Variability of Diel Vertical Migration in the Marine Planktonic Copepod *Pseudocalanus newmani* in Relation to Its Predators[1]

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We report results of a 3-yr field study of the vertical distributions and diel vertical migration (DVM) of *Pseudocalanus newmani* in the central basin of Dabob Bay, Washington, USA. Our results include two novel findings. First, a statistically significant relationship exists between strength of DVM in *P. newmani* and the potential predation impact of its planktonic invertebrate predators. Second, a strong "normal" DVM (up at night, down during the day), unique for *P. newmani* in 5 yr of sampling at this locale, occurred at a time when the zooplanktivorous fish *Ammodytes hexapterus* was unusually abundant and preying on the copepod; this DVM may have been induced by the fish. DVM behavior of *P. newmani* was highly variable, with changes in behavior commonly occurring on a time scale of weeks; in one case the copepod switched from a normal migration pattern to a reverse migration pattern (down at night, up during the day) in less than 5 wk. These observations, combined wth those of previous research, indicate that *P. newmani* has an exceptionally diverse repertoire of migration behavior, any particular expression of which is most likely manifested by individual copepods exercising phenotypic behavioral plasticity in response to potential predation.

Voici le compte rendu d'une étude sur le terrain ayant duré 3 ans, et portant sur la répartition verticale ainsi que la migration verticale nycthémérale du *Pseudocalanus newmani*, dans le bassin central de Dabob Bay, Washington, É.-U. Les résultats obtenus mènent à deux conclusions inédites. D'une part, il existe une relation importante, sur le plan statistique, entre l'intensité des migrations verticales nycthémérales chez le *P. newmani* et la prédation éventuelle exercée sur ce copépode par des invertébrés planctoniques. D'une part, une forte migration verticale nycthémérale, que l'on peut qualifier de «normale» (ascendante la nuit et descendante le jour) mais unique chez le *P. newmani* en 5 ans d'échantillonnage à cet endroit, s'est produite au cours d'une période où l'espèce zooplanctonophage *Ammodytes hexapterus* était particulièrement abondante et consommait de ce copépode; cette forte migration peut être imputable à ce poisson. Le comportement du *P. newmani* présentait de grandes variations, des modifications du comportement habituel s'étalant couramment sur des semaines; dans un cas, le copépode a inversé en moins de 5 sem son comportement migratoire normal (descendant la nuit et remontant le jour). Ces observations confirment celles d'une étude antérieure et indiquent que le *P. newmani* présente un répertoire extrêmement diversifié de comportements migratoires; en effet, tout copépode soumis à une prédation éventuelle démontre une plasticité de comportement phénotypique qui se manifestera très probablement de façon particulière selon les individus.

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Of the several hypotheses advanced to explain the adaptive value of diel vertical migration (DVM) behavior in zooplankton (Kerfoot 1985; Lampert 1989), evidence implicating predator evasion has recently accumulated from theoretical studies (Frost 1988; Gabriel and Thomas 1988; Mangel and Clark 1988), field observations (see brief review by Bollens and Frost 1989a; Levy 1990; Stirling et al. 1990; Bollens et al. 1992), and experimental manipulations of predators (Bollens and Frost 1989b, 1991; Dawidowicz et al. 1990; Leibold 1990; Neill 1990; Tjossem 1990; Ringelberg 1991). The DVM behavior of the marine planktonic copepod *Pseudocalanus newmani* Frost has played a particularly prominent role in the furtherance of the predator evasion hypothesis. Ohman et al. (1983) and Ohman (1990) inferred that 'reverse'' DVM (at depth during the night, near the surface at day) in adult female *P. newmani* in the deep, central basin of Dabob Bay (Washington) was a means of avoiding planktonic invertebrate predators that forage nocturnally in the surface layer. Further, ''normal'' DVM behavior (near the surface at night, at depth during the day) in *P. newmani*, not observed at the deep station, but occurring commonly at a nearby shallower station with a relatively depauperate assemblage of invertebrate predators, was suggested to be a means of avoiding zooplanktivorous fish that forage diurnally in the surface layer (Ohman 1990). With respect to the reverse migration of *P. newmani* at the deep station, Ohman (1990, fig. 12) presented field data relating the proportion of the population residing at depth at night during midsummer to the abundance of invertebrate predators above this depth at night; the relationship, while suggestive, was not, however, statistically significant.

Here, we report results of a 3-yr field study of the vertical distributions and DVM behavior of *P. newmani* in the deep, central basin of Dabob Bay and address the issue of how predators might induce changes in its DVM behavior.

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Materials and Methods

The field site was the deep (193 m), central basin of Dabob Bay, Washington, USA (47°45′N, 122°50′W). Twelve cruises were undertaken between 1985 and 1987: 25–26 April 1985, 25–26 June 1985, 20–22 August 1985, 8–15 October 1985, 6–8 May 1986, 9–11 June 1986, 5–6 August 1986, 13–15 August 1986, 10–12 June 1987, 15–17 July 1987, 12–14 August 1987, and 20–21 October 1987. During 1985 and 1986 the vertical distribution of adult female *P. newmani* was determined using a vertically hauled, multiple sample, closing net (1.0 m^2, 333-μm mesh) described by Frost (1988). On these cruises the following six discrete depth strata were sampled: 0–10, 10–25, 25–50, 50–75, 75–125, and 125–175 m. In May 1985 the two surface strata were combined into a single stratum of 0–25 m. During the 1987 cruises, we used a vertically hauled, single sample, closing net (1.0 m diameter, 216-μm mesh) described by Miller et al. (1984) and sampled 0–25, 25–50, and 50–175 m strata. On all 12 cruises, duplicate samples were collected near noon and midnight on each of two consecutive days. Abundance of adult females of *P. newmani* in preserved samples was determined from the mean abundance in replicate subsamples taken with a Folsom splitter, Stempel pipette, or automatic pipette.

For each of our 12 cruises, as well as for 15 dates reported in Ohman et al. (1983) and Ohman (1990; data kindly provided by the author), we calculated two separate indices of DVM in *P. newmani*. First, we calculated the weighted mean depth (WMD) of adult females for each daytime and nighttime vertical series of samples, where WMD = $(\Sigma n_i d_i)/\Sigma n_i$ and n_i is abundance (number per cubic metre) at depth d_i, taken to be the midpoint of each depth stratum. The amplitude of migration (ΔZ) was then calculated as the difference between the mean daytime WMD and the mean nighttime WMD, with positive values indicating normal DVM and negative values indicating reverse DVM. Each ΔZ value was tested for statistical significance using a *t*-test (two-tailed) to compare mean daytime and nighttime WMDs. Second, we calculated the proportion of adult female *P. newmani* migrating on a diel cycle across a reference depth of 25 m by calculating the difference between the mean proportion of the population above 25 m at midnight and the mean proportion of the population above 25 m at midday (i.e. *V* as described by Bollens and Frost 1989a). Although the choice of reference depth for this index is somewhat subjective, 25 m is the depth across which *P. newmani* most commonly migrates when exhibiting DVM at this locale (Ohman et al. 1983; Ohman 1990; this study).

Abundances of planktonic invertebrate predators in the upper 25 m at night were determined from the same samples used to determine the vertical distributions of *P. newmani*. We enumerated the carnivorous copepod *Euchaeta elongata* (copepodid IV, copepodid V, and adult female stages), the chaetognath *Sagitta elegans*, and the euphausiids *Euphausia pacifica* and *Thysanoessa longipes* (>10.5 mm, i.e. late juveniles and adults). These taxa represent the major invertebrate predators of *P. newmani* at this locale (Ohman 1986, 1990). To estimate the potential mortality imposed by the predator populations, we determined maximal potential predation rates (number of female *P. newmani*·d^{-1}) by multiplying predator density by experimentally derived maximal ingestion rates obtained from the literature. These maximal ingestion rates are 4.52, 16.1, and 18.7 female *P. newmani*·predator^{-1}·d^{-1} at 8°C for copepodid IV, copepodid V, and adult female *E. elongata*, respectively (Yen 1983), 2.26 female *P. newmani*·predator^{-1}·d^{-1} at 8°C for *E. pacifica* (Ohman 1984), and 2.20 female *P. newmani*·predator^{-1}·d^{-1} at 13°C for *S. elegans* (Reeve 1980). Maximal ingestion rate for *T. longipes*, which was always much less abundant than *E. pacifica*, was assumed to be equal to that for *E. pacifica*. These maximal predation rates were then adjusted for seasonal changes in temperature by applying the temperature predicted to occur in the middle of the 25–0 m stratum on each date (minimum of 8°C on February 1, maximum of 14°C on August 1; Ohman 1986), assuming a Q_{10} of 2.0.

On most dates, we obtained estimates of light attenuation in the surface layer from measurements of Secchi depth or vertical profiles of submarine irradiance using a LiCor 190SB underwater quantum sensor. Phytoplankton standing stock was measured as concentration of chlorophyll *a* in samples collected at five to seven depths in the upper 30 m (see Frost 1988; Ohman 1990). Sampling of planktivorous fish and gut content analysis of fish were done as described in Bollens and Frost (1989a).

Results and Discussion

Pseudocalanus newmani exhibited diverse migration behavior (Table 1). Considering only those sampling dates with sufficient replication for statistical testing (20/27 cases), *P. newmani* usually did not migrate (i.e. mean daytime WMD was not significantly different from mean nighttime WMD on 11 of 20 dates). Reverse DVM occurred on eight dates, thus doubling the number of cases reported by Ohman (1990). Normal migration was observed only once during 6–8 May 1986 (Table 1).

Simple linear regression (functional regression, Ricker 1973) was used to examine the dependence of the strength of DVM in *P. newmani* (*V*) on the potential predation rate of invertebrate predators (Fig. 1). For this analysis, we combined data from our 11 cruises with that from 11 cruises reported in Ohman (1990) in which concurrent sampling of *P. newmani* and its invertebrate predators was undertaken. The strength of DVM in *P. newmani* showed a highly significant (negative) dependence on potential predation rate regardless of which index of migration was used as the dependent variable (for *V*: $Y = 17.10 - 0.075X$, $r = -0.722$, $n = 22$, $P < 0.01$; for ΔZ: $Y = 9.194 - 0.044X$, $r = -0.762$, $n = 22$, $P < 0.01$). Moreover, both of these migration indexes also showed significant (negative) dependences on the absolute abundance of invertebrate predators (for *V*: $Y = 24.30 - 0.486X$, $r = -0.595$, $n = 22$, $P < 0.01$; for ΔZ: $Y = 13.36 - 0.281X$, $r = -0.465$, $n = 22$, $P < 0.05$).

The single instance of normal vertical migration (6–8 May 1986: Table 1; Fig. 2A), unique for *P. newmani* at this locale in 5 yr of sampling (Ohman 1990; this study; B. W. Frost, unpubl. data), occurred at a time when late larval and juvenile *Ammodytes hexapterus* (Pacific sandlance) were unusually abundant (Bollens and Frost 1989a). This fish is a known zooplanktivore (Hart 1973) and was actively feeding on adult female *P. newmani* at this time (Table 2). Gut content analyses were also done on five other species of fish collected at the station on this date (Bollens and Frost 1989a). Guts of four of these species (*Oncorhynchus keta* (chum salmon), *Gasterosteus aculeatus* (threespine stickleback), *Clupea harengus* (Pacific herring), and an unidentified osmerid (smelt)) contained no *P. newmani*, while guts of the fifth species (*Oncorhynchus gorbuscha* (pink salmon)) contained only trace amounts of *P. newmani* (<1% of gut contents by number or weight). Indeed, in 3 yr of regular trawl sampling of pelagic

TABLE 1. Daytime and nighttime weighted mean depths (WMDs) and summary statistics for adult female *P. newmani* at the central, deep station of Dabob Bay. 1973–80 calculations generated from data in Ohman et al. (1983) and Ohman (1990); 1985–87 calculations generated from unpublished data available from the authors upon request. See text for details regarding calculations. Negative (positive) values of ΔZ and V indicate reverse (normal) DVM. Probability that mean nighttime and mean daytime WMDs different by chance: $*P < 0.05$; $**P < 0.01$; $***P < 0.001$; ns = not significant. Blank cells indicate samples not collected or summary statistics not applicable given lack of replication on that date.

	Daytime WMDs (m)					Nighttime WMDs (m)					Day vs. night comparisons		
Dates	1	2	3	4	Mean	1	2	3	4	Mean	ΔZ (m)	*t*-statistic	V (%)
3-4 Aug. 1973	38.4	34.0			36.2	72.8	85.0			78.9	−42.7	6.58*	−56.9
1-2 Aug. 1978	36.4					56.1					−19.7		+4.8
24 Aug. 1978	23.2					51.7					−28.5		−46.7
28-30 Sept. 1978	19.2	24.9			22.1	23.3	18.0			20.7	+ 1.4	0.36ns	+5.0
11-12 Jan. 1979	11.5					13.9					− 2.4		−1.6
15-16 Mar. 1979	27.8					25.0					+ 2.8		+2.5
11-12 Apr. 1979	21.2					20.2					+ 1.0		+5.1
4-7 June 1979	28.6	24.2			26.4	28.5	51.9			40.2	−13.8	1.16ns	−24.6
10-11 July 1979	32.3					44.9					−12.6		−34.2
25-31 July 1979	28.1	30.8			29.5	75.2	72.3			73.8	−44.3	22.35**	−67.2
14 Aug. 1979	14.1	16.9			15.5	41.8	36.9			39.4	−23.9	8.50*	−66.7
5-7 Dec. 1979	24.9	24.0	23.2		24.0	24.9	25.1			25.0	− 1.0	1.57ns	+11.1
9-10 July 1980	11.0					16.2					− 5.2		−24.2
26-28 July 1980	21.1	21.9			21.5	30.8	25.4			28.1	− 6.6	2.42ns	−36.0
16-19 Aug. 1980	21.6	26.4			24.0	54.1	48.2			51.2	−27.2	7.15*	−43.7
25-26 Apr. 1985	31.8	30.4	34.9	30.0	31.8	30.2	29.1	29.2	26.2	28.7	+ 3.1	2.21ns	+10.9
25-26 June 1985	15.1	13.7	18.6	17.4	16.2	17.2	19.0	13.7	14.4	16.1	+ 0.1	0.06ns	−25.9
20-22 Aug. 1985	30.6	29.2	26.9	26.0	28.2	46.1	55.3	33.7	48.3	45.9	−17.7	3.83**	−26.8
8-15 Oct. 1985	12.8	15.6	7.9	7.0	10.8	10.9	10.9	11.5	9.1	10.6	+ 0.2	0.10ns	+2.8
6-8 May 1986	44.3	42.0	37.8	40.3	41.1	19.7	13.9	15.5	19.2	17.1	+24.0	12.19***	+53.6
9-11 June 1986	9.8	9.0	13.1	10.3	10.6	19.5	22.0	13.2	13.8	17.1	− 6.5	2.78*	−13.3
5-6 Aug. 1986	28.3	35.9	49.9	59.5	43.4	36.3	37.9	40.2	51.5	41.5	+ 1.9	0.24ns	−4.9
8-15 Oct. 1986	9.6	12.5	13.0	16.0	12.8	10.3	9.3	14.8	10.3	11.2	+ 1.6	0.89ns	+5.3
10-11 June 1987	19.8	21.9	22.6	26.6	22.7	21.8	21.7	22.1	20.6	21.6	+ 1.1	0.75ns	+4.3
14-17 July 1987	33.4	31.4	29.7	26.4	30.2	50.8	48.0	58.8	47.5	51.3	−21.1	7.03***	−22.5
12-14 Aug. 1987	20.5	31.1	34.1	27.2	28.2	51.8	42.9	40.1	43.3	44.5	−16.3	4.21**	−33.3
20-21 Oct. 1987	27.5	45.0	56.3	54.2	45.8	30.6	25.4	39.3	42.8	34.5	+11.3	1.47ns	+18.2

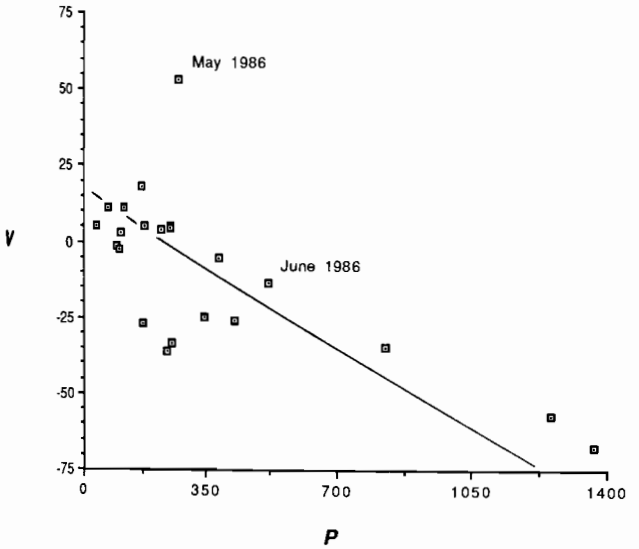

FIG. 1. Linear regression of the dependence of the strength of diel vertical migration (V) of adult female *P. newmani* in the deep, central basin of Dabob Bay on potential predation rate (P, number of female *P. newmani* removed·m^{-3}·d^{-1}) ($Y = 17.10 - 0.075X$, $r = -0.722$, $n = 22$, $P < 0.01$). Line fitted by functional regression (Ricker 1973).

fish and analyses of their gut contents at this station (e.g. Bollens and Frost 1989a and unpublished data for 1987), *P. newmani* rarely exceeded these trace levels in the diets of fish and never was as dominant a dietary item as in *A. hexapterus* in May 1986. The unique normal DVM exhibited by *P. newmani* during 6–8 May 1986 may have been induced by its unusually abundant predator, *A. hexapterus*.

For 21 sampling dates, we had estimates of light attenuation coefficient and phytoplankton standing stock (as milligrams of chlorophyll *a* per square metre, integrated over the upper 30 m). We found no significant correlation between either of these and either measure of strength of DVM in *P. newmani* (all correlation coefficients positive, but <0.3, $N = 21$).

These results suggest that DVM in *P. newmani* at this locale was largely a response to predation pressure from invertebrates and thus corroborate and lend a strong statistical basis to findings previously reported by Ohman et al. (1983) and Ohman (1990). Our results are novel, however, in indicating that the behavioral repertoire of *P. newmani* at this locale also includes normal DVM behavior. Thus, while no migration or reverse DVM was the most common behavioral mode in *P. newmani* at this locale (Table 1), with the latter behavior hypothesized to be induced by invertebrate predators, the normal DVM suggests an occasional inducing role for visual predators such as zooplanktivorous fish. Levy (1990) reported similar diversity of migration behavior in a freshwater cladoceran (*Bosmina*) and also suggested that different migration patterns were responses to presence and behavior of specific types of zooplanktivores.

Vertical migration behavior of *P. newmani* at this locale was not only highly variable, but could also sometimes change rather rapidly, e.g. from strong normal DVM behavior in May of 1986 to weak reverse migration just 5 wk later (Table 1; Fig. 2).

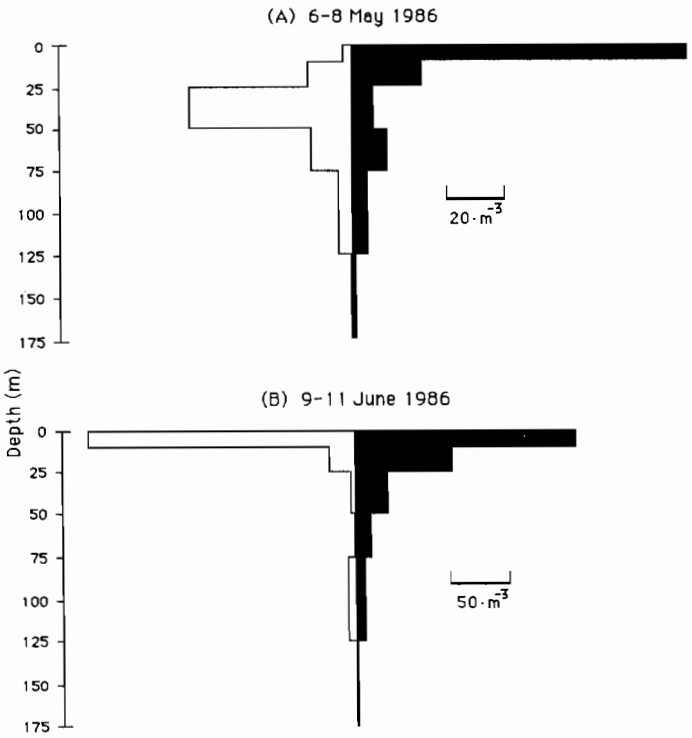

FIG. 2. Vertical distribution of adult female *P. newmani* in the central, deep basin of Dabob Bay. Each daytime (white) and nighttime (black) vertical distribution is the mean of four vertical series of samples collected in pairs near noon and midnight on each of two consecutive days.

TABLE 2. Composition of the diet, as percent of total numbers of different prey types, in seven juvenile (48–55 mm standard length) *A. hexapterus* collected at the deep, central station in Dabob Bay, on 1 May 1986. "Other" consisted of miscellaneous crustaceans, largely calanoid copepods and larval euphausiids. See Bollens and Frost (1989a) for details of collection and analysis of stomach contents.

Prey category	%
Calanus pacificus	11
Oithona similis	27
Pseudocalanus newmani	31
Other	31

Although we have no direct measurements of advection with which to address the possibility of substitution of behavioral types at this station, we believe that the change in behavior was not due to exchange of populations within Dabob Bay, for in concurrent sampling at the shallow station, *P. newmani* exhibited a weak (statistically nonsignificant) normal DVM during 9–10 June 1986 (B. W. Frost, unpubl. data). Ohman (1990) also observed differences in migration behavior of *P. newmani* sampled concurrently at the two stations.

The rapid shift of migration behavior at the deep station has implications for the mechanism by which predation might induce such changes. For instance, selective predation could impose differential mortality on genetically distinct behavioral types within the prey population and thus, over time, cause the observed changes in DVM behavior. Alternatively, individual copepods could simply be exercising phenotypic plasticity in their DVM behavior and thus effect very rapid changes in migration patterns.

The possibility of a population – genetic level behavioral response is supported by electrophoretic studies of freshwater cladocerans showing different genotypes of the same species to exhibit differences in DVM behavior (Weider 1984) and phototaxis (Dumont et al. 1985; De Meester and Dumont 1988, 1990). However, the change in behavior in *P. newmani* from normal migration in May 1986 to reverse migration in June 1986 occurred during a period of substantial increase in abundance of adult females of *P. newmani* (from 2497 ± 171 to 4380 ± 456·m^{-2} (mean ± SE), which would require the hypothesized mechanism of selective predation to inflict very much greater mortality on normal migrators in order for the reverse migrators to grow rapidly and become dominant in only 5 wk. However, the occurrence during this period of moderate to high potential invertebrate predation (Fig. 1), on the one hand, and an unusually high abundance of planktivorous fish (Bollens and Frost 1989a) actively feeding on *P. newmani* (Table 2), on the other hand, suggests that both behavioral types would be expected to experience substantial mortality, and thus a very much greater rate of mortality on normal migrators during this period seems unlikely.

Given this probable limitation on differential mortality to cause such rapid shift in migration behavior, the more likely explanation for the change we observed in DVM behavior in *P. newmani* is phenotypic behavioral flexibility of individual copepods. This interpretation of our field results is consistent with recent experimental findings showing individual phenotypic flexibility in DVM behavior in two other species of copepods (Bollens and Frost 1989b, 1991; Neill 1990). However, while such a hypothesis is suggested by our field data on *P. newmani*, it will ultimately need to be tested experimentally.

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