Acoustic observations of the swimming behavior of the euphausiid *Euphausia pacifica* Hansen

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A high-resolution, 445 kHz, multi-beam sonar and new data-processing techniques were used to characterize the swimming behavior of the euphausiid *Euphausia pacifica* Hansen, in Saanich Inlet, British Columbia. The instrument was deployed when the euphausiids were at depth during the day and during dusk periods of population ascent. Three-dimensional swimming paths of individual euphausiids were reconstructed by linking successive, acoustically-determined positions. Median swimming speeds were 1.8 cm s^{-1} during the day and 2.2–3.5 cm s^{-1} during dusk periods of vertical ascent. The presence of a fish at distances of 20–300 cm did not affect the swimming speed or turning of the euphausiids, suggesting that they did not respond to the presence of a potential predator at these distances. Euphausiids moved primarily obliquely in the vertical plane, with few individuals moving directly up or down, even during periods of vertical migration at dusk. We hypothesize that oblique swimming trajectories of euphausiids may reduce vulnerability to visual predators by allowing them to maintain bioluminescent counter-illumination during vertical migration.

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Introduction

The swimming behavior of motile zooplankton can alter perceived food availability, metabolic demand, and the risk of predatory attack. If animals are able to locate and maintain themselves within areas of increased food concentration, their ingestion rates will increase (Price, 1989; Saiz *et al.*, 1993). Increased motion enhances the probability of encountering a predator, particularly if predators are slow moving (Gerritsen and Strickler, 1977; Rothschild and Osborn, 1988). Motility can also affect the probability of detection by predators, as more active prey are more conspicuous to predators relying on visual (Janssen, 1982) or hydrodynamic (Tiselius *et al.*, 1997) cues to locate prey. Many zooplankton, particularly the abundant calanoid copepods and euphausiids, employ rapid escape responses to evade an attacking predator (Verity and Smetacek, 1996). At larger spatial scales, many zooplankton exhibit diel vertical migration (DVM), avoiding food-rich but well illuminated surface strata during the day in order to reduce

vulnerability to visual predators (Lampert, 1989). Although pelagic organisms can use motility to alter predation risk and food availability, increased activity comes at a cost: for many taxa, metabolic demand increases steeply with swimming speed (e.g. Torres and Childress, 1983; Buskey, 1998a, b).

To understand bioenergetic and predator–prey processes in zooplankton, it is necessary to characterize their swimming behavior. However, the swimming behavior of zooplankton in their natural environment remains poorly understood. In large part, this can be attributed to the difficulty of direct observation and the lack of instrumentation that can be used to observe behavior remotely. The sampling methods (pumps, nets, and echosounders) commonly used in zooplankton studies integrate information over many individuals, making it difficult to infer the behavior of single animals (Pearre, 1979). Interest in zooplankton behavior (e.g. Marine Zooplankton Colloquium I, 1989) has stimulated the development of novel techniques and instrumentation that are capable of resolving individual

zooplankton. Optical methods such as video instruments (reviewed in Schulze *et al.*, 1992; Foote, 2000) have the advantage of high spatial resolution but the drawback of observing relatively small volumes of water. Optical techniques have the additional disadvantage that they often require artificial illumination, which may alter zooplankton behavior. An alternative approach is to use acoustics to determine the swimming behavior of planktonic organisms. With acoustics, the movements of animals can be studied in relatively large volumes of water because of the comparatively low attenuation of sound (e.g. Torgersen and Kaartvedt, 2001). However, most acoustic systems used for zooplankton studies lack the resolution to identify and follow individuals (reviewed in Smith *et al.*, 1992; Foote and Stanton, 2000). With the development of OASIS, an instrument package combining a high-resolution, multibeam sonar and a camera for concurrent optical–acoustic imaging of macrozooplankton (Jaffe *et al.*, 1998), it is now possible to identify, localize, and track individual zooplankters (McGehee and Jaffe, 1996; Jaffe *et al.*, 1999).

In this study we use OASIS to characterize the swimming behavior of the euphausiid *Euphausia pacifica* Hansen, and test whether the euphausiids alter their swimming behavior when in the proximity of planktivorous fish. *E. pacifica* is a dominant species in the North Pacific (Brinton *et al.*, 1999) and is a strong vertical migrant, ascending into surface strata at night (Brinton, 1976). Other than what has been inferred from diel patterns of vertical distribution, little is known about the swimming behavior of individuals. Euphausiids are highly mobile, possess well-developed sensory capabilities, and are capable of considerable behavioral flexibility (e.g. Hamner *et al.*, 1983; Price, 1989; Strand and Hamner, 1990). In order to quantify the swimming behavior of individual euphausiids, we have developed a tracking technique that takes advantage of the ability of the OASIS package to localize individual zooplankton. The spatial positions of acoustically-localized zooplankton are improved by applying a newly developed algorithm (Jaffe, 1999). Using these methods, the swimming behavior of *E. pacifica* is compared during two distinct periods: while the animals are at depth during the day, and during the dusk ascent into near-surface waters.

Methods

Data collection

OASIS comprises a 445 kHz, multi-beam sonar used to localize individual zooplankters, and a digital camera used to identify a subset of the acoustic targets (Jaffe *et al.*, 1998). The sonar is designed for three-dimensional (3D) localization and tracking of macrozooplankton in 64 2° by 2° acoustic beams arranged in an 8 by 8 array. The instrument provides 3D locations by measuring target range within a beam and determining vertical and azimuthal positions using the beam transitions (Jaffe *et al.*, 1995). The

components are mounted on an aluminum frame equipped with a large current vane to keep the instrument oriented into the mean flow. The sonar was mounted to point slightly downwards, with an angle of −27° from the horizontal. OASIS is equipped with ancillary sensors including pressure and temperature sensors, a compass, and pitch and roll sensors.

The instrument package was deployed in August 1996, in Saanich Inlet, British Columbia (48°34.4′N, 123°30.4′W). The area was selected as a study site because the macrozooplankton there are dominated by a resident population of *E. pacifica*, whose depth distribution is restricted to the upper strata that can be sampled by OASIS (<125 m) as a consequence of the presence of anoxic waters at depth (Mackie and Mills, 1983; De Robertis, 2001). During OASIS deployments in this protected fjord the conditions were extremely calm. OASIS was lowered into strata dominated by euphausiids, 85 m during the day, and 40 m at dusk, and was allowed to record data at 2 Hz for an extended period, 30 min during the day, and 60 min at dusk. In these deployments, the sonar imaged a volume of 4.3 m^3, hereafter referred to as an acoustic image, at a range of 2–5 m from the instrument.

Individual acoustic targets >−95 dB were localized in 3D space using the methods described in De Robertis (2001). Laboratory and *in situ* analyses have demonstrated that, for the assemblage encountered during this study, *E. pacifica* dominated backscattering from zooplankton, which could be differentiated from reflections from planktivorous fishes (primarily juvenile walleye pollock *Theragra chalcogramma* and juvenile herring *Clupea harengus pallasi*), using a −66 dB threshold (De Robertis, 2001). As juveniles, both these fishes prey heavily on euphausiids (Brodeur, 1998; Robinson, 2000). In addition, the validation studies demonstrated that, on average, euphausiid target strength (TS) increases linearly with body size over body lengths ranging from 5 to 22 mm.

Target tracking

Euphausiid swimming trajectories were reconstructed by linking the positions of acoustic targets in successive acoustic images. Individuals were followed over time by searching for an acoustic target in the vicinity of the euphausiid's last-known position in the subsequent acoustic image (Figure 1). Three rules were used to track targets. First, a volume corresponding to target displacements of ±1 beam (±2°) and ±10 range samples (±7.5 cm) was demarcated around a target to be tracked. Given the sample interval of 0.5 s, this resulted in maximum-allowable velocities of 15 cm s^{-1} in range, and 12–36 cm s^{-1} in azimuth and elevation, depending on range. Second, if a single target was located within this volume in the next acoustic image, it was assumed to be the same animal as that identified in the previous image. Finally, tracks were discontinued if either 0 or >1 targets were present in this
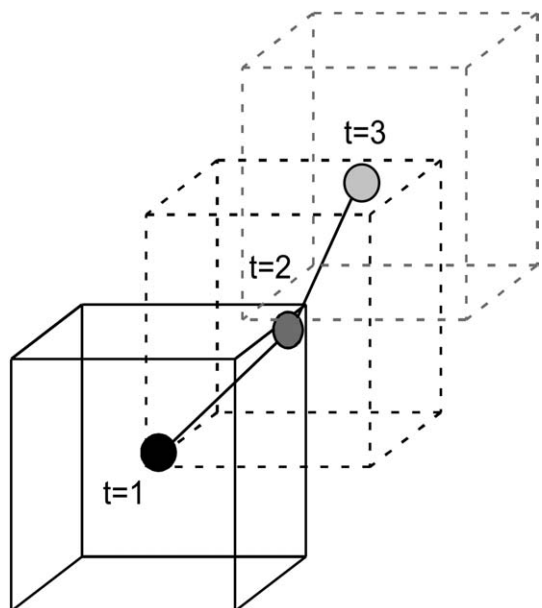
Figure 1. The procedure used to track a target over sequential acoustic images. A volume centered on the last-known target position is searched for the presence of the same target in the subsequent acoustic image. In this illustration, a target is tracked over three sequential acoustic images.

volume. This process was repeated for sequential acoustic images, resulting in a time series of spatial positions. The upper bound on animal-movement rates imposed by the tracking scheme was selected to allow measurement of routine swimming, which is $<10 \, \text{cm s}^{-1}$ for captive *E. pacifica* (Miyashita *et al.*, 1996). However, this upper bound is too low to consistently detect the much faster escape responses, which are in the range of 10–30 body lengths s^{-1} (Ignatyev, 1997). Preliminary studies indicated that tracking acoustic targets close to the $-95 \, \text{dB}$ detection threshold was ineffective, as weak acoustic targets were likely to drop below the detection threshold and out of view as they were being tracked. To minimize this problem, a minimum TS of $-91 \, \text{dB}$ was imposed as a criterion to initiate tracking.

Refinement of target localization

Although range resolution is $\sim 1 \, \text{cm}$, the $2°$ beam width dictates the elevation and azimuth resolution of the sonar, which is range dependent: it varies from 6 to 18 cm for the deployments considered here which is insufficient to resolve the short-term movements of zooplankton. A recently developed method was used to improve localizations of euphausiid positions in elevation and azimuth. This algorithm (described in Jaffe, 1999) refines the position of a target within a beam by comparing the observed backscatter with a series of model predictions for a simulated

target positioned over a grid that is finer ($0.25°$) than the sonar beam resolution ($2°$). Targets are localized within a beam by finding the modeled target position that best fits the observed backscatter. Laboratory studies have shown that for a high signal-to-noise situation, this interpolation results in a ~ 5-fold improvement in the spatial resolution of the sonar (Schell and Jaffe, submitted for publication).

The algorithm assumes that only a single animal is present at a given range. To identify when multiple targets contribute to the recorded backscatter and violate the single-target assumption, the goodness-of-fit between model prediction and the observed data was employed. The intensity of the observed and modeled acoustic backscatter was scaled such that the maximum backscatter was 1000, and the mean-squared error between the modeled and observed backscatter was computed. Initial tests indicated that the performance of the algorithm was degraded when the target was located in beams at the edge of the array where information from the adjacent side lobes was missing. Thus, targets detected in the periphery of the array and those with a mean-squared error greater than an empirically derived threshold of 1.5×10^6 were assumed to yield biased positional estimates and were rejected. This goodness-of-fit criterion will reject an increasing proportion of positions as target density increases because of backscatter from multiple targets at the same range. However, the method will identify targets which can be tracked successfully under high-density conditions as each position is tested for the influence of multiple targets. Using this technique, we have been able to successfully track a subset of acoustic targets at densities exceeding 30 targets $>-91 \, \text{dB m}^{-3}$, which corresponds to high densities of adult euphausiids. Tracks for which a minimum of five, sequential, valid positions was available were used in further analyses.

Compensation for water flow and platform motion

Tracks generated using the method described above reflect the movements of euphausiids relative to the instrument package. These motions include fluid flow and rotation of the instrument about the suspension wire as well as displacements due to swimming. If the coordinate system is defined relative to the horizontal, where U is the forward component, V is the azimuth component and W is the elevation component, the swimming motions of tracked euphausiids can be represented as follows:

$$\Delta U_{swim} = \Delta U_{obs} - \Delta U_{mf} - \Delta U_{rot}(r, \theta, s) \quad (1)$$

$$\Delta V_{swim} = \Delta V_{obs} - \Delta V_{mf} - \Delta V_{rot}(r, \theta, s) \quad (2)$$

$$\Delta W_{swim} = \Delta W_{obs} - \Delta W_{pitch} - \Delta W_{mf} \quad (3)$$

where the subscript swim refers to swimming motions, obs refers to the observed displacement, mf to the mean fluid flow, rot refers to the rotation of the sonar about the suspension wire, and pitch refers to the vertical motions

from the pitching of the instrument. r is the distance of the target from the sonar in the UV plane, θ is the angle of vector r in the UV plane, and s is the angular rotation of the sonar about the wire.

The swimming motions of the tracked animals can be isolated from other sources of motion provided some simplifying assumptions are made. By assuming that the swimming speeds of individual euphausiids are not correlated, the effect of mean flow in the horizontal plane (ΔU_{mf}, ΔV_{mf}) can be removed by subtracting the correlated part of the observed motions once ΔU_{rot} is accounted for. If motion introduced by the pitching of the instrument and vertical water flow is negligible compared to animal swimming (i.e. $\Delta W_{pitch} \ll \Delta W_{swim}$ and $\Delta W_{mf} \ll \Delta W_{swim}$), one can approximate animal swimming in the vertical plane as $\Delta W_{swim} \cong \Delta W_{obs}$.

ΔU_{rot} and ΔV_{rot}, the velocity components introduced by the platform rotation, were calculated for each tracked target from the angular velocity recorded by the onboard compass and the target location. The compass record was smoothed using Lowess (Cleveland, 1979) with a 10-s smoothing window to reduce the effect of instrumental noise and short-period variations. The resulting azimuth rotation component ΔV_{rot} averaged 0.24–0.87 cm s^{-1}, while ΔU_{rot} averaged 0.01–0.02 cm s^{-1}.

Mean-flow components in U and V were estimated by fitting the time series of U and V displacements after correction for platform rotation. A running mean of all target displacements observed in a 7-s interval was computed under the assumption that the mean flow was stable over this time period. This correlated component was then subtracted from the rotation corrected U and V velocity components to estimate ΔU_{swim} and ΔV_{swim}, the motions attributed to swimming behavior.

A tilt meter mounted on the instrument package indicated that the assumption that ΔW_{pitch} is low was reasonable, as the instrument's pitch changed slowly (range of $\bar{X} \pm SD$ 0.01 ± 0.02 to $0.02 \pm 0.03° \, s^{-1}$) over a total range of $<0.6–1.1°$ during each of the deployments. Motions of this magnitude would introduce an error of <0.15 cm s^{-1} in estimates of vertical displacement. Vertical water velocity, ΔW_{mf}, was assumed to be much less than animal-swimming velocities of several cm s^{-1}, and the vertical component of animal swimming was represented as $\Delta W_{swim} \cong \Delta W_{obs}$.

Overall, ΔU_{swim} ranged from 17 to 69% of ΔU_{obs}, and ΔV_{swim} ranged from 50 to 75% of ΔV_{obs}. Swimming behavior accounted for a smaller fraction of the total observed motion in V, which was primarily a result of the influence of current-induced motion of euphausiids towards the stationary sonar. The assumption most likely to be violated was that motions introduced by the rotation of the instrument package around the suspension wire could be accurately separated from swimming motions on the basis of the compass reading. This assumption was violated in cases where weak currents did not allow the current

vane to stabilize the instrument, resulting in short-period oscillations. This shortcoming was evident in several (n = 4) OASIS deployment records, in which the rotation of the instrument introduced azimuthal motions into the swimming trajectories. In order to avoid this effect, we used the criterion that ΔV_{swim} should not consistently exceed ΔU_{swim} to identify three acoustic records for further analysis: two records of 60-min duration taken at 40-m depth starting 6 min after sunset (20:22–21:22 on 11 and 12 August 1996) as the euphausiid population was ascending towards the surface, and a 30-min record from 85-m depth (10:40–11:49 on 12 August 1996) in the daytime, vertical-abundance maximum.

Analysis of tracks

In order to reduce the influence of measurement error on the swimming motions of the euphausiids, the measured trajectories were smoothed using a Kalman smoother. The related Kalman filter is widely used in tracking applications (Bar-Shalom and Li, 1998), but we did not require real-time tracking and chose to take advantage of the additional performance offered by a Kalman smoother. The Kalman smoother (Rauch *et al.*, 1965) fit the data to the piecewise-constant, white-acceleration model of Bar-Shalom and Li (1998). This model assumes that targets move at approximately a constant velocity with small accelerations that are constant over a single time sample. Motion along each axis was assumed independent from the other axes. The measurement noise variance used in the model was 2 cm^2 in range and 0.25° in elevation and bearing angle. A process noise variance of 2 cm^2 was used for each axis.

Results

The tracking procedure resulted in numerous tracks of short duration (e.g. Figure 2). In the two dusk sequences, 1611 and 3024 tracks were recorded over a 60-min period and 2229 tracks were recorded over 30 min during the day. Median track length ranged between 7 and 9 sequential positions (e.g. Figure 3), and maximum track length was 107 positions. Tracks tended to be longer when animal abundances were low and when TS was high. The TS (median of all values for a given trajectory) of tracked targets ranged between −90 and −81 dB, which corresponds approximately to euphausiid body sizes of 12–22 mm at 445 kHz (De Robertis, 2001).

The OASIS measurements indicate that *E. pacifica* does not move rapidly when at depth during the day (Figure 4A, median = 1.8 cm s^{-1}). Vertical velocities were approximately symmetrical around 0 (Figure 4B, median = −0.1 cm s^{-1}). Daytime swimming activity did not change appreciably over the 30-min record (Figure 5A). During dusk ascent, euphausiids moved more rapidly than while at depth during the day, particularly between 20:40 and
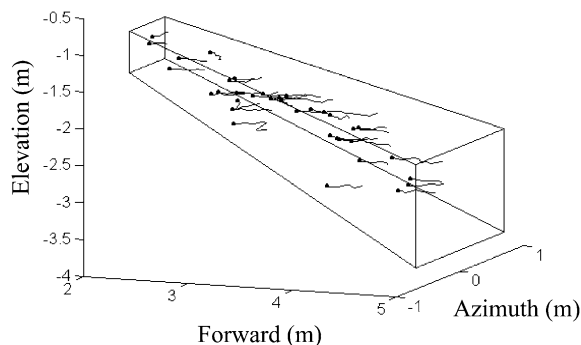
Figure 2. Tracks obtained over a 1-min period at 85-m depth during the day. The framed box demarcates the $4.3\,m^{-3}$ volume imaged, which was inclined at 27°. Lines represent the paths of individual euphausiids and the final position is indicated by a dot. The trajectories have not been corrected for the effects of water flow and exhibit correlated motions towards the stationary sonar, which is oriented into the flow by a current vane.

21:00 (Figure 5B, C). This peak in euphausiid activity coincided with elevated abundances of euphausiids observed by acoustic echo counting (Figure 5B, C, upper continuous lines). In all cases, most observed swimming speeds were substantially lower than the upper bound ($\sim26\,cm\,s^{-1}$) imposed by the tracking procedure.

In order to describe the major temporal changes in euphausiid swimming behavior at dusk, the 60-min dusk records were divided into 20-min periods designated here as early, peak, and late ascent. On both 11 and 12 August median speed was low during early ascent (1.4 and $1.3\,cm\,s^{-1}$, respectively), increased sharply during peak ascent (3.5 and $2.2\,cm\,s^{-1}$, respectively), and subsequently decreased (1.9 and $1.2\,cm\,s^{-1}$, respectively) during the late-ascent period (Figure 6). Speeds during peak ascent were higher than those observed during the day. Vertical velocity was low during early ascent, increased towards the surface during peak ascent, and returned to a more symmetrical distribution during the late-ascent period (Figure 7, Table 1). This indicates that most euphausiids ascending above 40 m did so during the 20-min peak period.

Few euphausiids were observed to move directly upwards or downwards during the day and at dusk. During
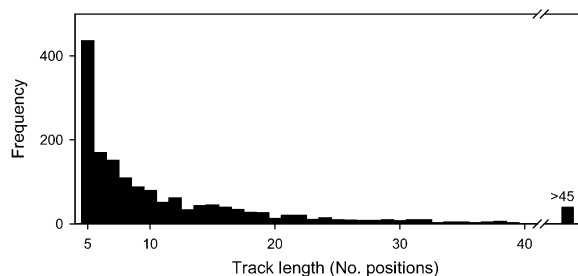

A.
n=2229

Frequency

TS <-86 dB
-86<TS<-81 dB
-81<TS<-66 dB

Swimming speed (cm s^{-1})
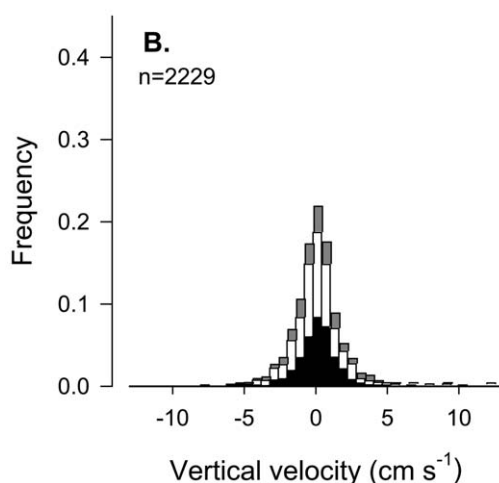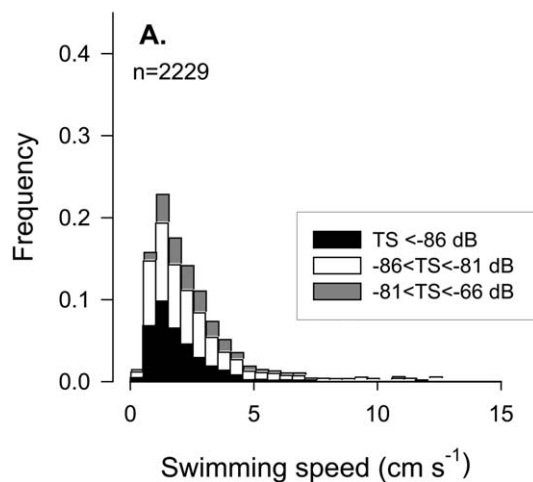
B.
n=2229

Frequency

Vertical velocity (cm s^{-1})

Figure 4. Histograms of (A) swimming speeds and (B) vertical velocities of euphausiids tracked during the daytime at 85-m depth. Tracked targets (n = 2299) are separated into three target-strength classes based on the maximum observed TS.

the daytime and all phases of dusk ascent, the swimming direction in the vertical plane differed significantly from the expectation under an isotropic swimming direction (G-test for uniformity, p < 0.001 in all cases). Compared to the daytime situation, more euphausiids were observed to move towards the surface during peak ascent, but few animals moved with steep angles towards the ocean surface (Figure 8). Only a small fraction (range 3.6–10.1%) of tracked euphausiids moved either up or down at angles within ±15° of the vertical during any phase of ascent and 5.0% of tracked euphausiids moved within ±15° of the vertical during the day. If the euphausiids did not exhibit a preferred swimming direction in the vertical plane, one would expect one-sixth or 16.7% of animals to swim at angles within ±15° of the vertical.

Figure 3. The distribution of track lengths for euphausiids tracked during the dusk ascent on 12 August 1996 (n = 1611).
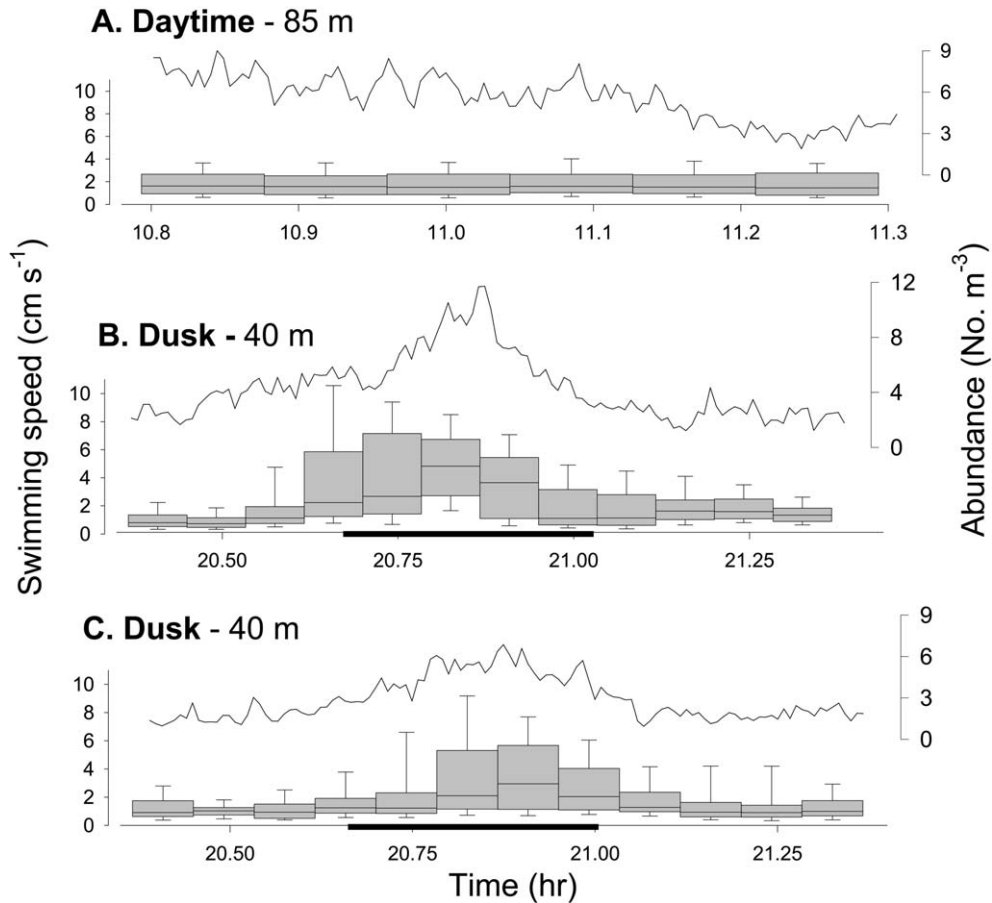
Figure 5. The temporal trends in euphausiid swimming speed during (A) daytime, and (B,C) dusk ascent into surface waters. Box plots demarcate the 10th, 25th, 50th, 75th, and 90th percentiles of observations over 5-min periods. Continuous lines and right-hand axes indicate the abundance of acoustic targets >-91 dB for each record. The heavy line along the abscissa demarcates the period defined as the peak ascent.

Swimming speeds during peak ascent were asymmetric (Figure 8), with those euphausiids moving towards the surface moving 1.5–1.8 times faster than those moving downwards (Table 1). Population ascent into surface waters was not synchronous: during peak ascent 60–70% of tracked euphausiids were observed to ascend towards the surface (Table 1), and many individuals moved quite slowly (Figure 7).

In all cases, size classes of acoustically-reflective targets corresponding to larger euphausiids moved more rapidly than lower TS targets (Figs. 4 and 7). In all deployments, the swimming speed was correlated with maximum TS (Figure 9, $p < 0.001$ in all cases), indicating that, on average, larger animals tend to move more rapidly although little of the observed variability was described by this relationship. Maximum TS of a tracked target was selected as an indication of body size in order to reduce the influence of animal orientation on TS (cf. McGehee *et al.*, 1998).

A total of 390 euphausiid targets of <-66 dB were tracked in the presence of acoustic targets >-66 dB corresponding to planktivorous fish. No fish were observed during the daytime deployment. In order to determine whether euphausiids alter their swimming behavior in the proximity of fish, the distance of each tracked euphausiid to the nearest fish was computed for all cases in which a target was tracked in the same acoustic image as a fish. Euphausiids in the immediate proximity of fish could not be tracked because acoustic backscatter from fish interfered with the tracking and localization algorithms.

On both dates (Figure 10A), the distance from a fish target was not correlated with euphausiid swimming speed ($p > 0.1$ in both cases). The net to gross displacement ratio (NGDR, Buskey, 1984) was used to characterize the degree of turning as a function of fish proximity. NGDR is the ratio of net displacement over a time interval to the total distance traveled. NGDR was not correlated with distance to the nearest fish target (Figure 10B, $p > 0.1$ in both cases),

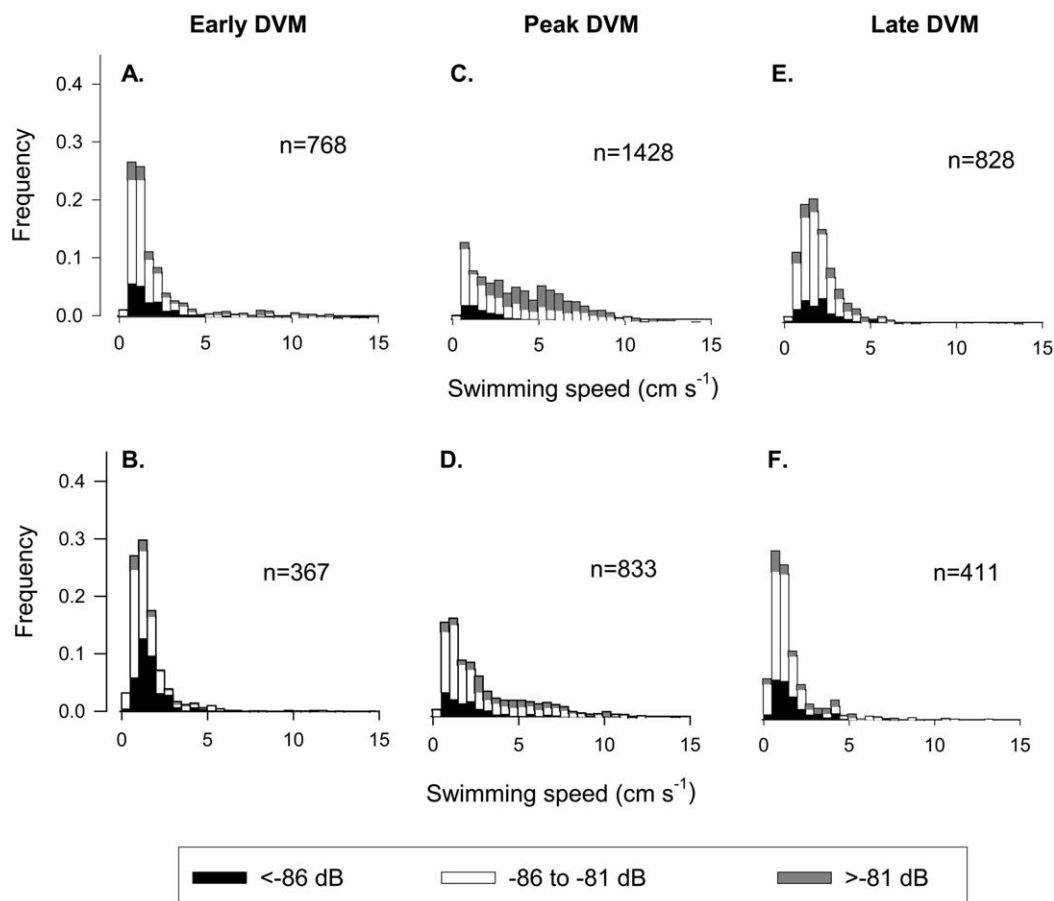**Early DVM**   **Peak DVM**   **Late DVM**

Figure 6. Histograms of 3D, euphausiid-swimming speeds during the dusk ascent. The 60-min records have been divided into three intervals, (A–B) 20:22–20:42 (early ascent), (C–D) 20:42–21:02 (peak ascent), and (E–F) 21:02–21:22 (late ascent). The upper row of plots is for 11 August and the lower row is for 12 August. The number of observations is indicated in each case. The tracked targets have been divided into three target-strength classes based on the maximum observed TS.

indicating that turning did not increase in the proximity of a predator. Taken together, net displacement and NGDR provide no evidence that euphausiids alter their swimming behavior at distances of 20–300 cm from a potential predator.

Discussion

The range of *E. pacifica* swimming speeds reported here is $\sim$0–17 cm s^{-1} or approximately 0–8 body lengths s^{-1}. These speeds compare favorably with previous reports of euphausiid swimming speed, which range between 0 and 10 body lengths s^{-1} (Table 2). However, most of the observations were at the lower end of this range, particularly during the daytime and prior to and after peak ascent (range of medians 1.2–1.9 cm s^{-1}). This reduced activity is consistent with previous OASIS estimates of daytime, *E. pacifica* swimming speed (0.3–1.2 cm s^{-1}, and 1.0–1.2 cm s^{-1} for records in 1996) based on target displacements in range (Jaffe *et al.*, 1999). As discussed in Jaffe,

et al. (1999), reduced swimming activity will confer two major advantages: reduced encounter rates with ambush predators and lower metabolic costs.

Swimming speed increased with TS, which, on average, increases with body size in euphausiids. The difference in swimming activity between animals of different sizes was more pronounced at dusk, indicating that larger animals move disproportionately rapidly during the dusk ascent. Our observations of size-dependent swimming speed and vertical swimming direction indicate that *E. pacifica* does not hover in place to maintain its depth during the day. Rather, most euphausiids swim slowly in oblique trajectories $<$60° from the horizontal plane. Median vertical velocity during the day was very close to 0 (-0.05 cm s^{-1}), indicating that this behavior could lead to a stable depth distribution of the population if individuals periodically reverse direction. Euphausiid vertical distributions during daytime are associated with isolumes (Boden and Kampa, 1965), and responses to light intensity are likely to control vertical position: when it is too bright, animals move

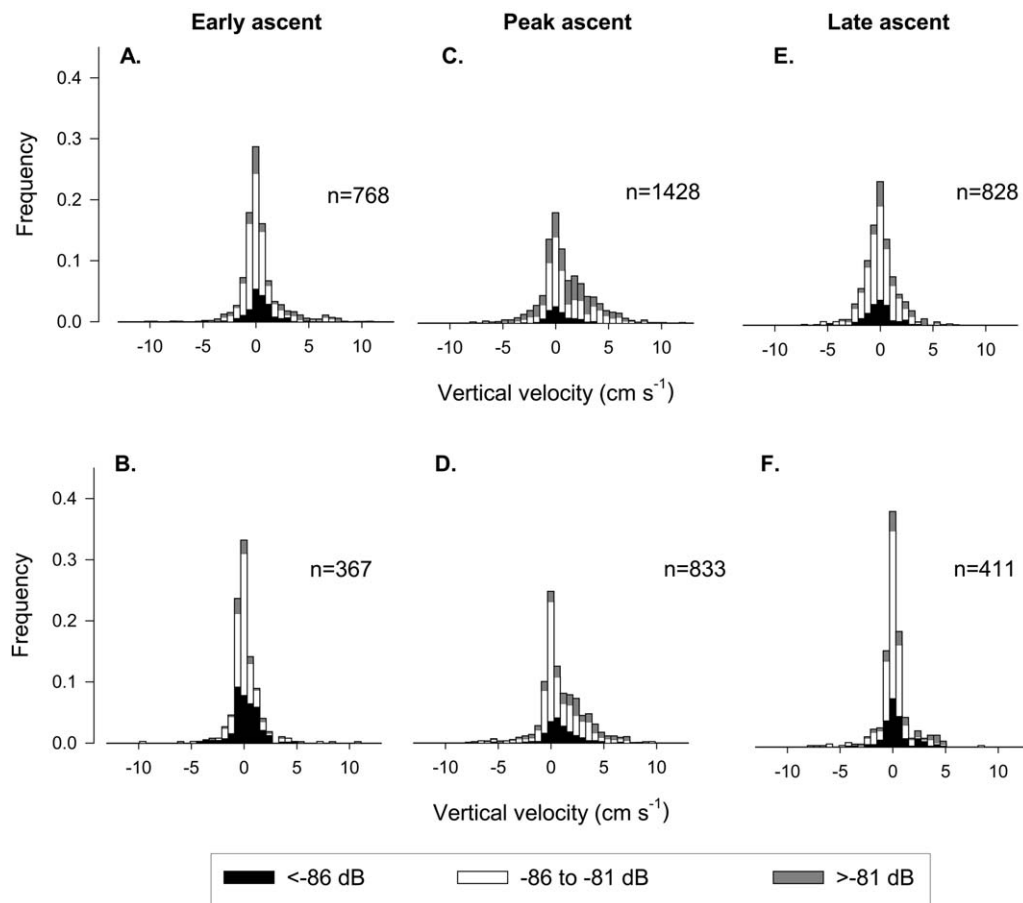**Early ascent**   **Peak ascent**   **Late ascent**

Figure 7. Histograms of euphausiid vertical swimming velocities during the dusk ascent. The 60-min records have been divided into three intervals, (A–B) 20:22–20:42 (early ascent), (C–D) 20:42–21:02 (peak ascent), and (E–F) 21:02–21:22 (late ascent). The upper row of plots is for 11 August and the lower row is for 12 August. The number of observations is indicated in each case. The tracked targets have been divided into three target-strength classes based on the maximum observed TS.

obliquely down, and when conditions are too dark, animals reverse course and ascend obliquely. Oblique swimming increases the time required between course corrections. Similar oblique swimming trajectories have been documented for the euphausiid *Thysanoessa raschii* responding to a stratified food layer (Price, 1989).

At dusk, the Saanich Inlet *E. pacifica* population overtakes the irradiance level with which it is associated during the day (Boden and Kampa, 1965). OASIS echo counts during the dusk ascents revealed that planktivorous fish were abundant with average densities of 9.2 and 3.0 fish $1000 \, m^{-3}$. This indicates that the ascending euphausiids were vulnerable to attack by visual predators at this time, but there was no evidence that the euphausiids altered swimming speed or direction when in the proximity of fish. Hence, although euphausiids may be able to assess overall predation risk by proxy, using cues such as light intensity or chemical signals (Forward and Rittschof, 1999), they may be unable to directly detect and avoid individual predators at spatial scales of 20–300 cm.

E. pacifica exhibited substantial variability in swimming behavior during ascent into surface waters. At any given time, a sizeable fraction of the animals was not ascending. During peak periods of dusk migration comparatively more animals moved in the $5-10 \, cm \, s^{-1}$ range, but a large fraction of the animals continued to move quite slowly. Animals moving upwards moved more rapidly than those moving downwards. Surprisingly, *E. pacifica* did not ascend directly into surface waters, but rather, ascended primarily obliquely at angles of $<\sim60°$ relative to the horizontal. Oblique ascents require euphausiids to swim further during vertical migration. Euphausiid swimming is hydrodynamically inefficient and energetically costly (Torres and Childress, 1983; Torres, 1984), and oblique vertical migration should elevate metabolic costs.

We hypothesize that the increased energetic cost of oblique migrations may be offset by a reduction in vulnerability to visual predators. Pelagic organisms contrast sharply with the bright background of downwelling light when viewed from below and are thus conspicuous to

Table 1. Swimming speeds and vertical swimming angles of *E. pacifica* during the daytime and during the dusk ascent. Dusk ascents have been divided into 20-min periods termed early, peak, and late ascent. Swimming angle is defined here as deviation of the swimming path from the horizontal plane ($-90°$ is straight down and $90°$ is directly upwards). Ascending euphausiids are defined as those with positive vertical velocities and those with negative vertical velocities are defined as descending. The binomial test was used to test the null hypothesis that 50% of the population was ascending (NS = $p > 0.05$, *$p < 0.05$, ***$p < 0.001$).

Record	n	Swim angle (degrees from horizontal) ($\bar{X} \pm SD$)	% Ascending	Swimming speed of animals ascending ($cm\,s^{-1}$) (median, 95% CI)	Swimming speed of animals descending ($cm\,s^{-1}$) (median, 95% CI)
Daytime 12 Aug 1996	2299	1.9 ± 42.3	48.0 (NS)	1.6 (1.5–1.7)	2.0 (1.9–2.1)
Early ascent 11 Aug 1996	769	3.0 ± 41.7	52.8 (NS)	1.5 (1.4–1.7)	1.3 (1.2–1.4)
Early ascent 12 Aug 1996	367	-0.3 ± 40.4	46.3 (NS)	1.5 (1.3–1.6)	1.2 (1.1–1.3)
Peak ascent 11 Aug 1996	1429	12.5 ± 37.6	63.0 (***)	3.9 (3.7–4.2)	2.6 (2.3–3.0)
Peak ascent 12 Aug 1996	834	18.9 ± 38.7	67.8 (***)	2.5 (2.3–2.7)	1.4 (1.3–1.7)
Late ascent 11 Aug 1996	832	-1.3 ± 44.5	47.1 (NS)	1.9 (1.8–2.0)	1.8 (1.7–2.0)
Late ascent 12 Aug 1996	410	3.9 ± 40.8	54.9 (*)	1.2 (1.1–1.3)	1.2 (1.1–1.3)

upward-looking visual predators (Muntz, 1990; Thetmeyer and Kils, 1995). All but one species of euphausiid possess ventral photophores, which produce downward-directed luminescence and are thought to camouflage the dark silhouette of the body from upward-looking predators (Clarke, 1963, Herring and Locket, 1978). However, counter-illumination can only be maintained while the luminescent organs point downwards, in the same direction as the downwelling light. By avoiding steep swimming trajectories, *E. pacifica* may avoid body orientations that compromise the effectiveness of counter-illumination during ascent.

Some pelagic organisms have adaptations that serve to keep photophores pointed downwards over a range of swimming directions. Hatchetfish can keep their body horizontal and photophores pointed down while swimming upwards or downwards (Janssen *et al.*, 1986). Euphausiid photophores are capable of rotating almost 180° in the dorso-ventral plane (Hardy, 1962), and counter-rotate relative to the eyes, which orient towards a directional light source (Land, 1980). In nature, this mechanism will orient the eyes upward towards the downwelling light and the photophores downwards over a range of body orientations. In the decapod shrimp *Sergestes similis* downward-directed light emission is greatest for horizontal body orientations, and decreases with increasing body angle (Latz and Case, 1982). Compensation for body tilt is asymmetric: when inclined 90° upwards, 15% of maximal emission is directed downwards, while for the 90° downward orientation, luminescence is 56% of the maximum. Although analogous measurements have not been made on euphausiids, it is likely that the effectiveness of photophore rotations decreases at steep-body orientations.

In Saanich Inlet, *E. pacifica* consistently avoided swimming trajectories that deviated greatly from the horizontal, even during dusk ascent. Although *E. pacifica* avoided swimming at steep vertical angles, analysis of video footage from a submersible dive (Alvin dive 3202 in the San Diego Trough) indicates that euphausiids have the physiological capability to swim directly upwards. Some of the euphausiids (suspected to be *E. pacifica*) at 270-m depth at 12:30 local time were observed to ascend directly upwards as they followed the lights of the ascending submersible.

It is important to recognize that the angle of euphausiid body orientation relative to the horizontal is not equivalent to the angle of swimming displacements. Euphausiids are denser than seawater and must orient their bodies upwards relative to the horizontal to create hydrodynamic lift to avoid sinking (Kils, 1981). The body angle required to overcome sinking decreases with swimming speed. For example, a 49 mm Antarctic krill requires a body angle of 55° to hover, while a body elevation of 10° is sufficient to compensate for gravity if the animal moves at $10\,cm\,s^{-1}$ (Kils, 1981). In the laboratory, active *E. pacifica* swim with body angles of $15 \pm 24°$ relative to the horizontal and hover at body angles of $37 \pm 13°$ (Miyashita *et al.*, 1996). Euphausiids can thus increase their swimming angle by increasing either their body angle or their swimming speeds. While ascending, *E. pacifica* avoided steep trajectories and exhibited asymmetric swimming speeds with animals moving upwards swimming about 1.5 times faster than those moving downwards. Thus, the increased vertical swimming angle observed during ascent can be attributed at least in part to increases in swimming speed as well as changes in body orientation. Our observations of oblique swimming trajectories are consistent with laboratory and field observations that euphausiids avoid body orientations that deviate greatly from the horizontal such as directly upwards or downwards (Kils, 1981; Hamner *et al.*, 1983; Price, 1989; Miyashita *et al.*, 1996).

There are certainly other possible explanations for the observed oblique swimming trajectories. The simplest of these is that the euphausiids orient to gravity or to light (Land, 1980; Kils, 1981), but do not produce downward-directed luminescence. In addition, if the euphausiids rotate
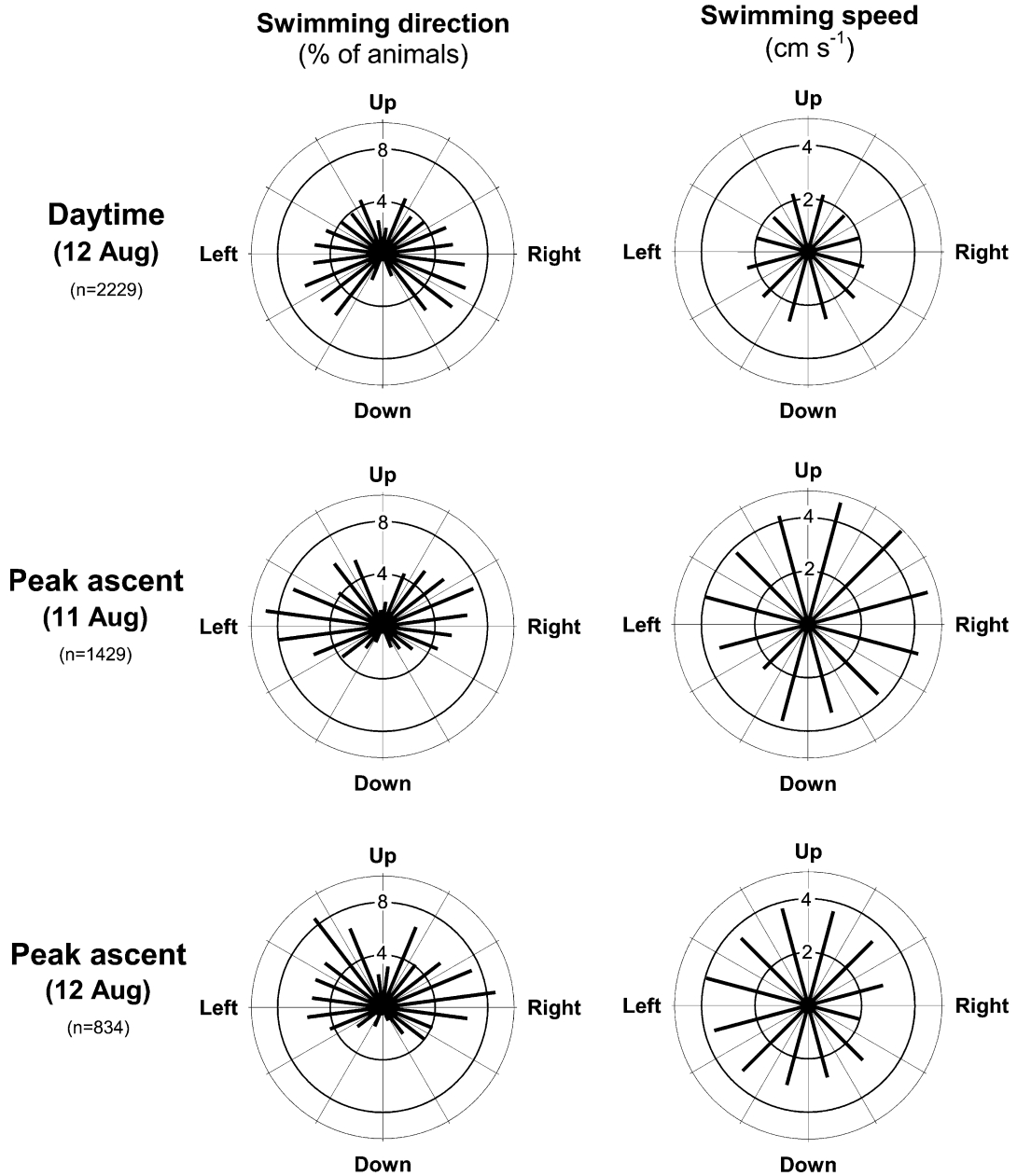
Figure 8. Euphausiid vertical swimming direction and swimming speed during daytime at depth and during the peak 20 min (20:42–21:02) of dusk ascent on 11 and 12 August. Swimming direction is defined as the vertical angle of the swimming path relative to the horizontal plane. The length of each line in the direction plots represents the percentage of animals swimming in a given direction (15° bins), and the direction of each line indicates the swimming angle relative to the horizontal dimension. The contours indicate 4 and 8% of tracked individuals. The length of the lines in the speed plots (30° bins) represents the mean speed for euphausiids observed to move in that direction. The contours indicate swimming speeds of 2 and 4 cm s^{-1}.

around the anterior–posterior axis as they swim, as has been observed for euphausiids responding to submersible lights (Widder *et al.*, 1992), the ventral photophores would not always point downwards, and bioluminescent counter-shading could not be maintained. This type of body rotation, which is inconsistent with counter-shading, cannot

be resolved with the tracking methods described in this study.

One of the primary assumptions of the approach employed here is that uncorrelated motions reflect swimming motions. If the euphausiids formed schools or swarms, their swimming trajectories would include a sizable correlated

A. y=0.06*x+7.51 r²=0.03

A. y=0.06*x+7.51 r^2=0.03

B. y=0.24*x+22.98 r^2=0.13

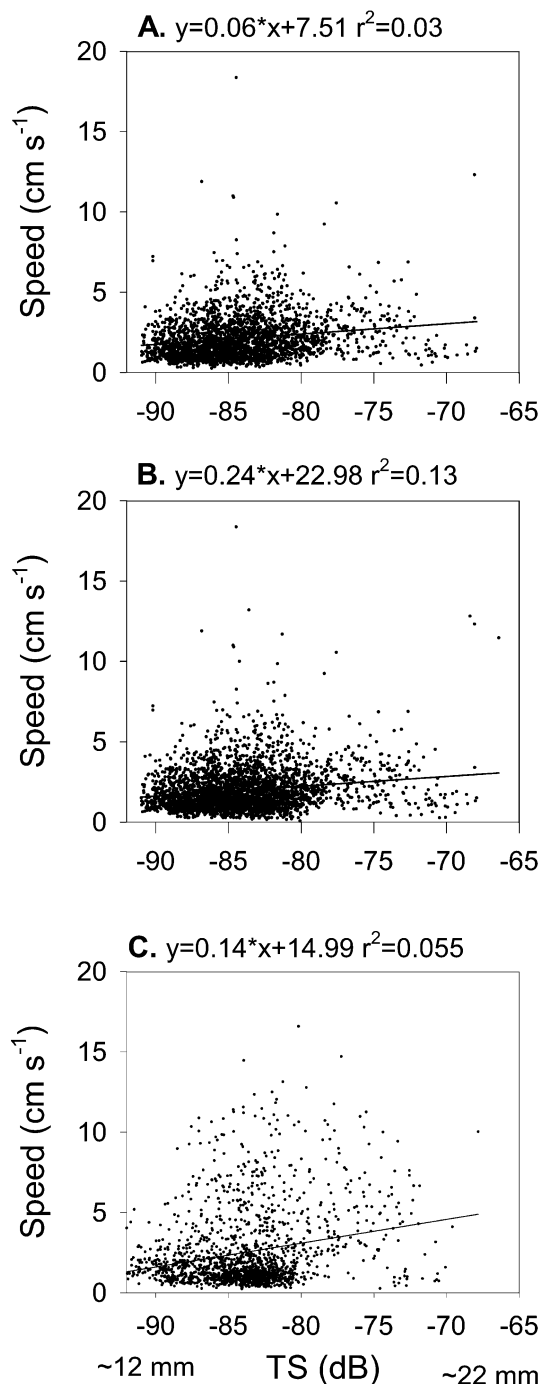**C.** y=0.14*x+14.99 r^2=0.055

~12 mm   TS (dB)   ~22 mm

Figure 9. Swimming speed as a function of the maximum-observed TS for euphausiids tracked during (A) daytime and (B–C) the dusk ascent.

component and their swimming behavior would be under-estimated. Although *E. pacifica* is known to form social aggregations in other environments (Mauchline, 1980; Hanamura *et al.*, 1984), analysis of *E. pacifica* spatial
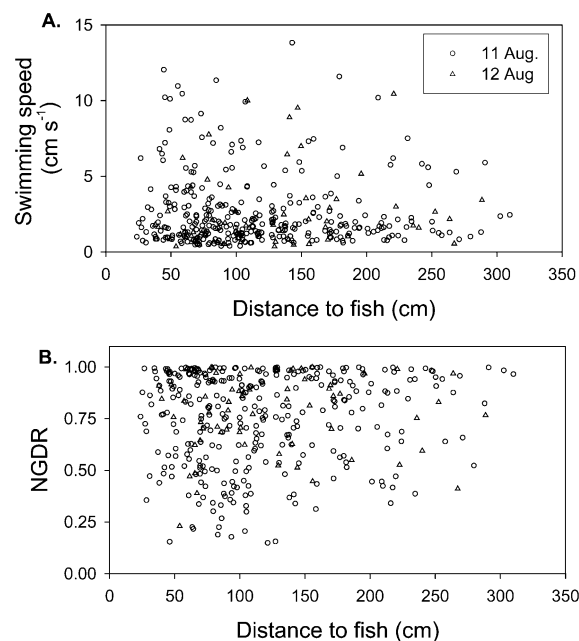
Figure 10. Euphausiid swimming behavior as a function of fish proximity. (A) Swimming speed as a function of distance to a fish. (B) Net to gross displacement ratio (NGDR) as a function of distance to a fish. NGDR is the ratio between the net displacement over a time interval and the total distance traveled.

distributions made concurrently with these measurements (De Robertis, 2002) indicate that the euphausiids did not engage in social behavior.

The motions of the tracked euphausiids were corrected for the influence of current flow and instrument rotation. However, any inadequacies in procedure used to remove the effects of instrument motions and currents in the horizontal plane will likely attribute some of these motions to animal swimming. If horizontal swimming motions are consistently overestimated relative to vertical motions, vertical swimming angles will be biased towards the horizontal. Numerical simulation of this bias indicates that for animals with isotropic swimming directions, the horizontal components of motion would have to be over-estimated by 150–430% relative to the vertical component in order to account for the observation that 10.1–3.6% of animals had swimming trajectories within ±15° of the vertical. Thus, this effect is unlikely to account for our observations of oblique, euphausiid swimming trajectories.

In Saanich Inlet, *E. pacifica* may be particularly vul-nerable to visual predation because visual predators are abundant and the euphausiids are associated with irradiance levels two or three orders of magnitude more intense than those experienced by the same species in more oceanic environments (Boden and Kampa, 1965). Moreover, they appear to be unable to detect the presence of potential predators and are therefore likely to be surprised by them. However, despite the apparent inability to locate and avoid

Table 2. Previous reports of euphausiid swimming speed. Measurements are for routine swimming and do not include the more rapid escape responses. When speeds of adults were measured but body size was not reported the mean adult body size from Brinton *et al.* (1999) was used to normalize swimming speed to body length (BL). These body lengths are indicated in parentheses. Measurements are for unaggregated individuals unless indicated.

Species	Statistic	Method	Body length (mm)	Swim speed (cm s^{-1})	Swim speed (BL s^{-1})	Source
Euphausia pacifica	Range (n = 6845)	3D acoustic tracking	~12–22	0–17	0–8	This study
Euphausia pacifica	Median	3D acoustic tracking	~15	1.8 (day) 1.2–3.5 (dusk)	0.8–2.3	This study
Euphausia pacifica	Mean	1D acoustic tracking	~15	0.3–1.2	0.2–0.8	Jaffe *et al.* (1999)
Euphausia pacifica (swarming)	Mean	Diver estimate	16.5	8–10	4.8–6.1	Hanamura *et al.* (1984)
Euphausia pacifica	Range (n = 62)	Aquarium video record	16	0–9	0–5.63	Miyashita *et al.* (1996)
Euphausia pacifica	Range (n = 34)	Experimental chamber	14–17	0–9.7	0–6.25	Torres and Childress (1983)
Euphausia americana	Mean ± SD	Aquarium video record	12	4.9 ± 1.7	4.1	Land (1992)
Thysanoessa inermis	Range (n = 3)	Plankton wheel	Adult (28)	1.1–3.46	0.4–1.2	Hardy and Bainbridge (1954)
Thysanoessa raschii	Mean (n = 30)	Mesocosm video record	Adult (22)	2–4.5	0.9–2.1	Price (1989)
Euphausia superba	Mean	Aquarium video record	45–50	5–6	1.1	Kils (1981)
Euphausia superba (schooling)	Max	Drop camera	35–55	18–45	5.1–8.2	Kils (1981)
Euphausia superba (schooling)	Max	Diver estimate	~36	20–40	5.5–11.1	O'Brien (1987)
Euphausia superba (schooling)	Mean (n = 50)	Mesocosm observation	48	9–17	1.9–3.5	Strand and Hamner (1990)
Meganyctiphanes norvegica	Range (n = 6)	Plankton wheel	Adult (34)	2.6–6	0.8–1.8	Hardy and Bainbridge (1954)
Unidentified euphausiid (likely *Euphausia pacifica*)	Max	Submersible video record	Adult (~18)	8.9, 16.3	5.0–9.1	M. Ohman (unpublished)
Various species	Range	Aquarium film record	Adult (13–32.5)	1.0–17.6	0.6–11.5	Ignatyev (1997)

planktivorous fish, euphausiids are able to minimize the risk of encountering predators by remaining inconspicuous. Behaviors such as DVM and bioluminescent camouflage that reduce the probability of detection by visually orienting predators may thus be at a premium in such comparatively high-risk environments.

Acknowledgements

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