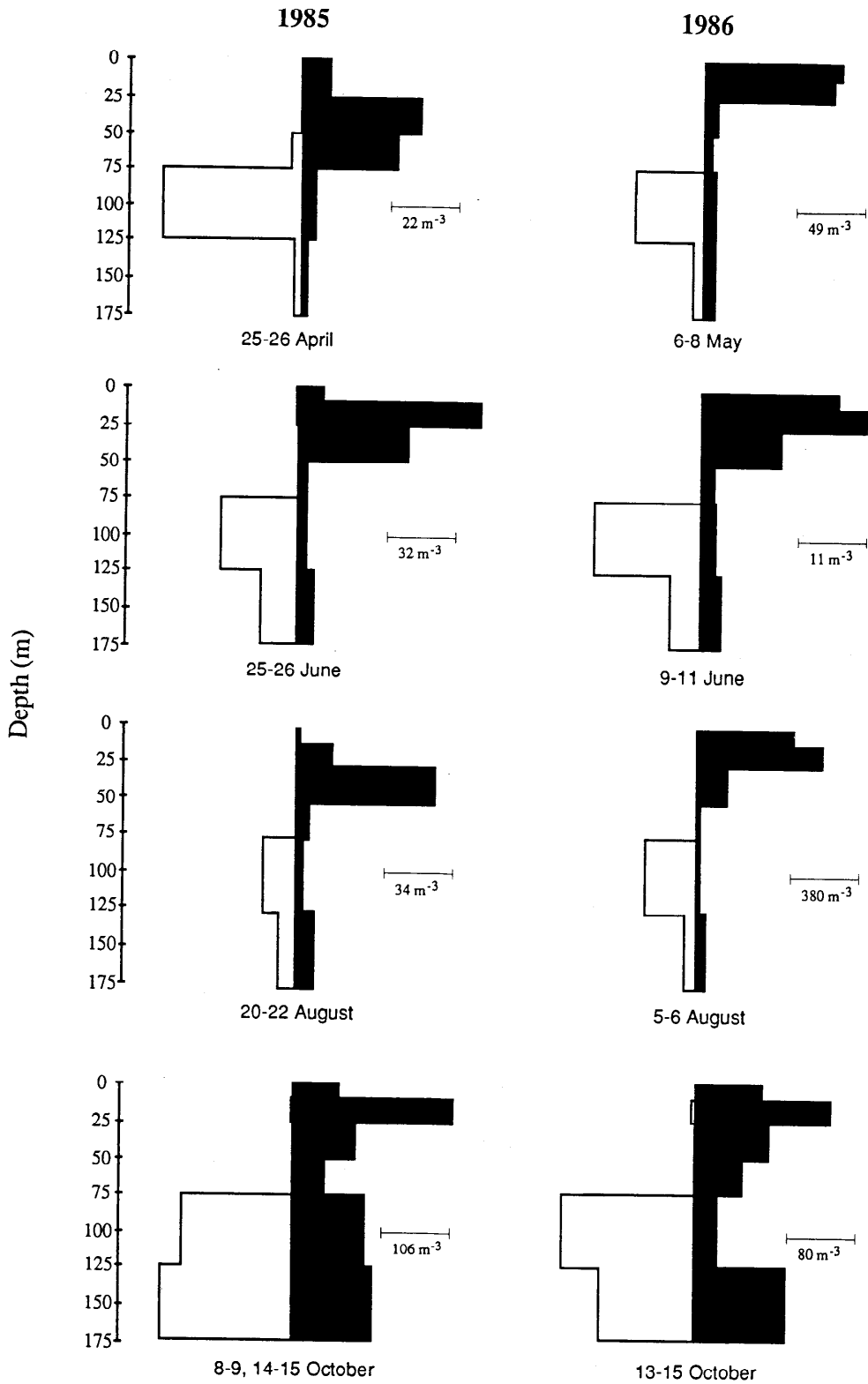
the surface layer in the daytime, whereas the migratory behavior of *C. pacificus* was more variable.

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. 1. Vertical distribution of adult females of *Metridia lucens* in 1985 and 1986. For each set of dates, day (clear) and night (opaque) vertical distributions are means of four vertical series of samples collected in pairs near noon and midnight on each of two consecutive days.



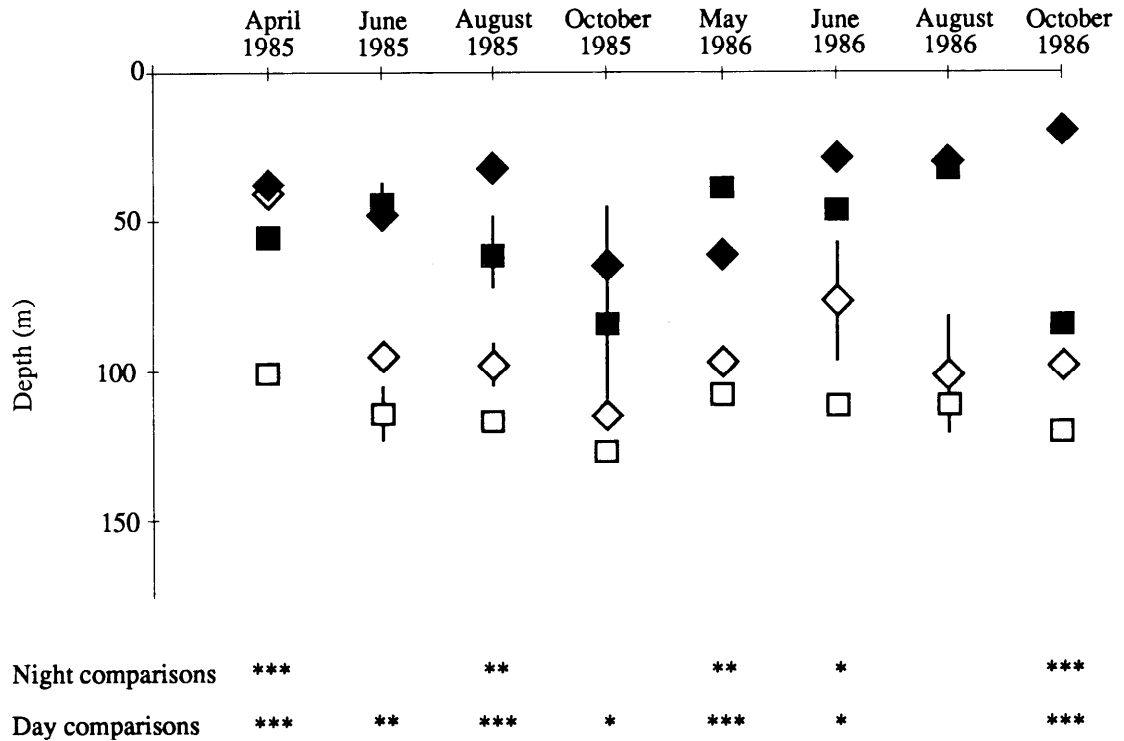


Fig. 2. Mean daytime (open) and nighttime (closed) weighted mean depths of adult females of *Metridia lucens* (squares) and *Calanus pacificus* (diamonds) in 1985 and 1986. Symbols are means (± 1 SE) of four weighted mean depths determined from replicate series of daytime or nighttime samples collected 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 ($P > 0.05$).

emphatic statement that “evidence of a diurnal migration . . . is so clear that we can hardly doubt its reliability” (p. 301). 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_i), availability (p_i), and electivity (E_i) of various species and size classes of zooplanktivorous fish for adult female *Calanus pacificus* and *Metridia lucens*. All nonzero values have been rounded to two decimal places.

Date	Size class (mm)	Calanus			Metridia		
		r_i	p_i	E_i	r_i	p_i	E_i
June/July 1985							
<i>Gasterosteus aculeatus</i>	50-99	0.16	0.02	0.80	0	0.16	-1.00
<i>Merluccius productus</i>	≤49	0.18	0.02	0.82	0	0.16	-1.00
	50-74	0.06	0.02	0.56	0	0.16	-1.00
<i>Oncorhynchus keta</i>	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
<i>Oncorhynchus tshawytscha</i>	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							
<i>Clupea harengus pallasii</i>	100-149	0.01	0.06	-0.69	0.02	0.61	-0.94
	≥150	0.00	0.06	-0.99	0.96	0.61	0.22
<i>G. aculeatus</i>	50-99	0.00	0.06	-0.94	0	0.61	-1.00
<i>M. productus</i>	≤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
	≥150	0.05	0.06	-0.02	0	0.61	-1.00
<i>O. keta</i>	≥150	0.00	0.06	-0.86	0.04	0.61	-0.88
<i>O. tshawytscha</i>	100-149	0.03	0.06	-0.23	0.01	0.61	-0.97
<i>Porichthys notatus</i>	50-99	0	0.06	-1.00	0.06	0.61	-0.83
October 1985							
<i>M. productus</i>	≥150	0.00	0.08	-0.93	0	0.17	-1.00
April/May 1986							
<i>Ammodytes hexapterus</i>	50-99	0.04	0.04	-0.02	0	0.09	-1.00
<i>C. h. pallasii</i>	100-149	0.01	0.04	-0.48	0	0.09	-1.00
<i>O. keta</i>	≤49	0.01	0.04	-0.71	0	0.09	-1.00
	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							
<i>C. h. pallasii</i>	≥150	0	0.00	-1.00	0.02	0.02	-0.09
<i>O. keta</i>	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
<i>Oncorhynchus kisutch</i>	100-149	0.00	0.00	-0.05	0	0.02	-1.00
August 1986							
<i>C. h. pallasii</i>	50-99	0.10	0.03	0.53	0	0.34	-1.00
<i>G. aculeatus</i>	50-99	0.04	0.03	0.14	0.02	0.34	-0.90
<i>M. productus</i>	≤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
<i>O. keta</i>	100-149	0.06	0.03	0.30	0.00	0.34	-0.99
<i>O. tshawytscha</i>	100-149	0.03	0.03	-0.03	0	0.34	-1.00
October 1986							
<i>C. h. pallasii</i>	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
	≥150	0.05	0.07	-0.21	0.17	0.18	-0.02
<i>G. aculeatus</i>	50-99	0.00	0.07	-0.97	0.00	0.18	-1.00
<i>M. productus</i>	50-99	0.04	0.07	-0.31	0.04	0.18	-0.65
<i>O. keta</i>	≥150	0	0.07	-1.00	0.01	0.18	-0.94
<i>O. tshawytscha</i>	≥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.

Date	Calanus consumed		Metridia consumed		Calanus: Metridia	P
	No.	Prop.	No.	Prop.		
20 Apr 91	17	0.65	9	0.35	1.89	0.1686
20 Apr 91	4	0.57	3	0.43	1.33	1.0000
20 Apr 91	5	0.24	16	0.76	0.31	0.0266
20 Apr 91	17	0.81	4	0.19	4.25	0.0072
20 Apr 91	15	0.75	5	0.25	3.00	0.0414
22 Mar 92	6	0.55	5	0.45	1.20	1.0000
22 Mar 92	12	0.71	5	0.29	2.40	0.1435
22 Mar 92	13	0.68	6	0.32	2.17	0.1671
22 Mar 92	15	0.83	3	0.17	5.00	0.0075
Subtotal	104	0.65	56	0.35	1.86	<0.001
2 Apr 92	14	0.74	5	0.26	2.80	0.0636
2 Apr 92	11	0.42	15	0.58	0.73	0.5572
2 Apr 92	13	0.93	1	0.07	13.00	0.0018
2 Apr 92	9	0.39	14	0.61	0.64	0.4049
11 Apr 92	11	0.79	3	0.21	3.67	0.0574
11 Apr 92	14	0.88	2	0.13	7.00	0.0042
11 Apr 92	18	0.75	6	0.25	3.00	0.0227
11 Apr 92	16	0.84	3	0.16	5.33	0.0044
Subtotal	106	0.68	49	0.32	2.16	<0.001
Total 1–17	210	0.67	105	0.33	2.00	<0.001

a deeper (260 m), offshore station in the Gulf of Maine and found *C. finmarchicus* to exhibit DVM, with maximum abundances at 114–138 m during the day and 6–42 m at night, while *M. lucens* showed slightly deeper distributions and more pronounced DVM. In contrast, at a shallower station (65–75-m depth) on Georges Bank Clarke (1934) reported *C. finmarchicus* to exhibit only very weak DVM, with maximum abundance at 15–25 m during the day and 5 m at night; however, *M. lucens* at this station exhibited pronounced DVM between 35 and 65 m during the day and 15 and 25 m at night.

Bamstedt and Tande (1988) reported on *C. finmarchicus* and *Metridia longa* in Kosterfjorden, western Sweden, in late winter and found adult females of both species to exhibit DVM across 50 m, but *M. longa* showed a stronger tendency to avoid the surface during the day. Krause and Radach (1989) reported that *M. lucens* (all copepodid stages combined) was be-

low 60-m depth throughout spring in the North Sea, whereas the distributions of adult female *C. finmarchicus* were more variable, with daytime distributions becoming deeper and DVM more pronounced as spring progressed. In the Southern Hemisphere, Atkinson (1989) noted that *Calanus simillimus* and *Calanus propinquus* off South Georgia Island in austral summer were confined almost exclusively to the upper 250 m, whereas *Metridia gerlachei* and *M. lucens* were highly abundant throughout the upper 1,000 m of the water column. In general, these previous studies corroborate our own findings: *Metridia* was deeper day and night and showed more pronounced DVM than *Calanus*.

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 electivity 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_i) 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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Submitted: 5 November 1992

Accepted: 23 April 1993

Revised: 21 June 1993

Limnol. Oceanogr., 38(8), 1993, 1837–1841

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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-

Acknowledgments

Thanks to Winfried Lampert, Bill DeMott, Herwig Stibor, and three anonymous reviewers for comments which improved the manuscript, and to Nancy Zehrbach for linguistic help.