these bands had access to high-quality food by remaining at the high altitudes they were also more likely to encounter severe winter snowstorms and cold. Third, the winter of 1979–80 (when these bands disappeared) was severe, and each of several snowstorms deposited over 65 cm of snow at about 1760 m. Accumulation at higher elevations and ridgelines, where the missing horses were found, would be much greater.

It is unlikely that snow was a density-dependent mortality factor, because of 42 skeletons located so far, 31 (74 percent) were situated above 2000 m and 28 (67 percent) were above 2300 m. The rest of the skeletons were found between 1400 and 2005 m. Because most horses spend less time at high altitudes (*6*), and all sites were searched for similar periods of time, the disproportionate number of bodies found at higher elevations $[\chi^2(1) = 9.52; P < .01]$ suggests that unpredictably heavy snow accumulation is a principal mortality agent in the Granites as it may be elsewhere in the Great Basin. For instance, during the winter of 1977 an estimated 300 horses (50 percent of the population) died in the Buffalo Hills (*8*), an insular area 12 km west of the Granites. Although these animals existed at high densities (*8*), and individuals probably were in poor physical condition, it seems that snow precipitated the heavy mortality.

Drought is another factor that has contributed prominently in catastrophic mortality in Great Basin horses. For instance, the remains of nine young horses that died in mud apparently after following their mothers to drink were found in the Owyhee Desert of northern Nevada (Fig. 1B). The foals, from different bands and varying in age from 2 weeks to 2 months, and a yearling, were not able to pull themselves from the mud (*8*).

Similar death assemblages have been reported for other large extant mammals, although the extent to which catastrophic mortality influences demography is not known. Mud-induced die-offs occurred in zebras (*Equus zebra*) (*9*) and in cape buffalo (*Syncerus caffer*), the latter which "died at water's edge after becoming too weak to pull themselves out" (*10*) while massive deaths of wildebeest young (*Connochaetes taurinus*) also occur (*11*). Even mountain zebras have perished in sudden snowstorms in the mountains of South Africa (*12*).

Population size or density (*13*) may well be indirect mortality agents and are certainly important in determining spatial relations. However, weather related variables such as heavy snow accumulation apparently increase the susceptibility of entire groups to mortality and may be more debilitating to mountain dwelling Great Basin horses than once believed.

The data on mortality in Granite Range horses suggest that generalizations about the social structure of paleomammals from fossil assemblages should be made with caution. For instance, if nothing was known about the social organization of horses several different conclusions might have arisen had only one of the assemblages in the Granites been found. If the discovery was that of the two females and juvenile, it could be argued that females and young formed the only permanent associations for that species. However, if the stallion and his harem were located instead, the conclusion might be that bands were the primary social units. Thus although skewed sex and age ratios may indicate some aspect of sociality, there are limitations to the extent to which they can be used to reconstruct the social structure of fossil mammals.

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Reverse Diel Vertical Migration: An Escape from Invertebrate Predators

Abstract. *The marine copepod* Pseudocalanus *sp. exhibits an unusual reverse diel vertical migration in Dabob Bay, Washington, concurrently with a normal vertical migration by nocturnal invertebrate predators. Reduced spatial overlap with predators appears to decrease mortality rate of adult female* Pseudocalanus. *A life table analysis suggests that the demographic disadvantage associated with daily migration across a thermal gradient can be overcome if mortality is reduced by as little as 16 percent.*

In aquatic environments, pelagic representatives of phyla as diverse as cnidarians and chordates undertake conspicuous vertical excursions on a diel cycle. Among the hypotheses advanced to explain the adaptive significance of diel vertical migrations, three have broad application to the evolution of this behavior in the ocean and in lakes. Two concern metabolic (*1, 2*) or fecundity (*3*) advantages that may accrue to individual animals that migrate vertically when waters are thermally stratified. A third suggests that animals migrate to avoid visually feeding vertebrate predators (*4*).

We report that reverse diel vertical migration (nocturnal descent) allows a species of marine copepod to avoid nonvisually feeding invertebrate predators. This reverse migration recurs at the same location in different years and is not predictable by hypotheses other than the avoidance of nocturnal predators. A few instances of reverse migration behavior by zooplankton have been observed in marine (*5*) and freshwater (*6*) environments, although none in the ocean have been linked to predator-prey interactions.

At the deepest location (185 m) in Dabob Bay, a temperate fjord in Puget Sound, Washington (47°45′N, 122°49′W), which is oxygenated year-round, adult females of the small suspension-feeding copepod *Pseudocalanus* sp. (*7*) underwent a reverse diel vertical migration in early August 1973 (Fig. 1A). This behavior was observed again in late July 1979 in different food conditions (Fig. 1B), and on other occasions in midsummer (*8*). Ovigerous females also reverse migrate (*9*). Late July through early August is the period of the peak annual abundance of at least two species of predatory invertebrates in Dabob Bay, the chaetognath *Sagitta elegans* (*10*) and the copepod *Euchaeta elongata* (*11*). These two species and the euphausiid *Euphausia pacifica* exhibit normal (nocturnal ascent) diel vertical migration behavior (Fig. 1C) concurrently with the reverse migration by *Pseudocalanus*. At times of year when the abundance of these predators is greatly reduced, or at a shallow station in Dabob Bay where few predatory zooplankton occur, no reverse migration by *Pseudocalanus* has been observed (*8*).

Laboratory feeding experiments with seven species of common zooplankters potentially predatory on *Pseudocalanus* in Dabob Bay have shown that *Euchaeta elongata* (*11*), *Sagitta elegans* (*12*), and *Euphausia pacifica* (*8*) exhibit the highest rates of predation on *Pseudocalanus* females (*13*). *Euchaeta* and *Sagitta* are obligate predators. *Pseudocalanus* is the preferred prey of *E. elongata* in Dabob Bay (*11*) and frequently is the predominant prey of *S. elegans* (*8, 14*). *Euphausia pacifica* is omnivorous, but whether individuals selectively ingest small copepods or other prey is not known.

Feeding rates of mature individuals of *S. elegans* and *E. elongata* are higher at night than during the day (*8, 11, 14*). The greatest impact of these predators on *Pseudocalanus* would, therefore, be expected to occur during nighttime hours, when the predators migrate toward the surface. Yet the reverse migration by *Pseudocalanus* reduces overlap with these predators, apparently decreasing mortality. *Euchaeta elongata* and *S. elegans* alone could reduce the abundance of *Pseudocalanus* females, their preferred prey, at the estimated fractional rate of 0.105 to 0.237 per day in late July 1979 (*15, 16*), in the absence of avoidance behavior by *Pseudocalanus*. By contrast, the estimated finite mortality rate of females at the time of the reverse migration is lower by at least a factor of two: 0.003 to 0.054 per day (*17*).

Pseudocalanus females descend rather than ascend nocturnally. This pattern is incompatible with the assumptions of one current metabolic model of diel vertical migration behavior (*2*). Another metabolic model (*1*) has been rejected (*3*) in favor of one which emphasizes the demographic effects of larger clutches

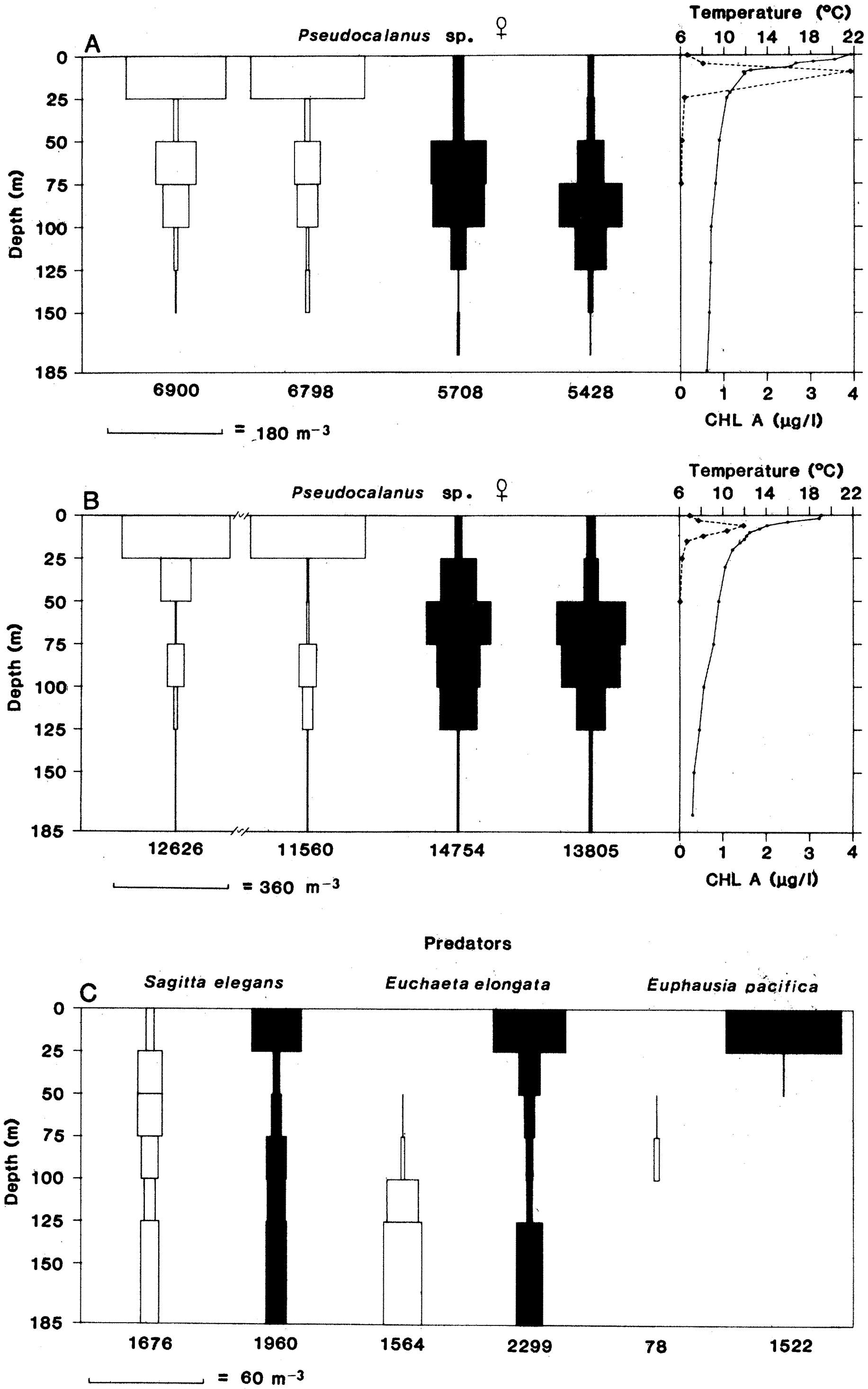

Fig. 1. Day (open) and night (shaded) vertical distributions of the copepod *Pseudocalanus* sp. and three species of predatory zooplankton at station D in Dabob Bay. (A) *Pseudocalanus* sp. females on 3–4 August 1973. (B) *Pseudocalanus* sp. females on 25 July 1979 (day 1) and 30 July 1979 (day 2; nights 1 and 2). (C) *Sagitta elegans*, *Euchaeta elongata* (copepodid V and adult female stages), and *Euphausia pacifica* (individuals > 10.5 mm, total length) 25–30 July 1979. Predator abundances are averages from the samples in (B); a similar pattern was observed in 1973. Low daytime numbers of *E. pacifica* are due to visually aided net avoidance, since 105-kHz acoustic evidence shows that *E. pacifica* adults are concentrated between 40 and 100 m by day (*24*). Duplicate sample series were taken within 90 minutes, except as noted, with a closing Puget Sound net (1 m in diameter, 216-μm mesh; vertical hauls). The total number of individuals per square meter is shown beneath each vertical series; scale bar indicates population density with animals assumed to be randomly dispersed within each sampled depth stratum. Temperature and chlorophyll a (*CHL A*) casts were made within 10 hours of the night series.

produced by vertically migrating individuals. The genus *Pseudocalanus* was the original subject for this demographic model, which we reexamine in Table 1.

The demographic consequences of migrating across a 4°C temperature gradient (Table 1, column 3) are compared with the population growth rate of a similar, nonmigratory *Pseudocalanus* population (Table 1, column 2). Ovigerous as well as nonovigerous females spend half the day below the thermocline, and part-time residence in cooler waters does result in larger body size and clutch size (Table 1), as suggested by McLaren (*3*). However, the longer development times in cooler waters result in decreased survivorship, which is not compensated by the larger clutch size of vertical migrants. Survivorship declines more rapidly than fecundity increases. Thus, when both populations experience the same daily mortality rate, a migrant *Pseudocalanus* population shows a lower realized rate of increase than one which remains continuously near the surface.

If, however, migrating females experience a 50 percent reduction in mortality rate (d_3) due to avoidance of predators, as estimated above, their rate of increase exceeds that of the nonmigrants (Table 1, column 4). Only a 16 percent reduction in the mortality rate of females (that is, $d_3'/d_3 = 0.84$) (Fig. 2) results in an advantage for migrants. Small decreases in mortality can confer important benefits on vertical migrants.

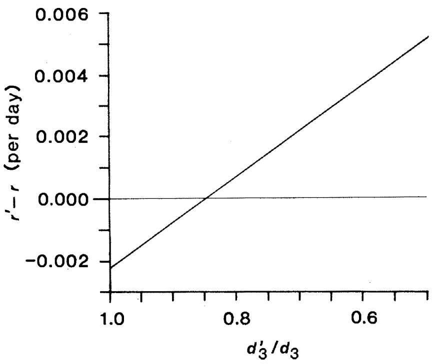

Fig. 2. The difference between the realized rate of increase of a migratory population of *Pseudocalanus* (r') and that of a nonmigratory population (r) as adult mortality rate for a migrant (d_3') decreases relative to that for a nonmigrant (d_3).

The question remains why the invertebrate predators reside at depth by day rather than foraging on *Pseudocalanus* near the surface. Large-bodied zooplankton are particularly vulnerable to visually hunting planktivorous fish, which tend to select larger (*18, 19*) or more visible (*20*) prey. Analysis of the stomach contents of the planktivorous fish captured in surface waters of Dabob Bay in July 1979 (*21*) revealed a positive electivity (*22*) toward most large zooplankton species. In contrast, the electivity toward *Pseudocalanus* by one species (juvenile chum salmon) was strongly negative and by the other (stickleback) was neutral. Where prey larger or more pigmented than *Pseudocalanus* are available, the alternative prey are ingested preferentially by these stages of these fish species (*23*). Thus the risk of capture by these visual predators appears to be greater for the large-bodied predatory zooplankters than for *Pseudocalanus*.

In closed aquatic systems such as small lakes, predation by selective planktivores may lead to local extinctions of preferred prey species (*18*). In open marine ecosystems the population density of predators is typically lower than that in small lakes and ponds, and prey may be able to find vertical refuges. Predation pressure—by either invertebrate or vertebrate planktivores—is therefore unlikely to cause extinctions in pelagic regions of the ocean, though it may be a dominant agent shaping diel vertical migration and other behavioral responses of marine zooplankton.

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Table 1. Life table analysis for *Pseudocalanus*. Early developmental stages (nauplius I to copepodid III) remain continuously in the surface stratum at 13°C near the chlorophyll maximum (*3, 15*). Later stages of nonmigrants (copepodid III through adult females) also remain continuously at 13°C, but those of migrants spend half the day at 9°C. Instantaneous mortality rates satisfy: $d_1 = 4d_2 = 4d_3$ and $r = 0.0$ for the nonmigrant (*3*). Temperature-dependent development times are from Thompson (*25*), as analyzed by Corkett and McLaren (*26*), and the size-fecundity relation from McLaren (*3*). Females are assumed to produce ten clutches (*26*). The value of r, the realized rate of increase, is obtained from $\sum_x l_x m_x e^{-rx} = 1.000$, where l_x is age-specific survivorship and m_x is age-specific fecundity.

Variable	Nonmigrant	Migrant	
		Mortality unchanged	Adult mortality reduced
Development time (days)			
Egg	2.63	3.11	3.11
Nauplius I to adult	24.88	26.47	26.47
Mortality rate (per day)			
d_1, nauplius I to copepodid III	0.1879	0.1879	0.1879
d_2, copepodid III to adult	0.0470	0.0470	0.0470
d_3, adult female	0.0470	0.0470	0.0235
Survivorship (proportion)			
Nauplius I to adult	0.03192	0.02961	0.02961
Adult (between clutches)	0.88372	0.86401	0.92952
Fecundity			
Prosome length of female (mm)	0.850	0.870	0.870
Clutch size (eggs)	5.81	6.31	6.31
Rate of increase (r) (per day)	0.000	−0.002	0.005

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7. The systematics of *Pseudocalanus* are in need of revision (*26*). Total length of females averaged 1.2 mm.
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9. Since females carry eggs in an attached egg sac, the vertical distribution of eggs must follow that of females. Ovigerous females could not be confined to the 0- to 25-m stratum at night. On the basis of egg counts, in 1979 each shallow-dwelling female would have had to carry 138.3 eggs; this far exceeds the clutch size expected for females of their body size (13.2 eggs per female) (*3, 8*); see also S. G. Afrikova [*Biol. Morya* **37**, 68 (1976)] for evidence of migration by ovigerous females of *Pseudocalanus*.
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16. The measure is based on predators in the upper 25 m at night (Fig. 1C), feeding at a prey density

of 1.0 *Pseudocalanus* female per liter, well below saturating prey concentrations. Predation rates would be higher if prey patches were considered.

17. Estimated from the population model of F. Argentesi, R. de Bernardi, and G. di Cola [*Mem. Ist. Ital. Idrobiol.* **31**, 245 (1974)], applied from 30 July to 8 August 1979. Stage durations from J. Vidal [*Mar. Biol.* **56**, 135 (1980)]. Copepodid stage abundances determined approximately weekly in summer from two or three replicate vertical hauls with a 73-μm mesh net.
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21. Sampling with a surface trawl (6.1 m wide) from 3 to 0 m, or a surface dip net, on 10–11 July 1979. Adult stickleback (*Gasterosteus aculeatus*) ranged from 71 to 82 mm and juvenile chum salmon (*Oncorhynchus keta*) from 63 to 98 mm, standard length.
22. Electivity measures the similarity between prey composition in a predator's diet and that in the environment. Electivity index is the logarithm of *Q* [J. Jacobs, *Oecologia* **14**, 413 (1974)]. Ambient zooplankton abundance determined with a 216-μm, 1-m diameter net hauled vertically from 0 to 5 m (four replicates).
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Accumulation of D-Aspartic Acid with Age in the Human Brain

Abstract. *An age-related accumulation of D-aspartic acid was detected in the white matter of ten normal brains from individuals aged 30 to 80 years. Gray matter showed no systematic increase in D-aspartic acid. The rate constant for D-aspartate formation in the brain is equal to the predicted value calculated for 37°C. Accumulation of the uncommon D-aspartate isomer in myelinated white matter implies that there is little or no turnover of this tissue, and this may have a bearing on dysfunction of the aging brain or on other diseases of myelin.*

The degree of racemization (conversion) of amino acids from the biologically common L configuration to the uncommon D configuration has been correlated with the age of fossil proteins in ocean sediments (*1*) and in archeological bones and shells (*2*). The observation that aspartic acid undergoes racemization and accumulation in the stable protein of living tooth enamel (*3*) and dentine (*4*), as well as in the eye lens nucleus (*5*), led to the prediction that racemization should correlate with aging in any metabolically "stable" protein in warm-blooded animals (*6*).

Because myelin proteins in nerve tissue are relatively stable, with slower turnover than those of other proteins (*7*), we believed that racemization might be detectable in nerve tissue protein during the human life span and that aspartic acid in the white, myelin-rich, inner portion of human brains should racemize and accumulate in proportion to the age of an individual. D-Aspartic acid accumulates in human tooth enamel and dentine at a rate of about 0.1 percent per year (*3, 4*) and in human eye lens nucleus at about 0.14 percent per year (*5*). We now report that D-aspartic acid accumulates at a similar rate in the white, myelin-rich, inner core of human brain.

Human brains obtained from subjects who had no history of abnormal pathology were frozen immediately after autopsy and were kept frozen until analyzed. White (myelin-rich) matter was separated from nonwhite (gray) tissue by dissection from the inner portion of the brain. The dissected fractions were homogenized in cold 10 percent trichloroacetic acid to precipitate the protein. The protein samples were hydrolyzed at 100°C for 6 hours in 6*N* HCl, followed by purification and isolation of aspartic acid by ion-exchange chromatography (*8*). *N*-Trifluoroacetyl-L-prolyl-D,L-aspartic acid methyl esters (volatile diastereomeric dipeptides) were synthesized, and the ratio of the amount of D-enantiomer to that of L-enantiomer (*D*/*L*) was determined on a gas chromatograph (Perkin-Elmer Sigma 2) fitted with a nitrogen-phosphorus detector and a 15-m fused-silica capillary column containing SE-54 as the bonded phase (J&W Scientific).

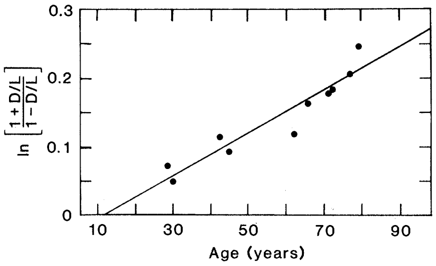

Fig. 1. Relationship between age and the ratio of D- to L-aspartic acid in the white matter of ten normal human brains.

The *D*/*L* value for laboratory-induced racemization was 0.016, which does not significantly alter the results reported.

The results of aspartic acid analyses for the white matter samples of ten normal brains were plotted (Fig. 1); a least-squares fit of the data resulted in the kinetic equation

$$\ln\left[\frac{1 + D/L}{1 - D/L}\right] = [(3.14 \pm 0.38) \times 10^{-3}]t - 0.036 \quad (1)$$

where *t* is the age of the individual. The data are presented in the form of a reversible first-order rate equation (*9*) rather than the irreversible equation used for the enamel and dentine results (*3, 4*), D-aspartic acid being present in sufficient concentration in the brain to make the use of the irreversible first-order rate equation invalid. The slope of the line represented by Eq. 1 corresponds to $2k_{\mathrm{Asp}}$, where k_{Asp} is the rate of formation of D-aspartate in the brain. Thus, in the white matter, $k_{\mathrm{Asp}} = 1.57 \times 10^{-3}$ year^{-1} compared with the calculated value for k_{Asp} at 37°C (body temperature) of 1.50×10^{-3} year^{-1}. Analyses of eight gray matter samples by the same procedure did not show any correlation of *D*/*L* values with age.

Bada and Helfman (*2–6*) proposed the use of the D- to L-aspartic acid ratio to estimate the age of long-lived animals. We tested the possibility of a similar estimate in the human brain by analyzing a sample that was of unknown age when received. Analysis produced a *D*/*L* value of 0.0826, indicating an age of 64 years. The actual age was subsequently found to be 66 years, in good agreement with the experimentally determined value.

McFadden and Clarke (*10*) reported that all of the methylated aspartic acid isolated from erythrocyte membrane and cytoskeletal proteins has the uncommon D configuration, suggesting the presence of a system of widely distributed enzymes that recognize racemized aspartyl residues for subsequent repair. Our discovery that D-aspartic acid accumulates with age in the white matter of human brain might indicate that the McFadden and Clarke repair mechanism fails to penetrate or to function in the white matter or that there is little or no metabolic turnover of the proteins in white matter. The fact that there is no systematic increase in *D*/*L* values for aspartate in gray matter implies a far more rapid turnover or a functioning repair mechanism in this portion of brain tissue.

The line in Fig. 1 represents the best straight line fit to the data. However, data are lacking for the younger age