

## Original papers

# Ovigerity, selective predation, and variable diel vertical migration in *Euchaeta elongata* (Copepoda: Calanoida)

S.M. Bollens\* and B.W. Frost

School of Oceanography, WB-10, University of Washington, Seattle, WA 98195, USA

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**Summary.** We present a statistical analysis of a previously published (Yen, 1983) but heretofore unanalyzed data set on the vertical distributions and diel vertical migration (DVM) of adult females of the marine planktonic copepod *Euchaeta elongata* in Dabob Bay, Washington, USA. Non-ovigerous females were strongly migratory on all four dates sampled, residing between 75–175 m during the day and at shallower depths during the night, commonly entering the upper 50 m of the water column. In contrast, ovigerous females were non-migratory or weakly migratory, largely remaining between 100–175 m both day and night, and entering the upper 50 m of the water column only rarely. Thus non-ovigerous females always migrated much more strongly, as measured by both amplitude of migration and the proportion of animals migrating, than did ovigerous females. These results led us to hypothesize that differential susceptibility to visually orienting predators was the cause of these differences in DVM behavior in female *E. elongata*, and we subsequently undertook an experimental study of the feeding selectivity of the copepod's natural predator, Pacific herring (*Clupea harengus pallasii*). Pacific herring exhibited a highly significant preference for ovigerous over non-ovigerous adult female *E. elongata*. The demographic consequences of variable DVM in adult female *E. elongata* were investigated by way of life table analyses. Results indicated that under conditions of thermal stratification of the water column there is a distinct demographic disadvantage (reduced rate of realized population growth) incurred by non-migratory or weakly migratory ovigerous females due to delayed egg development at cooler subsurface temperatures. We conclude that ovigerous female *E. elongata* remain at depth both day and night to avoid visually orienting predators, and that such behavior must afford the copepod a demographic advantage of no less than a 26% reduction in adult mortality to offset the demographic cost of delayed egg development.

**Key words:** Ovigerity – Selective predation – Diel vertical migration – Zooplankton – *Euchaeta elongata*

Diel vertical migration (DVM) behavior, whereby aquatic animals change their vertical distribution in the water column on a 24-hour cycle, is widespread among aquatic animals inhabiting lakes and seas. DVM is often variable within a given species of planktonic animal, having been shown to vary with developmental stage (Nicholls 1933; Uye et al. 1990), geographic location (Frost 1988; Ohman 1990), and season and year (see recent review by Bollens and Frost 1989a). Additionally, DVM has been suggested to vary with the reproductive condition of adult female copepods (Yen 1983; Vuorinen 1987) and shrimp (Apollonio et al. 1986). For example, data presented by Yen (1983) on the vertical distributions of the planktonic copepod *Euchaeta elongata* in Dabob Bay, Washington (USA) suggested differences in DVM in ovigerous and non-ovigerous adult females, with the ovigerous females being the less migratory, remaining at depth both day and night.

Ovigerity, the practice of carrying eggs, is a feature of the life histories of several genera of planktonic calanoid copepods (Hutchinson 1967; Sekiguchi 1974). In the case of *E. elongata*, ovigerous adult females have a conspicuous external egg sac (Fig. 1) that we hypothesized might render these animals more vulnerable to visual predators. Indeed, considerable evidence has accumulated from both field and experimental work showing that many planktivorous fish exhibit a dietary preference for ovigerous over non-ovigerous cladocerans (Mellors 1975; Gliwicz 1981; Koufopanou and Bell 1984; Tucker and Woolpy 1984) and copepods (Sandstrom 1980; Dawidowicz and Gliwicz 1983; Hairston et al. 1983; Vuorinen et al. 1983; Winfield and Townsend 1983).

In the case of Dabob Bay, there is marked vertical heterogeneity in the distribution of planktivorous fish (Bollens and Frost 1989a). Qualitative hydroacoustic observations (105 kHz) indicated that many fish re-

\* Present address and address for offprint requests: Biology Department, Woods Hole oceanographic Institution, Woods Hole, MA 02543, USA



**Fig. 1.** Ovigerous adult female of *Euchaeta elongata*, with dark blue external egg sac attached to the abdomen. Total length of animal approximately 6.9 mm (Photograph by K. E. Fischer)

mained in surface waters both day and night, while others migrated off the bottom at dusk to spend the nighttime hours in surface waters; thus nighttime abundances of fish were greater at the surface than at depth. These observations, combined with the exponential decline of moonlight with depth, indicate that nighttime predation pressure must be greater at the surface than at depth. Thus, we hypothesized that any differences in the nighttime vertical distributions and diel migration behavior of ovigerous and non-ovigerous female *E. elongata* would be due to differential susceptibility to visually orienting predators.

Additionally, we were interested in the demographic consequences of variable DVM in *E. elongata*. For example, previous theoretical work using life tables has shown that copepods residing at sub-optimal temperatures (e.g., below the seasonal thermocline) can experience delayed development and thus reduced rate of realized population growth (McLaren 1974; Ohman et al. 1983; Vuorinen 1987; Frost 1988; Ohman 1990). For such behavior to persist, the demographic costs of residence in cooler, subsurface waters must be offset by a demographic advantage of equal or greater magnitude. Thus we used life table analyses to examine the tradeoffs for *E. elongata* between growth (development) and mortality resulting from variable DVM behavior (i.e., from different partitionings of time spent in warm, well-lit surface waters and cooler, darker subsurface waters).

The specific goals of the present study were thus three-fold. First, to analyze the data in Yen (1983) to determine if apparent differences in vertical distribution and DVM of ovigerous and non-ovigerous female *E. elongata* were statistically significant. Second, to undertake an experimental study of the feeding selectivity of Pacific herring (*Clupea harengus pallasii*), an abundant zooplanktivorous fish in Dabob Bay (Bollens and Frost 1989a) known to feed on adult *E. elongata* at night (Bollens, unpublished), designed to evaluate the role of selective predation in differentially impacting ovigerous and non-ovigerous female *E. elongata*. And third, to use life table analyses (McLaren 1974; Ohman et al. 1983; Vuorinen 1987; Frost 1988; Ohman 1990) to compare the demographic consequences of variable DVM of adult female *E. elongata*.

## Methods

### *Vertical distributions and diel vertical migration*

Zooplankton were sampled on four dates (15–16 December 1972; 18–19 February 1973; 21–22 July 1973; 3–4 August 1973) in the deep (193 m), central basin of Dabob Bay, Washington, USA. On each date duplicate samples were collected with a 1 m diameter, 216  $\mu\text{m}$  mesh Puget Sound net (Miller et al. 1984) by hauling the net vertically through the following depth strata: 175–150; 150–125; 125–100; 100–75; 75–50; 50–25; and 25–0 m. Samples were immediately rinsed from the net and preserved in 10% buffered seawater-formalin solution. All adult female *E. elongata* in each sample were enumerated in the laboratory, and the reproductive status (ovigerous when an external egg sac was present; non-ovigerous when egg sac absent) of each individual was noted. The occasional free egg sac was assumed to have been detached during collection and thus the number of free egg sacs in each sample was subtracted from the count of non-ovigerous females and added to the count of ovigerous females.

Statistical analyses to determine the presence or absence of DVM behavior in ovigerous and non-ovigerous females were done by calculating weighted mean depths for each day and night profile and employing a *t*-test to compare means of the daytime and nighttime weighted mean depths. If the difference between mean daytime and nighttime weighted mean depths was statistically significant, the magnitude of this difference was considered a measure of the amplitude of DVM. Additionally, as a measure of the proportion of the population exhibiting DVM into and out of the thermally stratified surface layer (assumed to be the upper 50 m), we calculated the difference between the fraction of the population below 50 m at midday and the fraction of the population below 50 m at midnight (i.e.,  $V$  as in Bollens and Frost [1989a]).

### *Clutch size and egg development rates*

Clutch size and egg development rate are critical input parameters for life table analyses, and we therefore estimated these parameters in the following way. Adult female *E. elongata* were collected in Dabob Bay on 22 May 1989 and returned to the laboratory in Seattle. Clutch size (number of eggs per ovigerous female) was determined by microscopic examination of 20 ovigerous females. For determination of egg development rates, individual adult females were placed in a 1-l jar filled with seawater (pumped from 30 m depth in Dabob Bay in October 1988), and approximately 40–50 live, small copepods were added to each jar to serve as prey. Thirty individual adult female *E. elongata*, either ovigerous (external egg sac present) or ripening (darkly pigmented ovaries), were

kept in the dark at each of two temperatures, 8° C and 12° C. Each individual jar received new prey (approximately 40–50 small copepods) and a 50% change in seawater every 4–8 days. The reproductive status (ripening, ovigerous, or hatched) of each female was checked every 3–12 h (only those jars containing active nauplii were considered as legitimate hatch times), and the egg development times were calculated as the time between egg sac formation and hatching.

### Fish predation

Several hundred adult female *E. elongata* were captured and sorted (approximately 50 per 4-l jar) in Dabob Bay on 18 August 1988 as described above. These copepods, together with one dozen Pacific herring (total length 15–25 cm) obtained from a local bait dealer, were transported in an icewater-filled cooler to Friday Harbor Laboratories (San Juan Island, Washington, USA) the following day. The *E. elongata* were stored in an 8° C coldroom and the herring were placed in a 314-l (107 cm long × 47 cm wide × 62 cm deep) outdoor flow-through saltwater (440 µm filtered) tank. Rectangular (102 cm long × 42 cm wide × 62 cm deep) plexiglass enclosures with 571 µm mesh screen on the bottom were placed approximately 3 mm off the bottom of each of two other, identical flow-through tanks that were shaded from man-made light.

On the evening of 22 August 1988 two herring were placed in each of the two flow-through enclosures/tanks and allowed to acclimate over night. At 0430 the next morning the flow of water through the two enclosures was shut off; at 0500 a mixture of exactly 50 ovigerous and 50 non-ovigerous adult female *E. elongata* was introduced into each enclosure. Sunrise occurred at 0616 and there was no moonlight (moon beyond the horizon); thus lighting conditions during the experiment simulated late dusk or early dawn, or perhaps nighttime conditions of bright moonlight. The herring were allowed to feed, unobserved, for 70 min in one enclosure and 115 min in the other, after which time the fish were dip netted from the enclosure. The enclosure was then lifted vertically from the tank so that all water and remaining copepods were filtered through the bottom. These copepods were then immediately identified as to status (ovigerous or non-ovigerous) and enumerated. The occasional free egg sac was paired with an egg-free female and added to the count of ovigerous females. Those copepods not retained on the bottom of the enclosure were presumed eaten by the fish.

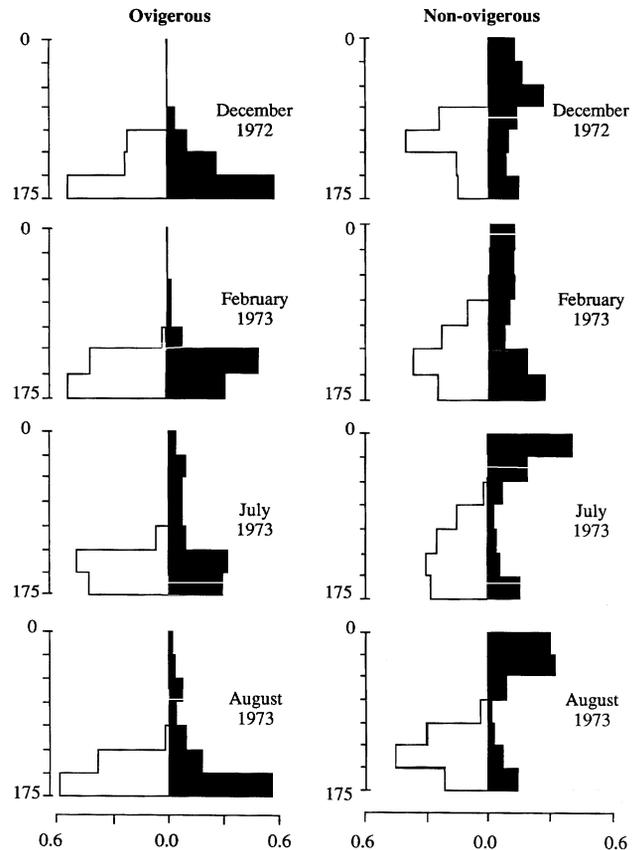
Results from the two replicate enclosures/tanks were pooled and the binomial distribution (Sokal and Rohlf 1981) was used to test for differences between the observed frequencies of ovigerous and non-ovigerous females consumed and the expected frequencies assuming a ratio of 1:1 (i.e., neutral selection by the fish).

## Results

### Vertical distributions and diel vertical migration

Striking differences in the vertical distributions of ovigerous and non-ovigerous adult female *Euchaeta elongata* were evident on all four dates. Ovigerous females were always concentrated between 100–175 m during the day, with a small percentage of the population residing in shallower waters during the night, especially in the summer (Fig. 2). Non-ovigerous females were likewise concentrated at depth (75–175 m) during the day, but a much larger proportion of the population resided at shallower depths during the night than did the ovigerous females (Fig. 2).

The statistically significant differences between mean daytime and nighttime weighted mean depths indicates



**Fig. 2.** Vertical distribution of adult female *Euchaeta elongata* on four dates in Dabob Bay, Washington, USA. Each daytime (clear) and nighttime (darkened) vertical distribution is the mean of two vertical series of samples collected near noon and midnight. Scales are the proportion of the copepod population in the seven sampled layers

the presence of DVM in non-ovigerous female *E. elongata* on all four dates, and ovigerous females on the two summer dates (Table 1). Ovigerous females were apparently non-migratory during winter, as indicated by the absence of statistically significant differences between mean daytime and nighttime weighted mean depths (Table 1), although the statistical power of the test is low for distinguishing slight differences (“effect size” as in Rotenberry and Wiens, 1985). The magnitudes of these differences, or amplitudes of DVM, indicate that non-ovigerous females migrate much greater distances (mean amplitude of 4 dates = 51.7 m) than do ovigerous females (mean = 10.8 m) ( $P < 0.05$ ,  $t$ -test, 6 df; Table 1). Additionally, the  $V$  values indicate that a very much larger percentage of non-ovigerous females migrate across 50 m (mean = 44.3%) than do ovigerous females (mean = 4.9%) (Table 1).

### Clutch size and egg development rates

Clutch size of field collected ovigerous female *E. elongata* was  $18.6 \pm 1.0$  eggs (mean  $\pm$  s.e.,  $n = 20$ ). Egg development times, confirmed by the presence of viable nauplii at time of hatching, were calculated as  $14.3 \pm 0.13$  days

**Table 1.** Vertical distributions and diel migrations of non-ovigerous and ovigerous adult females of *Euchaeta elongata* in Dabob Bay. WMD (weighted mean depth) =  $(\sum n_i d_i) / \sum n_i$ , where  $n_i$  is abundance (number per  $m^3$ ) at depth  $d_i$  ( $d_1 = 12.5$ ,  $d_2 = 37.5$ ,  $d_3 = 62.5$ ,  $d_4 = 87.5$ ,  $d_5 = 112.5$ ,  $d_6 = 137.5$ , and  $d_7 = 162.5$  m). Day and night mean WMDs were compared by *t*-test for each date: \*\*, probability

that observed difference between day and night mean WMDs occurred by chance is  $< 0.01$ ; \*  $0.01 < P < 0.05$ ; for all other pairs, day and night mean WMDs not significantly different ( $P > 0.05$ ). Amplitude of DVM ( $\Delta Z$ ) assigned value of zero when day and night mean (WMDs not significantly different. All values are in m, except  $V$  (%))

#### Ovigerous females

Dates		WMD#1	WMD#2	Mean WMD	$\Delta Z$	$V$
15–16 XII 1972	Day	141.4	147.4	144.4		
	Night	145.3	149.4	147.3	0	0
18–19 II 1973	Day	157.6	148.5	153.1		
	Night	140.8	138.9	139.8	0	0.5
21–22 VII 1973	Day	144.8	148.6	146.7		
	Night	118.8	119.2	119.0**	27.6	13.4
3–4 VIII 1973	Day	151.0	152.0	151.5		
	Night	136.9	133.9	135.4**	16.1	5.8

#### Non-ovigerous females

Dates		WMD#1	WMD#2	Mean WMD	$Z$	$V$
15–16 XII 1972	Day	116.1	119.9	118.0		
	Night	85.0	77.1	81.0*	37.0	28.3
18–19 II 1973	Day	127.6	134.2	130.9		
	Night	101.2	99.4	100.3*	30.6	24.4
21–22 VII 1973	Day	126.2	131.7	128.9		
	Night	50.0	72.0	61.0*	67.9	61.5
3–4 VIII 1973	Day	129.5	136.8	133.1		
	Night	66.3	57.8	62.1**	71.1	63.1

(mean  $\pm$  s.e.,  $n = 4$ ) at  $8^\circ$  C, and  $8.26 \pm 0.68$  (mean  $\pm$  s.e.,  $n = 3$ ) at  $12^\circ$  C. The small sample size was due to females either shedding their egg sacs before hatching, or less often, dying or producing malformed, non-viable nauplii. These rates are faster than that of 18.8 days at  $8^\circ$  C found by Yen (1983), who used a method assuming continuously hatching eggs (Edmondson 1960; Burgis 1980), and 18.7 days at  $10^\circ$  C for the congener *E. norvegica* reported by Hopkins (1977), who used the same method as this study.

#### Fish predation

When presented with equal proportions of ovigerous and non-ovigerous adult female *E. elongata* as potential prey, Pacific herring ingested 4.67 times as many ovigerous as non-ovigerous adult females, indicating a highly statistically significant preference for ovigerous prey ( $p = 0.006$ , binomial,  $n = 17$  copepods [14 ovigerous, 3 non-ovigerous] eaten).

#### Life table analyses

The potential population growth rate of *E. elongata* can be calculated using a simple life table approach (McLaren 1974; Ohman et al. 1983; Vuorinen 1987; Frost 1988; Ohman 1990). Specifically, we probed the

demographic consequences of DVM in adult female *E. elongata* by using life table analyses to contrast populations containing migratory and non-migratory (residing at depth both day and night) adult females. We assumed conditions of a sharp seasonal thermocline separating a deep layer of  $8^\circ$  C water from a surface layer of  $12^\circ$  C water. An approximate temperature gradient of  $4^\circ$  C is typical of spring and autumn in Dabob Bay, and is a conservative estimate of summertime stratification (Ohman 1986). Migrants were assumed to spend 12 hours per day in each stratum, while non-migrants spend 24 h per day in their preferred stratum.

All naupliar stages of *E. elongata* in Dabob Bay reside below the thermocline both day and night (Frost, unpublished), and thus always develop at approximately  $8^\circ$  C. Early copepodid stages (I–III) are only very rarely found above 50 m (Damkaer 1964) and were thus assumed to also develop at  $8^\circ$  C. Copepodid stages IV and V, however, undertake DVM (Ohman 1990), and thus were assumed to experience a daily mean temperature of  $10^\circ$  C. By applying the mean ratio of maturation time:egg development time (18.9:1.0) of the five species of calanoid copepod given in Landry (1983) to the egg development time of *E. elongata* at  $8^\circ$  C, and a correction for the slightly enhanced development of migratory copepodid stages IV and V (i.e., 52.9 days at  $10^\circ$  C if migratory vs 66.9 days at  $8^\circ$  C if nonmigratory), we estimated the development time for adult female *E. elongata* (fertilization to maturity) to be 256.1 days. If adult females con-

**Table 2.** Values of various life history parameters that serve as input in the four life table analyses (scenarios 1–4) used to contrast the demographic consequences of migratory and non-migratory behavior in ovigerous adult female *Euchaeta elongata*. The value of  $r$ ,

the realized rate of population increase, is obtained from  $\sum l_x m_x e^{-rx} = 1.0000$ , where  $l_x$  is age-specific survivorship and  $m_x$  is age-specific fecundity. See text for details

Life History/ Environmental Parameter	Scenario 1	Scenario 2	Scenario 3	Scenario 4
	Adults Migratory/ Perfect Survivorship	Adults Migratory/ Population Steady State	Adults Non-migratory/ Mortality unchanged	Adults Non-migratory/ Adult mortality reduced
Temperature (°C)	8.0–12.0	8.0–12.0	8.0	8.0
Egg development time (days)	11.3	11.3	8.3	8.3
Maturation time (fertilization-maturity, days)	256	256	253	253
Clutch size (female eggs per ovigerous adult female)	9.3	9.3	9.3	9.3
Number of consecutive clutches per adult female	10.0	10.0	10.0	10.0
Mortality, immature stages ( $d^{-1}$ )	0	0.01473	0.01473	0.01473
Mortality, adult stage ( $d^{-1}$ )	0	0.01473	0.01473	0.01091
Realized rate of population increase ( $r$ , $d^{-1}$ )	0.01473	0	–0.00071	0

tinue to migrate upon becoming ovigerous, the eggs will experience an average temperature of 10° C, and thus take 11.3 days to develop (mean of 8° C and 12° C development times estimated above). All life table calculations were made with adult females producing ten consecutive clutches (assumed) of 9.3 female eggs per clutch (from above, assuming 1:1 sex ratio of eggs). The interclutch interval was assumed to be zero.

These estimates of development and fecundity, combined with the assumption of perfect survivorship, can be applied to a life table analysis of a population containing migratory ovigerous females to generate a realized rate of population growth ( $r$ ) of 0.01473  $d^{-1}$  (scenario 1, Table 2). For ease of comparison with subsequent scenarios, we have included an instantaneous daily mortality term, applied to all developmental stages, of 0.01473  $d^{-1}$  such that  $r$  of a population containing migratory adults equals zero (scenario 2, Table 2).

We next estimated the demographic cost of ovigerous females being non-migratory (remaining at depth day and night) by reducing the egg development time to that at 8° C, and obtained  $r = -0.00071$  (scenario 3, Table 2). For this non-migratory behavior to persist, the demographic cost of delayed egg development must be balanced by a demographic advantage of equal or greater magnitude. The obvious candidate for such an advantage is reduced mortality afforded ovigerous females by avoidance of visually orienting predators inhabiting the surface layer. The magnitude of reduced mortality of adult females necessary to balance the costs of delayed egg development can be calculated by reducing the level of mortality of adult females in the life table analyses such that the realized rate of growth of the population of non-migratory females becomes zero, i.e., equal to that of the migratory population. This scenario indicates that a 26% reduction of adult mortality is necessary to offset the demographic cost of delayed egg development

in a population containing non-migratory ovigerous females (scenario 4, Table 2).

## Discussion

While ovigerous female *E. elongata* may on some occasions exhibit weak DVM, nonovigerous females are always more strongly migratory, as measured by both the amplitude of migration and the proportion of the population migrating. Furthermore, while non-ovigerous females commonly enter the upper 50 m of the water column at night, ovigerous females virtually never do so.

The preference of planktivorous fish for ovigerous over non-ovigerous copepod and cladoceran prey has been well studied in both the laboratory (Mellors 1975; Vuorinen et al. 1983; Winfield and Townsend 1983; Koufopanou and Bell 1984; Tucker and Woolpy 1984) and in the field (Mellors 1975; Sandstrom 1980; Bohl 1982; Dawidowicz and Gliwicz 1983). Our results showing Pacific herring to preferentially feed on ovigerous versus non-ovigerous adult female *E. elongata* are thus consistent with a large body of previous research. The basis for this preference, however, is unclear. Previous work on other planktivorous fish – zooplankton prey interactions have indicated selective predation can be influenced by prey size (Galbraith 1967; Brooks 1968; Doble and Eggers 1978; Mittlebach 1981; Eggers 1982; Koslow 1981), prey pigmentation (Zaret 1972; Mellors 1975; Vinyard and O'Brien 1975; Kislalioglu and Gibson 1976), and prey escape ability (Drenner et al. 1978). Any one or combination of these factors could account for the greater susceptibility of ovigerous versus non-ovigerous adult female *E. elongata* to Pacific herring predation.

We conclude that the non-migratory or weakly migratory DVM behavior of ovigerous female *E. elongata* (below 50 m day and night) is an adaptation to avoid

visual predators during a particularly vulnerable stage in the copepod's life history. Indeed, the threat of visual predators may well be the cause of both ovigerous and non-ovigerous female *E. elongata* avoiding the surface layer during daylight. However, adult *E. elongata* feed predominantly on small copepods that largely inhabit surface waters in Dabob Bay (Yen 1983), and thus adult females experience greatly improved feeding resources when entering the surface layer (Yen 1985). Non-ovigerous females apparently do so only under the cover of darkness. Such nightly forays into food-rich surface waters are not entirely without risk, however, as many planktivorous fish are known to feed at night, albeit at reduced levels relative to daytime (Blaxter and Hunter 1982; Bollens unpublished). Ovigerous female *E. elongata*, being even more susceptible to predation by planktivorous fish than are non-ovigerous females, must remain at depth both day and night to avoid being eaten, despite the demographic cost incurred of delayed egg development.

Furthermore, non-migratory ovigerous females may incur an additional demographic cost due to longer interclutch intervals associated with poorer feeding conditions at depth. We have not estimated this cost because we were unable to measure interclutch intervals in the laboratory. Thus the contrast we have drawn between migratory and non-migratory DVM behavior in ovigerous adult female *E. elongata* considers only the demographic cost of continuous residence in cooler, subsurface waters. Consequently, our calculation of a 26% reduction in adult mortality is a conservative estimate of the demographic advantage required to offset the costs of non-migratory behavior, and would be necessarily greater if food limitation occurred at depth.

Our invocation of differential predation risk as the regulator of vertical distributions and DVM in ovigerous and non-ovigerous copepods is similar to that of Vuorinen (1987), although with different consequences for the copepods. Working with the copepod *Eurytemora hirundoides* in the Archipelago Sea, Vuorinen (1987) explained the greater proportion of ovigerous females at depth during the day as predator avoidance behavior, with these females migrating into the food-rich surface layer to feed at night. In contrast, less conspicuous non-ovigerous female *E. hirundoides* were more evenly distributed day and night, and were thus less migratory than were ovigerous females.

In the case of *E. elongata* in Dabob Bay, ovigerous females are likewise more susceptible to visual predators than are non-ovigerous females, but predation risk is apparently so great for both types of copepods that they must avoid the surface layer in the daytime, with the less conspicuous but still vulnerable non-ovigerous females entering the food-rich surface layer only under the cover of darkness. The more pronounced predator-avoidance behavior of *E. elongata* in Dabob Bay as compared to *E. hirundoides* in the Archipelago Sea could be due to either greater predator abundances in Dabob Bay or greater susceptibility to fish predation of *E. elongata* (due, for example, to its larger body size: 6.9 mm vs 1.7 mm total length for *E. hirundoides*). Thus while the distributional patterns of the two species of copepod are quite different,

the underlying mechanism is the same: avoidance of visual predators. In both cases planktivorous fish constrain the vertical distributions and diel migrations of the copepods such that ovigerous females spend less time in the surface layer than do non-ovigerous females.

Under conditions of a thermally stratified water column, however, such avoidance of the surface layer has its attendant cost. All other things being equal, residence in colder subsurface waters can result in delayed egg development and thus a reduced rate of realized population growth. This argument has normally been presented as a demographic cost of DVM relative to the alternative of remaining in the warmer surface layer day and night, with persistence of DVM behavior requiring that this demographic cost be balanced by a demographic advantage (usually reduced mortality) of equal or greater magnitude (McLaren 1974; Ohman et al. 1983; Vuorinen 1987; Frost 1988; Ohman 1990). We present a similar argument for the cost of remaining at depth day and night relative to the alternative of undertaking DVM. We conclude that the non-migratory predator-avoidance behavior of ovigerous female *E. elongata* (residing below 50 m day and night) must afford the copepod a demographic advantage of no less than a 26% reduction in adult mortality to offset the demographic cost of delayed egg development.

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