

## Recruitment, growth, and diel vertical migration of *Euphausia pacifica* in a temperate fjord

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**Abstract.** The pelagic crustacean *Euphausia pacifica* Hansen was sampled with a multiple-sample 1.0 m<sup>2</sup> Tucker trawl and a multiple-sample 1.0 m<sup>2</sup> vertical net in Dabob Bay, Washington on 17 dates between May 1985 and October 1987. Size (stage) structure and abundance of the population were determined for each date, while vertical distribution and diel migration were determined for 13 dates. Although interannual variability in both timing and magnitude of events occurred, consistent patterns were discernable. The population produced a large pulse of larvae (2 to 5 mm) in late spring of each year, apparently in response to the vernal phytoplankton bloom. Much lower abundances of larvae occurred during summer and autumn of each year, and larvae were completely absent during winter. Recruitment to the juvenile (6 to 9 mm) and adult ( $\geq 10$  mm) stages was strongest during the summer, with abundances of these individuals peaking in summer and autumn. Individual growth rates, determined by modal progression analysis, were calculated for *E. pacifica*. Rates ranged from zero for some adult cohorts during the winter to 0.12 mm d<sup>-1</sup> for larvae during spring. The latter are among the highest ever reported for this species in the field. The vertical distributions and diel vertical migrations (DVM) of *E. pacifica* varied seasonally and between size (stage) classes. At night, all size classes were distributed in the surface layer (upper 25 m) irrespective of season or year. During the day, the larger/older stages were always distributed at middepths (50 to 125 m). In contrast, the daytime distribution of the larvae was more variable, being concentrated at the surface during spring and early summer of 1985, and at increasing depths later in the summer and autumn of 1985 and again in spring of 1986. This resulted in invariant DVM in the juveniles and adults, but variable DVM in the larvae, the latter of which is hypothesized to be a response to variable abundances of zooplanktivorous fish.

### Introduction

Euphausiids are often an abundant and conspicuous component of marine macroplankton, where they can play a significant role in the flow of energy and matter in pelagic food webs (Mauchline 1980). In the subarctic North Pacific, *Euphausia pacifica* is often the dominant species of euphausiid and in some areas reaches concentrations high enough to enable commercial exploitation (Odate 1979, Fulton and LeBrasseur 1984). The life history and ecology of *E. pacifica* in open ocean and open coastal waters have been well documented (e.g. Panomareva 1963, Smiles and Percy 1971, Brinton 1976, Fulton and LeBrasseur 1984), but *E. pacifica* can also be quite abundant in deep inland basins (Cooney 1971, Heath 1977), where studies of its population biology are generally less extensive. Ross et al. (1982) reported on the fecundity of *E. pacifica* in Puget Sound and several investigators have reported on daytime surface swarming of this species in Japanese coastal waters (Komaki 1967 and references therein, Terazaki 1980, Endo 1984, Hanamura et al. 1984), but other aspects of this species' life history and population biology in inland waters, such as growth and diel vertical migration (DVM), have gone largely unreported or are confined to unpublished reports (e.g. Cooney 1971, Hulsizer 1971, Heath 1977).

As part of a broader program investigating the vertical distributions and diel migrations of zooplankton in a temperate fjord (Dabob Bay, Washington, USA), we undertook a field study of the population biology of *Euphausia pacifica*. We report here our findings on recruitment, seasonal cycles of abundance, growth, and diel vertical migration behavior.

### Materials and methods

Samples were collected at a central, deep station (193 m max. depth) in Dabob Bay, Washington, USA (Fig. 1) on 17 cruises between May 1985 and October 1987 using a multiple-sample 1.0 m<sup>2</sup> Tucker trawl (Frost and McCrone 1974) with 500  $\mu$ m mesh nets, and less frequently with a multiple-sample 1.0 m<sup>2</sup> vertical net (Frost 1988)

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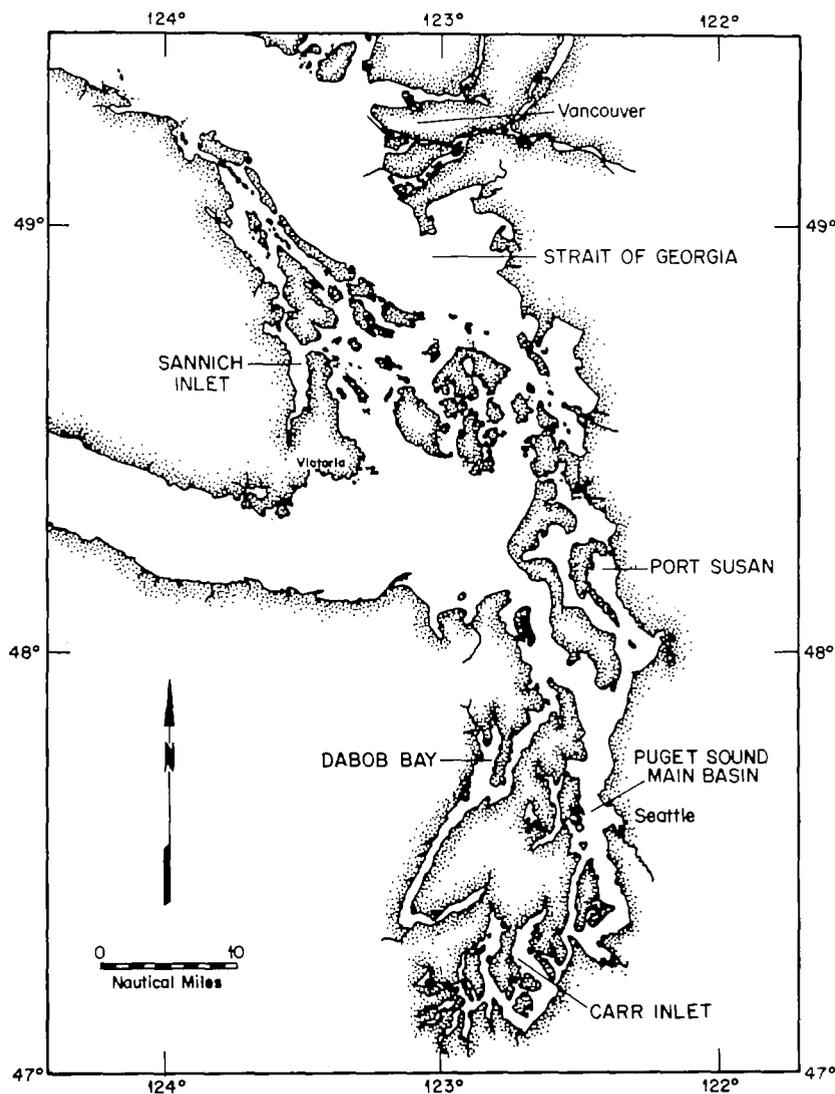


Fig. 1. Location of inland basins referred to in the text

with 333  $\mu\text{m}$  mesh nets. Dabob Bay exhibits very weak circulation as a result of a sill at the basin's mouth and very low freshwater input, which in turn favors repeated sampling of the same population of zooplankton over the course of at least several days (Frost 1988 and references therein).

At least two nighttime hauls from near bottom to the surface were collected with the Tucker trawl on each cruise (1 May, 18 June, 22 August, 15 October 1985; 13 February, 14 April, 5 June, 13 August, 22 October, 16 December 1986; 21 January, 23 February, 15 April, 5 May, 16 June, 18 August, 12 October 1987). On most cruises we assessed vertical distribution and possible DVM of euphausiids by towing the Tucker trawl and/or vertical net through multiple depth strata (usually 175 to 125, 125 to 75, 75 to 50, 50 to 25, 25 to 10, 10 to 0 m) near midnight and noon. Assessment of horizontal distributions within the bay was beyond the scope of the present study. Vertically stratified series of tows with the Tucker trawl were summed to give water column totals. The Tucker trawl was towed obliquely from 150 m (May 1985 to October 1985) or 175 m (April 1986 to October 1987) to the surface. Tow speeds averaged  $100 \text{ cm s}^{-1}$ . Volumes filtered, calculated from electronically telemetered data on flow meter counts and tilt angle of net, averaged ca.  $350 \text{ m}^3$  and ranged from  $80 \text{ m}^3$  (surface sample) to  $2700 \text{ m}^3$  (total water column sample). Catches were rinsed from the nets and immediately preserved in 10% formalin-seawater solution. Collection of samples with the vertical net is described in Frost (1988).

Samples were split in the laboratory with a Folsom splitter to obtain a subsample of at least 50 individual euphausiids of  $\geq 6 \text{ mm}$  length (measured from the anterior tip of rostrum to the posterior tip of telson). Additional splits of the subsample were sometimes made (i.e., May 1985, June 1985, April 1986, May 1987) to reduce the number of 2 to 5 mm individuals to ca. 50. All euphausiids in the subsamples were identified to species (using Boden 1950a, Boden et al. 1955, and Endo and Komaki 1979), enumerated and measured for length to the nearest mm. Abundances were calculated from volumes filtered (assuming 100% efficiency) as euphausiids  $\text{m}^{-3}$ .

Since developmental stage of individuals was not distinguished, we report some of our results as pooled data for the following different size classes, the choice of which was based on length-development stage relationships given for *Euphausia pacifica* in Boden (1950a) and Brinton (1976): late calyptopis and furcilia larvae as 2 to 5 mm, post-larval juveniles as 6 to 9 mm, adolescent and young adults as 10 to 14 mm, older adults as  $\geq 15 \text{ mm}$ . These groupings should be considered only as a rough guide, however, as size at development would be expected to vary seasonally and perhaps even interannually as a function of both temperature and food availability (Mauchline and Fisher 1969, Ross 1979, Mauchline 1980).

Two other species of euphausiids were present in our samples. *Thysanoessa longipes* Brandt comprised an average of 3.7% (maximum 11.8%), and *Tessarabrachion oculatus* Hansen an average of <1% (maximum 6%) of the euphausiids in our Tucker trawl sam-

ples. These very much less abundant species will not be discussed further.

Both avoidance and escapement of euphausiids are potential biases of our sampling gear. Net avoidance by euphausiids is a very contentious issue within the literature (Mauchline and Fisher 1969, Mauchline 1980). For example, Allen (1972) found no avoidance of towed 1.0 m nets by euphausiids, whereas Jerde (1967) found that euphausiids greater than 21 mm were able to avoid a towed 1.0 m net. Hovekamp (1989) claimed that abundance estimates of euphausiids were greater with plummet nets vs a 1.0 m<sup>2</sup> Tucker trawl, but examination of the data in his appendix shows this to be the case on only one of two dates; furthermore, he did not examine this effect as a function of euphausiid size. Brinton (1967) determined that his data were inconclusive regarding the avoidance capabilities of juvenile and adult *Euphausia pacifica*, but he suggested they could avoid the net in deep layers. Thus, while the degree to which *E. pacifica* can avoid a towed 1.0 m<sup>2</sup> Tucker trawl is unclear, this gear is likely underestimating the abundance of larger individuals, and thus our data on adults should be viewed cautiously. As for the vertical net, avoidance of this type of gear by *E. pacifica* is more pronounced than for the Tucker trawl (Hovekamp 1989, our data), and thus we present only data on larvae (2 to 5 mm) from the vertical net samples. Regarding the documentation of DVM, it is only important that daytime and nighttime water column totals are equal, i.e., that daytime and nighttime avoidance of the net, if present, are equal.

Regarding escapement of euphausiids, specimens smaller than 3 mm have been reported to pass through a 550 µm mesh net (Brinton 1976) and thus our Tucker trawl data on 2 mm euphausiids should be considered underestimates of abundance; we have chosen to present these data, however, to illustrate certain aspects of the early life history of *Euphausia pacifica* (e.g. seasonality of recruitment). The vertical net (333 µm mesh size) data should have no bias in the abundance of 2 mm individuals due to escapement.

Growth was determined by modal progression analysis. For each date a length-frequency distribution was determined and mean length of each modal group was calculated in the following way. Length-frequency distributions that were discontinuous (five cases) were considered to represent different modal groups and the mean of each group was calculated directly. In the 12 cases where the length-frequency distributions were contiguous, the means and standard deviations were calculated using probability paper methods described by Harding (1949) and Cassie (1950, 1954). Using the criterion advocated by Grant (1989), we considered any adjacent modal size groups as statistically significantly different if their mean lengths were separated by at least three standard deviations. In the 5 of 12 cases that failed to meet this criterion of statistical significance, we applied the Kolmogorov-Smirnov test (Sokal and Rohlf 1981) for deviation from normality, and all distributions were statistically distinguishable from a single normal curve. Therefore, all distributions were determined to consist of two or more modal groups, and the mean of each group was calculated using probability paper methods. For any given modal group, the change in mean length between sampling dates was calculated as mm d<sup>-1</sup>.

## Results

### Recruitment and seasonal abundance patterns

Although interannual variability in recruitment and seasonal abundance patterns occurred, the same general patterns were evident during our 30-mo field study (Figs. 2 and 3). A large pulse of larvae (2 to 5 mm size class) was present in the spring of each year. Peak springtime abundances of larvae were considerably greater in 1985 and 1986 (21 and 24 m<sup>-3</sup>, respectively) than in 1987 (6.0 m<sup>-3</sup>). Much reduced numbers of larvae were present throughout the summer and autumn of each year

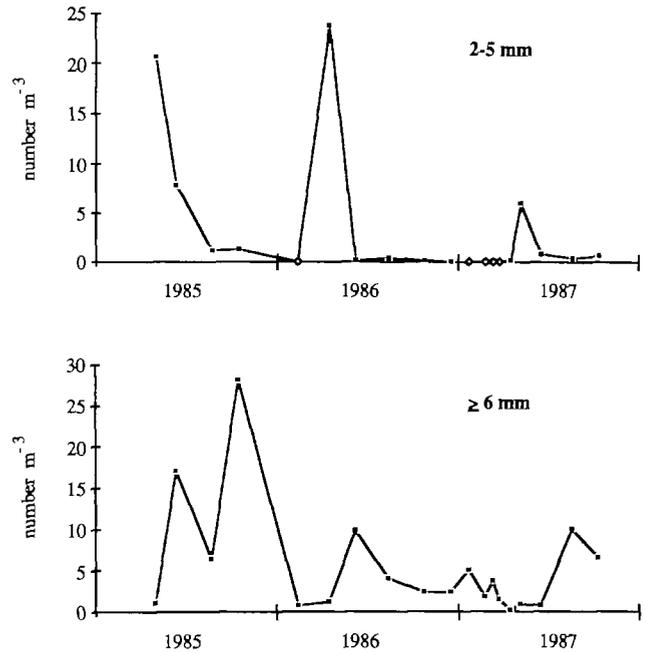


Fig. 2. *Euphausia pacifica*. Seasonal abundances of different size classes sampled with the Tucker trawl in Dabob Bay between May 1985 and October 1987. Filled squares are means of duplicate night-time hauls from near bottom to surface. Open diamonds represent zero values. Hatch marks on the abscissa separate years

(< 1.0 m<sup>-3</sup>). No individuals of this size class were present during the winter.

The springtime pulses of larvae were in turn followed by peak abundances of juveniles and adults (≥ 6 mm size classes combined) in the summer and early autumn of each year (Fig. 2), although the timing of these peaks varied somewhat (i.e., October in 1985, June in 1986, and August in 1987). In contrast to the larvae, juveniles and adults were more abundant in 1985 (28 m<sup>-3</sup>) than 1986 (9.7 m<sup>-3</sup>) or 1987 (9.9 m<sup>-3</sup>) (Fig. 2).

### Growth

Individual growth rates varied between seasons, years, and size classes of euphausiids (Fig. 3). Larvae (2 to 5 mm) produced in spring and early summer tended to have high growth rates (0.08 to 0.12 mm d<sup>-1</sup>), whereas larvae produced later in the summer tended to grow more slowly (0.04 to 0.08 mm d<sup>-1</sup>). Growth rates of larvae produced in October and December could not be determined due to uncertainty in tracking the progression of moults.

Juveniles (6 to 9 mm) resulting from the springtime pulses of larvae tended to grow at rates of 0.04 to 0.08 mm d<sup>-1</sup> during summer, and typically at the lower end of this range during autumn. Adolescents and adults (≥ 10 mm) showed considerable variability in their growth rates: moderately high rates (0.036 to 0.083 mm d<sup>-1</sup>) occurred virtually year-round, with lower rates occasionally interspersed among these (e.g. 0.003 mm d<sup>-1</sup> during June to August 1986, 0.016 mm d<sup>-1</sup> during Au-

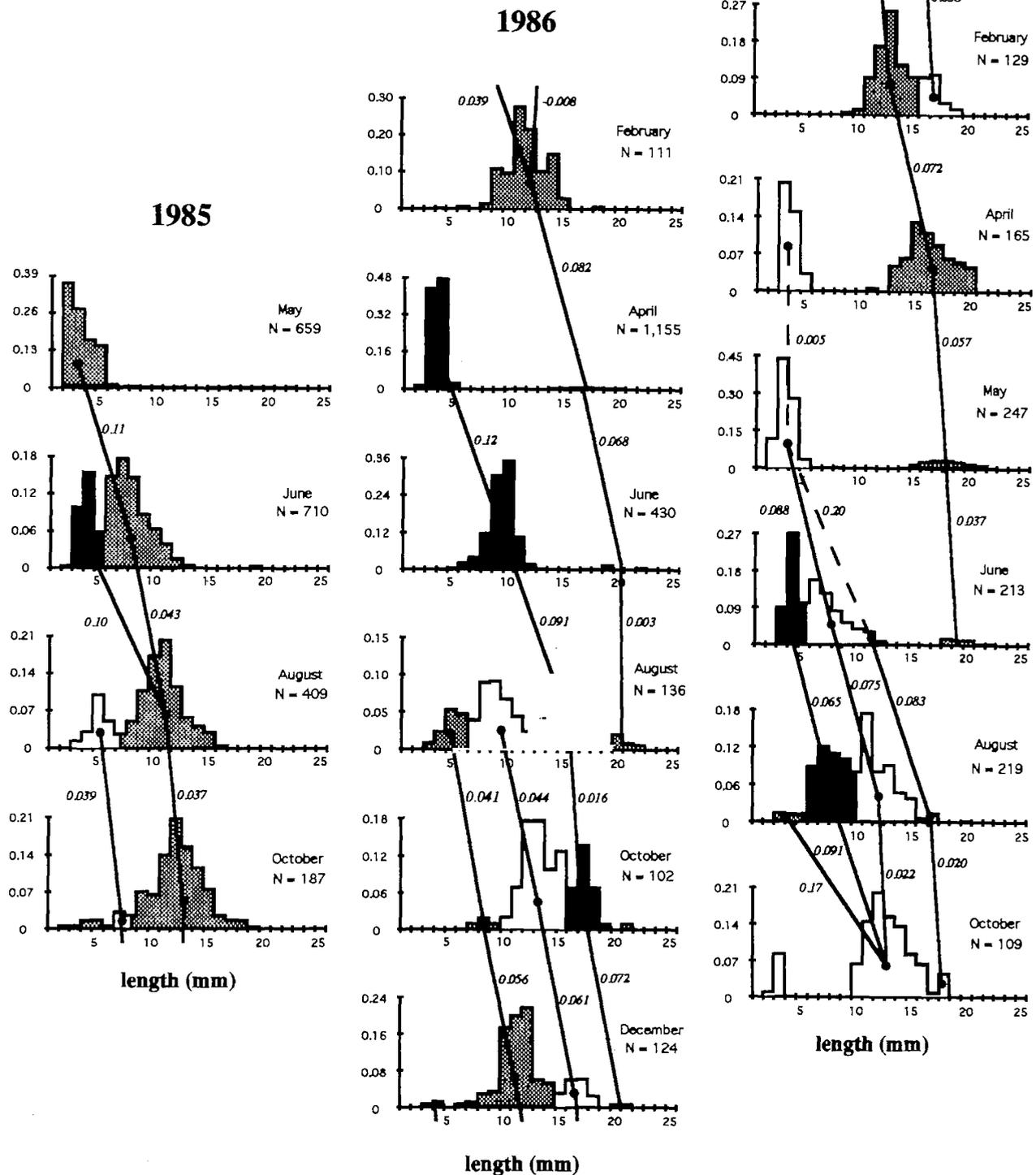


Fig. 3. *Euphausia pacifica*. Length-frequency distributions for each cruise to Dabob Bay. Duplicate nighttime hauls with the Tucker trawl from near bottom to surface summed for each cruise. Modes, determined as described in the text, are connected by lines to indicate modal progression between cruises. Numbers in italics next to

lines are estimates of individual growth rates ( $\text{mm d}^{-1}$ ). Continuous lines represent estimates of individual growth rates that are reasonable given previously reported rates; dashed lines indicate estimated rates that are more speculative. N: total no. of individuals measured for each histogram

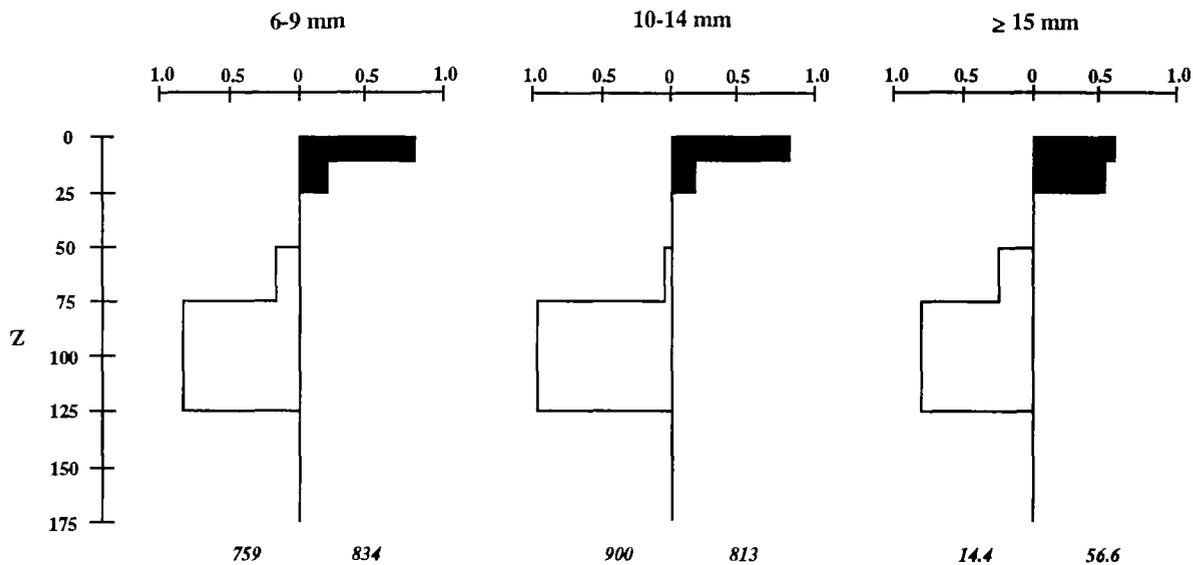


Fig. 4. *Euphausia pacifica*. Vertical distributions of different size classes in Dabob Bay on 5-6 June 1986. Similar distributions of these size classes observed on all other sampling dates. Open histograms are proportion of population in each stratum near noon; filled histograms are proportion of population in each stratum near

midnight. Proportions are means of duplicate samples collected with the multiple-sample Tucker trawl. Numbers in italics under each histogram is mean no. of ind.  $m^{-2}$ . Z: depth. In no case was there any significant difference between daytime and nighttime abundances ( $t$ -test,  $2N-2$  df,  $p > 0.05$ )

gust to October 1986). Zero or negative growth in this size class occurred briefly between October 1985 and February 1986 and again between December 1986 and January 1987.

#### Vertical distributions and diel migrations

Whereas all size classes of *Euphausia pacifica* were invariably concentrated in surface waters (0 to 25 m) at night, the daytime depth distributions and DVM behavior of *E. pacifica* varied between seasons, years and size classes of individuals. Adults and juveniles always exhibited DVM, residing at depth during the day (maximum concentrations ranging from 50 to 125 m) and ascending to the surface at night (e.g. Fig. 4). The subsurface daytime maxima and strong, seasonally invariant DVM behavior of these size classes were on all dates evident in hydroacoustic (105 kHz) observations made concurrently with the net sampling.

In contrast to the juveniles and adults, larval *Euphausia pacifica* exhibited highly variable DVM behavior (e.g. Fig. 5) as evidenced by large variations in daytime depths, with maximum concentrations ranging from the surface to 125 m. Thus, larvae appeared to be nonmigratory (residing in the surface both day and night) in May and June of 1985, but moderately or strongly migratory in August and October 1985, and in April 1986. In addition to DVM, *E. pacifica* exhibited an ontogenetic migration, as evidenced by the trend toward greater daytime depth with increasing size [i.e., larvae usually between 0 and 75 m (Fig. 5) and juveniles and adults between 50 and 125 m (Fig. 4)].

#### Discussion

In order to relate our results to previous findings, we review the existing literature on field studies of *Euphausia pacifica*, giving special emphasis to the large body of unpublished reports on this species in deep, inland basins of the northeast Pacific.

#### Recruitment and seasonal abundance patterns

Cooney (1971) sampled *Euphausia pacifica* at three locations in Puget Sound (Carr Inlet, Main Basin, and Port Susan; Fig. 1) and found a very similar recruitment pattern: 3 mm individuals (late furcilia) began to appear in April and were present in reduced numbers throughout August and into September. Hulsizer (1971) found larval *E. pacifica* present from April through August (peak abundance in June) in Port Susan, and from April to October (peak abundance in August) in Carr Inlet. These seasonal patterns of larval recruitment were attributed to overwintering adults spawning (probably iteroparitively) throughout spring and summer, with perhaps a small contribution of larvae coming from the maturation and reproduction of 0-yr (spring-hatched) adults by late summer.

Ross et al. (1982) found spawning of *Euphausia pacifica* in Port Susan to be most intense in April and May coincident with maximum phytoplankton abundance, and spawning continued at low levels well into summer. The absence of reproduction in the fall by 0-yr adults was attributed to food limitation preventing full maturation within the first year.

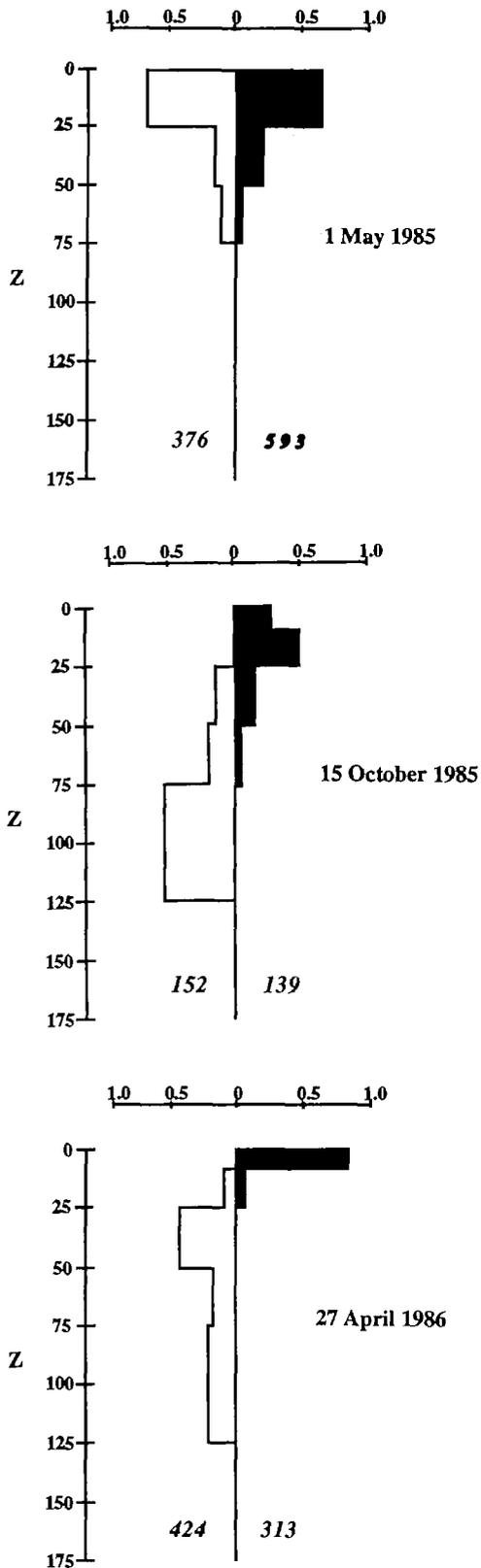


Fig. 5. *Euphausia pacifica*. Vertical distributions of larvae (2 to 5 mm size class) in Dabob Bay on different dates. Open histograms are proportion of population in each stratum near noon; filled histograms are proportion of population in each stratum near midnight. Proportions are means of duplicate samples collected with the multiple-sample vertical net. Number in italics under each histogram is mean no. of ind. m<sup>-2</sup>. Z: depth. In no case was there any significant difference between daytime and nighttime abundances ( $t$ -test,  $2N-2$  df,  $p > 0.05$ )

Heath (1977) studied the population biology of *Euphausia pacifica* in several different locations in the Strait of Georgia, British Columbia, Canada (Fig. 1) and found that spawning occurred from May to September (peak in May–June); spawning was closely related to phytoplankton availability. Recruitment of larvae usually peaked in summer, occurring ca. 1 mo after spawning, but considerable geographical variation existed in the timing of events. A distinct but less abundant fall cohort, appearing as 3 to 5 mm larvae in October, was usually present in low numbers, which the author attributed to spawning by 1-yr old rather than 0-aged adults.

Turning to offshore waters, Brinton (1976) showed that abundance of larval *Euphausia pacifica* off southern California peaked during May to August, apparently in response to upwelling and increased phytoplankton availability; however, some larvae were present all year round. Similarly, Smiles and Percy (1971) found peak abundances of furcilia larvae of *E. pacifica* off the Oregon coast to occur between August and December, presumably in response to summer upwelling and phytoplankton availability. But as was the case off southern California, Smiles and Percy (1971) found larvae present throughout the year. The common occurrence of abundant larvae off Oregon as late as December suggests that spawning may be occurring well after peaks in phytoplankton availability. Perhaps protozoan and/or metazoan microplankton, which might be expected to occur later in the upwelling season, are providing significant nourishment for pre-spawning adult *E. pacifica*.

The large springtime pulses of larval euphausiids in our samples suggest spawning of adults must have occurred a few to several weeks earlier, i.e., predominantly during early spring. Why is the period of (inferred) spawning of *Euphausia pacifica* in Dabob Bay compressed largely within a single season? Several alternative explanations can be offered. As mentioned above, the correlation between spawning of *E. pacifica* and phytoplankton blooms has been well documented for oceanic populations (Smiles and Percy 1971, Brinton 1976) and for populations in inland waters (Heath 1977, Ross et al. 1982). Given that Dabob Bay exhibits a regular and sizeable spring phytoplankton bloom (Fig. 6), the annual peak in (inferred) spawning of *E. pacifica* in the bay at this time may be a response to phytoplankton availability. However, Dabob Bay also exhibits a regular and conspicuous autumn bloom (Fig. 6). Do adult *E. pacifica* respond to the autumn bloom by reproducing, and why are there relatively few larvae present in later autumn and early winter (Fig. 3: October 1985, December 1986, and October 1987)? Food quality as well as quantity should be considered, as feeding in *E. pacifica* has been shown to be sensitive to the type of phytoplankton available (Parsons et al. 1967), and thus chlorophyll *a* may not be an adequate measure of food availability (Hulsizer 1971).

The reduced level of (inferred) spawning in the summer (Fig. 3: August 1985, August 1986, and August 1987) relative to spring is perhaps less perplexing given that phytoplankton abundance is much reduced in Dabob Bay at this time (Fig. 6). A question arises as to the nutritive source of this reproduction. *Euphausia pacifica* has

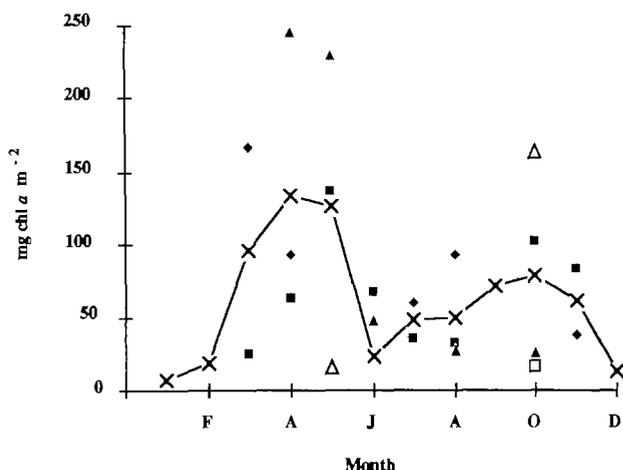


Fig. 6. Mean annual cycle of abundance of chlorophyll *a* (integrated from 30 m to surface) at the central, deep station in Dabob Bay (from Bollens et al. in press). (■) 1979, (□) 1981, (◆) 1982, (◇) 1983, (▲) 1985, (△) 1986, (×) mean

been shown to be omnivorous in the laboratory (Ohman 1984), and thus the potential for protozoan and metazoan microzooplankton, which might be expected to be particularly abundant during summer in coastal waters (e.g. Chester 1978), to significantly contribute to the diet and thus reproductive capabilities of *E. pacifica* in the field warrants further attention. If phytoplankton is the nutritive source of spawning, why is there apparently no spawning in winter (Fig. 3: February 1986, January, February and March 1987) when phytoplankton abundance is typically at levels only slightly lower than those in summer (Fig. 6)? Winter reproduction in Dabob Bay may simply be precluded by temperatures (8 °C) that are outside the spawning range for *E. pacifica* (Brinton 1976, Heath 1977), but the occurrence of reproductively active adults at even lower temperatures in the northwest Pacific (e.g. Terazaki et al. 1986) would argue against the interpretation.

As an alternative explanation for the reduced level of (inferred) spawning in Dabob Bay in summer and autumn relative to spring, the stage/age structure of the population, as dictated by predation, may be limiting spawning. As suggested by Ross et al. (1982) for Port Susan, as overwintered adults are removed from the population by predation throughout spring and summer, there remain few sexually mature 1-yr adults to spawn in late summer, and only a very small number of 0-aged adults (born in spring of that year) are able to mature fast enough, perhaps due to food-limitation in late summer/autumn, to spawn in their first year. However, in the case of Dabob Bay, 0-aged adults large enough to reproduce (12 to 18 mm) are relatively abundant by August of each year (Fig. 3). If these euphausiids spawn at this time, seasonal differences in intensity of predation on eggs and larvae might explain the low numbers of larvae present during summer and autumn. Indeed, both the carnivorous copepod *Euchaeta elongata* (Yen 1982) and the chaetognath *Sagitta elegans* (Ohman 1983) reach their annual peaks in abundance at this time, and cannibalism

is another potentially important source of mortality for eggs and larvae. The relative importance of food-limitation and predation as causes of the restricted period of larval production and recruitment in *Euphausia pacifica* in Dabob Bay need to be more fully investigated.

Turning briefly from seasonal patterns to estimates of absolute abundance, our peak abundances (water column totals) of larvae of 21 m<sup>-3</sup> in 1985, 25 m<sup>-3</sup> in 1986, and 6 m<sup>-3</sup> in 1987 are generally very high compared to those previously reported in the literature for offshore environments but are comparable to those reported by Heath (1977) for nearby Saanich Inlet, British Columbia, Canada (Fig. 1). For example, Smiles and Percy (1971) obtained average abundances of furciliae of 0.22 m<sup>-3</sup> off Oregon, and as many as 2.7 m<sup>-3</sup> at one station in November. Brinton (1976) found between 5 and 10 larvae m<sup>-3</sup>, and as many as 18 larvae m<sup>-3</sup>, during periods of maximum recruitment off southern California. Youngbluth (1976) reported occasional abundances of larvae in the central California Current of as many as 10 m<sup>-3</sup>, but these were almost always in specific depth strata rather than average values for the water column. In contrast, Heath (1977) found a maximum density of 25 m<sup>-3</sup> for larvae in Saanich Inlet in late June for the water column as a whole, and an order of magnitude higher densities in near-surface waters (0 to 12 m). The greater abundances of larvae in fjords such as Saanich Inlet and Dabob Bay could be due to physical maintenance of patches [i.e., reduced mixing and eddy diffusion; see, for example, Frost (1988) and references therein] and to generally high levels of primary production in these areas [Harrison et al. (1983) and references therein, Downs (1989)].

## Growth

Several previous studies have estimated individual growth rates of *Euphausia pacifica* using modal progression analysis. In offshore environments, Smiles and Percy (1971) obtained growth rates of 0.065 mm d<sup>-1</sup> for the entire life span of *E. pacifica* (and reaching as high as 0.095 mm d<sup>-1</sup> for juveniles), which is ca. twice that reported by Nemoto (1957) and Ponomareva (1963). Brinton (1976) found growth rates similar to those of Smiles and Percy (1971). Fulton and LeBrasseur (1984) reported growth rates of *E. pacifica* from British Columbia coastal waters of 0.05 and 0.08 mm d<sup>-1</sup> between January and April.

Considering deep, inland basins of the northeast Pacific, Heath (1977) found growth of *Euphausia pacifica* in the Strait of Georgia to be maximal during summer of the first year of life at 0.094 mm d<sup>-1</sup>, subsequently slowing during autumn and halting altogether in winter; average growth for the entire life span was 0.038 mm d<sup>-1</sup>. Similarly, Cooney (1971) found that growth of *E. pacifica* in the ≥ 10 mm size class from different regions of Puget Sound was not apparent between October and February, but reached 0.05 to 0.08 mm d<sup>-1</sup> between March and June; growth of the newly recruited size class (< 10 mm) was slightly higher, being 0.08 to 0.09 mm d<sup>-1</sup> between April and August.

Hulsizer (1971) found growth rates of *Euphausia pacifica* in Carr Inlet of  $0.075 \text{ mm d}^{-1}$  between February and June for 1-yr (7 to 24 mm) individuals and  $0.095 \text{ mm d}^{-1}$  between April and August for 0-aged (3 to 19 mm) individuals, whereas *E. pacifica* in Port Susan grew more slowly at rates of  $0.042 \text{ mm d}^{-1}$  from February to August for 1-yr old (8 to 22 mm) individuals and  $0.066 \text{ mm d}^{-1}$  from April to August for 0-aged (3 to 17 mm) individuals. Winter (October to February) growth was negligible ( $0.001$  to  $0.004 \text{ mm d}^{-1}$ ) at both locations.

These rates are within the range we report for *Euphausia pacifica* in Dabob Bay, although our estimates of summertime growth of larval cohorts and wintertime growth in some adult cohorts are among the highest reported for this species in the field. The extended period of growth including summer and autumn for all stage (age) classes contrasts sharply with the restricted period of spawning and larval recruitment in Dabob Bay. This again raises a question as to the nutritive source for growth later in the year, and we suggest that the importance of omnivory to diet and growth of *E. pacifica* would be a fertile area for future investigation.

Finally, we offer a warning. As has been pointed out elsewhere (e.g. Ricker 1969, Brinton 1976), results of modal progression analyses of field data can be biased by selectivity of sampling gear and by size-specific differences in growth and mortality. For example, the "piling-up" of modes (Brinton 1976, Heath 1977) of juveniles and adolescents later in the growing season (e.g. June to August 1985 and August to October 1987 in our data) can make interpretation difficult. This could reflect real differences in size-specific growth rates (e.g. higher rates for smaller individuals), or this could be due to increased mortality (such as from size-selective predation from planktivorous fish) or greater avoidance of the sampling gear by larger euphausiids, which would in turn lead to underestimation of growth rates of these larger individuals. In a similar manner selective mortality on smaller size classes of euphausiids could lead to overestimates of individual growth rates. Additionally, iteroparous spawning within a single season, such as is known to occur in *Euphausia pacifica* (e.g. Ross et al. 1982), can potentially generate broad peaks in apparent spawning which can in turn reduce the resolution with which individual spawning events and cohorts can be identified and tracked. Sampling variability is yet another potentially confounding effect. These limitations should be kept in mind when comparing growth rates determined by modal progression analyses. Finally, while all of the above authors used modal progression analysis to estimate growth rates, none explicitly discussed assumptions and tests for modality of length-frequency distributions, further complicating the comparison of estimated rates.

#### Vertical distributions and diel migrations

DVM in *Euphausia pacifica* is well documented in oceanic waters, where adults typically reside between 100 and 500 m during the day, and enter the surface 50 to 100 m at night (Esterly 1914, Boden 1950 b, Brinton 1962a, b, 1967, Alton and Blackburn 1972, Frost and McCrone

1974, Marlowe and Miller 1975, Youngbluth 1976). An exception to this pattern is reported by Ponomareva (1963), who claims (i.e., no data presented) that by winter of their second year adults in the Bering Sea remain between 200 and 500 m day and night.

Larvae, and to a lesser degree juveniles, show greater variability in their vertical distributions. For instance, Brinton (1967) sampled *Euphausia pacifica* in January–February in the California Current at both inshore and midshelf stations and found larvae at the midshelf station to be weakly migratory (0 to 200 m during the day; 0 to 100 m at night), but nonmigratory (upper 100 m both day and night) at the inshore station. Youngbluth (1976) found larval and juvenile *E. pacifica* to exhibit ontogenetically and geographically variable DVM during summer in the central California Current; both the amplitude of migration (vertical distance traveled) and proportion of the population migrating increased with developmental stage (age) and distance from shore. Terazaki et al. (1986) sampled *E. pacifica* in the spring at a shallow (80 m) station off northeastern Japan and found adults to perform DVM, being distributed below 30 m during the day and between 5 and 30 m at night; larvae (furcilia stages) exhibited very weak or nonexistent DVM, being more evenly distributed in the surface 50 m both day and night.

Several authors have reported on the daytime surface swarming of *Euphausia pacifica* in shallow coastal waters off northern Japan (Komaki 1967 and references therein, Terazaki 1980, Endo 1984, Hanamura et al. 1984). In these cases, larger (> ca. 12 mm) individuals, usually sexually mature adults, occurred in exceptionally high densities (several  $\text{liter}^{-1}$ ) in the surface 1 to 10 m of the water column.

The vertical distributions and diel migrations of *Euphausia pacifica* in deep, inland basins of the northeast Pacific Ocean have been reported by several investigators. Cooney (1971) found *E. pacifica* in Puget Sound occurring during the day chiefly in a diffuse sound scattering layer between 50 and 100 m. Sampling in Port Susan in July, Cooney (1971) found spatial segregation of size classes within the layer, with smaller euphausiids (3 to 6 mm) occurring in the upper portion (45 to 55 m) and larger ones occurring progressively deeper, the largest (15 to 20 mm) occurring almost exclusively in the bottom-most portion (65 to 70 m) of the scattering layer. Hovekamp (1989) examined the vertical distribution of *E. pacifica* in Dabob Bay and found them occurring between 50 and 125 m during the day and 0 and 75 m during the night.

Bary (1966) documented strong DVM of euphausiids ("almost only *Euphausia pacifica*", p. 656) in January and May in Saanich Inlet between 70 and 130 m in the day and 0 and 40 m at night. Greenlaw (1979) used a multi-frequency (79 to 169 kHz) hydroacoustic system to study *E. pacifica* in Saanich Inlet, and found their vertical distribution to be 80 to 130 m during the daytime while they were spread throughout the water column at night, with only the larger euphausiids migrating to the surface, and the smaller ones remaining at depth; these observations were not, however, confirmed by sampling with nets.

Our data on the vertical distribution of *Euphausia pacifica* in Dabob Bay indicate that juvenile and adult stages of *E. pacifica* experience considerable shoaling in their daytime distribution from what is usual in deeper, oceanic waters (i.e., 50 to 100 m vs 200 to 500 m). These observations are in general agreement with previous reports of this species in inland basins of the northeast Pacific. Our observations are notably different, however, from several accounts from Japanese waters in that our data show no indication of daytime surface swarming.

Although geographic variability in the DVM behavior of larval *Euphausia pacifica* has been reported previously, our study is the first report of seasonal and interannual variability of DVM behavior by larvae. This variability is remarkably similar to that of the planktonic copepod *Calanus pacificus* studied over the same time period and location by Bollens and Frost (1989 a). Bollens and Frost (1989 a) showed the strength of DVM (measured as the proportion of the population migrating) in adult female *C. pacificus* to be significantly correlated with the abundance of actively feeding zooplanktivorous fish, and suggested that the variability of migration behavior was related to the seasonal cycle of recruitment of fish in the bay, i.e., migration behavior was weak or nonexistent during seasons (e.g. spring) and years (e.g. 1985) when newly recruited predators were low in abundance. Larval *E. pacifica* are of similar size to adult *C. pacificus* (ca. 3 mm prosome length) and in Dabob Bay are preyed upon by virtually the same suite of planktivorous fish. Thirteen species of zooplanktivorous fish in Dabob Bay were analyzed for presence or absence of larval *E. pacifica* in the diet [see Bollens and Frost (1989 a) for details] and the following seven species were found to be predators: Pacific sandlance, *Ammodytes hexapterus*; Pacific herring, *Clupea harengus pallasii*; threespine stickleback, *Gasterosteus aculeatus*; Pacific hake, *Merluccius productus*; chum salmon, *Oncorhynchus keta*; chinook salmon, *Oncorhynchus tshawytscha*; and plainfin midshipman, *Porichthys notatus* [see Table 2 in Bollens and Frost (1989 a) for a similar list of predators on *C. pacificus*].

We therefore hypothesize that the shift in migration behavior in larval *Euphausia pacifica* from nonmigratory in spring of 1985 to migratory in summer and autumn of 1985, as well as the interannual variability in springtime migration behavior (1985 vs 1986), may, like that proposed for adult female *Calanus pacificus*, be a response to vertebrate predators. Recent experimental field manipulations have shown that the marine planktonic copepod *Acartia hudsonica* can exercise rapid changes in DVM behavior depending on the presence or absence of planktivorous fish (Bollens and Frost 1989 b, 1991), and similar results have been found for several freshwater zooplankters (Dawidowicz et al. 1990, Leibold 1990, Neill 1990, Tjossem 1990, Ringelberg 1991). However, the degree to which larval *E. pacifica* can exercise such flexibility in migration behavior in response to predators remains to be tested experimentally.

Our observations of seasonal patterns of recruitment, abundance, growth and DVM behavior in *Euphausia pacifica* in Dabob Bay, combined with those in the literature from other locales, lead us to make the following

conclusions and recommendations for future work. First, the relative importance of food-limitation and predation as causes of the restricted period of larval production (spring) and juvenile and adult recruitment (summer and autumn) of *E. pacifica* in Dabob Bay need to be more fully investigated. Second, the occurrence of extended periods of high rates of individual growth of *E. pacifica* in Dabob Bay, which are among the highest ever reported for this species in the field, suggests a potentially important role for omnivory during periods of low phytoplankton abundance (e.g. summer). Third, the variable DVM behavior of larval *E. pacifica*, which contrasts sharply with the strong, invariant DVM behavior of juveniles and adults, is hypothesized to be a response to variable abundances of zooplanktivorous fish, and should be tested experimentally.

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