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Size-dependent visual predation risk and the timing of vertical migration in zooplankton

Abstract—Zooplankton commonly exhibit diel vertical migration (DVM), descending from food-rich surface waters during the day. If DVM is a tradeoff between avoiding size-selective visually hunting predators and maximizing energy gain, smaller bodied prey should enter surface waters earlier and leave later than larger, more visually conspicuous organisms. Conventional sampling technologies lack the temporal resolution to test this prediction. Here, we report on the first test of this prediction using a new submersible optical–acoustic imaging system capable of resolving the timing of migration of the euphausiid crustacean *Euphausia pacifica* Hansen. Smaller bodied animals consistently ascended as much as 30 min earlier and descended up to 45 min later than adults. The timing of vertical migration reflects how the size-dependent risk of attack by visual predators alters the tradeoff between feeding and predator avoidance, supporting the predator-avoidance hypothesis for DVM.

The risk of attack by planktivorous fish increases with ambient light level and prey characteristics affecting visibility such as body size, morphology, pigmentation, mobility patterns, and gut contents (O'Brien 1987; Ryer and Olla 1999). Large-bodied and highly pigmented zooplankton are disproportionately vulnerable to visual predators and are subject to heavy mortality when fish are abundant (Hrbáček 1962; Brooks and Dodson 1965; Brodeur 1998). Therefore, morphological or behavioral characteristics that result in a reduction in the intensity of visual predation on zooplankton should confer a gain in fitness.

Many of the behaviors exhibited by zooplankters, such as reduced feeding during daylight, ontogenetic vertical migrations, seasonal diapause, and diel vertical migration (DVM), can reduce the risk of attack by predators (Ohman 1988; Verity and Smetacek 1996). Although the proximate stimulus for DVM is thought to be diel changes in ambient light intensity (Ringelberg 1995), the adaptive significance of the behavior has been controversial. After scrutiny of alternative hypotheses, the present consensus is that DVM typically concerns predator avoidance (reviewed in Lampert 1989, 1993). DVM is generally thought to minimize spatiotemporal overlap with visually hunting predators in food-rich surface strata during daylight hours, but the behavior can also be reversed to avoid encounter with carnivorous predators, which are themselves migrating to avoid visual predators (Ohman 1990). By performing DVM, migrants avoid surface strata at times when they are most vulnerable to predators. The principal costs associated with this reduction in mortality are the energetic costs of migration and the decreased potential for population growth through part-time residence in relatively low-food, deeper strata (Ohman 1990).

The predator-avoidance hypothesis for DVM can be framed in the context of selection between habitats in which rates of energy gain and mortality differ. If DVM is primarily a mechanism by which organisms balance the conflicting requirements of maximizing net reproduction and predator avoidance, the behavior should vary with vulnerability to

predators (Sih 1980; Bollens and Frost 1989; Lampert 1993). The risk of attack by visual predators varies with ambient light levels and thus should change steeply during twilight. Migration to a deeper, poorly illuminated habitat during the day reduces the probability of detection by a visual predator at the cost of decreased net energy gain. If zooplankton migrate during twilight periods of steep changes in irradiance, the daily risk of attack by visual predators should be sensitive to small changes in the times of migration. Models of zooplankton vertical habitat choice based on maximizing fitness suggest that the time of migration should vary with vulnerability to visual predators (Iwasa 1982; Fisken and Giske 1995). If DVM is a tradeoff between energy gain and mortality risk, the timing of exchange between the surface and deeper layers should not be identical for all size classes within a population. Rather, smaller prey should enter surface waters earlier and leave later than larger, more conspicuous organisms. Here, we present a field test of this prediction in a population of *Euphausia pacifica* Hansen using a newly developed optical–acoustic submersible imaging system (OASIS) that has sufficient temporal resolution to detect small changes in migration times.

Study site—We measured the time at which a population of *Euphausia pacifica* performed vertical migrations in Saanich Inlet, British Columbia (48°34.4′N, 123°30.4′W) in July/August of 1996 and 1997. Saanich Inlet has a narrow sill at its entrance, which restricts bottom water circulation resulting in anoxic waters below the sill depth for much of the year (Herlinveaux 1962). The crustacean macrozooplankton in this locality exhibits low species richness and is dominated by abundant *Euphausia pacifica* and the gammarid amphipod *Orchomene obtusus* Sars. There is little spatial overlap between these species, as *E. pacifica* aggregates above the oxycline during the day and migrates to surface waters at night, while *O. obtusus* is a weak vertical migrator and is found deeper in the water column (Bary et al. 1962; ADR unpubl. data).

OASIS allows acoustic localization of individual zooplankton with a 445 kHz multibeam sonar (described in Jaffe et al. 1995) in a 4 m³ volume of seawater at ranges of 2–5 m with concurrent optical verification of a subset of the acoustic targets that trigger a digital camera (Jaffe et al. 1998). Photographic identification addresses the major drawback of acoustic methods for zooplankton sampling, which unobtrusively sample large volumes but offer very little taxonomic information. The optical images confirmed previous reports (Bary et al. 1962; Herlinveaux 1962) of a large population of euphausiids (species composition from net samples averaged 98% *E. pacifica* in 1996 and 85% in 1997) dominating the macrozooplankton, as well as the presence of planktivorous fish (walleye pollock *Theragra chalcogramma* Pallas and Pacific herring *Clupea harengus pallasi* Valenciennes) known to prey heavily on euphausiids.

Acoustic calibrations—To characterize the acoustic signatures of euphausiids of different body sizes, we conducted a series of laboratory measurements on tethered live euphausiids (primarily *Euphausia gibboides*) ranging from 4 to 21 mm body length in a 20 m³ laboratory tank. The euphausiids were tied to a human hair and suspended in a known location in the sonar's field of view, and 500 determinations of target strength (TS) were made for each individual over a period of 15 min. For these measurements, the sonar was inclined at an angle of 27° relative to the surface of the water to mimic the sonar's orientation during deployments. The tether was acoustically undetectable above the experimental target recognition threshold of −101 dB (corrected value—*see below*) and did not constrain the orientation of euphausiids relative to the sonar. Reverberation at the periphery of the tank required placing the euphausiids in an acoustically quiet area at a range of 1.15 m, which is in the near field (<2.4 m) of the acoustic beam for this system. In the near field, the acoustic pressure field is complex and does not fall off smoothly with distance (Lockwood and Willette 1973), as assumed by theoretical corrections for the spreading of acoustic beams. To correct for this effect, a correction of +3 dB was obtained by measuring the changes in the TS of a standard target moved at successively greater distances from the sonar in a larger freshwater tank and applied to the data. An additional series of measurements showed that the +3 dB near field correction is appropriate across the acoustic beam. In addition to the laboratory measurements, the TS of euphausiids triggering the optical images in situ in Saanich Inlet was determined following the methods in Jaffe et al. (1998), providing an independent measure of the relationship between body size and TS.

The corrected laboratory measurements of the TS of tethered euphausiids exhibited substantial variability (standard deviations ranged from 1.2 to 8.2 and averaged 5.7 dB). In many cases, particularly for the smaller size classes, the acoustic return was below the target recognition threshold. The laboratory and in situ OASIS TS determinations are qualitatively similar (Fig. 1A), but statistical analysis of values above the noise floor reveals a marginally significant difference in the slopes determined with each of the two methods (ANCOVA: $F_{1,94} = 2.96$, $p = 0.089$), and thus separate regressions have been computed for each measurement technique. We have identified two factors that could account for this discrepancy. Our empirical correction for the near field could be inadequate, or the euphausiids detected in the optical images might have a higher TS because they tend to be at a broadside orientation that leads to higher TS (Jaffe et al. 1998), whereas the laboratory determinations integrate over many orientations. The TS of euphausiids is known to be highly dependent on orientation (McGehee et al. 1998), and we suspect that the observed differences are due to a bias in animal orientation.

Linear regression analysis indicates that both the median values of laboratory measurements ($y = 0.86x − 101.16$, $r^2 = 0.61$, $F_{1,57} = 89.6$, $p < 0.001$) and the in situ OASIS TS determinations ($y = 0.56x − 94.3$, $r^2 = 0.23$, $F_{1,37} = 11.3$ $p < 0.005$) show a positive relationship between euphausiid body size and TS in the 6–22 mm size range (Fig. 1A). Higher variability and lower r^2 values are to be expected for the in situ measurements, as the regressions are for single realizations rather than medians of many realizations, as in the case of the laboratory measurements. Both types of TS determinations are consistently lower than predicted by a previous empirical length vs. TS relationship derived from
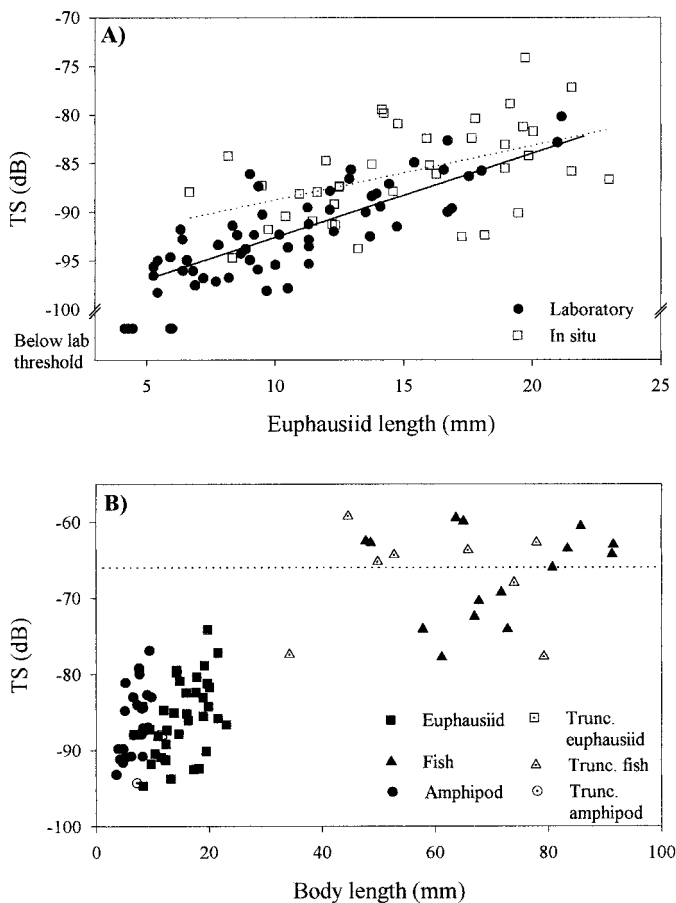
Fig. 1. Relationship between acoustic target strength (TS) and organism body size. (A) TS determinations for 65 individual tethered euphausiids in a tank (median of 500 determinations for each specimen), and in situ measurements of the TS of 39 individual euphausiids triggering the OASIS digital camera (single determinations for each specimen). The solid line represents a linear regression for tethered euphausiids and the dotted line a regression for in situ determinations. (B) In situ measurements for the taxa observed in the OASIS images. Symbols distinguish between organisms that were imaged completely in the optical field and those whose bodies were truncated, for which the standard length was estimated if >50% of the body was in view. The horizontal line demarcates the −66 dB criterion used to distinguish fish and zooplankton. Some of the in situ TS determinations ($n = 40$) presented here have been reported previously (Jaffe et al. 1998), although that paper contains a calibration error: all TS's reported there have been adjusted by −6 dB.
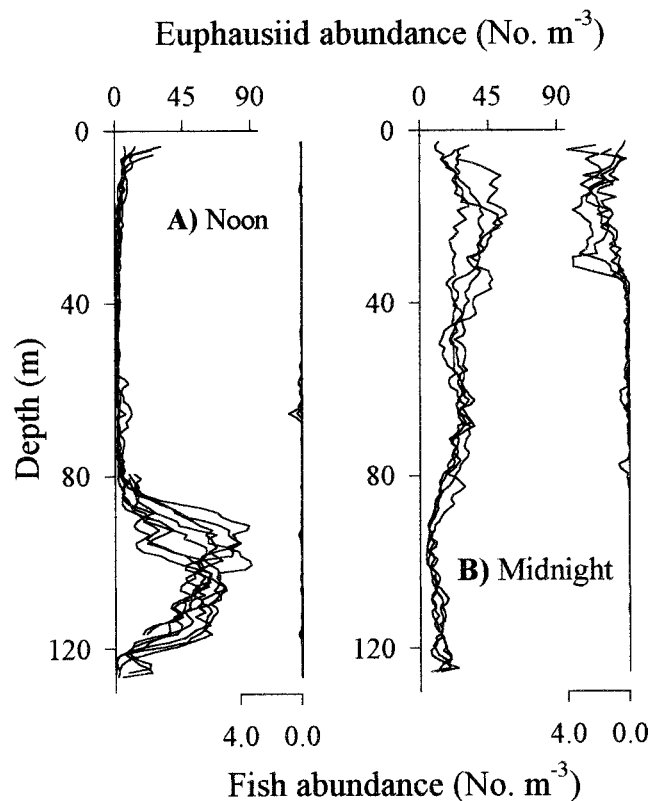

Fig. 2. Day/night OASIS echo-counting profiles of fish and of zooplankton dominated by euphausiids. (A) Vertical profiles of euphausiids (left axis) and fish (right axis) during midday. Euphausiids are defined as targets with an acoustic target strength (TS) of −95 to −66 dB and fish as targets with a TS > −66 dB. (B) Midnight vertical profiles of euphausiid (left axis) and fish (right axis) abundance. All profiles are from 1997.

several species of crustaceans at 420 kHz (Wiebe et al. 1990). This discrepancy is likely attributable to differences in animal orientation, as the position of the sonar relative to the tethered animals is different in our study, as well as the use of different species of experimental animals. Together, our measurements reveal that OASIS is reliably capable of detecting euphausiids of body sizes greater than ~7 mm using our field target threshold of −95 dB, and that TS increases with body size.

Despite some overlap, the TS of the fish in the optical images was higher than that of the euphausiids and amphi-

pods (Fig. 1B), enabling us to define a TS cutoff of −66 dB as a criterion by which to distinguish fish from zooplankters. None of the 32,500 corrected laboratory measurements on tethered euphausiids exceeded this value. This cutoff will underestimate the number of fish present and is conservative in the sense that it will erroneously identify some fish as euphausiids, but is unlikely to identify euphausiids as fish.

Field measurements—Repeated vertical echo-counting profiles indicated that the euphausiids migrated from a daytime depth of 90–110 m to surface strata at night, and that fish and euphausiids overlapped mainly in the upper 40 m at night (Fig. 2A, B). We discovered that in our twilight recordings, smaller animals appeared earlier during dusk (Fig. 3A) and disappeared later during dawn (Fig. 3B).

During dusk and dawn, the abundance of euphausiids migrating to/from the surface was monitored at a single depth intermediate to the day/night position of the population. OASIS was positioned at a depth of 40 m (1996) or 50 m (1997), allowed to face into the prevailing current, and recorded the abundance of acoustic targets for an extended period. Our ability to resolve acoustic backscatter from individual euphausiids enabled us to characterize the size distribution of the euphausiids migrating past the instrument
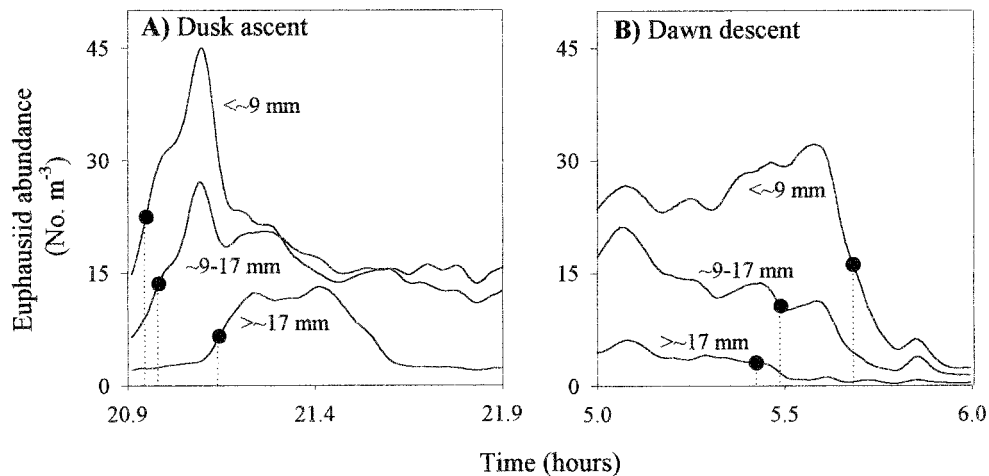
Fig. 3. Examples of dusk and dawn echo counting of three size classes of euphausiids as they migrate past OASIS. (A) Euphausiid abundance during dusk ascent recorded at 50 m depth. The three lines represent three acoustic size classes (−95 to −93, −93 to −86, and −86 to −66 dB, which correspond to the median TS of <9 mm, 9–17 mm, and >17 mm euphausiids, respectively). Larger animals ascend later than smaller animals. The timing of DVM is characterized by the temporal median (black circle), i.e., the time at which the observed abundance reaches 50% of the maximum, before/after the maximum values in ascents/descents. (B) As in (A), but for dawn descent. Larger animals descend earlier than smaller animals.

and resolve small size-dependent changes in the time of ascent/descent. This was done for five ascents and six descents of the population during the two summer cruises. Acoustic data were recorded at rates of 1 and 2 Hz during ascents and 0.167 and 0.1 Hz during descents in 1996 and 1997, respectively. For each recording, we analyzed the period in the record encapsulating the migration, which corresponds to the first 60 min of the ascents (recording started ~2/20 min after sunset in 1996/1997), and 60 min before to 30 min after sunrise in the case of descents.

We processed the acoustic data to a list of TS and three-dimensional position for each target detected. Targets were identified as local maxima above a −95 dB threshold within each beam using the methodology described in Jaffe et al. (1999). The target lists were sorted into 25 1 dB TS categories (−95 to −70 dB), which are consistent with reflections from individual euphausiids. Targets with a TS between −69 and −66 dB were excluded from this analysis because of low numerical abundance. The abundance of targets as a function of time in each TS category was smoothed with a running mean of 5-min duration weighted by a standard normal distribution. We characterized the timing of DVM with a statistic we define here as the temporal median, the time at which the observed abundance reaches 50% of the maximum before/after the maximum observed values in the ascents/descents. The temporal median is reported relative to local sunset/sunrise.

Analysis of the twilight ascents/descents of the population revealed that the timing of ascent and descent was not uniform for all size classes of euphausiids, as shown by departures from a horizontal line in Fig. 4. On all occasions, the null hypothesis of no dependence of the timing of DVM on body size can be rejected, as smaller bodied euphausiids consistently ascended as much as 30 min earlier and de-

scended as much as 45 min later than the adults. Lower data-acquisition rates during descents permitted less smoothing, resulting in more variable estimates of the temporal median, particularly for the less abundant, more reflective targets. TS classes for which no temporal median was observed were excluded from the analysis. This occurred commonly in ascent records, which were usually initiated too late to capture the behavior of the smallest animals.

Discussion—The development of a sampling technology allowing the enumeration of different size classes of zooplankton with a high temporal resolution has afforded us the opportunity to test a poorly studied facet of the predator-avoidance hypothesis for DVM. Our observations of size-dependent timing of DVM in *E. pacifica* are consistent with the consequences of the changing risk of attack by visual predators and therefore support the predator-avoidance hypothesis for DVM. This inference is based on the premises that visual predation is an important source of mortality and that rates of energy gain for zooplankton are higher in near-surface waters. These assumptions appear to be reasonable for this environment, as our optical–acoustic sampling and profiles of phytoplankton pigments (unpubl. data) suggest that visual predators are abundant and that food concentrations are greatly elevated in near-surface waters. Since all size classes of euphausiids entered the surface layer after sunset, the results are inconsistent with an alternative hypothesis based on energetic considerations predicting that migratory herbivores should ascend 1–2 h before sunset (Enright 1977).

One must consider the possibility that nonadaptive explanations can explain the observed differences in the times of arrival and departure from the surface layer on proximate grounds alone. If size-dependent physiological constraints
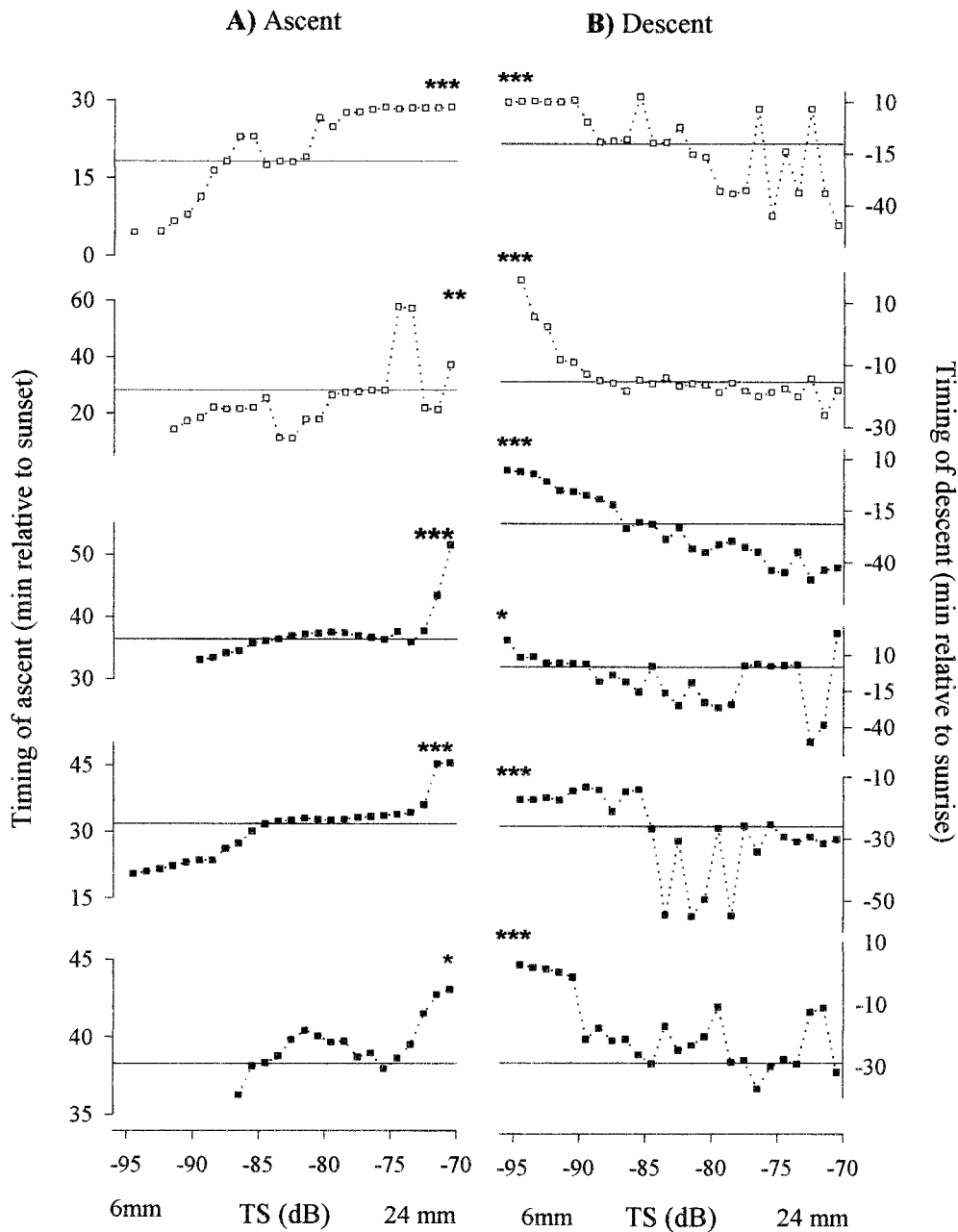
Fig. 4.   Timing of vertical migration derived from twilight echo counting of a series of acoustic size classes during (A) ascent of the euphausiid population on five different nights, and (B) descent during six different dawns. White and black symbols correspond to records made in 1996 and 1997 respectively. The timing of DVM is estimated by the temporal median for acoustic size classes ranging from target strengths of -95 to -70 dB, which correspond to 6 to 24 mm euphausiids based on our calibration measurements. The temporal median is reported relative to local sunrise/ sunset. A horizontal line has been drawn through the -85 to -86 dB size class for reference. In each case, the null hypothesis of no dependence of the timing of DVM on body size is rejected (one tailed Spearman rank correlation $*p < 0.05$, $**p < 0.01$, $***p < 0.001$, no correction for multiple testing).

limit migrations, an adaptive explanation for size-dependent differences in migration times would be inappropriate. For example, if smaller animals are limited to shallower daytime depths than adults due to a less developed swimming ability, they may arrive in the surface waters prior to the adults,

which would have to travel farther. Additionally, size-dependent differences in the ability to perceive the light cue for DVM could account for differential initiation of the migration or differential daytime depths. However, there seems to be no inherent limitation of ocular function or swimming

ability preventing *Euphausia pacifica* from living deeper or responding to lower irradiance levels as a cue to migrate, as both juvenile and adult *E. pacifica* migrate to deeper daytime depths with lower light intensities in oceanic environments than in Saanich Inlet (Boden and Kampa 1965; Brinton 1967). Thus, the observed size-dependent timing of DVM appears to be associated with changes in behavioral decisions rather than physiological constraints.

The small number of fish detected during the daytime at this deep central station suggests that the fish are moving from the periphery of the fjord to deeper waters to feed at night (cf. Bohl 1990). It may appear advantageous for the euphausiids to remain in surface waters during daylight hours in this situation, as the reduced daytime predator abundance may offset the increased effectiveness of individual predators. However, fish have flexible behavior that can change quickly, and if euphausiids remained in surface waters by day the fish would likely respond by foraging in surface waters during the day.

We would be remiss not to consider the possibility that the temporal trends in the abundance of the acoustic size classes on which our conclusions are based are artifacts of either: (1) registering multiple weak scatterers as a single strong target at high abundances, or (2) systematic changes in animal orientation resulting in a temporal trend in TS (McGehee et al. 1998). It is unlikely that multiple targets are being mistakenly interpreted as single strong targets to any great extent, as the lowest TS's are often recorded concurrently with the highest abundances. During 1997, we had sufficient optical images of euphausiids to confirm that at dusk smaller animals ascended into surface waters prior to larger ones. Thus, we are confident that our observations are due to differential behavior on the part of the euphausiids.

Additionally, we have also assumed that acoustic scatterers with a TS < -66 dB represent euphausiids, although this range overlaps with the in situ determinations of the TS of the amphipod *O. obtusus,* which is also locally abundant. However, this should not affect our conclusions, as depth-stratified net sampling conducted during these cruises showed that *O. obtusus* was rare above 65 m (ADR unpubl. data).

Although the detailed timing of DVM has been poorly studied due to sampling difficulties, we are aware of three studies characterizing the time of migration of zooplankters of different body sizes that can be compared to our results. Enright and Honegger (1977) conducted a series of vertical net hauls that revealed that *Calanus pacificus* stage C5 copepodites consistently ascended earlier than adults, which are somewhat larger in body size, although the time of migration relative to sunset varied with sampling date. Andersen and Sardou (1994) documented that smaller bodied colonies of *Pyrosoma atlanticum* undergo DVM with smaller amplitudes than larger colonies and that smaller colonies ascend earlier and descend later than larger ones. Additionally, recent submersible observations in Oceanographer Canyon have documented that smaller bodied species of euphausiids (*Thysanoessa gregaria*) consistently ascend prior to larger species (*Nematoscelis megalops* and *Meganyctiphanes norvegica*), although all species occupy similar daytime depths (T. Frank and E. Widder, pers. comm.). In these cases, the

observations are consistent with the size-dependent mortality/energy gain tradeoff that we propose here, as all taxa feed primarily in surface waters and are subject to predation by pelagic fish (Blaber and Bulman 1987; Bollens and Frost 1989). Studies focusing on the more easily measured amplitude of DVM have established that the amplitude and phase of DVM are not fixed but vary with predation risk (Ohman 1990) and food concentration (Gliwicz and Pijanowska 1988). Ontogenetic shifts in the amplitude of DVM are common, as younger, less vulnerable, stages often do not migrate or they descend to shallower daytime depths than adults (Zaret and Suffern 1976; Bollens et al. 1992).

The size-selective nature of predation in aquatic systems leads to predictable changes in vulnerability during development. Changes in the risk of attack alter the mortality/energy gain tradeoff, with those individuals able to compensate by shifting the timing and amplitude of DVM achieving a fitness advantage. This tradeoff operates widely in terrestrial and aquatic taxa: favorable habitats are often risky, and organisms will avoid dangerous but profitable foraging areas at the cost of decreased growth and fecundity (Sih 1980; Ohman 1990; Lima 1998). The proposed ultimate mechanism for size-dependent timing of DVM is based on the potential for increased energy gain in surface waters and diel changes in vulnerability to predators. These conditions prevail in both freshwater and marine pelagic environments, and we thus anticipate that our results are broadly applicable, with more conspicuous organisms exhibiting shorter residence times in surface waters than less vulnerable ones.

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