

## NOTES

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### Zooplanktivorous fish and variable diel vertical migration in the marine planktonic copepod *Calanus pacificus*

**Abstract**—As a field test of the hypothesis that variable diel vertical migration in zooplankton is a response to variations in the abundance of visually orienting predators, we sampled juvenile and adult planktivorous fish inhabiting a temperate fjord (Dabob Bay, Washington) concurrently with the vertical distributions of a population of adult female *Calanus pacificus* (Copepoda: Calanoida) known to exhibit seasonally variable diel vertical migration. Results of nighttime trawling on seven dates between April 1985 and October 1986 and subsequent stomach content analyses showed that eight species of fish, comprising 45 different size classes, fed on adult female *C. pacificus*; all species of fish showed marked seasonal and interannual variations in their abundances. The extent to which the population of *C. pacificus* exhibited diel vertical migration was determined for each cruise date by calculating the proportion of the population crossing 75-m depth on a diel cycle. A statistically significant regression was obtained between strength of diel vertical migration in *C. pacificus* and abundance of fish actively preying on the copepod. We propose that the timing and magnitude of changes in the migration behavior of *C. pacificus* in Dabob Bay are directly linked to the year-class strengths of the dominant species of planktivorous fish.

Observations of diel vertical migration have been well documented for aquatic organisms in diverse phyla. These observa-

tions have generated much debate over the proximate and ultimate causes of vertical migration behavior, with several hypotheses being proposed to explain its possible adaptive significance (*see* Kerfoot 1985 for a recent review). Predation from visual predators is perhaps the most often hypothesized selective pressure responsible for the evolution of vertical migration in zooplankton (Zaret and Suffern 1976; Pearre 1979; Kerfoot 1985; Gliwicz 1986*a*; Lampert 1987; Frost 1988). Previous studies supporting the predation hypothesis can be divided into two general categories: theoretical arguments based on demographic and energetic models showing that only through reduced mortality from avoidance of predators can vertical migration confer an advantage in population growth to diel migrants (Stich and Lampert 1981; Ohman et al. 1983; Lampert 1987; Frost 1988), and field studies purporting to show a relationship between the presence or abundance of predators and the extent to which vertical migration is exhibited by planktonic prey (Kozhov 1963; Zaret and Suffern 1976; Williamson and Magnien 1982; Fancett and Kimmerer 1985; Gliwicz 1986*a,b*; Luecke 1986).

The first approach has placed theoretical limits on adaptive significance of migration behavior, while at the same time providing a specific hypothesis for further testing. The second approach, attempting to provide direct field evidence linking prey behavior with the presence or abundance of predators, has provided much circumstantial support for the predation hypothesis but has often suffered from ambiguous results due to the use of widely separated field sites (e.g. the comparative lake studies of Zaret and Suffern 1976 and Gliwicz 1986*a*), that thereby allow variable environmental factors to

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obfuscate the role of predation. In addition, the use of nonquantitative techniques for assessing predators and their feeding habits has too often left open the question of direct linkage between predator and prey (e.g. Kozhov 1963; Williamson and Magnien 1982; Fancett and Kimmerer 1985; Gliwicz 1986a).

In short, although predator avoidance is the most commonly proposed explanation for the adaptive significance of diel vertical migration, field evidence lags behind the theoretical arguments. What is needed is a time series of concurrent, quantitative observations of predator abundances and prey migration under variable conditions of vertical migration behavior of the prey. Therefore, the most judicious choice for a field test would be a single prey species that exhibits variable diel vertical migration and would include the measurement, over time, of all environmental parameters (both physical and biological) hypothesized to affect migration behavior.

The marine planktonic copepod *Calanus pacificus* has been shown to exhibit seasonal and intergenerational variability in diel vertical migration off southern California (Enright and Honegger 1977; Koslow and Ota 1981; Huntley and Brooks 1982) and both seasonal and interannual variability in Dabob Bay, Puget Sound, Washington (Runge 1981; Frost 1988). Frost (1988) has shown that this variation in Dabob Bay is unrelated to those environmental factors previously proposed to provide an energetic or mortality-independent demographic advantage to diel migrants (namely, food availability, in situ growth rate of females, and thermal stratification of the water column). These results led him to hypothesize that diel vertical migration in adult females of *C. pacificus* is a response to visually orienting zooplanktivores, most likely planktivorous fish. Planktonic invertebrate predators were eliminated from consideration because all the species potentially preying on adult *C. pacificus* in Dabob Bay are non-visual predators, most forage nocturnally, and many are diel vertical migrators themselves (Frost unpubl.). In this note we present results of an 18-month field study, undertaken concurrently with the study of Frost

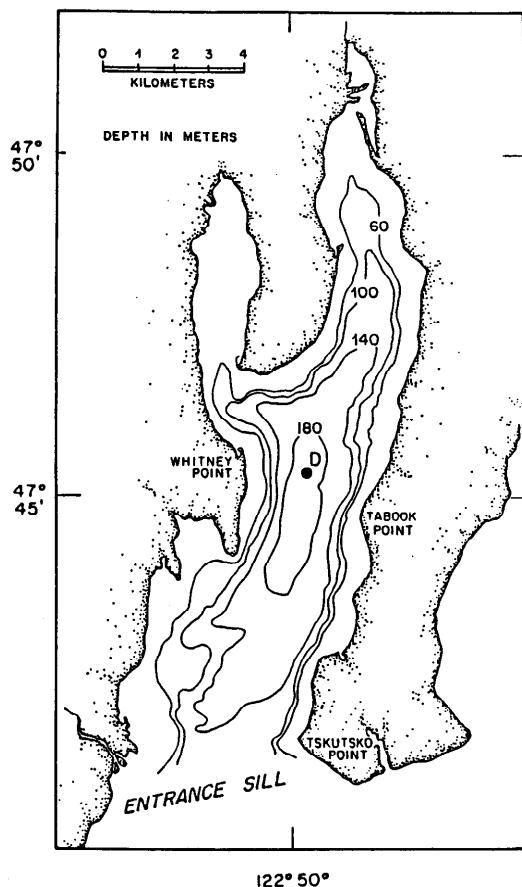


Fig. 1. Bathymetry of Dabob Bay and the location of the central, deep station (D—193 m).

(1988), assessing the abundances and feeding habits of potential predators of *C. pacificus*. Our purpose was threefold: to quantitatively estimate the abundance of planktivorous fish between seasons and between years; to identify, from stomach contents, those fish actively feeding on adult female *C. pacificus*; and to relate the abundance of actively feeding predators to diel vertical migration behavior in adult female *C. pacificus*.

Dabob Bay (Fig. 1) was chosen as the site of our study because its circulation regime is favorable to repeated sampling of populations of planktonic organisms (Frost 1988 and references therein). Abundances of planktivorous fishes and the vertical distribution of adult female *C. pacificus* were determined at a central, deep (193 m) station during June, August, and October 1985 and

late April–early May, June, August, and October 1986. Additionally, zooplankton, but not planktivorous fish, were sampled in late April 1985.

Two trawl types were deployed on each cruise to sample juvenile and adult planktivorous fishes. Qualitative hydroacoustic observations (105 kHz) with upward- and downward-looking transducers indicated that some fish vertically migrated, typically descending during the day to the very bottom (i.e. well below the distribution of *Calanus*)—a depth which effectively precludes these fish from preying on *Calanus* during the day. Other fish remained in the surface layer both day and night; our daytime trawling, however, yielded no catches, due no doubt to the well-known daytime avoidance capabilities of pelagic fish. Thus, we trawled only at night and assume that nighttime abundances are indicative of potential predators of *Calanus* in the surface layer throughout the day. A midwater trawl with mouth area of 81.0 m<sup>2</sup> (9.0 × 9.0 m) and stretch-mesh size ranging from 8.9 cm nearest the mouth to 1.3 cm in the cod end was used to sample from 50 m to the surface and, less frequently, from 25 m to the surface. The depth of the net was monitored with a bathygraph. The mouth of the net was kept open by two 230-kg doors rigged to the bridles. Tow speed averaged 150 cm s<sup>-1</sup> (range: 120–180 cm s<sup>-1</sup>) and volumes filtered, calculated from mouth area and length of tow, ranged from 115,000 to 449,000 m<sup>3</sup>.

A surface tow net with mouth area of 18.3 m<sup>2</sup> (3.0 × 6.1 m) and mesh size grading from 8.9 cm nearest the mouth to 0.6 cm at the cod end was used to sample the surface 3 m. Two pipes with floats at the top and weights at the bottom were attached to the sides of the net to keep the mouth vertical. The surface tow net was kept fully open by deployment between two boats (the 20-m RV *Clifford A. Barnes* and a 5-m Boston Whaler). Average tow speed was 80 cm s<sup>-1</sup> (range 50–100 cm s<sup>-1</sup>) and volumes filtered ranged from 7,300 to 31,700 m<sup>3</sup>. Two or three tows were taken with each net on each cruise.

Catches were immediately removed from the cod end, and all fish were identified to

species (except salmonids) then counted, weighed, and measured for length (fork length for those fish possessing forked tails and standard length for all other species). Lengths were measured to the nearest 1 cm for fish >5 cm, and to the nearest 0.5 cm for fish <5 cm. *Squalus acanthias* (spiny dogfish) and *Porichthys notatus* (plainfin midshipman) were counted and weighed but not measured for length. Gut cavities of all salmonids (*Oncorhynchus* spp.) were injected with a small volume of Formalin (0.5–3.0 ml) to halt digestion; salmonids were then preserved in 10% buffered seawater Formalin for species identification and measurement (fork length to the nearest millimeter) in the laboratory. Of the remaining nonsalmonid fishes, 10–20 individuals were selected from predetermined size classes (see below) for each species and injected and preserved with Formalin. The total time between bringing the catch aboard and preservation of the fish and their stomach contents was usually ~10 min, but never >20.

Abundance estimates for each trawl type were calculated by averaging the number of fish per unit of volume for the two to three tows of each gear type. Because capture efficiencies are assumed to be 100% for both trawl types, abundance estimates are conservative. Estimates of the number of fish per unit of volume of near-surface water (50 m to surface) were calculated with a weighted average of the mean abundance estimates of the two gear types, assuming that the surface tow net sampled from 3 m to the surface and that the midwater trawl sampled from 50 m to 3. This latter assumption is based on the fact that no fish were caught in independent surface tows (3 m to surface) with the midwater trawl, due presumably to the disturbance of surface waters by the vessel.

Each species of fish was divided into the following size classes for stomach content analyses: ≤49, 50–99, 100–149, ≥150 mm. Salmonids were further divided into 50–74 and 75–99 mm. The choice of size classes was sometimes based on a previously observed change of diet with size (e.g. the switching from epibenthic to neritic prey at ~50 mm in pink and chum salmon, as shown by Okada and Taniguchi 1971 and

Table 1. Abundances of planktivorous fish [No.(10<sup>4</sup> m<sup>3</sup>)<sup>-1</sup>] in near-surface water (50–0 m) at the central station in Dabob Bay. Estimates are a weighted average of the two trawl types.

Planktivorous fish	1985			1986			
	Jun	Aug	Oct	Apr/May	Jun	Aug	Oct
<i>Ammodytes hexapterus</i> (Pacific sandlance)				10.6	0.001	0.02	
<i>Clupea harengus pallasii</i> (Pacific herring)		0.71	0.41	0.21	0.31	0.11	9.82
<i>Engraulis mordax</i> (northern anchovy)				0.014		0.035	
<i>Gasterosteus aculeatus</i> (threespine stickleback)	0.036	0.76	0.023	0.19	0.052	1.58	2.32
<i>Merluccius productus</i> (Pacific hake)	1.53	4.36	1.6	0.54	1.88	13.4	5.35
<i>Microgadus proximus</i> (Pacific tomcod)							0.009
<i>Oncorhynchus gorbusha</i> (pink salmon)				0.057			
<i>Oncorhynchus keta</i> (chum salmon)	1.23	0.83	0.093	1.91	3.66	0.51	0.18
<i>Oncorhynchus kisutch</i> (coho salmon)	0.022				0.91		
<i>Oncorhynchus tshawytscha</i> (chinook salmon)	0.086	0.067			0.11	2.23	0.14
<i>Porichthys notatus</i> (plainfin midshipman)		0.158	0.158	0.24	0.18	0.66	0.20
<i>Psychrolutes paradoxus</i> (tadpole sculpin)				0.04			
Unidentified embiotocid (surfperch)						0.023	
Unidentified osmerid (smelt)							0.019
Unidentified salmonid						0.023	0.018
Total	3.01	6.89	2.29	13.8	7.12	18.6	18.1

Simenstad et al. 1980) and at other times was based on the need for keeping the total number of fish stomachs analyzed to a reasonable number given limited resources. For each cruise date, 5–14 individuals (when available) were selected from each size class of each species of fish for microscopic examination of stomach contents. The stomach from the esophagus to just posterior to the pylorus was dissected from each fish. Prey organisms were sorted, identified, and enumerated under a dissecting microscope.

Prey were identified to the lowest possible taxon (usually species) and developmental stage allowed by the state of digestion. In the case of *C. pacificus*, the later copepodid stages and the sex of the adults were almost always identifiable. The actual number of stomachs analyzed from any one size class and species depended on a somewhat subjective assessment of the interstomach variability of contents at the time of dissection. When abundance and composition of prey types were relatively consistent among stomachs, only five individual stomachs from that size class were analyzed; when variability was greater or abundance lower, a many as 14 stomachs were analyzed from each size class. For the purposes of this paper, we report only on the presence or absence of adult female *C. pacificus* in the stomach contents.

Sampling and sample analysis for the ver-

tical distribution and abundance of adult female *C. pacificus* are described elsewhere (Frost 1988).

A combined total of 4,225 fish representing 14 species were caught during the seven cruises to Dabob Bay. Spiny dogfish (*S. acanthias*) was discounted as a potential predator of *C. pacificus* based on a review of the literature (Hart 1973 and references therein) and is not included in the catch results. Our catch results show the abundance of planktivorous fish in Dabob Bay to vary seasonally, both for individual species and total fish (Table 1). The seasonal occurrence of various size classes of the different species in our catches corresponds well with published (e.g. Hart 1973; Miller and Borton 1980; Garrison and Miller 1982) and unpublished (Bollens et al. in prep.) accounts of the life histories of these fishes in the neritic northeast Pacific.

Considering seasonal variations in abundance of total fish in 1985, the most striking feature was the twofold to threefold greater abundance in August as compared to either June or October. This was due largely to the much greater numbers of *Merluccius productus* in August. Having hatched as larvae in late winter and early spring (Bailey and Yen 1983; Bollens et al. in prep.), this species had by August attained a size great enough to be retained by our nets (30–60 mm). Similarly, *Clupea harengus pallasii* and *Gaster-*

*osteus aculeatus* reached their highest abundances in our catches in August, due largely to young-of-the-year fish available to our nets on this cruise. Juvenile salmonids (*Oncorhynchus* spp.), although present on all three cruises in 1985, were most abundant during June and August, a time during which these species are known to migrate through Puget Sound on their way to oceanic waters (Simenstad et al. 1982).

Striking seasonal variations in the abundance of individual species and total planktivorous fish were observed in 1986 as well. In late April–early May, juvenile *Ammodytes hexapterus* was overwhelmingly dominant in our catches. This species spawns early in winter (Trumble 1973) and would therefore be expected to produce young-of-the-year that are available to our nets at an earlier date (i.e. spring) than the other species of planktivorous fish in Dabob Bay, most of which spawn in late winter–early spring (Bollens et al. in prep.). In June, abundances were relatively low for all species, except larger juveniles of *M. productus* (age-I and age-II) and juvenile salmonids (especially *Oncorhynchus keta*). The very much reduced catches of *A. hexapterus* in June and later were likely due to initiation of demersal behavior in the young-of-the-year juveniles (Reay 1970 and references therein; but see Macer 1966), thereby greatly reducing susceptibility to capture by our sampling gear. The highest abundance of total planktivorous fish in 1986 was obtained in August, when young-of-the-year *M. productus* and *G. aculeatus* were extremely abundant in our catches. Juvenile salmonids, especially *Oncorhynchus tshawytscha*, were also abundant during August. Total abundance of fishes remained high in October, when young-of-the-year *C. harengus pallasi*, *M. productus*, and *G. aculeatus* were all abundant.

In comparing years, the seven dominant species in our catches (*A. hexapterus*, *C. harengus pallasi*, *G. aculeatus*, *M. productus*, *O. keta*, *Oncorhynchus kisutch*, and *O. tshawytscha*) were all more abundant in 1986 than 1985, due mostly to larger numbers of young-of-the-year fishes in 1986. Furthermore, *C. harengus pallasi*, *G. aculeatus*, and *M. productus* young-of-the-year juveniles

remained abundant during October 1986, in stark contrast to the very small catches we obtained in October 1985. Interannual differences in the abundances of *A. hexapterus* are more difficult to assess given that this species seems to be available to our sampling gear (upper 50 m of the water column at night) only in the relatively early stages of its life history, corresponding to a season (spring) when we sampled with trawls in 1986, but not in 1985. Results from ichthyoplankton surveys, however, showed larval *A. hexapterus* to be present in spring 1986 but absent during 1985 (Bollens et al. in prep.). Additionally, juvenile (young-of-the-year) and adult *A. hexapterus* were caught in our trawls in June and August 1986, whereas no *A. hexapterus* individuals were caught in summer or fall 1985. These observations suggest that had we trawled for juvenile and adult fishes in May 1985, abundances of young-of-the-year *A. hexapterus* would have been lower than we observed in May 1986, i.e. the 1986 year-class of *A. hexapterus* was probably larger than the 1985 year-class.

A total of 396 fish (comprising 13 species) collected at the central station during the seven cruises in 1985 and 1986 were analyzed for stomach contents. Data on presence or absence of adult female *C. pacificus* were the basis for determining which planktivorous fishes actively preyed on *C. pacificus* on any single cruise date. Eight species comprising 45 different size classes were found to have adult female *C. pacificus* in their stomachs. On any one cruise date, a minimum of five and a maximum of 10 species/size classes were found to be feeding on *C. pacificus*. The seasonal and interannual variability is striking (Table 2).

We quantified the degree to which the population of *C. pacificus* undertakes a normal diel vertical migration (up at night, down during the day), or the "strength" of migration behavior (herein denoted as  $V$ ), by calculating the difference between the fraction of the population above a given depth at midnight and the fraction of the population above that same depth during midday. This parameter is then a measure of the fraction of the population migrating across a particular depth on a diel cycle.

Table 2. Abundances of planktivorous fish [No.(10<sup>4</sup> m<sup>3</sup>)<sup>-1</sup>] found to prey on adult female *Calanus pacificus* in near-surface water (50–0 m) at the central station in Dabob Bay. Estimates are a weighted average of the two trawl types.

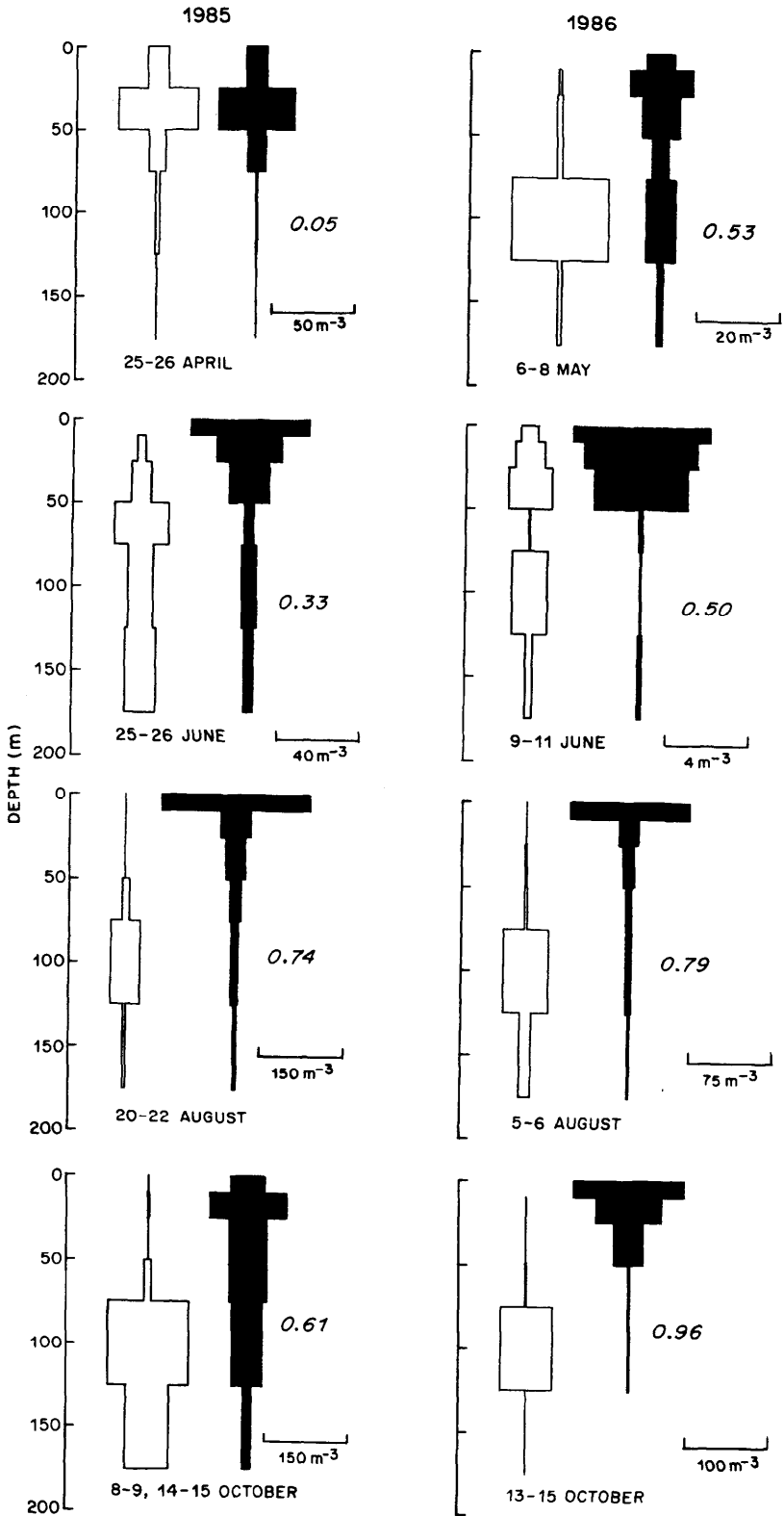
Planktivorous fish	1985			1986			
	Jun	Aug	Oct	May	Jun	Aug	Oct
<i>Ammodytes hexapterus</i>							
50–99 mm				10.6			
<i>Clupea harengus pallasii</i>							
50–99 mm		0.61	0.29		0.08	5.03	
100–149 mm		0.07	0.05	0.19			4.53
≥ 150 mm		0.04	0.07			0.02	0.25
<i>Engraulis mordax</i>							
100–149 mm						0.04	
<i>Gasterosteus aculeatus</i>							
50–99 mm	0.04	0.04				0.82	2.07
<i>Merluccius productus</i>							
≤ 49 mm	0.04	2.69				3.44	
50–99 mm	0.04	0.69				7.37	2.28
100–149 mm							
≥ 150 mm	1.38	0.99	1.21				
<i>Oncorhynchus keta</i>							
≤ 49 mm				0.20			
50–74 mm				1.10	0.31		
75–99 mm	0.34			0.53	2.65		
100–149 mm	0.85	0.48	0.09		0.59	0.51	
≥ 150 mm		0.34					
<i>Oncorhynchus kisutch</i>							
100–149 mm					0.81		
<i>Oncorhynchus tshawytscha</i>							
75–99 mm	0.07						
100–149 mm	0.02	0.07				2.24	
Total	2.78	6.01	1.71	12.6	4.36	14.5	14.2

Although the maximum depth or amplitude of migration of *C. pacificus* varies seasonally, this species, when migratory, always descends to at least 75 m in the daytime (Fig. 2). This depth, therefore, was chosen as the reference depth across which we measured the proportion of the population undertaking diel migration. It should be emphasized that we do not present calculations of the amplitude of the vertical migration, but rather the percentage of the population undertaking migration across 75-m depth.

Both seasonal and interannual differences in the strength of diel vertical migration in adult female *C. pacificus* are apparent. The extent to which *C. pacificus* exhibits vertical migration in the spring and early summer varies between years, being extremely small in late April ( $V = 0.05$ ) and small in June

( $V = 0.33$ ) 1985, vs. moderate in both early May ( $V = 0.53$ ) and June ( $V = 0.50$ ) 1986. *Calanus pacificus* was strongly migratory in late summer (August) of both years ( $V = 0.74$  for 1985;  $V = 0.79$  for 1987). In early fall (October), *C. pacificus* vertically migrated during both years, but the degree of migration varied considerably, being greater in 1986 ( $V = 0.96$ ) than 1985 ( $V = 0.61$ ).

The dependence of the strength of the diel vertical migration exhibited by *C. pacificus* ( $V$ ) on the abundance of planktivorous fish actively feeding on *C. pacificus* in the surface 50 m of the water column was examined with simple linear regression (Fig. 3). The regressions for individual years (1985 and 1986) suggest a dependence, but the slopes of these lines do not differ statistically from zero. Combining the data for both



years, thus increasing the number of observations, resulted in a statistically significant regression. Whether the dependence is actually linear is somewhat uncertain given the broad confidence intervals for the slope and intercept.

In general, the proportion of the population of adult female *C. pacificus* undertaking diel vertical migration is both seasonally and interannually variable and is related to the abundance of actively feeding planktivorous fish. We propose that the timing and magnitude of these behavioral changes in *C. pacificus* are directly linked to the year-class strengths of the various species of planktivorous fish in Dabob Bay in the following way. If the abundance of fish is thought to be the cause of the moderate migration behavior of *C. pacificus* in May 1986 ( $V = 0.53$ ), then the large number of young-of-the-year *A. hexapterus* (comprising 77% of all planktivorous fish and 84% of all predatory fish) might be largely responsible. Although the relationship between the abundance of planktivorous fish and the presence or absence of migration behavior in *C. pacificus* in spring is difficult to assess given the lack of data on fish abundance in spring 1985, there is reason to believe, as discussed above, that the 1986 year-class of *A. hexapterus* was much larger than the 1985 year-class.

We therefore suggest that the abundance of young-of-the-year *A. hexapterus*, being an early winter spawner and thus producing juvenile fish of a size capable of preying on adult *C. pacificus* by spring, determines whether *C. pacificus* is migratory in late April–early May. As summer progresses, young-of-the-year of other, later-spawning species of planktivorous fish (*C. harengus pallasii*, *G. aculeatus*, and *M. productus*) begin to attain a size large enough to feed on adult *C. pacificus*. Additionally, abundances of seaward-migrating juvenile salmonids increase from spring to early summer. The abundances of young-of-the-year juveniles of the later-spawning nonsalmonids (*C. ha-*

*rengus pallasii*, *G. aculeatus*, and *M. productus*) then reach a maximum in late summer and may persist into autumn, coinciding with the time when the proportion of the population of adult *C. pacificus* undertaking diel vertical migration also reaches a maximum.

The strong dependence of our abundance estimates on the mesh size of our sampling gear begs the question of the possible role that smaller or younger fish might play as predators of *C. pacificus*. We were not able to adequately sample late larval and early juvenile stages of fish (20–40 mm long). These stages of pelagic fish are known to avoid plankton nets (Murphy and Clutter 1972), and it has been shown that a gap in sampling capability may exist until these fish grow large enough to be caught by commercial-sized nets and larger midwater trawls (Mais 1974; Methot 1986). Therefore, the abundances and feeding habits of these sized fishes, and thus their potential predatory impact on adult female *C. pacificus*, were impossible for us to assess. Previous studies, however, have shown that larval stages of marine fishes only rarely take prey as large as adult *Calanus* (Blaxter 1965; Hunter 1980). As a first approximation then, fish smaller than those retained by our trawls (i.e.  $\leq 20$ –40 mm) are assumed not to be feeding on adult *C. pacificus*.

This relationship between the presence or abundance of predators and the vertical migration behavior of zooplanktonic prey has been suggested before. Gliwicz (1986b) stated that seasonal differences existed in both the abundance of predators and the vertical migration of several species of zooplankton in tropical Lake Cahora Bassa. Though he claimed that vertical migrations were “most pronounced” in late August–early September, he didn’t present data for any other sampling date, thereby precluding comparison of migration behavior with abundance of predators. Additionally, his reference to “most pronounced” migration likely refers to the amplitude of migration (rather than

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 Fig. 2. Vertical distribution of adult females of *Calanus pacificus* in Dabob Bay in 1985 and 1986. For each set of dates, day (clear) and night (darkened) vertical distributions are means of four vertical series of samples collected in pairs near noon and midnight on each of two consecutive days. Numbers in italics are values of  $V$ , calculated as described in text.



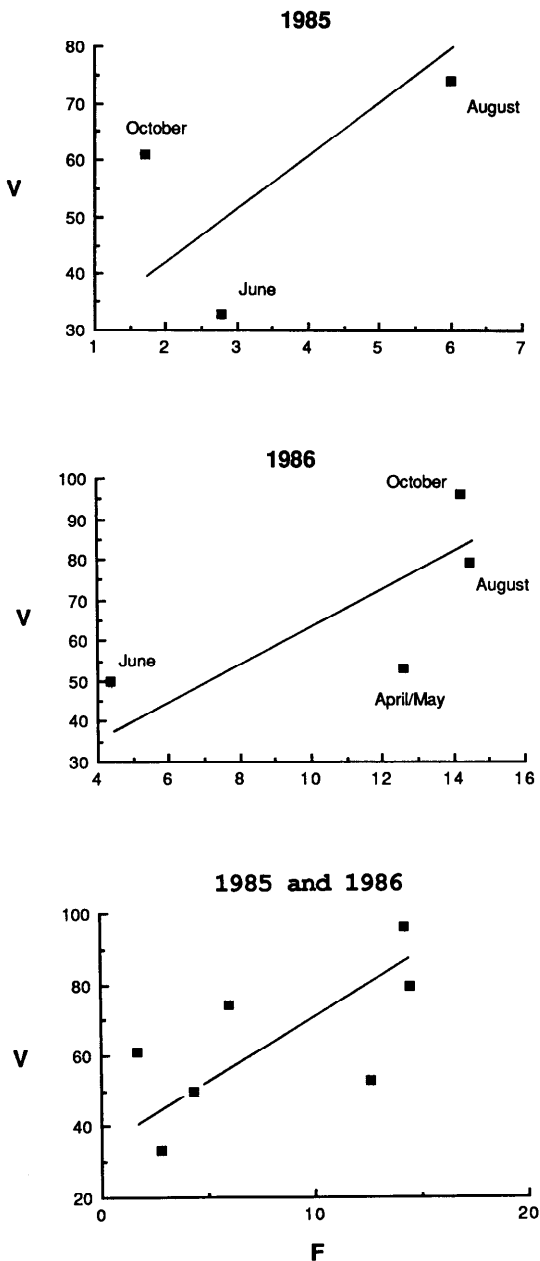


Fig. 3. Linear regressions for the dependence of the strength of diel vertical migration ( $V$ , from Fig. 2) in adult female *Calanus pacificus* on the abundance of predatory fish in the upper 50 m of the water column at night ( $F$ , from Table 2) during 1985, 1986, and both years combined. Lines fitted by functional regression (Ricker 1973); only the line for both years combined ( $V = 3.77F + 33.76$ ) has a slope differing significantly from zero ( $t_{0.05,5} = 2.94$ ,  $P < 0.05$ ; 95% C.L. of slope 0.48, 7.06; 95% C.L. of  $y$ -intercept 2.41, 65.11).

the proportion of the prey population undertaking migration), which he attributes to light (proximate factor) rather than predators (a possible ultimate cause).

Narver (1970) concurrently sampled sockeye salmon (*Oncorhynchus nerka*) juveniles <1-yr old and the zooplankton of Babine Lake, British Columbia, during June–October. The cladoceran *Bosmina coregoni* and the calanoid copepod *Heterocope septentrionalis* exhibited seasonally variable diel vertical migration behavior. *Heterocope septentrionalis* was nonmigratory in June (concentrated near the surface both day and night) but became increasingly migratory, both in amplitude and proportion of the population migrating, during summer and autumn. *Bosmina coregoni* showed a reverse diel vertical migration (i.e. near the surface during the day and at depth at night), which Zaret (1980) attributed to response to the normal diel vertical migration of the predatory *H. septentrionalis*. Although the amplitude of the reverse migration of *B. coregoni* was shown by Narver to increase in summer and fall, the proportion of the population exhibiting this behavior appears to have been fairly constant during all sampling periods. The increased amplitude of the migrations of both zooplankters might be simply a result of increased clarity of the lake in summer and fall (as shown by Narver's Secchi disk data).

The change from nonmigratory to migratory behavior (i.e. the proportion of the population migrating) in the case of *H. septentrionalis*, however, suggests a more fundamental change in the environment and resulting behavior than that caused by changing light regime. On the basis of Narver's standard net tows, the abundance of sockeye increased between early July and mid-August, then declined through October. *Heterocope septentrionalis* was a dominant prey of sockeye on all sampling dates (between July and October). Although not discussed by Narver, the increase in abundance of sockeye during July and August corresponds closely to the change in behavior of *H. septentrionalis* from nonmigratory to migratory. Although other environmental parameters were not measured and other possible factors influencing migration can-

not therefore be ruled out (e.g. thermal stratification and food availability), Narver's observations suggest the predation hypothesis as an explanation for initiation and enhanced display of vertical migration behavior in *H. septentrionalis*.

Similarly, Tessier (1986) presented data for *Daphnia catawba* in Lake Lacawac, Pennsylvania, showing a change in diel vertical migration behavior from nonmigratory in April to migratory in June and July. He also found that recruitment and growth of the dominant planktivorous fish, *Perca flavescens*, occurred in spring and summer, respectively, indicating close correspondence of seasonal changes in migration behavior of prey with increasing abundance of predators.

Kozhov (1963) described seasonal changes in both the amplitude and intensity of diel vertical migrations in the zooplankton of Lake Baikal. Changes in migration amplitude were attributed to changing light regimes, while changes in intensity of migration were attributed to periods of active feeding by planktivorous fish. The intensity of migration (percent of total population undertaking migrations) of copepodid stages of *Epischura baicalensis* was very weak in spring but pronounced in late summer when the dominant planktivorous fishes (*Cottomephorus* spp., *Coregonus* spp., and *Comphorus* spp.) migrated offshore and actively fed in surface waters. Although lacking quantitative data on the seasonal variability of predator abundances, Kozhov's observations lend support to the predation hypothesis as an explanation for seasonal variability of diel vertical migration in zooplankton.

Interannual variability in diel vertical migration of zooplankton and its possible relationship to predator abundance have received even less attention than seasonal variability. Ohman (1983) related the reverse diel vertical migration of a small calanoid copepod (*Pseudocalanus* sp.) to the normal diel vertical migration of known invertebrate predators for a single location and season over several years. He found strong correlation between the proportion of adult female *Pseudocalanus* sp. below 50 m at night and the number of *Sagitta elegans* and

*Euchaeta elongata* above 50 m at night. Luecke (1986) presented diel vertical distributions of *Chaoborus flavicans* in Lake Lenore, Washington, and showed a change from nonmigratory to migratory behavior in this species spanning the period of introduction of cutthroat trout (*Salmo clarki henshawi*) into the lake. Similarly, Dorazio et al. (1987) reported on a summer shift in net zooplankton (especially *Daphnia pulex*) of Lake Michigan from nonmigratory to migratory between 1983 and 1985. During this period visual observations of planktivorous fishes (alewife and bloater chub) suggested increasing numbers of predators, although abundances and feeding habits of the fishes apparently were not quantified.

These previous reports corroborate our own field observations on the dependence of variable migration behavior in planktonic animals on the variation in abundance of their predators, and while correlation is not necessarily causation, it is suggestive that *C. pacificus* may be undertaking diel vertical migration in an effort to avoid visually orienting predators, i.e. planktivorous fish. This possibility is all the more likely given the inability of any of the energetic or demographic models hypothesizing enhanced growth or reproduction from diel vertical migration to explain the variable nature of this behavior by *C. pacificus* in Dabob Bay (Frost 1988). That is, both our demographic models (Frost 1988) and our field observations point to predator avoidance as the adaptive significance of diel vertical migration.

Even if the variable diel vertical migration behavior of planktonic prey in these previous reports and our Dabob Bay field study are indeed responses to predators, the actual mechanism by which predators trigger this response is an open question. Ever since the seminal work of Hrbáček et al. (1961) and Brooks and Dodson (1965) over two decades ago, studies of predator-prey interactions in the plankton have focused on selective predation as the mechanism by which predators affect their prey. Indeed, such a mechanism is implicit in earlier theoretical analyses of induction of diel migratory behavior in zooplankton (Wright et al. 1980; Ohman et al. 1983), and observed

intraspecific genetic differences between migratory and nonmigratory genotypes of freshwater cladocerans (Weider 1984; Dumont et al. 1985) support the possibility of such a mechanism. Recently, however, there has developed a greater appreciation of the ability of prey organisms to respond phenotypically, both morphologically (Havel 1987) and behaviorally (Petranka et al. 1987; Kats et al. 1988), to the chemical exudates of predators, and such a mechanism for the induction of diel vertical migration behavior in zooplankton has been suggested by Frost (1988) and Dodson (1988).

Our data are consistent with either mechanism of induction, but the rapid rate of change of migration patterns in 1985—none in May, weak in June, strong in August, and moderate in October—would require very different rates of population growth between the two prey genotypes (migratory genotype  $r >$  nonmigratory genotype  $r$  between May and August; nonmigratory genotype  $r >$  migratory genotype  $r$  between August and October), perhaps to a degree that excludes such a genotypic change in the population as a reasonable possibility.

What is required to more fully test our field data against these two possible mechanisms of induction is to include rate measurements of both predation and prey responses. The necessary data (stomach contents, temperature, and feeding periodicity of fish for gut evacuation rates and thus predation rates; egg production rates, development times, and mortality rates of *C. pacificus*) are currently being analyzed and will allow us to place limits on the rate at which *C. pacificus* could respond at a population-genetic level to predation from planktivores.

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