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## THE DEMOGRAPHIC BENEFITS OF DIEL VERTICAL MIGRATION BY ZOOPLANKTON<sup>1</sup>

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**Abstract.** Three types of diel vertical migration behavior were expressed within a fjord population of the calanoid copepod *Pseudocalanus newmani*: (1) reverse migration (nocturnal descent), (2) normal migration (nocturnal ascent), and (3) no detectable migration. Reverse migration by *P. newmani* occurred in all three study years, but only at a deep (185 m) station at times of year when normally migrating predatory zooplankton (the copepod *Euchaeta elongata*, the chaetognath *Sagitta elegans*, and the omnivorous euphausiid *Euphausia pacifica*) were abundant. A predator-exclusion “natural experiment” tested the hypothesis that the reverse migration is a predator avoidance mechanism: at a shallow (55 m) station within the same fjord, large predatory zooplankton were absent or reduced markedly in abundance. In conditions of reduced nocturnal predation by predatory zooplankton, no reverse migration by *P. newmani* was detected on any of 11 cruises, consistent with the hypothesis. Instead, at the shallow station, where diurnal predation by planktivorous fish was of increased importance, normal diel vertical migration by *P. newmani* was observed on several occasions. No migration was detectable at either the deep station or the shallow station at times of year of low feeding activity of predators in surface waters. The predominant migration behavior (reverse, normal, or no migration) varied depending whether the primary source of mortality was predation by nocturnally feeding zooplankton or visually hunting planktivorous fish, and appeared unrelated to resource distributions or temperature gradients.

The relative advantage of the three migration behaviors is explored with theoretical life table analyses. Re-examination of the demographic advantage hypothesis proposed by McLaren (1974) illustrates that vertical migration across a thermocline carries a fitness cost, not a benefit. The realized rate of increase of a migrant population of *Pseudocalanus* is found to be lower than a nonmigrant population for all combinations of surface temperatures, positive thermal stratification, and ratios of mortality for early and late developmental stages. However, avoidance of predators by vertical migrants reverses the outcome of this analysis. Predator avoidance by *Pseudocalanus*, accompanied by reduced mortality rates, confers a fitness advantage upon a population that migrates across a thermocline. Remarkably small reductions in mortality rates (as little as 12%) confer this advantage, whether migrants avoid nonvisually hunting predatory zooplankton by night or visually hunting planktivorous fish by day.

The behavioral variation documented here confirms that diel vertical migration is dynamic rather than a fixed, invariant behavioral trait within a population. In environments where predation pressure and other factors vary through time, studies of limited scope and short duration are unlikely to illuminate the ultimate causes for diel vertical migration. The heritability of the vertical migration trait is unclear. The different phenotypic responses reflected within this single population of *P. newmani* may reflect altered behavior of individuals. Alternatively, this behavioral variation may represent a balanced polymorphism maintained by differential mortality of genotypes experiencing selection pressures that vary through time.

**Key words:** *balanced polymorphism; Copepoda; diel vertical migration; population dynamics; predation; Pseudocalanus newmani; zooplankton behavior.*

### INTRODUCTION

The behavior of individuals can profoundly alter the dynamics of populations (Tolstoy 1889, Hassell and May 1985, Ohman 1988, Roughgarden et al. 1989). Yet behavioral studies are frequently carried out in

isolation without attention to their consequences for birth rates, death rates, and population trajectories through time (Hassell and May 1985, May 1986). Conversely, investigations seeking to explain population fluctuations require close attention to animal behavior to account successfully for the mechanisms underlying population change (Steele and Henderson 1981, McCauley and Murdoch 1987). In an explicit link be-

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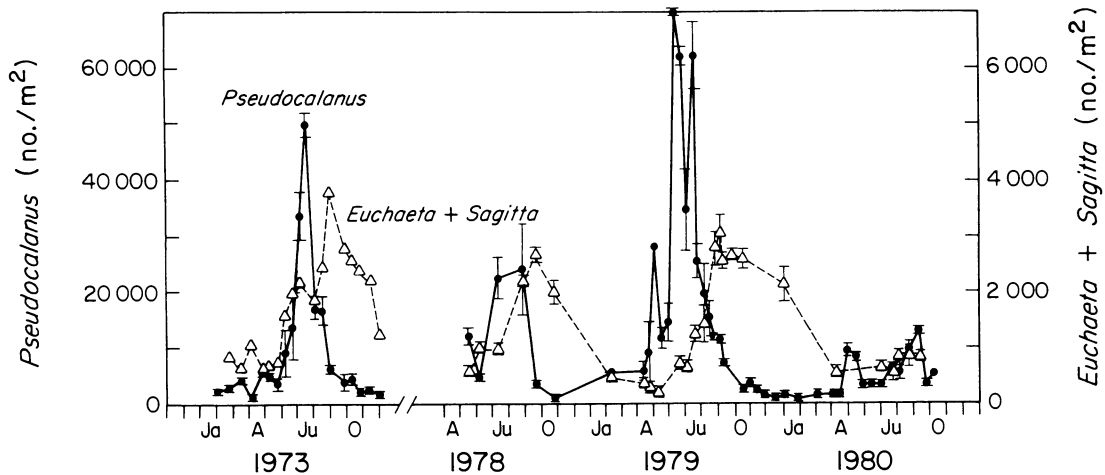


FIG. 1. Temporal variation ( $\bar{X} \pm SD$ , when SD available) in abundance of the suspension-feeding copepod *Pseudocalanus newmani* and predators (the carnivorous copepod *Euchaeta elongata* and the chaetognath *Sagitta elegans*), at Station D in Dabob Bay.

tween behavior and population dynamics, Parker (1985, Fig. 2.3) illustrates how prey and predator behaviors that vary with the behavioral "strategy" adopted by their adversary can generate unexpected stable, cyclical population oscillations.

Within the behavioral repertoire of zooplankton (see Kerfoot and Sih 1987, Paffenhöfer and Price 1988), diel vertical migration (DVM) is perhaps the most broadly distributed trait, occurring in diverse animal phyla, widespread geographical locales, and in marine and freshwater habitats. Despite the widespread nature of DVM and associated implications for population level processes, conflicting views persist regarding its adaptive significance (see reviews by Longhurst 1976, Kerfoot 1985, Bayly 1986, Haney 1988). Part of the confusion stems from the variable characteristics of the behavior. DVM may vary among developmental stages of a species, between times or places for a single species, and between coexisting species (Enright and Honegger 1977, Stich and Lampert 1981, Ambler and Miller 1987, Williams et al. 1987, Frost 1988, Gliwicz and Pijanowska 1988, Haury 1988, Lampert 1989). Efforts to test hypotheses for the adaptive significance of this behavior must therefore recognize that selection pressures vary in time, space, and among species.

The present study is the behavioral component of a larger investigation of the processes controlling population growth of the copepod *Pseudocalanus newmani*. Trajectories of the abundance of *P. newmani* and two of its principal predators illustrate the recurrent seasonality of predator abundance in Dabob Bay and suggest a prey-predator oscillation (Fig. 1). The seasonal population growth of *P. newmani* appears not to be a consequence of periodic resource limitation (Ohman 1985), but of diapause of late copepodid stages combined with the seasonal impact of predation by carnivorous zooplankton (Ohman 1985, 1986). A pre-

liminary report documented the occurrence of reverse diel vertical migration behavior of *P. newmani* at times of year of peak predator abundance (Ohman et al. 1983), demonstrating the opposite phasing of predator (nocturnal ascent) and prey (nocturnal descent) vertical migrations and the fitness gain to the reverse migratory *Pseudocalanus*. The present contribution analyzes the variability of DVM by *P. newmani* in light of the seasonal dynamics of predation pressure and tests the hypothesis that DVM is a predator avoidance mechanism against alternatives.

The hypothesis that reverse DVM is a mechanism for avoidance of nocturnally feeding predatory zooplankton (Ohman et al. 1983) has specific consequences, each of which is investigated here. (1) Developmental stages of *P. newmani* less subject to nocturnally phased predation should show less tendency to reverse migrate. (2) Co-occurring species of zooplankton less subject to attack by nocturnal predators should not reverse migrate. (3) In the absence of nocturnal predation pressure *P. newmani* adults should cease to reverse migrate. A natural experiment served to exclude large, vertical migrant predatory zooplankton, in an explicit test of the third postulate. A site was located within the study region where predatory zooplankton were excluded altogether, or reduced dramatically in abundance, but characteristics were otherwise suitable for expression of DVM by *P. newmani*. The DVM behavior of *P. newmani* is thus contrasted in sites characterized by high and low abundance of nocturnally feeding predators. The third postulate is also tested by comparing seasonal and year-to-year differences in predation pressure with variations in DVM behavior.

This study also re-evaluates the demographic advantage hypothesis proposed by McLaren (1974). Among other quantitatively posed hypotheses for the

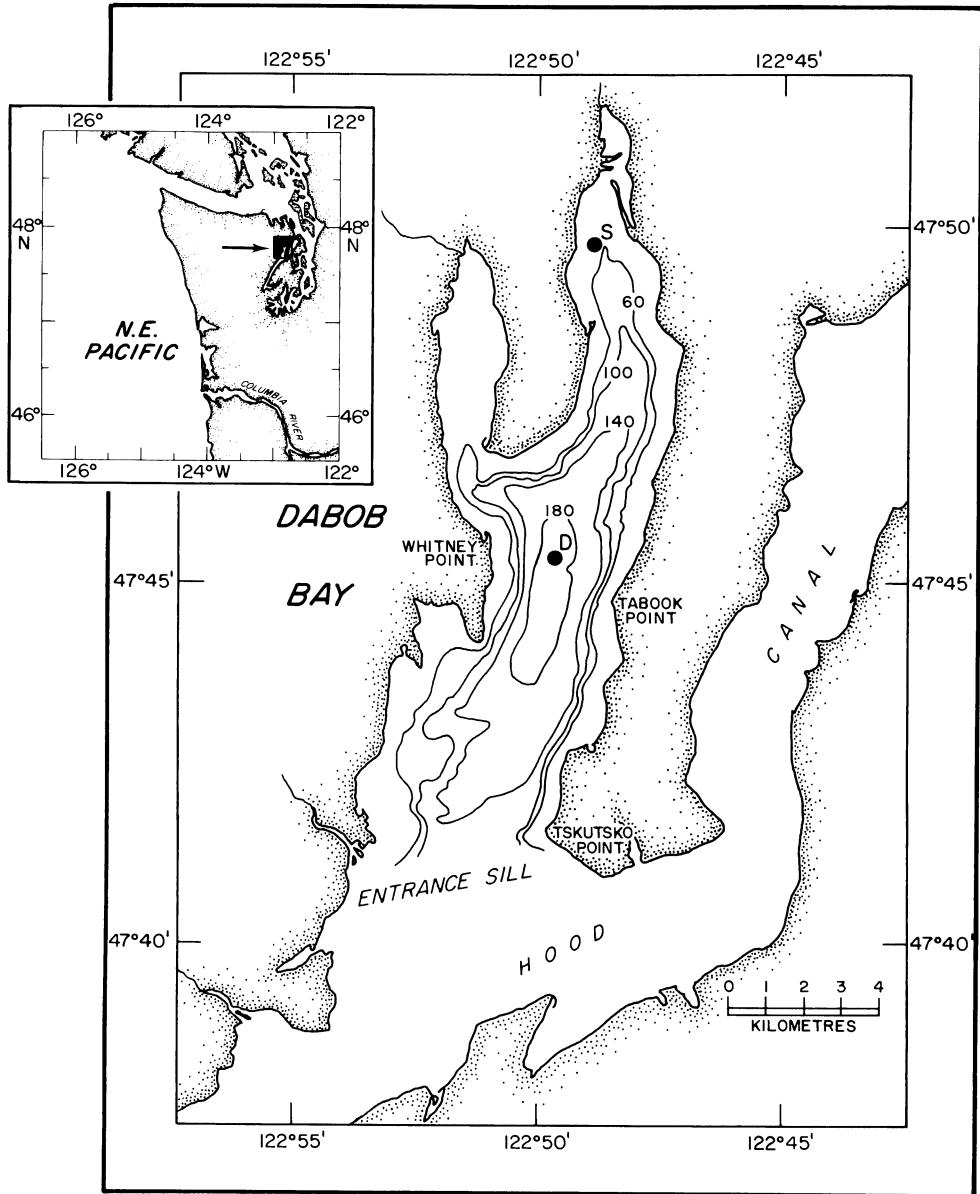


FIG. 2. Bathymetry of Dabob Bay and positions of Stations D and S. Inset map identifies location of the study site within Puget Sound.

adaptive value of DVM (Enright 1977, Wright et al. 1980, Gabriel and Thomas 1988, Mangel and Clark 1988), McLaren's was the first to assess the relative advantage of different behaviors in terms of both survivorship and fecundity schedules, using population growth rate rather than individual ingestion or somatic growth as measures of fitness. Following development of his demographic model, McLaren (1974) concluded that "it does not seem worth pursuing further analytical extensions of the model without more information from nature." On the basis of the new information from natural populations presented here, this model is now

re-examined. A series of life table analyses is carried out to explore the demographic consequences of diel vertical migration for *Pseudocalanus* in Dabob Bay and more generally for zooplankton in thermally stratified waters in the ocean and in lakes.

The terminology adopted here is as follows. The term "normal" diel vertical migration will refer to a pattern of nocturnal ascent by individuals that reside at depth by day. "Reverse" DVM will refer to nocturnal descent by individuals that reside near the surface by day (Hutchinson 1967). "Nonmigrant" will refer to individuals that occupy the same depth stratum by day and

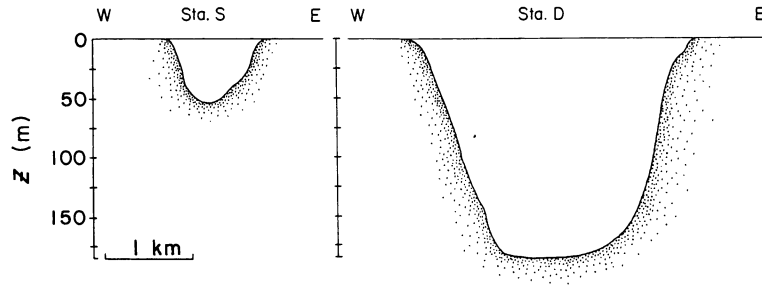


FIG. 3. Cross sections through Dabob Bay at Station D and at Station S, looking northward.

by night, whether near the surface or at depth. Other nuances of migratory behavior are described by Hutchinson (1967) and Pearre (1979).

## METHODS

### Sampling

Zooplankton were sampled at two locations in Dabob Bay, Washington State (Fig. 2): Station D (mean lower low water depth = 185 m) and Station S (mean = 55 m). Cross sections through Dabob Bay illustrate the differing bathymetry at these two locations (Fig. 3). Vertically stratified zooplankton samples were taken with a 216- $\mu$ m mesh, 1-m diameter Puget Sound net (a modification of the Juday design) retrieved vertically at  $\approx 45$  m/min. The net was closed during ascent, within 1 m of the target depth, by a messenger-operated net tripper. Samples were preserved in a 10% solution of Formalin/seawater buffered with sodium borate, to which butylated hydroxytoluene was added to retard oxidation of zooplankton pigments. At Station D on two cruises (11–12 January 1979 and 13–15 August 1979) and at Station S on two cruises (26–28 September 1978 and 13–15 August 1979) vertical distributions were determined from overlapping net hauls rather than by the standard procedure employing vertically stratified hauls. A mechanical failure on the research vessel permitted only one vertical series to be completed at Station D on 25 July 1979; following repairs and return to the research site the remaining vertical series at this station were completed on 30–31 July. To minimize differences between stations in incident solar radiation, both stations were sampled on the same day when possible or, alternatively, on consecutive days. Deck lights on the research vessel were turned off during night hauls in the upper 25 m.

Vertically stratified zooplankton sampling was carried out in three study years: 1978, 1979, and 1980. Standard sampling depths at Station D in 1978 were: 185–100, 100–80, 80–60, 60–40, 40–20, and 20–0 m. In 1979 they were: 185–125, 125–100, 100–75, 75–50, 50–25, and 25–0 m. In 1980 the standard depths differed from 1979 only near the surface: 25–14, 14–5, and 5–0 m. The standard depths at Station S in 1978 and 1979 were: 55–40, 40–20, and 20–0 m, and in 1980 they were: 55–40, 40–20, 20–14, 14–5, and 5–0

m. Departures from these standard depths, as well as the particular dates sampled, are visible in the figures or are noted in the text.

All stratified sampling for zooplankton was performed from conventional surface ships. Additional vertical hauls for integrated abundance of *Pseudocalanus* and sampling for hydrographic properties were performed from a pontoon aircraft on many occasions when time did not permit stratified sampling to be done. Station D, but not Station S, was sampled in this manner, using a 73- $\mu$ m mesh, 0.5 m diameter net. The time series of abundance of *Pseudocalanus newmani* females for 1979–1980 was obtained from this series. For details see Ohman (1986).

*Pseudocalanus newmani*, other small copepods, and euphausiid furciliae were usually enumerated from multiple aliquots subsampled with a Stempel pipette. *P. newmani* were counted from entire samples when rare. Larger and less abundant zooplankton were counted from quantitative splits obtained with a Folsom splitter. Three species of *Pseudocalanus* occur within Puget Sound: *P. newmani*, *P. moultoni*, and *P. mimus* (Frost 1989). For all enumerations *P. newmani* was distinguished from the other two species. On no date sampled during this study did *P. moultoni* or *P. mimus* constitute >6% of total *Pseudocalanus* females in Dabob Bay. In previous publications where I used the designation *Pseudocalanus* "sp." in reference to Dabob Bay *Pseudocalanus*, the sole species referred to was *P. newmani*.

Water samples for analysis of phytoplankton pigments were collected in Niskin bottles and filtered through Gelman A/E glass-fiber filters or Nitex screens (Runge and Ohman 1982). Pigments were extracted in 90% aqueous acetone either by sonication or cold extraction in the dark at 4°C, and were analyzed fluorometrically for chlorophyll and pheopigments after the methods in Lorenzen (1966). Vertical temperature profiles were determined by a conductivity-temperature-depth sensor or bathythermograph.

### Life table analyses

Life table analyses explored the demographic effects of diel vertical migration across a thermocline. The *Pseudocalanus* population was assumed to live in a

two-layer, stratified water column. In the case of the nonmigrant *Pseudocalanus*, all developmental stages remained continuously in the surface layer. For the migrant *Pseudocalanus* population, vertical migration across the thermocline began at copepodid stage III (CIII). Thus, for the migrant population, nauplius I (NI) to CIII remained continuously in the surface layer, then CIII to CVI (and the eggs attached to adults) migrated daily between the surface and deep layers, spending half the day in each stratum.

Embryonic development time (ED, in days) was determined as a function of temperature ( $T$ , in degrees Celsius) from the relation of Corkett and McLaren (1978):

$$ED = 1845(T + 11.45)^{-2.05}. \quad (1)$$

Average embryonic development time (EDAV) was weighted for the fraction of development (0.5) completed at the day temperature (EDDT) and the night temperature (EDNT) as:

$$EDAV = 1/[0.5/EDDT + (0.5/EDNT)]. \quad (2)$$

Development time of postembryonic developmental stages was determined from ED, together with application of the equiproportional rule. The equiproportional rule states that a given developmental stage occupies the same proportion of the total development time at any constant temperature (Corkett et al. 1986). The appropriate constant for each postembryonic developmental stage, to be multiplied by ED, was obtained from Table I in Ohman (1986).

Body size of *Pseudocalanus* CIII has been found to be relatively constant, irrespective of temperature during early development (McLaren 1974, Vidal 1980). Subsequent growth, from CIII to adult, was described as an inverse function of temperature (McLaren 1974) and expressed as final adult prosome length (PL, in millimetres):

$$PL = 0.597[1 + 10.82 \cdot (13.4 + T)^{-0.99}]. \quad (3)$$

Fecundity (EN, number of female eggs) was described as a function of prosome length (McLaren 1974), assuming a sex ratio of 1:1:

$$EN = 10.39 \cdot PL^{3.58}. \quad (4)$$

The exponent of the relation between egg number and prosome length actually observed for *P. newmani* in Puget Sound is somewhat smaller (Ohman 1985, Eq. 9) than for the species of *Pseudocalanus* studied by McLaren. Nonetheless, Eq. 4 is used here to retain direct comparability with McLaren's (1974) analysis and to give larger animals the maximum fecundity advantage. Predicted egg numbers from the two equations diverged by no > 18% over the range of prosome lengths of *P. newmani* considered in this analysis.

Instantaneous mortality rates (per day) applied over different life history stages and were chosen to meet the constraints described below.  $d_1$  applied from the

beginning of nauplius I (NI) to the beginning of copepodid III (CIII) for all populations.  $d_2$  referred only to nonmigrant populations, from the beginning of CIII to the adult stage.  $d_3$  referred only to migrant populations, also from the beginning of CIII to the adult stage. Because females carry eggs in an attached sac, the mortality rate of eggs was assumed to be equivalent to that of adult females. All calculations were made in terms of female offspring alone, assuming a sex ratio of 1:1. After the terminal molt, females underwent a prereproductive period equivalent to the egg duration and then produced 10 successive clutches (Corkett and McLaren 1978).

Life tables were then constructed from these development times, instantaneous mortality rates, size-fecundity relations, and reproductive schedules. The Euler equation was solved for  $r$ , the realized rate of increase, from:

$$\sum_x l_x m_x e^{-rx} dx = 1.000, \quad (5)$$

where  $l_x$  is age-specific survivorship and  $m_x$  is age-specific fecundity.  $r$  was solved iteratively with a life table program written in Turbo Pascal. Unlike the algorithm of Ohman et al. (1983), the present algorithm did not truncate mortality or development rates, but computed values to machine precision.

## RESULTS

### Comparisons of Station D and Station S

Temperature profiles at Station D and Station S showed comparable structure (Fig. 4). The depth and shape of the thermocline were similar at the two stations in summer, and temperature inversions occurred at both stations in winter. A subsurface chlorophyll maximum characterized both stations from May until September. The concentration of chl *a* was similar at most depths, except at the depth of the chlorophyll maximum layer where chl *a* sometimes differed by a factor of two (or more in March) between stations. Water column properties were similar at both stations, as indicated by pairwise comparisons of several properties measured at both stations on 10–19 cruises (Table 1). *Pseudocalanus newmani* occurring at either of the two localities apparently experienced similar phytoplankton, temperature, and irradiance conditions.

In contrast, the abundance of predatory zooplankton differed markedly between the two stations. The three predominant predators of adult *Pseudocalanus newmani* (see Ohman 1986) were largely excluded from the shallow station (Table 2). Most significantly, *Euchaeta elongata* was very rare at Station S where, in 10 cruises, only three specimens of *E. elongata* were found. However, at Station D as many as 2104 *Euchaeta elongata*/m<sup>2</sup> were found. The predation potential of these predators is considerable: each *Euchaeta* CV or female has a potential daily ingestion rate of 16 or 19 adult *Pseudocalanus*, respectively ( $I_{max}$ , Yen 1983).

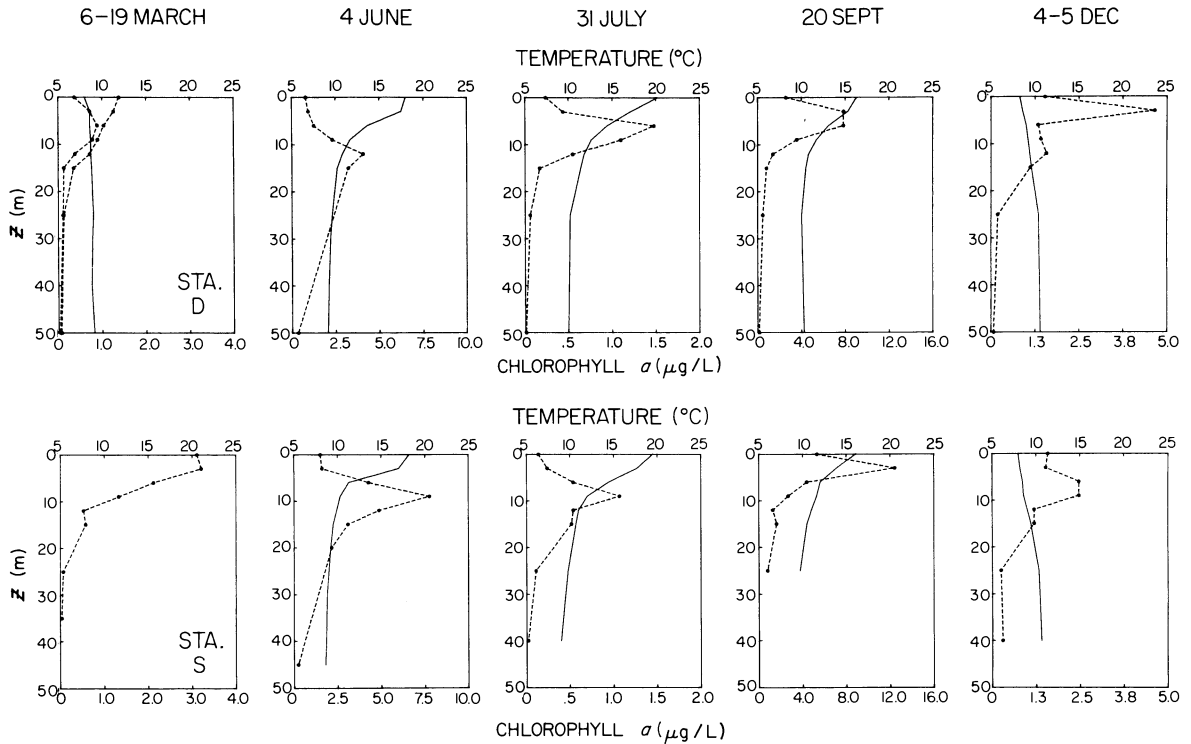


FIG. 4. Comparative vertical profiles of chl *a* (---) and temperature (—) at Station D (top row) and Station S (bottom row), for representative seasons. (No temperature profile was determined at Station S in March.) March profiles from 1980, others from 1979.

The chaetognath *Sagitta elegans* was, on average, 13.7 times as abundant at Station D. Each adult *S. elegans* can ingest up to 5 *Pseudocalanus* females/d (Reeve 1980). Only nighttime samples were used for comparing *Euphausia pacifica* abundances (they avoid nets by day), making fewer estimates available. On average *Euphausia pacifica* was 16.4 times as numerous at Station D. Each adult *E. pacifica* can attack as many as 2.4 *Pseudocalanus* females/d (Ohman 1984). Gelatinous predators were never numerous, but ctenophores averaged 8.0 times as abundant and hydromedusae 3.3 times as abundant at Station D (differences not significant,  $P > .05$ , Wilcoxon matched-pairs signed-ranks test).

TABLE 1. Comparison of water column properties at Station D and Station S during 1978–1980 (Wilcoxon matched-pairs signed-rank tests, two-tailed). *N* indicates the number of cruises. Secchi depth is proportional to the average light extinction coefficient. Chl *a* < 73  $\mu\text{m}$  indicates the proportion of total particulate chl *a* that passed through a 73- $\mu\text{m}$  mesh Nitex screen.

Variable	<i>N</i>	<i>P</i>
Secchi depth (m)	19	>.10
Temperature difference (3 m – 30 m)	15	>.10
Maximum chl <i>a</i> ( $\mu\text{g/L}$ )	12	>.10
Integrated chl <i>a</i> ( $\text{mg/m}^2$ )	12	>.10
Chl <i>a</i> < 73 $\mu\text{m}$ (%)	10	>.10

Some evidence suggests that the abundance of fish differed between the two stations, in the opposite direction from the abundance of carnivorous zooplankton. Visual observations and limited sampling with a surface Tucker trawl confirmed the presence of epipelagic schooling fish at both stations in summer, but fish schools were larger and sighted more frequently at Station S (M. D. Ohman, *personal observation*). Fish sampling, carried out by surface townet only at Station D in July, captured adult threespine stickleback (*Gasterosteus aculeatus*) and juvenile chum salmon (*Oncorhynchus keta*), although other planktivorous fish species also occur there (Ohman 1986). A south-to-north acoustic transect of Dabob Bay made with a low-frequency (49 kHz) echosounder suggested more subsurface acoustic backscatterers in the shallow region of Dabob Bay, in the vicinity of Station S. Presumably, due to the transducer frequency used and signature of the echoes, the acoustic backscatterers were fish.

Note that even for the same abundance of planktivorous fish in shallow and deep regions, the impact of fish on *Pseudocalanus* adults would be greater in the shallow region. Threespine stickleback in Dabob Bay prefer larger and more visually conspicuous zooplankton prey when available, yet ingest *P. newmani* females in proportion to their relative abundance in the water column (Ohman 1986). Thus, where larger carnivorous zooplankton are deficient, as at the shallow station,



TABLE 2. Comparative abundance of predatory zooplankton at Station D and Station S in Dabob Bay (means  $\pm$  SD).  $N = 2$  to 7 profiles, except  $N = 1$  where SD is omitted.  $P$  value in bottom row reports the results of two-tailed Wilcoxon matched-pairs signed-rank test.

Date	Station	Total water column abundance (number/m <sup>2</sup> )		
		<i>Euchaeta elongata</i> *	<i>Sagitta elegans</i>	<i>Euphausia pacifica</i>
31 Jul-1 Aug 1978	D	320 $\pm$ 32†	1852 $\pm$ 44	836
	S	0	169	99
24-25 Aug 1978	D	1635 $\pm$ 226	2185 $\pm$ 187	598 $\pm$ 469
	S	0 $\pm$ 0	122 $\pm$ 80	180 $\pm$ 66
26-29 Sep 1978	D	1119 $\pm$ 114	1545 $\pm$ 210	342 $\pm$ 251
	S	0 $\pm$ 0	82 $\pm$ 61	90 $\pm$ 24
4-7 Jun 1979	D	838 $\pm$ 145	389 $\pm$ 83	2322 $\pm$ 1328
	S	1 $\pm$ 2	529 $\pm$ 60	242 $\pm$ 101
10-12 Jul 1979	D	687 $\pm$ 266	987 $\pm$ 278	4001 $\pm$ 3928
	S	0 $\pm$ 0	1270 $\pm$ 685	38 $\pm$ 11
25-31 Jul 1979	D	2104 $\pm$ 287	1746 $\pm$ 246	2148 $\pm$ 823
	S	0 $\pm$ 0	482 $\pm$ 18	69
13-15 Aug 1979	D	1478 $\pm$ 112	1690 $\pm$ 114	588 $\pm$ 414
	S	0 $\pm$ 0	103 $\pm$ 19	58 $\pm$ 2
4-6 Dec 1979	D	1667 $\pm$ 319	1289 $\pm$ 273	234 $\pm$ 249
	S	0 $\pm$ 0	5 $\pm$ 4	1 $\pm$ 1
11-12 Mar 1980	D	324 $\pm$ 23	252 $\pm$ 47	107 $\pm$ 86
	S	0 $\pm$ 0	3 $\pm$ 4	0
26-29 Jul 1980	D	407 $\pm$ 74	596 $\pm$ 181	248 $\pm$ 17
	S	0 $\pm$ 0	160 $\pm$ 224	11 $\pm$ 16
Median ratio of abundance (Station D/Station S)		>100	13.7	16.4
$P$		<.01	<.02	<.01

\* Abundance of *E. elongata* is the sum of copepodid stage Vs (CVs) and adult females, except that CVs were not enumerated in the one instance noted.

† *E. elongata* females only.

*Pseudocalanus* will be a more important prey item. In field or laboratory situations where their preferred prey are absent, sticklebacks will readily ingest small copepods (e.g., Landry 1978, Vuorinen et al. 1983, Bollens and Frost 1989). Also, Kerfoot (1975) observed a predation gradient in Union Bay adjoining Lake Washington, where carnivorous zooplankton were the predominant predators in deeper waters and planktivorous fish predominated in shallow waters.

In summary, the predation regimes at the two stations differed in the significantly greater abundance of large, vertically migrating, predatory zooplankton at Station D than at Station S. Evidence points towards greater relative importance of planktivorous fish at Station S than at Station D. Temperature profiles, light extinction, and phytoplankton properties did not differ in a systematic manner between the two stations.

#### Comparative migrations of *Pseudocalanus newmani* at Station D and Station S

The vertical migration behavior of *P. newmani* at the deep station was compared with vertical migration behavior at the shallow station in three study years (1978, 1979, and 1980). These results will be presented chronologically, followed by parallel results for predators. The relatively small variation in total abundance

among profiles on each date (Figs. 5-8) suggests that a single population was sampled over a diel period.

Migration behavior was compared on three cruises conducted in the first study year (1978). In early August, *P. newmani* females reverse migrated at Station D (Fig. 5). The daytime modal depth was 20-40 m; at night the population mode descended to 60-80 m. Three weeks later in August, when the population size had decreased severalfold (Figs. 1 and 5), part of the population at Station D continued to exhibit reverse migration (Fig. 5). Five weeks later, in September, there was no evidence for diel vertical migration (Fig. 5). In September, virtually the same temperature difference (3.8°C, 3-30 m) was observed as in late August (3.9°).

On none of these three occasions did *P. newmani* females reverse migrate at Station S (Fig. 5). In early August, late August, and late September *P. newmani* females migrated normally. The population mode at 20-40 or 40-55 m by day ascended to the 0-20 m stratum by night. This normal migration persisted as the population size declined from  $\approx 35\,000/\text{m}^2$  to  $150/\text{m}^2$  (Fig. 5). The same temperature difference (3.8°) was observed in September at Station S, where *P. newmani* females migrated normally, as at Station D they did not migrate.

Sampling began at Station D in January of the following year, but not until June at Station S. At Station

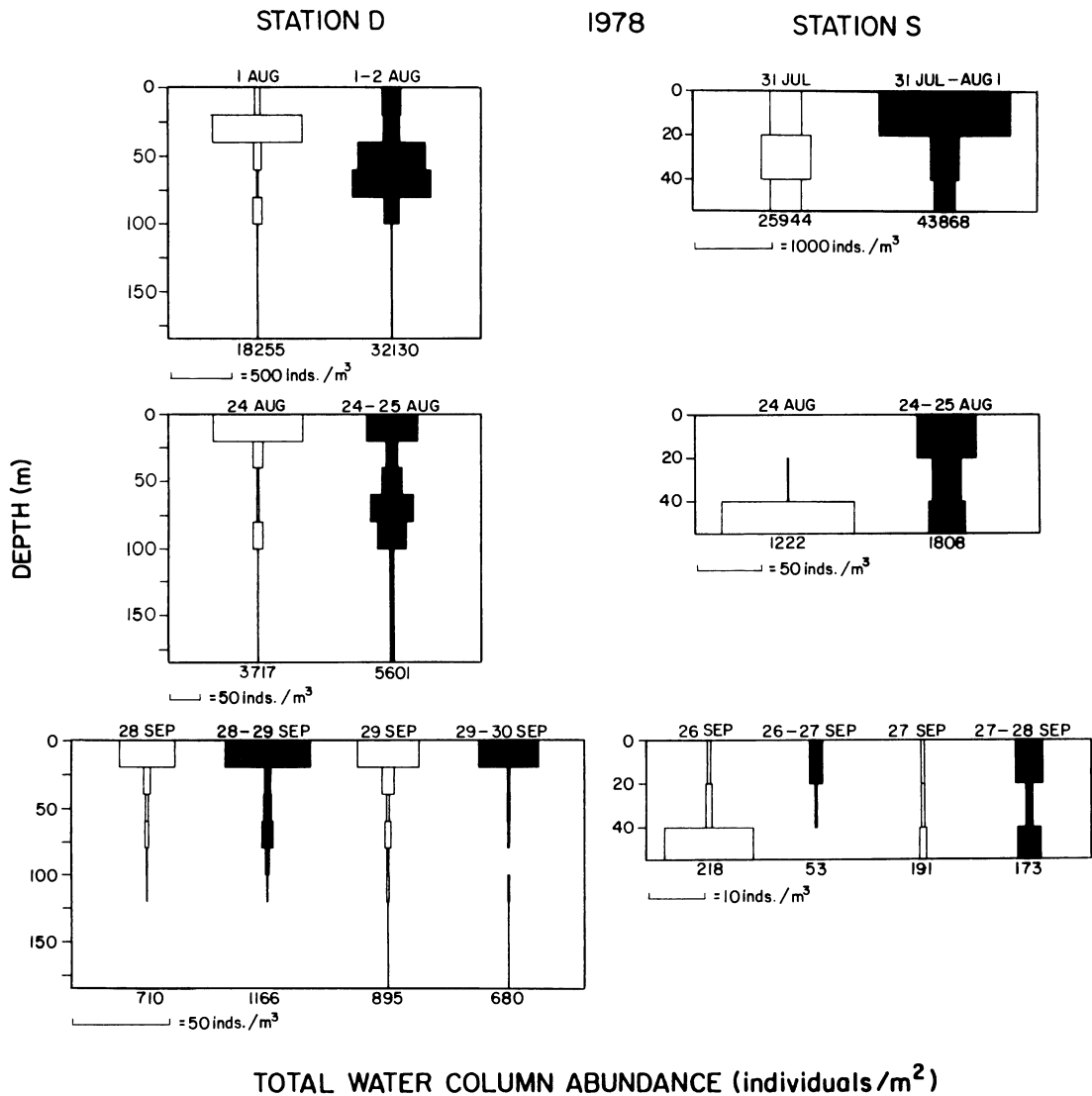
*Pseudocalanus newmani*

FIG. 5. Day (open) and night (shaded) vertical distribution of *Pseudocalanus newmani* females at Station D and Station S in July, August, and September 1978. Vertical profiles of abundance illustrate the daytime (open) and nighttime (shaded) vertical distributions. The width of each histogram bar is proportional to the average population density (number per cubic metre) within the sampled stratum, with the scale indicated beneath each plot. The area of each histogram bar is proportional to the fraction of the population occupying that stratum. The water column total abundance (individuals per square metre) is indicated beneath each histogram. Multiple vertical profiles within one panel indicate replicate series of samples. Note expanded vertical (depth) scale for Station S.

D the population mode resided continuously in the near-surface stratum both day and night. No evidence for diel vertical migration of *P. newmani* females was detected in January, March, or April (Fig. 6), during which time the population size increased. Over this interval the maximum chlorophyll concentration in the euphotic zone increased thirtyfold from 0.2 to 6.6  $\mu\text{g}$  chl *a*/L (see Fig. 13, below), without any apparent effect on vertical migration behavior.

In June there was little evidence for vertical migra-

tion behavior of *P. newmani* females at Station D (Fig. 7). Possible limited nocturnal descent on 7 June did not include a major fraction of the population. Note the absence of strong migration despite an 8° vertical temperature difference (Fig. 4). By early July, following a fourfold decrease in abundance of *P. newmani* females in the water column, part of the population now descended from the surface to below 25 m at night (Fig. 7). By late July, the reverse vertical migration was fully developed (Fig. 7). The population shifted from

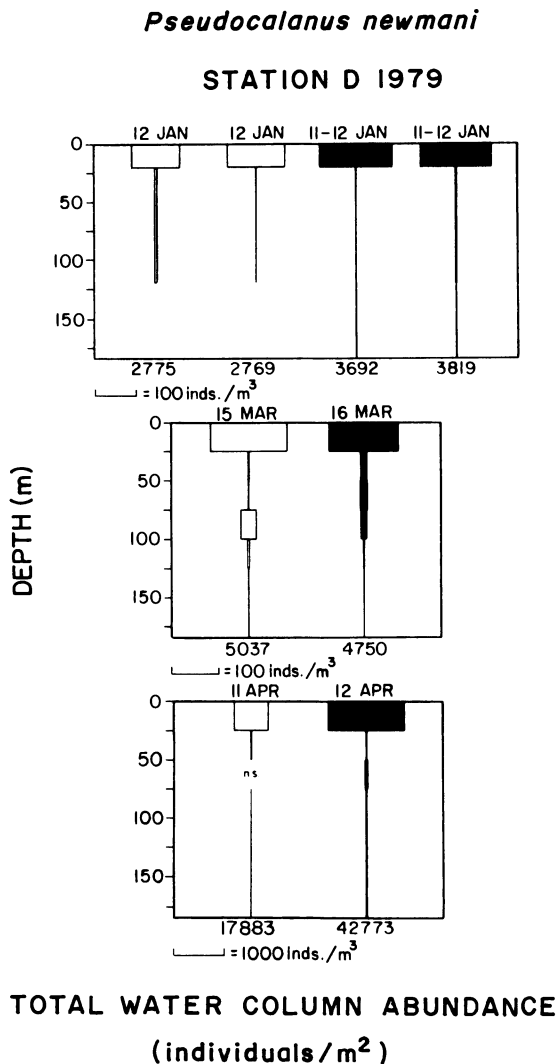


FIG. 6. Day and night vertical distribution of *Pseudocalanus newmani* females at Station D in January, March, and April 1979. The population at Station S was not sampled. (Symbols as in Fig. 5.)

0 to 25 m by day to 50 to 100 m at night, or even deeper (Fig. 7). This was a coherent population response, involving vertical descent of 94–95% of the population.

Two weeks later, in August, the reverse migration was still detectable (Fig. 7). Lack of a functioning closing device for the net required sampling by overlapping vertical net hauls on this date and only three strata were sampled (25–0, 50–0, and 185–0 m). Hence the vertical location of copepods dwelling below 50 m cannot be resolved in this series. By December, at which time the population size had declined further, vertical migration behavior was, as in the previous winter, not detectable (Fig. 7).

Comparative sampling at Station S on the same five

cruises revealed a remarkably different pattern. In June at Station S, as at Station D, there was little evidence for diel migration (Fig. 7). At both stations the vertical temperature gradient was 7°–8°. In early July, following a severalfold decline in population numbers, there was a clearly defined normal migration. The daytime mode at 40–55 m ascended at night to 0–20 m. This normal migration at Station S occurred concurrently with an emergent reverse migration at Station D. As observed in the previous year, migrations were in opposite directions at Station S and Station D. In late July there was no evidence for migration at Station S, although normal migration was again evident in August (Fig. 7). By December there was no evidence for migration at Station S (as was also the case at Station D).

In March of the 3rd yr there was again no evidence for migration at Station S (Fig. 8). Finer resolution vertical sampling was carried out in July and August at both stations to define more clearly the vertical location of *Pseudocalanus* within the euphotic zone. At Station D in early July the daytime modal depth was between 5 and 14 m (Fig. 8), and some of the population appeared to descend below this depth at night (Fig. 8). By late July a reverse migration was again well developed: the daytime mode near the surface descended to 50–75 m at night. About 3 wk later the reverse migration was again very pronounced, with daytime residence in a depth layer overlapping that of the chlorophyll maximum and nocturnal descent to a modal depth of 50–75 m (Fig. 8). Despite the predominance of reverse migration in both the late July and early August sampling intervals, a small but detectable fraction of the population appeared in the upper 5 m at night. That is, one small part of the population migrated normally even as most of the population reverse migrated.

Behavior at the shallow station was markedly different, as observed in the previous 2 yr. *P. newmani* females exhibited a well-defined normal migration in late July, with the population mode ascending from 40 to 55 m by day to 5 to 14 m by night (Fig. 8). This normal diel vertical migration behavior persisted at Station S into August.

A summary of the seasonal change in median depth of the population at Station D and Station S illustrates the differing behaviors at the two stations (Fig. 9). This summary illustrates the trend primarily for 1979 when sampling was the most complete. At Station D in the daytime and Station S at night, the median depth of the population was in the upper 15–20 m. This depth overlapped the region of maximum chlorophyll concentration (see Fig. 13). By July, a reverse vertical migration emerged clearly at Station D (Fig. 9A) and a normal migration at Station S (Fig. 9B). Normal migration was again apparent at Station S in August and September. By December no evidence of vertical migration, either reverse or normal, was detectable at either station.

*Pseudocalanus newmani*

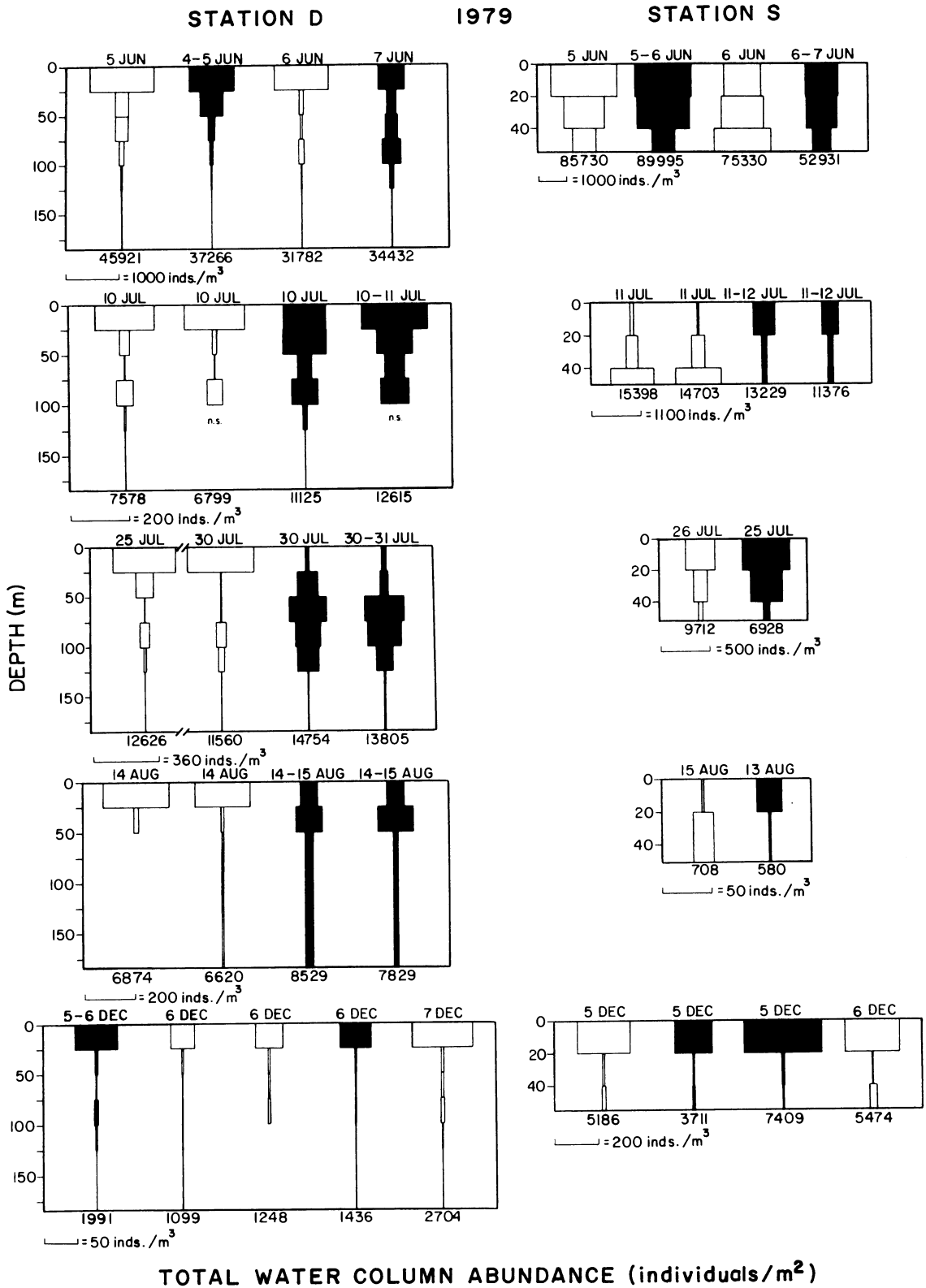


FIG. 7. Day and night vertical distribution of *Pseudocalanus newmani* females at Station D and Station S in June, July, August, and December 1979. (Symbols as in Fig. 5.)

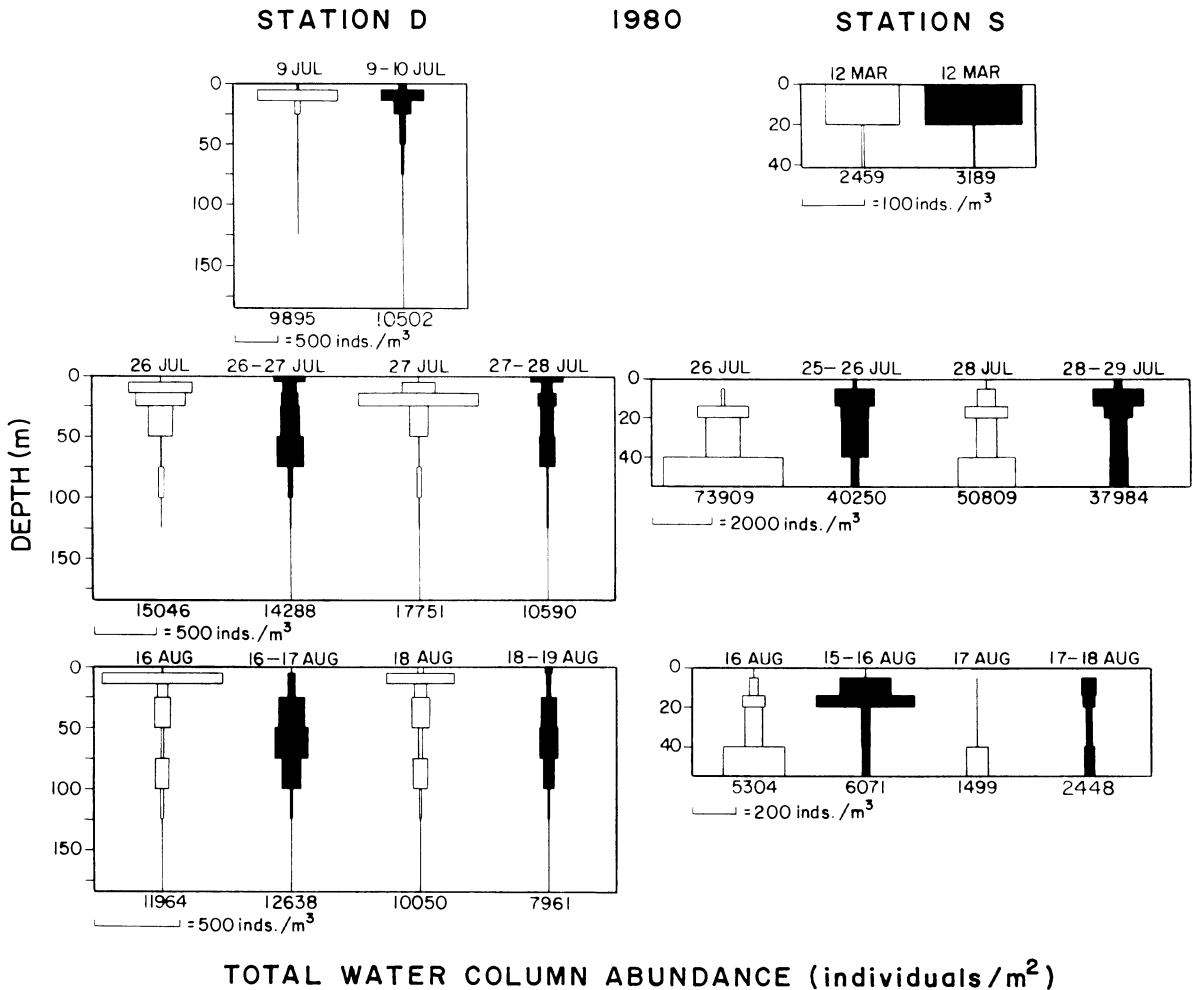
*Pseudocalanus newmani*

FIG. 8. Day and night vertical distribution of *Pseudocalanus newmani* females at Station D and Station S in March (Station S only), July, and August 1980. (Symbols as in Fig. 5.)

*Predator migrations at Station D*

The seasonal peak in expression of reverse vertical migration at Station D in late July coincided with the peak abundance of predatory zooplankton (Fig. 1). However, not only the abundance of predators, but also the extent of spatial overlap of predators with prey, determine prey-predator encounter frequencies. The vertical distribution of predators of *P. newmani*, as well as the distribution of the prey, was found to change seasonally. The vertical migration behavior of predators was analyzed only at Station D, from representative profiles taken in March, July, and December. At Station S predatory zooplankters were generally too limited in abundance to analyze vertical distributions.

Late developmental stages of *Euchaeta elongata* (copepodid stage CIV, CV, and adult female) attack adult female *Pseudocalanus*, with ingestion rate increasing with predator developmental stage (Yen 1983).

Thus the diel migration of these stages, as well as adult males, was investigated (Fig. 10). In March, July, and December, all stages of *Euchaeta elongata* remained primarily below 75–100 m by day. At night, a fraction of each stage ascended into the upper 25–50 m. As exemplified by the adult females, this fraction varied through time. In March, 26% of the adult female *E. elongata* entered the upper 50 m at night, in late July 42% ( $\bar{X}$ ), but by December only 6% of these carnivores entered the upper 50 m by night. In December, the total water column abundance of *Euchaeta* was not much lower than in July (960 vs. 985 females/m<sup>2</sup>, respective medians), but few females migrated out of deeper strata. Hence, the predation risk for epipelagic prey was substantially lower in December. Other developmental stages of *Euchaeta elongata* exhibited comparable behavior, with a larger proportion of the CIVs, CVs, and adult males entering the upper 50 m

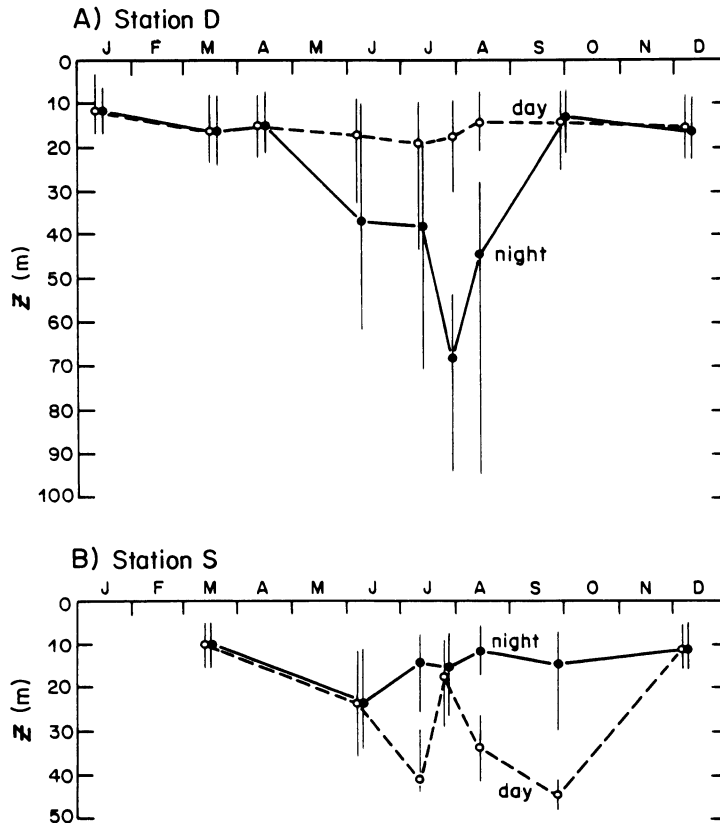


FIG. 9. Seasonal change in day (○---○) and night (●—●) median depth of *Pseudocalanus newmani* females, at (A) Station D and (B) Station S. The distributions are from vertical series in 1979 excepting September (1978; both stations) and March (1980; Station S only). Vertical lines indicate the vertical distance between the 25<sup>th</sup> and 75<sup>th</sup> percentiles of the population distribution.

at night in July than in either March or December (Fig. 10).

A similar pattern was observed for *Sagitta elegans* (Fig. 11). The daytime population mode was below the surface in March and July, but near the bottom in December. In spring and summer the nighttime population mode ascended to the upper 25 m. By December the population mode remained below 125 m at night as well as during the day (Fig. 11). King (1979) documented fully the seasonal and stage-specific changes in *S. elegans* migration behavior. Changes in chaetognath stage of development and feeding activity parallel this change in migration behavior. Later in the year the population shifts to an increasingly higher fraction of juvenile (stage II) chaetognaths, a smaller proportion of the population enters the surface layer at night, and a smaller fraction ingests *Pseudocalanus* (Ohman 1986). Again, the integrated water column abundance of *Sagitta elegans* differed little between July and December, but the number of chaetognaths entering surface waters to prey on epipelagic copepods diminished greatly by December.

*Euphausia pacifica*, unlike *Euchaeta elongata* and *Sagitta elegans*, is an omnivore, not an obligate carnivore. Phytoplankton and other microplankton are

typically more suitable prey for *E. pacifica* than small copepods, although *E. pacifica* can attack and injure adult *Pseudocalanus* (Ohman 1984). Vertical migration behavior of *E. pacifica* differs from that of the two obligate carnivores in that virtually all late furcillae and adults enter the upper 25 m at night, regardless of time of year (Fig. 11). By day the population is characteristically between 50 and 100 m, although the markedly smaller day catches indicate visually aided net avoidance (cf. Brinton and Townsend 1981). The nocturnal abundance of *E. pacifica* was greater in July than in March or December.

The pronounced normal diel vertical migration of predators of *P. newmani* in late July occurred concurrently with the reverse migration by *P. newmani* females. Although only 4 yr of data are available for the late July–early August peak of predator abundance (4th yr from Ohman et al. 1983), there is a suggestive correspondence between interannual differences in intensity of reverse migration by *P. newmani* and the abundance of obligate predators entering the upper 50 m at night (Fig. 12,  $r^2 = 0.90$ ,  $P < .10$ , Model II regression). Spatial, seasonal, and year-to-year differences in migration behavior of *P. newmani* are associated with predator abundance.

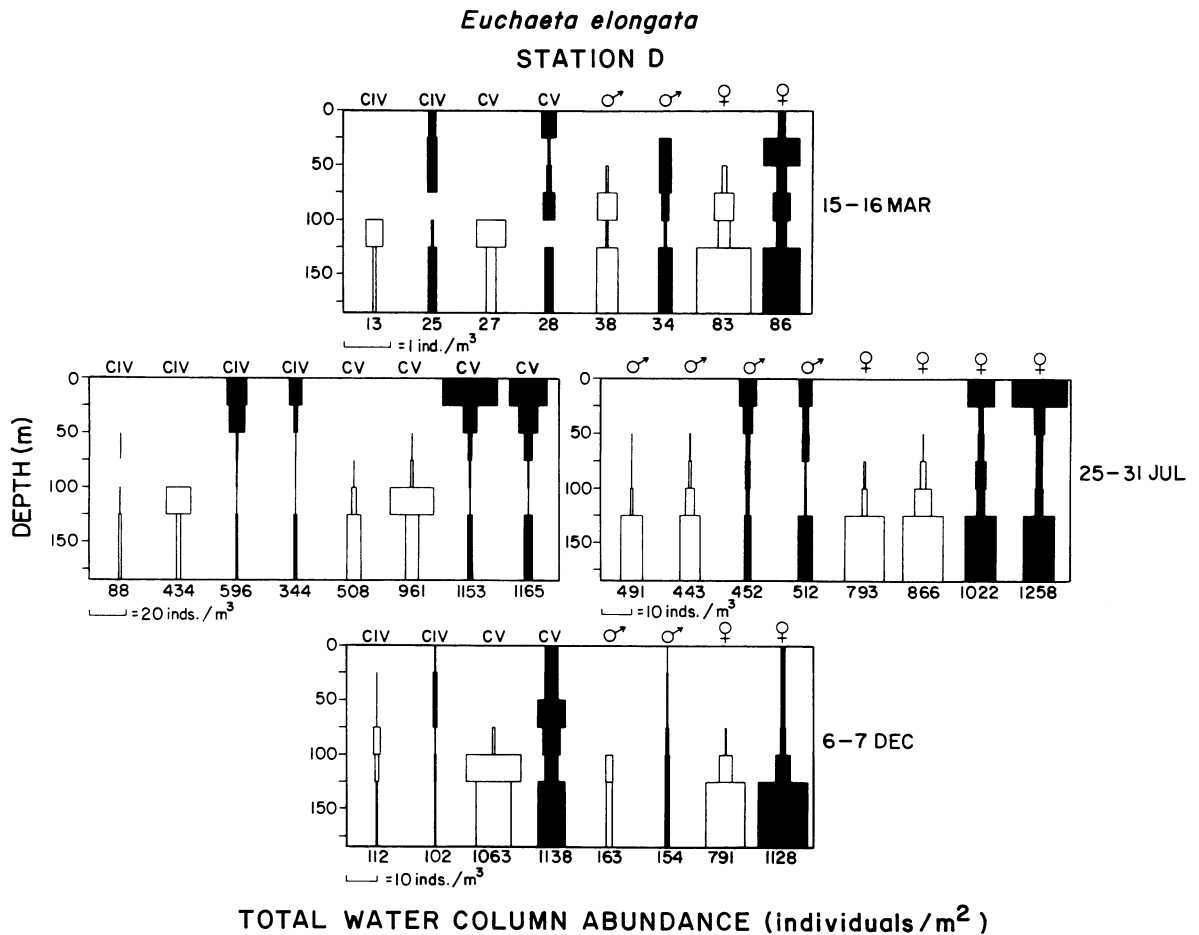


FIG. 10. Day and night vertical distribution of *Euchaeta elongata* copepodid stage IV, copepodid stage V, adult males, and adult females at Station D in March, July, and December 1979. (Symbols as in Fig. 5.)

#### *Food limitation effects*

To examine a possible association between resource limitation and diel vertical migration of *P. newmani*, I reproduce some data from Ohman (1985). Food concentrations required to sustain maximum growth of CV *Pseudocalanus* were estimated as a function of temperature from results in Vidal (1980). These food requirements were compared with ambient food concentrations approximated from chl *a* and size-fractionated chl *a*. In addition, an integrative measure of the suitability of particulate food to support maximal reproductive rates of *Pseudocalanus newmani* females was obtained from temporal variations in fecundity.

On most dates ambient phytoplankton bearing chl *a* (Fig. 13) met or exceeded the critical concentration for growth of *Pseudocalanus*, often severalfold (Fig. 14A). Occasionally the ambient food supply fell below requirements, most notably in late July 1979. Following this interval of food-limited ingestion, fecundity declined (Fig. 14B).

The one clear episode of food limitation in July of 1979 was a time of pronounced reverse migration. Two weeks later phytoplankton concentrations had in-

creased substantially and the reverse migration still occurred. Food conditions in July 1980 were sufficient for maximal growth and egg production, in strong contrast with the previous July, yet reverse migration was again clearly defined. Conversely, on numerous occasions in March, April, June, and September, food conditions were sufficient to support maximal growth and reproduction, yet no vertical migration was detected. The reverse migration by *P. newmani* females bears no apparent relation to periods of high or low food abundance.

#### *Variations in migration behavior by developmental stages and by other species*

Developmental stages of *Pseudocalanus newmani* differed in the expression of reverse diel vertical migration. The behavior of all copepodid stages of *P. newmani* was analyzed from one series when a strong migration was expressed by adult females. The net mesh size used (216  $\mu\text{m}$ ) undersampled the smallest copepodid stages, CIs and CIIs. However, this bias should be consistent between day and night and should not

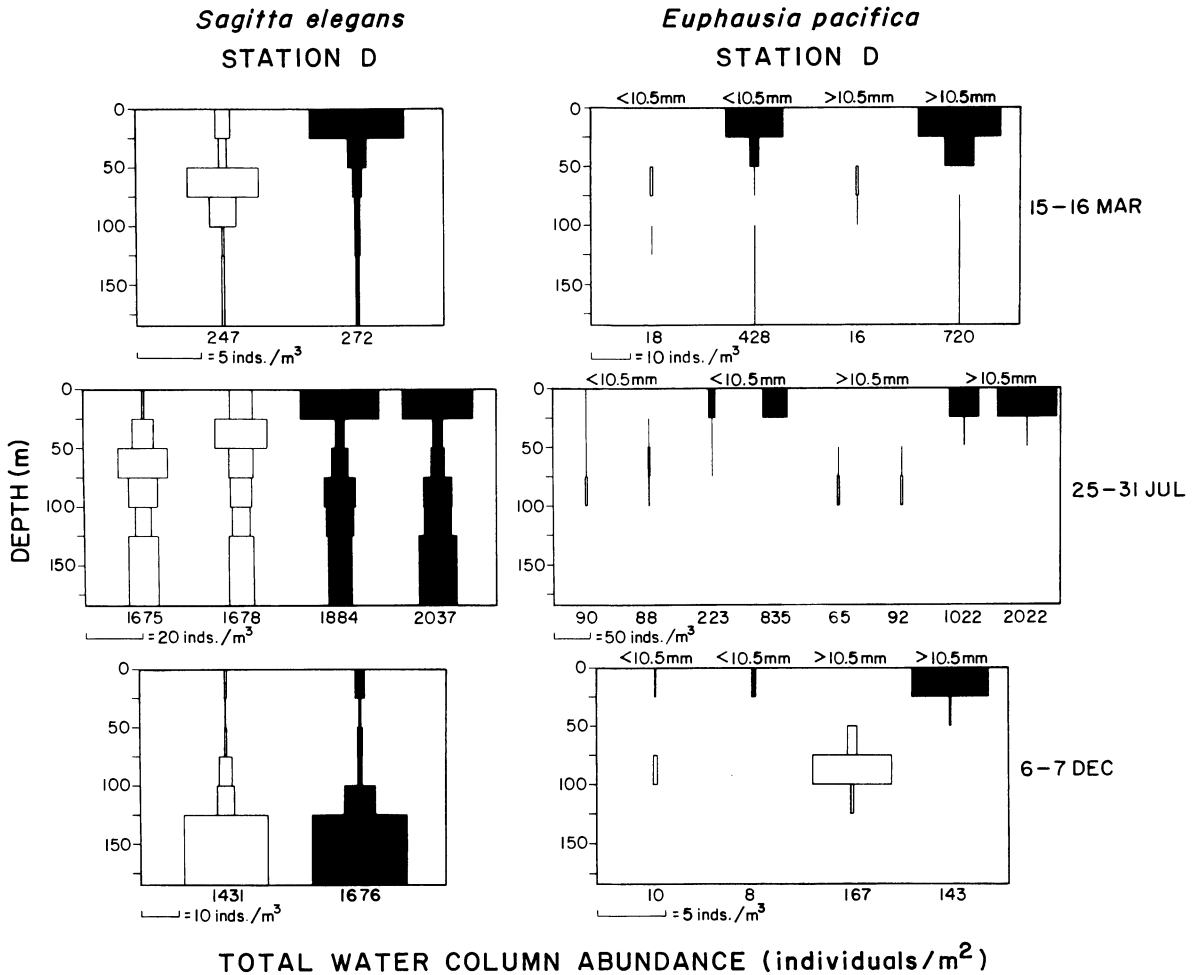


FIG. 11. Day and night vertical distribution of *Sagitta elegans* (left) and two size classes of *Euphausia pacifica* (<10.5 mm total length; >10.5 mm total length) at Station D in March, July, and December 1979. In the case of *E. pacifica*, daytime histograms reflect avoidance of the plankton net. (Symbols as in Fig. 5.)

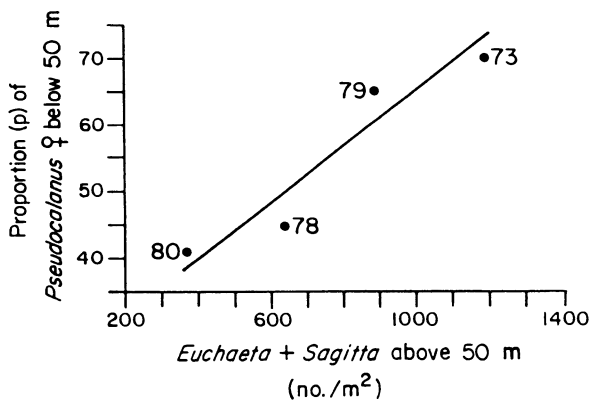


FIG. 12. Relationship between the proportion ( $p$ ) of *Pseudocalanus newmani* females reverse-migrating at Station D in late July-early August and the abundance ( $A$ ) of predatory zooplankton (*Euchaeta elongata* females and *Sagitta elegans*) in the upper stratum at night, for four different years. ( $p = 0.042A + 23.2$ ,  $P < .10$ ,  $r^2 = 0.90$ , Model II regression.)  $p$  is expressed as the arcsine  $\sqrt{p}$  transformation.

distort the vertical distributions of these stages. Most adult males and copepodid stage Vs, as well as adult females, reverse migrated (Fig. 15). A fraction of the CIVs also descended, but little evidence for reverse migration was detected in CIIs, CIIs or CIs. A summary survivorship curve illustrated that when averaged over a season, young copepodid stages (CI-III) experience lower mortality than later copepodids (Ohman 1986). This suggests that there is a higher potential gain through reverse migration for later developmental stages. The lower limit to the stage of onset of migration is also influenced by morphological constraints.

No evidence of diel vertical migration was detected among three other species of small copepods that co-occurred with *P. newmani* (Fig. 16). Two are relatively small cyclopoid copepods (*Oithona similis*,  $\approx 0.43$  mm, and *Oithona spirostris*, 0.71 mm prosome length) and one is a calanoid (*Paracalanus parvus*, 0.71 mm). Therefore body size alone is not sufficient to predict the propensity of zooplankton to reverse migrate.



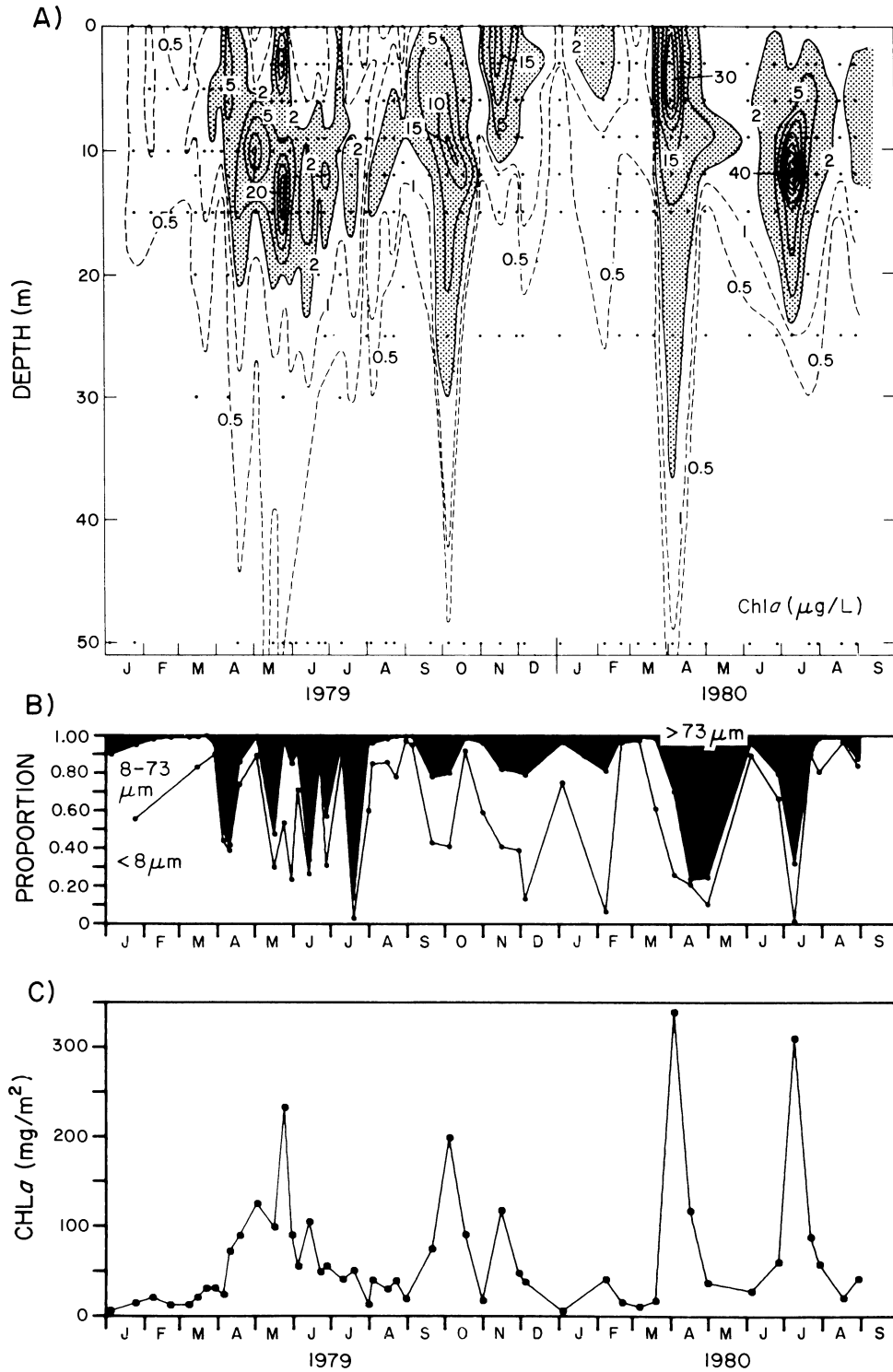


FIG. 13. Temporal variation in chlorophyll *a* at Station D in Dabob Bay. (A) Concentration of chl *a* at discrete depths. Shaded region and solid contour lines indicate chl *a* concentrations of  $> 2 \mu\text{g/L}$ ; dashed contours indicate chl *a* concentrations  $< 2 \mu\text{g/L}$ . Dots indicate depths sampled on each date. (B) Proportion of chl *a* in three size fractions:  $< 8 \mu\text{m}$ ,  $8-73 \mu\text{m}$ , and  $> 73 \mu\text{m}$  (shaded region) for samples taken at a depth of 6–12 m. The samples were located in, or near, the chlorophyll maximum layer. (C) Chl *a* concentration integrated vertically between the depths 0–30 m.

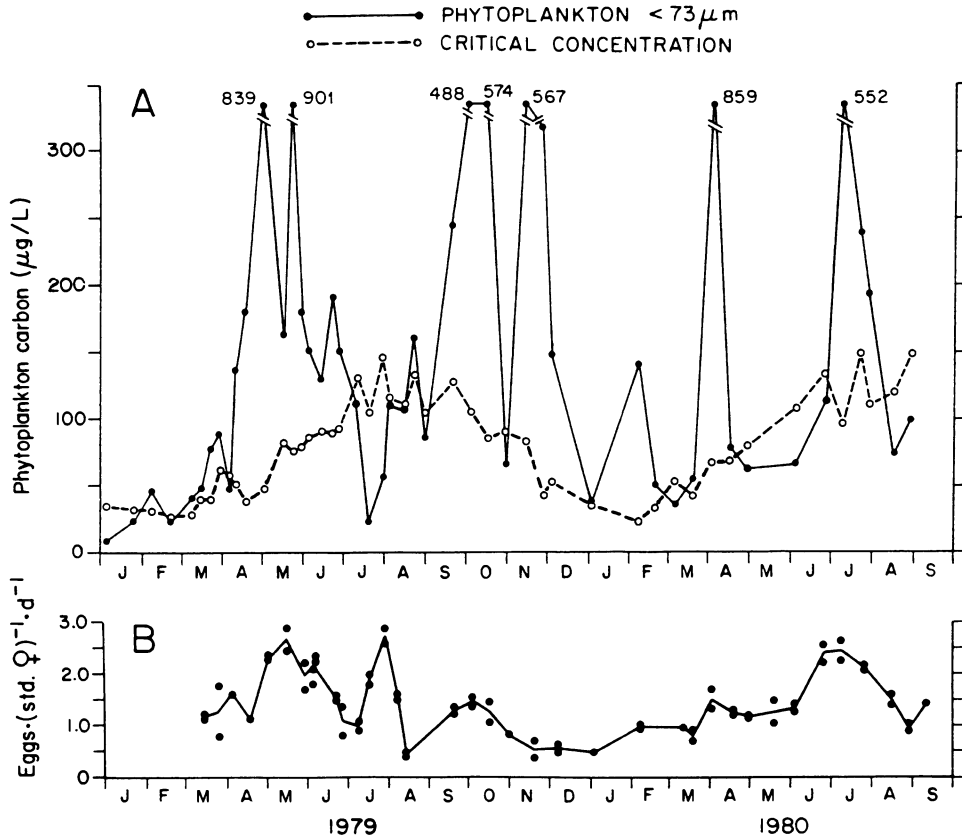


FIG. 14. Station D. (A) Temporal variation in concentration of carbon in phytoplankton  $< 73 \mu\text{m}$  (near the chlorophyll maximum) compared with the critical concentration for growth of copepodid V of *Pseudocalanus*. (B) Temporal variation in reproductive rate of adult female *Pseudocalanus*. Egg production rate (eggs per standard female per day) corrected for seasonal changes in female body size and temperature. Both figures are reproduced from Ohman (1985).

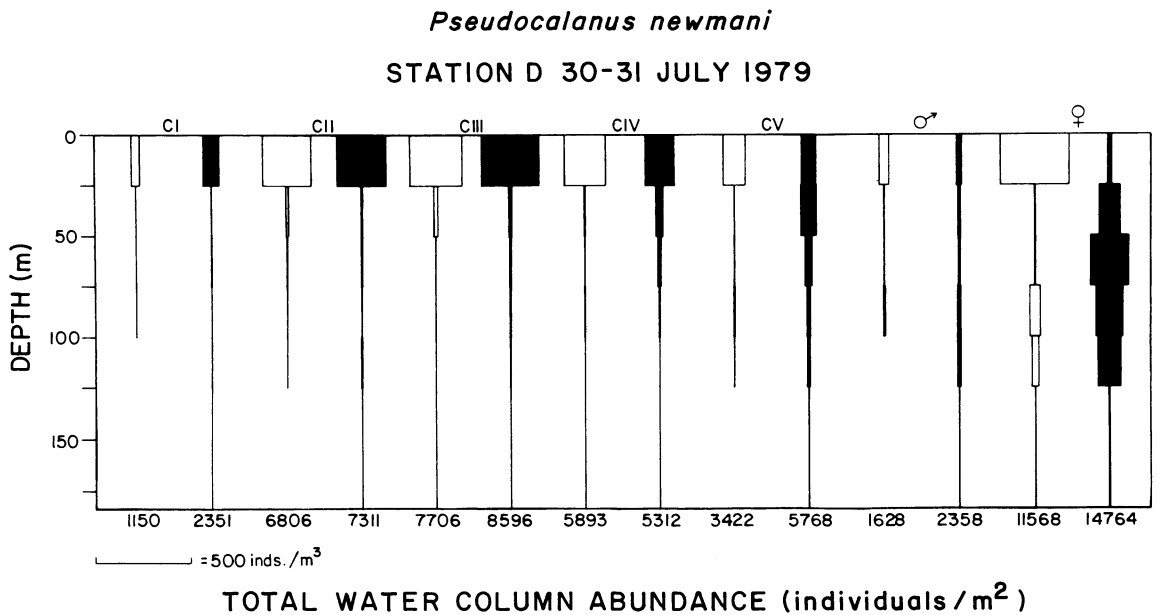


FIG. 15. Day and night vertical distribution of all copepodid stages of *Pseudocalanus newmani* at Station D in July 1979. (Symbols as in Fig. 5.)

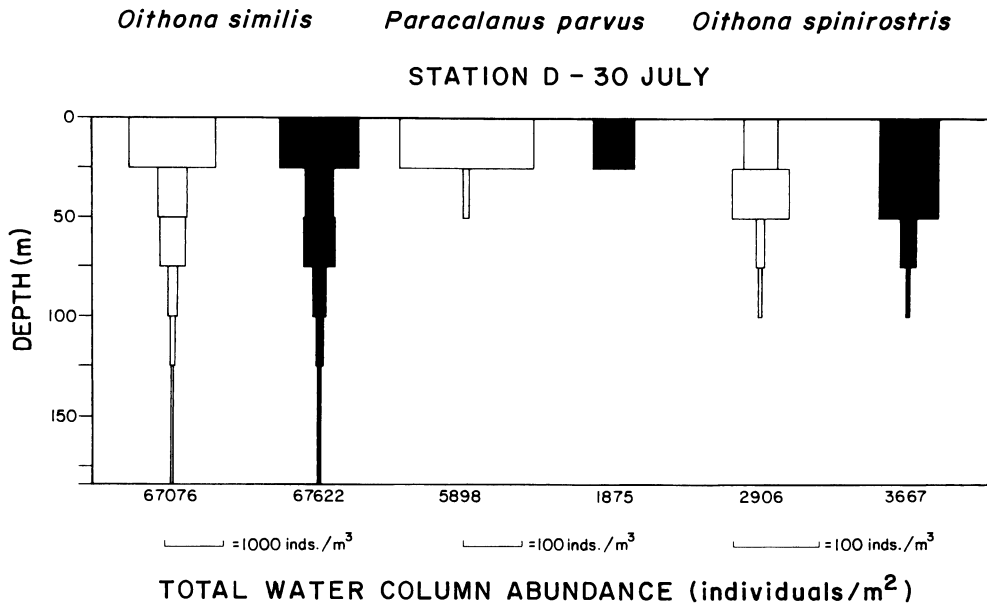


FIG. 16. Day and night vertical distributions of adult females of *Oithona similis*, *Paracalanus parvus*, and *Oithona spinostris* at Station D on 30 July 1979. (Symbols as in Fig. 5.)

#### Life table analyses

The demographic consequences and adaptive significance of diel vertical migration behavior were explored with a series of life table analyses, for comparison with the hypothesis developed by McLaren (1974). They extend the analyses presented in Ohman et al. (1983). Most of the assumptions made by McLaren have been borne out by subsequent data. For example, results from Dabob Bay suggested that with a limited number of exceptions during a 2-yr field study, *P. newmani* grows and develops at food-satiated, temperature-dependent maximum rates (Ohman 1985). The inverse relation between body size and temperature was confirmed in the laboratory (Vidal 1980) as well as in the field (Ohman 1985), as was the positive relation between body size and clutch size (Ohman 1985). These patterns are also well known for other calanoid copepods. McLaren assumed that diel vertical migration commences at copepodid stage III; in Dabob Bay it was detectable from copepodid IV onward. However, to make life table analyses comparable to those of McLaren (1974), migration is assumed to commence at stage CIII, and departures are evaluated later. On average, mortality rates are higher in younger stages than in older stages as McLaren assumed, although an unanticipated plateau region of low mortality at stage CI-CII was found (Ohman 1986). If average mortality rates are computed over just two life history intervals, i.e., from nauplius I to copepodid III ( $d_1$ ) and from CIII through the adult female ( $d_2$ ), then the ratio of  $d_1 : d_2$  is  $\approx 2$ . This value is within the range of early : late mortality ratios used in McLaren's analysis, but differs from the ratio of 4 used by Ohman et al. (1983).

A final assumption of McLaren (1974), that newly molted females vertically migrate but then cease migrating and remain in warm waters at the onset of egg laying, is not substantiated by the data. Ovigerous females of *P. newmani* migrate vertically, as well as non-ovigerous females (Ohman et al. 1983, note 9). Afrikova (1976) also documented vertical migration of ovigerous females of *P. elongatus*. Vuorinen et al. (1983; also Vuorinen 1987) demonstrated that ovigerous females of the copepod *Eurytemora hirundoides* have a stronger migration response than non-egg-bearing females. Hence, the difference between the model of McLaren (1974) and that used here concerns the migratory behavior of ovigerous females. Eggs, borne by female *Pseudocalanus* in an attached sac, are here permitted to cross the thermocline on a daily basis along with adults. Otherwise, I use similar or identical quantitative relationships to those adopted by McLaren.

In examining the results of life table analyses it should be noted that the realized rate of increase,  $r$ , measures the population growth rate under conditions of natural mortality. It does not reflect the intrinsic rate of natural increase from laboratory study. Comparisons between the realized rate of increase of a migrant population and that of a nonmigrant population are depicted graphically as their difference ( $r_{\text{migrant}} - r_{\text{nonmigrant}}$ ). For all cases throughout Figs. 17-20 the nonmigrant population is at equilibrium ( $r_{\text{nonmigrant}} = 0$ ). At equilibrium, when  $r = 0$ , the net reproductive rate,  $R_0$ , is equal to 1.

In all conditions of positive thermal stratification (surface water warmer than deeper water) migrants suffer a disadvantage by comparison with nonmigrants (Fig. 17). In Dabob Bay, elsewhere in the ocean, and

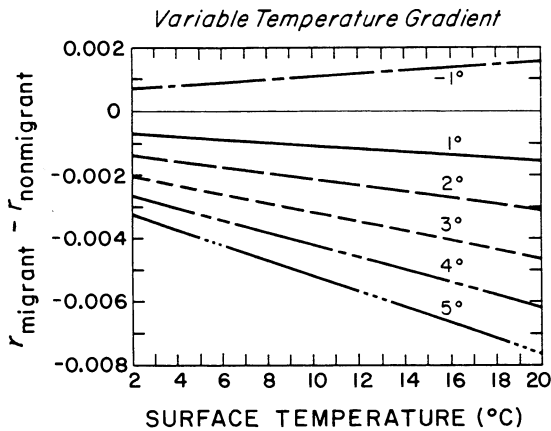


FIG. 17. Difference in realized rate of increase,  $r$ , between a vertical migrant and a nonmigrant population of *Pseudocalanus* as a function of surface temperature and the vertical temperature gradient. Family of curves illustrates the effects as the temperature gradient (surface temperature - lower layer temperature) varies between  $-1^\circ$  and  $+5^\circ\text{C}$ . (Ratio of early/late mortality rates,  $d_1/d_2$ , is held constant at 2.0.) Line of no difference is illustrated for reference.

in lakes, the temperature gradient experienced by migrants frequently exceeds the  $5^\circ$  difference indicated in Fig. 17. As the temperature gradient increases further, the severity of retardation of population growth of migrants becomes greater still. A temperature inversion must exist for migrants to increase at a faster rate than nonmigrants. There is no combination of surface temperatures and positive thermal gradients where migrants can achieve a demographic advantage.

The basis for this effect is as follows. By spending half the day in cooler water copepods eventually attain a larger body size and consequent higher fecundity, as described by Eqs. 3 and 4. This point formed the basis for the hypothesis advanced by McLaren (1974). However, lower temperatures also slow developmental rates such that the total time spent in each developmental stage increases. Under the same daily mortality rate migrants, taking longer to mature than nonmigrants, experience lower survivorship to the adult stage and lower survivorship between clutches. The summation of survivorship times fecundity ( $\Sigma l_x m_x$ ) for the migrant is therefore lowered. The lower survivorship of migrants more than discounts their higher fecundity, resulting in a decreased rate of population growth for animals that cross a thermocline.

This demographic disadvantage increases as the surface temperature increases from  $2^\circ$  to  $20^\circ$  (abscissa in Fig. 17). With increasing surface temperatures, the increment in body size and in clutch size diminishes for the migrant residing part-time in cooler waters below the thermocline. For example, consider a constant  $4^\circ$  temperature gradient across the thermocline. When the surface temperature is  $8^\circ$  the migrant gains 13% in clutch size, but at a surface temperature of  $20^\circ$  the migrant gains only 6% in clutch size. Further, as the

magnitude of the vertical temperature gradient increases from  $1^\circ$  to  $5^\circ$ , the losses to the migrant increase.

Now consider the case where the temperature gradient is held constant at  $4^\circ$  and the ratio of early to late mortality rates ( $d_1/d_2$ ) varies (Fig. 18). This corresponds to conditions where predators that feed selectively on younger stages and those that feed selectively on older stages change in relative importance. For all ratios of mortality rates and at all temperatures the migrant again suffers by comparison with the nonmigrant. As  $d_1/d_2$  decreases from 6.0 to 2.0, the disadvantage to the migrant increases. That is, when mortality rates for early larval stages are only twice those of late copepodids and adults,  $r$  decreases more than when early stages experience six times the mortality rate of later stages. This effect occurs because the lower mortality of late stages in the latter (6:1) case permits higher survivorship to the age of first reproduction. As noted above, the 2:1 case is the most representative of the average conditions actually observed in this study site and underscores the loss in fitness experienced by a vertical migrant.

How then can this fitness loss associated with migration across a thermocline be overcome? Consider that the midsummer abundance of active predators of *Pseudocalanus* is greater in surface waters than in subsurface waters. If *Pseudocalanus* avoids predators by migrating below the surface layer at times of greatest predation risk, mortality rates should decrease (Fig. 19). When the mortality rates of copepodid stages CIV-CVI (the stages found above to migrate) are reduced by 50%, the migrants attain substantial gains in population growth rate. This effect holds for all temperature gradients.

Although a 50% (or greater) reduction in mortality

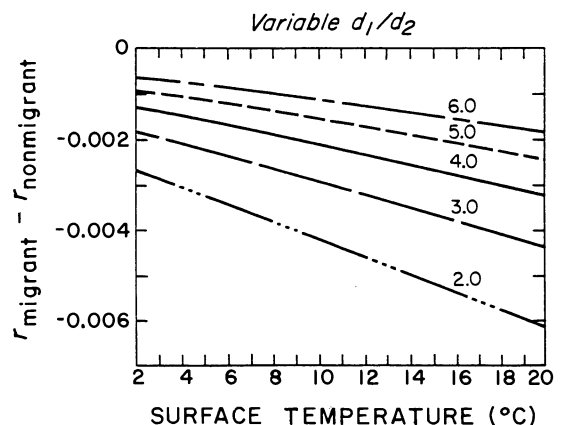


FIG. 18. Difference in realized rate of increase,  $r$ , between a vertical migrant and a nonmigrant population of *Pseudocalanus* as a function of surface temperature and the ratio of early/late mortality rates. Family of curves illustrates the effects as the ratio of early/late mortality rates,  $d_1/d_2$ , varies between 2.0 and 6.0. (Temperature gradient held constant at  $4^\circ\text{C}$ .)

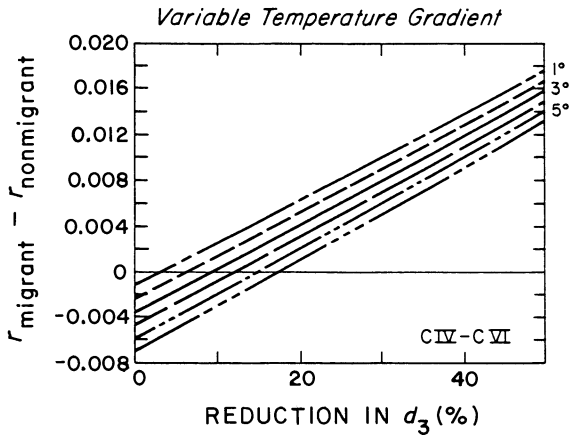


FIG. 19. Difference in  $r$  between a vertical migrant and a nonmigrant population of *Pseudocalanus* as a function of the reduction in the mortality rate of CIII to adult ( $d_3$ ) achieved by predator avoidance, and the vertical temperature gradient. Family of curves illustrates the effects as the temperature gradient varies between 1° and 6°C. ( $d_1/d_2 = 2.0$ , where  $d_1$  = mortality rate from nauplius I to CIII for all populations and  $d_2$  = mortality rate from CIII to adult in nonmigratory populations; surface temperature = 13°.)

rates by avoiding predators is plausible for natural populations (Stich and Lampert 1981, Ohman et al. 1983), it need not be this large for diel vertical migration to confer a significant advantage upon migrants. Consider the case when the temperature gradient is 4°, the surface stratum temperature is 13° and the ratio of early to late mortality is 2.0. These conditions are representative of those in late July when a strong reverse migration is expressed by *P. newmani*. Late mortality (CIV to adult) need only be reduced by 12% for migrants to achieve comparable growth rates to nonmigrants (zero line in Fig. 19). Greater reductions in mortality rates promote more rapid population growth by the migrant. That is, very slight reductions in mortality rates achieved through diel vertical migration overcome the slowed population growth rate associated with migration across a thermocline and result in significant gains for migrants.

Consider now the effect as the onset of vertical migration (and reduction in mortality rate) begins at progressively earlier developmental stages (Fig. 20). Commencement at the adult stage requires an 18% reduction in mortality for migrants to achieve an advantage, still a relatively small decrement. If migration commences as early as stage CIII, only a 10% diminution in mortality rate for migrants results in a higher rate of population growth for migrants.

DISCUSSION

Individuals within a single copepod population perform either reverse, normal, or no diel vertical migration, apparently depending on the more important source of mortality: predation by nocturnally feeding,

normally migrating carnivorous zooplankton, or visually hunting planktivorous fish. The variations in migration behavior of *Pseudocalanus newmani* are associated with differences in predation pressure in time and in space, and are not explainable by distributions of resources or temperature.

Growing evidence from other studies also suggests that predator avoidance is of overriding significance as an adaptive advantage of diel vertical migration (DVM) by zooplankton. Zaret and Suffern (1976) established the importance of planktivorous fish predation to DVM by the copepod *Diaptomus gatunensis* in an isothermal water column. Stich and Lampert (1981) contrasted nonmigrant *Daphnia galeata* with migratory *D. hyalina*. *D. hyalina* has the lower birth rate of the two, but is more abundant because of its lower death rate, apparently achieved through avoidance of predators. From their simulations, Wright et al. (1980) concluded that vertical migrations of both small-bodied cladocerans and larger bodied zooplankton were explained by the selectivity of planktivorous fish. Clark and Levy (1988) suggested that visually hunting planktivores whose predators also hunt by visual means have a narrow temporal window at dawn and dusk when vertical migration into surface waters is advantageous. Of several factors analyzed by Gabriel and Thomas (1988), the payoff of migration depended most markedly on the risk of predation.

Some other instances of changes in migration behavior in response to altered abundance of predators have been reported. Williamson and Magnien (1982) suggested that the onset of diel vertical migration by *Mesocyclops edax* was associated with increased fish density. After the introduction of trout into Lake Le-

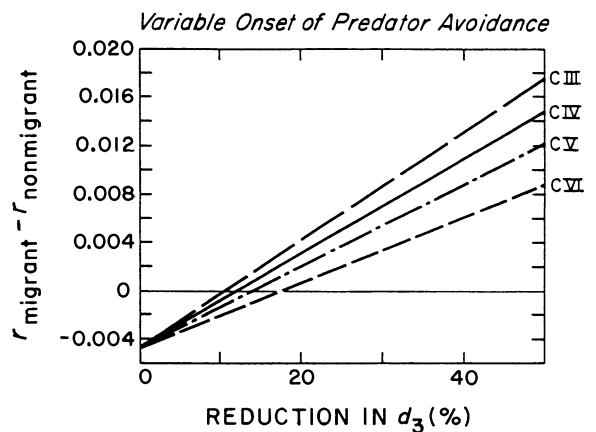


FIG. 20. Difference in  $r$  between a vertical migrant and a nonmigrant population of *Pseudocalanus* as a function of the reduction in the mortality rate of CIII to adult ( $d_3$ ) achieved by predator avoidance, and the developmental stage of onset of migration. Family of curves illustrates the effects as the onset of predator avoidance varies between copepodid stage III and stage VI (adult). ( $d_1/d_2 = 2.0$  as in Fig. 19; temperature gradient = 4°, surface temperature = 13°.)

nore, Washington, late-instar *Chaoborus* larvae and pupae began to migrate out of the water column by day, seeking refuge in sediments (Luecke 1986). Gliwicz (1986) found that the extent of vertical migration of *Cyclops abyssorum* in eight lakes of the Tatra Mountains was correlated with the length of time over which a lake had been stocked with planktivorous brook char. In Dabob Bay, Frost (1988) concluded that variability in migration behavior of *Calanus pacificus* could only be accounted for by avoidance of visually feeding planktivores. Bollens and Frost (1989) observed the induction of DVM of *Acartia hudsonica* in experimental enclosures containing planktivorous sticklebacks.

Such observations, along with the present ones, indicate that vertical migration behavior varies through time, and that extended study under different field conditions is necessary to make substantive progress on the subject of the adaptive nature of diel vertical migration.

Normal diel vertical migration by predators of *Pseudocalanus* at the deep station is, in turn, an effective means to avoid their own predators. Preference by planktivorous fish for larger or more visible prey (e.g., Brooks and Dodson 1965, Parsons and LeBrasseur 1970, Zaret 1980, Koslow 1981) suggests that carnivorous zooplankton will benefit by avoiding fish by day in the same water column where *Pseudocalanus* avoids carnivorous zooplankton by night. The reduced abundance of these large-bodied zooplankters at the shallow station may result from fish cropping where there is no opportunity for predatory zooplankton to attain a deepwater refuge through DVM.

Body size alone is not a sufficient predictor of reverse migration responses, as three other species of small-bodied copepods occurring in the water column with *Pseudocalanus* showed no evidence of migration. Interspecific differences in prey activity patterns (e.g., Gill 1987) and predator selectivity (Sullivan 1980, Yen 1985) will be critical determinants of prey mortality rates and, consequently, of the survivorship gain attainable by DVM.

Predatory zooplankton do not alter their migration behavior in late summer to feed on deep-dwelling *Pseudocalanus*, apparently because they shift to alternate prey items (Ohman 1986). This would permit *P. newmani* to return to continuous residence in the surface layer at Station D in September. Gabriel and Thomas (1988) noted that when predation risk is low, nonmigration is a preferred, and evolutionarily stable, strategy. The dynamic model of Mangel and Clark (1988), which uses some parameters from Ohman et al. (1983), also suggests that the optimal migration behavior for a single cohort of *Pseudocalanus* changes through time. Mangel and Clark's model is quite different from the life table approach taken here (where I incorporate survivorship and fecundity schedules as explicit functions of temperature gradients). Their model suggests that the transition from migratory to nonmigratory

behavior occurs as the risk of losing future reproduction varies with time.

#### *Alternative hypotheses*

McLaren's (1974) demographic advantage hypothesis is perhaps the most far-reaching alternative to the predation hypothesis yet articulated. It is built upon a series of biological observations that hold widely for diverse planktonic populations. Only one key assumption has not been substantiated by this and other studies, namely the nonmigratory behavior of egg-bearing females. The demographic advantage hypothesis requires that once ovigerous, females cease migrating across a thermocline and remain continuously in the warmer surface stratum. However, the present work indicates that ovigerous females of *P. newmani* migrate just as non-egg-bearing females do. Furthermore, in one study where egg-bearing *Euchaeta* showed restricted migrations by comparison with non-egg-bearing females (Yen 1983), the ovigerous females remained below the thermocline rather than above it. Modifying this assumption changes the outcome of the life table analyses, such that there is no plausible region of surface temperatures, temperature gradients, or ratios of early : late mortality rates where migrants can attain a demographic advantage over nonmigrants. Vertical migrants much achieve a reduction in mortality to predominate in a population.

Demographic advantages from thermal gradients have also not been substantiated experimentally. Orcutt and Porter (1983) determined that the rate of increase of *Daphnia parvula* was always greater at a high constant temperature than in fluctuating temperature conditions. Stich and Lampert (1984) found that both *Daphnia galeata* and *D. hyalina* attained earlier reproduction and a larger cumulative number of offspring in simulated nonmigration conditions (constant food and temperature) than in simulated migration conditions (high temperature and high food for part of the day and low temperature and low food for part of the day). In the absence of other benefits, vertical migrants in thermally stratified waters will consistently suffer a disadvantage by comparison with nonmigrants that remain continuously in the surface stratum.

McLaren (1963) proposed a metabolic advantage hypothesis, which he subsequently rejected (Lock and McLaren 1970, McLaren 1974), though the number of authors who have not recognized the fallacies in the earlier hypothesis is remarkable. This hypothesis incorporated erroneous metabolic effects on body size, used an asymptotic growth function that is not applicable to copepods, and did not consider the effects of natural mortality (see McLaren 1974). Another metabolic model (Enright 1977) assumed that migrants reduce diurnal grazing pressure on phytoplankton to permit maximal photosynthesis and prey growth by day. This assumption is inconsistent with the reverse migration by *Pseudocalanus* at Station D, where algal

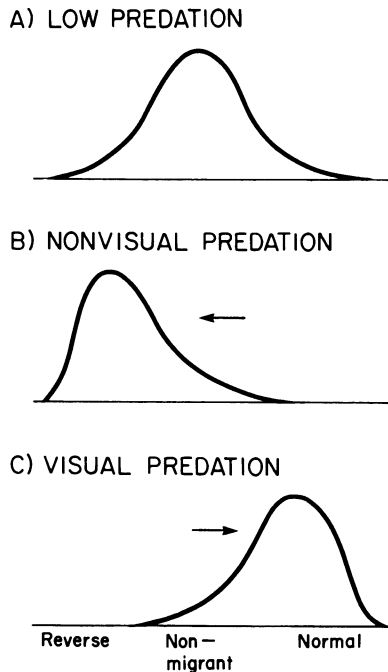


FIG. 21. Hypothesized relative abundance of three vertical migration phenotypes (reverse migrant, nonmigrant, and normal migrant) under different predation regimes. (A) Low predation pressure, (B) high predation pressure by nonvisual predators, and (C) high predation pressure by visual predators.

prey are freed from *Pseudocalanus* grazing pressure at night, not by day. Other assumptions of the metabolic model proposed by Enright (1977) were not substantiated by the experimental tests of Lampert et al. (1988).

Several investigators (e.g., Conover 1968, Pearre 1973, Mackas and Bohrer 1976, Huntley and Brooks 1982, Dagg 1985) have suggested that diel vertical migration is a hunger-motivated response, i.e., that hunger causes ascent into food-rich layers and descent occurs when zooplankters become satiated after an interval of feeding. A specific prediction follows from this hypothesis: migrations should be strongest when zooplankters are food satiated and should not occur in conditions of food limitation (Huntley and Brooks 1982). This prediction is at variance with the present observations. In April and June particulate food for *Pseudocalanus* was abundant (Fig. 13A) and adult females exhibited nearly optimal reproductive rates (Fig. 14B), indicating that both individual and population growth occurred at food-satiated rates. However, there was little or no evidence for diel migration by *Pseudocalanus* in these conditions. Conversely, in late July 1979, the single clearest episode of food limitation experienced during a 2-yr period (Fig. 14), *Pseudocalanus* exhibited a strong reverse migration, again contrasting with the predictions of the hunger/food limitation argument.

More generally, the food limitation hypothesis also

fails to account for the opposite phasing of *Pseudocalanus* migrations at the deep and shallow stations, as well as size/developmental stage variations in vertical migration behavior. Since younger developmental stages have lower food requirements (e.g., Vidal 1980), they should be more frequently food satiated, yet younger stages show less, rather than more, tendency to migrate. Migrations by nonfeeding males of *Euchaeta elongata* and *Pseudocalanus newmani* are also inconsistent with hunger-motivated responses. Nor does the hypothesis explain why migration should occur on a 24-h cycle rather than with some other periodicity, such as the duration of a feeding bout. Also, hunger causes *Daphnia magna* to become less, rather than more positively phototactic (De Meester and Dumont 1989), as would be implied by the food limitation hypothesis. It appears that, if food supply and hunger modify the vertical migration behavior of zooplankton in any way, it is not through the mechanism proposed above.

Food supply may affect the vertical distribution of predators like *Sagitta elegans* and *Euchaeta elongata*, but in an indirect manner through its relationship with diapause. Most *S. elegans* and *E. elongata* remain at depth in December when the epipelagic food supply is greatly diminished. This appears to be an effect of food supply on life histories and overwintering behavior rather than on diel vertical migration behavior per se.

#### Life table analyses

The remarkable feature of the life table analyses is the small mortality reduction that makes migration behavior advantageous. For conditions approximating those observed at the time of the peak reverse migration, migrants will replace nonmigrants if migration-related predator avoidance diminishes mortality rates of late developmental stages by only 12%. Comparison of these reductions with estimated predation rates on *Pseudocalanus* (Ohman 1986) in Dabob Bay suggests that such reductions can be readily accomplished in nature.

The changing predominance of different migration behaviors can be illustrated in a hypothetical manner. At times of low predation pressure the nonmigrant would become the dominant phenotype (Fig. 21A), since it reproduces and develops at maximum rates and suffers no increase in mortality by remaining near the surface. Under intense predation by nocturnally feeding, nonvisual predators, reverse migrants would have the highest population growth rate and would come to predominate (Fig. 21B). Conversely, under high predation by visually feeding predators the normal migrants would become the dominant phenotype (Fig. 21C). Which of the three vertical migratory behaviors manifested by *Pseudocalanus newmani* has the greatest advantage therefore depends on the absolute intensity of predation as well as the relative importance of nocturnal vs. diurnal predators.

All available morphological evidence indicates that members of a single species, *Pseudocalanus newmani*, exhibit the three different migration behaviors. This intraspecific variability could be due to phenotypic plasticity of migration behavior depending upon environmental stimuli, or to changing relative abundances of different genotypically determined behaviors.

Concerning the first possibility, all measured environmental variables, except predator abundance, were similar at the two stations, suggesting that predator contact is the only likely environmental stimulus that could account for the difference in behavior between stations. This would require that *Pseudocalanus* respond to tactile, hydrodynamic, or chemosensory cues from predatory zooplankton with a directional, downward swimming, or sinking response. As yet there is no evidence that this evasion response exists. Vertical traps or rapid vertical sampling could be designed to examine the detailed timing of prey descent and predator ascent, to determine whether reverse migration is initiated upon the ascent of predators or begins prior to it. In another approach using field enclosures, Bollens and Frost (1989) concluded that avoidance of sticklebacks by *Acartia hudsonica* was not a chemically mediated response.

The three vertical migration phenotypes may represent distinct genotypes. The predominance of one genotype over the other could occur through differential mortality of those individuals that do not exhibit predator avoidance. Seasonal changes in predation pressure on *Pseudocalanus* could lead to seasonally changing selection coefficients and hence changes in the dominant vertical migration phenotype. For this mechanism to operate on a seasonal time scale, population growth must be sufficiently rapid for new generations of *Pseudocalanus* with differing gene frequencies to replace one another relatively quickly. Ohman (1985) inferred that as many as 8–9 generations of *P. newmani* can occur in Dabob Bay within a year.

Reverse migration behavior is most pronounced after seasonal population crashes (Figs. 1 and 7) that follow peak predation by carnivorous zooplankton (Ohman 1986). Hence the timing is appropriate for mortality of nonmigrants to account for the emergence of reverse migration behavior. Also, when most *P. newmani* females are reverse migrating, a very small fraction of the population may exhibit alternate behavior (as in July 1980). This persistence of behavioral variation is essential if seasonally changing selection pressures were to maintain a balanced polymorphism.

Using allozyme markers, Weider (1984) detected differences in vertical migration behavior among genotypes of *Daphnia pulex* cooccurring within a pond. The relative abundance of different genotypes varied as pond conditions changed (Weider 1985). De Meester and Dumont (1988, 1989) isolated clones of *Daphnia magna* with different phototactic responses and vertical

distributions. The coexistence of positively phototactic, negatively phototactic, and “gypsy” clones within a single lake (De Meester and Dumont 1988) may be relevant to the behavioral polymorphism of *Pseudocalanus newmani* in Dabob Bay. Although Gliwicz (1986) suggested that hundreds or thousands of generations would be required for development of migratory behavior in a population (excluding populations in shallow lakes), the genetic variance found by Weider and De Meester and Dumont would permit rapid responses to changing conditions. Also, relatively rapid changes in migration behavior as noted above (Williamson and Magnien 1982, Luecke 1986), albeit in shallow environments, suggest that evolutionary changes may occur much more quickly than Gliwicz (1986) estimates.

#### Generality of results

In no other situation has a single copepod species been found to exhibit such a clearly defined, predictable range of behaviors within one region as *P. newmani* in Dabob Bay. Unambiguous reverse migrations, not attributable to sampling error, have been noted for a number of other taxa (e.g., Hutchinson 1967, Narver 1970, Dumont 1972, Hure and Scotto di Carlo 1974, Federenko 1975, Hairston 1980, Hamner et al. 1982, Bayly 1986), but these other species appear not to exhibit the range of behaviors shown here. In other situations, species of *Pseudocalanus* have been found to be nonmigratory (e.g., Minoda 1971, Corkett and McLaren 1978) or to exhibit normal migrations (Zagorodnyaya 1975, Afrikova 1976, Kamba 1977, Corkett and McLaren 1978). However, no other reverse migration by *Pseudocalanus* appears to have been reported. Several characteristics of the species studied and the study region account for the manifestation of the three behaviors.

First, unlike many taxa, *P. newmani* is highly susceptible to predation by both nonvisually hunting zooplankton and visually hunting planktivorous fish. Adult *P. newmani* are relatively small bodied; the prosome length of adult females averages 0.86 mm (Ohman 1985). They are the preferred prey of the predators *Euchaeta elongata* (Yen 1983, 1985) and *Sagitta elegans* (Ohman 1986). Although *Euphausia pacifica* obtains only a small ration from *Pseudocalanus* adults, the euphausiid can nonetheless fatally attack *Pseudocalanus* (Ohman 1984). In addition, numerous species and stages of planktivorous fish also ingest adult *Pseudocalanus* (Kamba 1977, Checkley 1982, Cohen and Lough 1983, Ohman 1986).

Second, there is a recurrent, seasonal pattern of predation on *Pseudocalanus* in Dabob Bay (Fig. 1; Ohman 1986) that is not common to all regions where *Pseudocalanus* and other small copepods occur. Peak predator abundances within Dabob Bay are relatively high. For example, the maximum abundance of *Euchaeta*



*elongata* (2104/m<sup>2</sup>, CVs and females) is several times that in the oceanic subarctic Pacific (Minoda 1971).

Third, reduced advective exchange between Dabob Bay and other basins of Puget Sound suggests that sub-populations of *Pseudocalanus* of different predation histories have less opportunity to be mixed. This also enhances the detectability of diel vertical migration behavior since, in advective environments, altered behavior is easily obscured against a background of small-scale patchiness. Especially in summer, extended periods of low winds interact with the minimal tidal currents (Kollmeyer 1965, Ebbesmeyer et al. 1975, Jamart and Winter 1978) to generate protracted residence times within the fjord (Christensen and Packard 1976). Episodes of deep-water replacement occur (Ebbesmeyer et al. 1975), but over an extended time period. Consequently, zooplankton in different regions of the fjord apparently remain semi-isolated for periods of time. This reduced advective exchange permits the development and maintenance of a predation gradient over  $\approx 10$  km and the expression of different behaviors.

Despite this unusual combination of characteristics that makes the behavioral "signal" of diel vertical migration so clearly detectable in Dabob Bay, the processes operating there should be applicable to other ocean regions. Species of *Pseudocalanus* and related predators cooccur over a large sector of the North Pacific Ocean (Bieri 1959, Brinton 1962, Gardner and Szabo 1982, Frost 1989) and elsewhere. The conditions of particularly high predation pressure by large vertical migrators in Dabob Bay may be viewed as loosely analogous with the acceleration of catalytic reactions with temperature. Just as commonly occurring chemical reactions may be accelerated at elevated temperatures without changing the fundamental nature of the catalytic process, the prey-predator interactions studied here in conditions of strong predation pressure are illustrative of interactions that occur commonly elsewhere, albeit more slowly in other environments where the consequences may be more difficult to detect.

The behavioral polymorphism demonstrated by *Pseudocalanus newmani* in Dabob Bay afforded an unusual opportunity to investigate the adaptive significance of diel vertical migration and its interaction with population growth. Several characteristics of the migrations appear consistent only with the hypothesis that the ultimate or evolutionary advantage of this behavior is predator avoidance. However, the classical statement of the predation hypothesis, i.e., diurnal avoidance of visually hunting fish, is incomplete. It ignores the importance of nocturnal avoidance of non-visually hunting zooplankton. Much as early discussions of size-selective predation by planktivorous fish (Hrbáček 1962, Brooks and Dodson 1965) gave way to greater understanding of the opposing effects of fish and predatory zooplankton in influencing the size structure and species composition of zooplankton assemblages (e.g., Kerfoot 1975, Zaret 1980, Kerfoot and

Sih 1987), increasing evidence suggests that these two groups of predators may have complementary consequences for zooplankton behavior.

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