

Light-cued Emergence and Re-entry Events in a Strongly Tidal Estuary

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ABSTRACT: Acoustic backscatter from an active sonar system (TAPS-6) over a range of six frequencies between 265 kHz and 3 MHz revealed characteristics of emergence and reentry events within 1 h of sunset and sunrise, respectively, at a site 10 m deep in the Damariscotta River estuary, Maine. Emergence traps indicated that the mysid shrimp *Neomysis americana* was the dominant migrator. Daily fluctuations in irradiance influenced the timing of dusk emergence. Local variability in irradiance apparently caused populations to emerge occasionally before sunset or to leave the surface after the beginning of nautical twilight near dawn. Emergence before sunset was marked by slower-than-average ascent, and departure from the surface after initiation of nautical twilight was marked by faster-than-average descent. This pattern would be expected for populations avoiding visual predators by concealment in dark waters. Mean ascent ($0.29 \pm 0.03 \text{ cm s}^{-1}$ [$\pm 1 \text{ SE}$]) and descent ($-0.26 \pm 0.02 \text{ cm s}^{-1}$) velocities showed little difference in magnitude, suggesting that a similar mechanism controls both. Ascent initiation times for the first such event of the night were consistent with a cue based on relative rate of change in light intensity and inconsistent with either the progress of isolumes or with absolute rate of change in light intensity.

Introduction

We use the term emergence to denote objectively determined, regular migration events of infauna or epifauna higher into the water column. We call the return migration reentry. The existence of emergence has been known for a long time (e.g., Herman 1962; Alldredge and King 1980), but the geographic distribution and timing of such events have not been widely quantified. Our definition and most others depend on the method of detection and on the algorithms applied to define an emergence event, a point that we make in this paper and its companion (Taylor et al. 2005) by using two different detection algorithms on the same data records. The algorithm in this paper detects the first emergence and last reentry of the night, whereas the companion paper's detects initiation time of the largest emergence event of the night or day.

Emergence is important for a number of reasons. One is its fundamental role in benthic-pelagic coupling. Emergent organisms often feed during their pelagic excursions (Lasenby and Langford 1973; Fulton 1982a,b). In so doing, they enhance their own exposure to both demersal and pelagic predators. Emergent species are often major dietary items for fishes and larger invertebrates (e.g., Mauchline 1982; Pihl and Rosenberg 1984). They also can be involved in benthic-pelagic coupling in a more subtle, indirect manner by enhancing

sediment resuspension (Roast et al. 2004). Emergence also plays a role in dispersal; it is notable that many emergent species (i.e., peracarid crustaceans) lack dispersing larval stages. Because individuals in general do not return to the spot that they leave, emergence decreases static stability of benthic community structure but also lends some dynamic stability; recovery of local emergent populations does not await a seasonal recruitment event. Emergence may also have substantial effects on the propagation of sound. Emergers can dominate volume reverberation of the entire shallow water column at high frequencies (Kringel et al. 2003). It is this feature that we exploit in recording their behaviors. More subtly, emergent organisms, especially those that bury themselves during the day, can influence sound propagation into sediments through their effects on surface roughness (Richardson et al. 2001). Emergence and reentry are underappreciated components of bioturbation.

Correlations of vertical migrations with irradiance and its time variation are well known (e.g., Foxon 1939; Forward 1976, 1988; Alldredge and King 1980; Gal 1999). Several hypotheses address the specific light-mediated mechanisms that cue emergence. Three hypotheses involve changing characteristics of light during twilight: the preferendum or isolume hypothesis, the rate of change hypothesis, and the relative rate of change hypothesis. The preferendum or isolume hypothesis (Russell 1927) postulates a specific irradiance (E), or isolume, that migrating organisms track in their movements through the water column. The rate-of-change

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hypothesis (Clarke 1930) postulates that emergence is triggered by a particular rate or duration of change in ambient light intensity (ΔE) from the ambient intensity (the adaptation intensity) serves as the cue to emerge. A third hypothesis speculates (Ringelberg et al. 1967), given some level of adaptation to ambient intensity, that the cue may better be described by the relative rate of change in light intensity ($\Delta E/E$).

Acoustic methods recently have changed spatial and temporal resolution of emergence events and the ability to test these hypotheses in the field. Kringel et al. (2003) found striking regularities in group vertical migration speeds and times at a 20-m deep site in Puget Sound, Washington, United States. That site has high tidal range (2 m) but modest tidal velocities (ca. 2.5 cm s^{-1}). Using a six-frequency acoustic backscatter device, we examined a site half as deep in the Damariscotta River estuary, Maine. Typical current speeds are an order of magnitude greater and tidal range is 50% greater than at the Puget Sound site. This paper examines the timing of the first emergence event that begins near sunset and its consistency with alternative hypotheses regarding the cues used by animals for emergence. The timing of this first emergence event of the night proved inconsistent with both irradiance and rate of change of irradiance as timing cues but consistent with relative rate of change of irradiance. Despite high tidal velocities, group migration velocities in both emergence and reentry were consistent and substantially slower than those observed at a deeper site with slower flows in Puget Sound.

Materials and Methods

This study was conducted at 10 m depth (mean lower low water) in the Damariscotta River estuary, in the vicinity of the University of Maine's Darling Marine Center campus in Walpole, Maine ($69^{\circ}34.9'W$, $43^{\circ}56.1'N$). Because of strong tidal exchange (tidal excursion approximately 3 m) and limited freshwater input ($0.63 \times 10^5 \text{ m}^3$ per tidal period in mid summer; McAlice 1993), water properties closely resemble those of nearby coastal seawater. By most criteria, the site behaves as though in a shallow coastal fjord rather than a river. Average tidal velocities fall near 25 cm s^{-1} (Mayer et al. 1996). Strong tidal currents and the relatively shallow depth (10 m) at the study site promote a tidally-mixed, fairly homogenous water column. Generally, the water is very turbid (attenuation coefficient, $k = 0.51 \text{ m}^{-1}$ at 10 m; Mayer et al. 1996). Bottom type varies along the 29-km long river, from rock and gravel to primarily sand and silt. Bottom type at the study site is silty sand. Water temperatures range from 1°C in February to 18°C in

September. Diatom blooms occur on the bottom (10 m) in spring and fall (Abello and Shellito unpublished data), but microelectrode observations revealed no net production of oxygen at the 10-m deep seabed during mid summer (Vopel and Thistle unpublished data).

Four replicate 1-m² emergence traps with 1-mm mesh (of the same design used by Kringel et al. 2003) were placed in the vicinity of the study site several times per week from May to December 2001 and June to November 2002 (daily from May through October 2002). To restrict contamination with plankton, traps were lowered by hand with the base perpendicular to the seafloor, then pulled upright upon reaching bottom. Collection bottles were changed daily, with emergent animals fixed in 4% formaldehyde and stored in 70% ethanol. *Neomysis americana* was divided into stages following Mauchline (1980). Males were classified by elongated fourth pleopods, females by the presence of a brood pouch, either empty or containing various stages of young, and juveniles by having none of these sexual characteristics.

Acoustic records were collected using two TAPS-6 units (Tracor Acoustic Profiling System, BAE SYSTEMS, San Diego, California). No more than one was operated on a given date in this study. TAPS was mounted in a metal frame, placed on the seafloor at the study site by divers, and positioned looking upward toward the air-water interface. Transducers at six frequencies (265, 420, 700, 1,100, 1,800, and 3,000 kHz) pinged simultaneously 24 times and integrated backscatter (S_v , in dB) over either 1-min or 2-min intervals, at each 12.5-cm depth bin in the water column above TAPS. As the height of the water column changed with the tides, so did the number of depth bins recording backscatter. We made extensive use of Matlab software (The Mathworks, Massachusetts) to process the voluminous acoustic data. Routines or M-Files are ASCII files written in the Matlab programming language and hereafter are specified as filename.m. All of them may be downloaded from <<http://www.marine.maine.edu/~jumars/preprints/Appendix.pdf>>.

Local tide height was determined as the middle of the range bin with the highest mean backscatter intensity across frequencies (tideline.m). Set by the position of TAPS in the frame, the transducers were approximately 1 m above the seafloor, and the average height of the water column above the transducers was 9 m.

We processed raw backscatter voltages cumulated over the 24 pings for each depth bin, frequency, and time with the program makermt.m (courtesy Charles Greenlaw, BAE SYSTEMS, San Diego, California). We applied manufacturer-determined calibration constants and corrections for beam

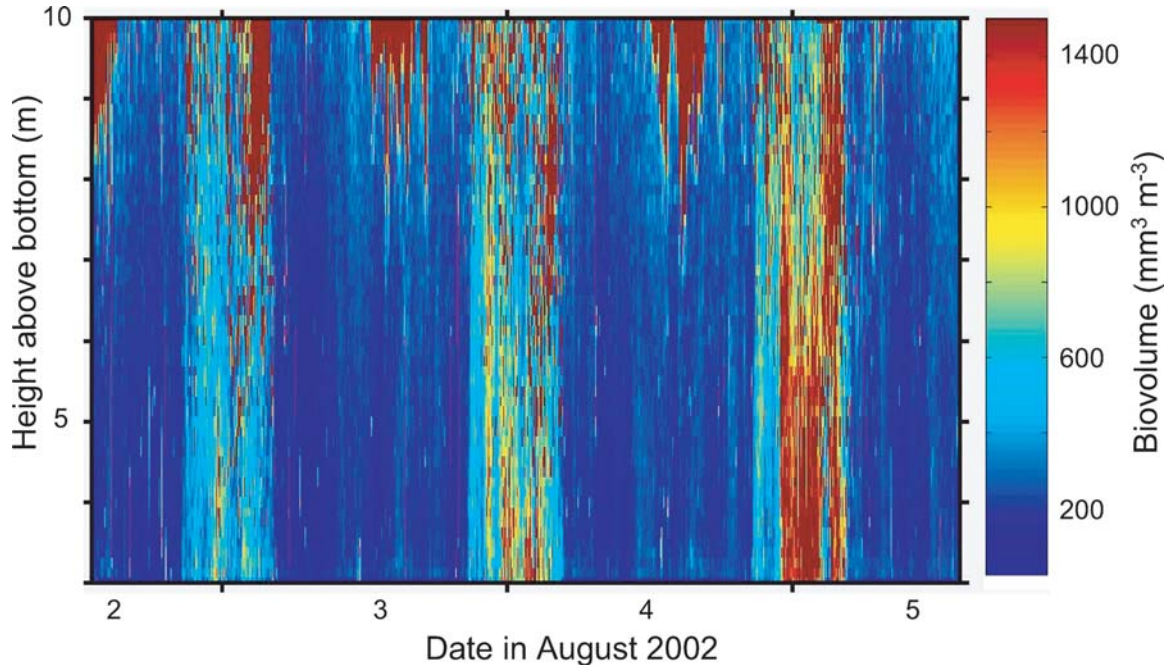


Fig. 1. Calculated biovolume versus height above the sediment for August 2–5, 2002. Due to ringing of the transducers and metal frame, the deepest reliable measurement is at 2 m above TAPS or 3 m above the bottom. Water depth varies with tidal phase, but the plot has been truncated uniformly at 10 m above the bottom. Tick marks are at midnight, local time (EDST). Daytime red pixels extending downward from the surface at this season do not reflect accurate biovolumes. They arise from a combination of injected bubbles from seabreeze-generated whitecaps and surface-schooling fishes. Over much of the water column a background biovolume of $200 \text{ mm}^3 \text{ m}^{-3}$ is observed during the day. Note the night-to-night variability over the three dates.

spreading in the first steps of processing, but they appeared to underestimate its vertical extent. We included an additional algorithm (`nospread.m`, written by the authors) to remove the otherwise persistent vertical gradients in backscatter. Acoustic ringing of the metal frame contaminated the lowermost 2 m of the record in some of the frequencies, so we eliminated backscatter data within 2 m of the transducers (within 3 m of the seafloor). Using an equivalent spherical radius model (Greenlaw and Johnson 1982, 1983) and taking into account the temperature and salinity of the water (`makets.m`, `invsndr.m`; courtesy of Charles Greenlaw, BAE SYSTEMS), we inverted those smoothed backscatter data to biovolume ($\text{mm}^3 \text{ m}^{-3}$). For several reasons we did not resort to more complex inversions that involve elongate shapes. Spherical inversions are remarkably robust (when converted to equivalent volumes of the real body shapes involved; Greenlaw and Johnson 1983; Pieper and Holliday 1984). Elongate-body models (e.g., McGehee et al. 1998) require observations or assumptions about animal orientation that we had little basis to make for mysids. Moreover we were more interested in timing issues of emergence than absolute biovolumes. In this analysis, we used only the sum of the biovolume across all size

classes or total biovolume (Fig. 1). We 19-point median smoothed (`smoothdata.m`) these processed biovolume data in time from 3 m above bottom to the surface.

For each depth bin, we calculated backward differences in total biovolume and transformed to percentages $[(100 \times (\text{time}_2 - \text{time}_1)) / \text{time}_1]$. To determine initiation times of emergence events, we plotted all points within 1 h of sunset that had increases in total biovolume of at least 20% from the previous minute (`findfirstpm.m`). Whenever this method located at least three points, we fitted a straight line to them via least-squares regression. If the slope differed significantly from zero, we extrapolated to find the intercept with the bottom (0 m) to yield time of emergence. Group ascent speeds were estimated from the slope of the line. To calculate time of reentry, we reversed this procedure (`findlastam.m`), fitting a line to points within 1 h of morning civil twilight (the time at which the sun is 6° below the horizon) that had decreases of at least 20% from the previous minute (`findlastam.m`). This method yielded a cluster of points during the night but few points after onset of civil twilight (Fig. 2). Analogous with the emergence-time estimate, we used the last of 20% decreases in a depth bin for the regression. It could be argued that time of leaving

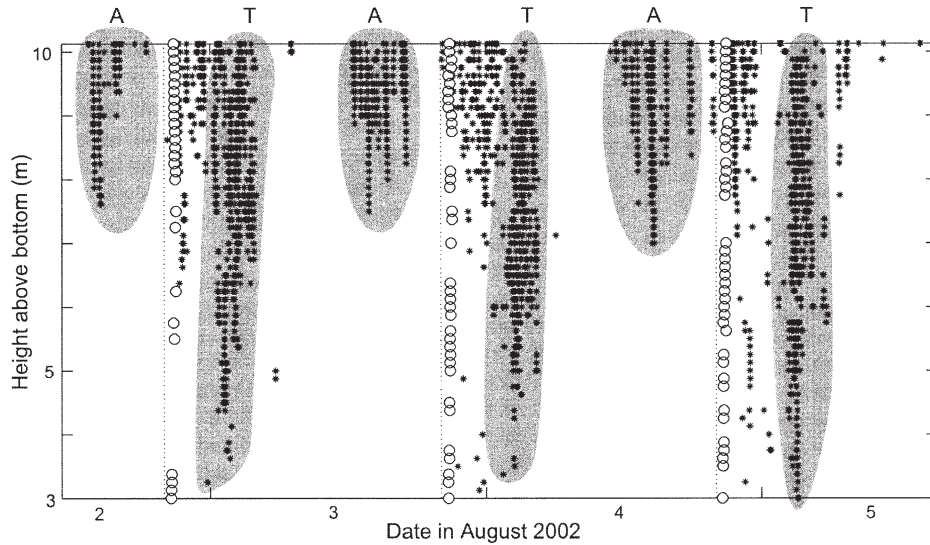


Fig. 2. Points (asterisks or white-filled circles) are plotted where in depth and when in time there is $\geq 20\%$ increase in acoustically estimated biovolume ($\text{mm}^3 \text{m}^{-3}$) from the prior minute at the same depth. Note that the same three days are displayed as in Fig. 2. Tick marks on the abscissa are positioned at midnight. The white-filled circles are the subset of points identified iteratively by the `findfirstpm.m` algorithm (see text) as belonging to the first emergence event of the night and were used to find both time of emergence (extrapolated intercept with zero distance above bottom) and rate of ascent (slope of the regression through these points). Dotted vertical lines are added to help visualize that, although they are very steep because of the time compression in the plot, the circles do not fall on a perfectly vertical line. Analogous procedures using a criterion of $\geq 20\%$ decrease near sunrise were used to determine re-entry times and descent speeds (not shown). Even more dramatic, tidally cued emergence events (T-labeled gray regions) are evident as dense arrays of points after midnight and are the subjects of the companion paper (Taylor et al. 2005). Afternoon, near-surface clusters of points (A-labeled gray regions) are due to combined effects of bubble injection during afternoon seabreezes and near-surface fish schooling (largely of juvenile alewives, *Alosa pseudoharengus*).

the surface is a more logical standard for the downward migration than is time of reaching the bottom. Noise near the surface (backscatter from the interface) and the need to define the interface in the acoustic signal makes this approach more difficult. Times of sunset and civil twilight were taken from tables http://aa.usno.navy.mil/data/docs/RS_OneYear.html for our local latitude and longitude. We applied this procedure to all of the days for which there were data, from July to October 2002. The method yielded 28 estimates of emergence times and velocities and 34 such estimates for reentry.

The first date in 2002 for which emergence and reentry algorithms yielded points was July 19. Set by instrument failure, the last day of the study was October 9. Data from another TAPS-6 instrument deployed in 2002 suggested that vertical migration continued past this date, and in 2001, vertical migration could be observed into November. Acoustic data from September 15 and September 26 to October 8, 2002 were recorded at 2-min intervals, and the remainder of the days in the period were recorded at 1-min intervals.

To test the hypothesis that diel vertical migration is modulated by a light cue during twilight, we correlated emergence and reentry times with

times of sunset and sunrise, respectively, for July to October 2002. To avoid assumptions of binormality, we used Spearman's ρ as a measure of correlation (Conover 1999). The square of this measure is analogous to the square of Pearson's product-moment correlation coefficient, but is an estimate of the proportion of the variance in the ranks of one variable that can be explained by variation in ranks of the other.

To better identify the cue used, surface PAR (photosynthetically active radiation, 400–700 nm, Licor 190SA) was averaged over 1-min intervals from continuous data. The nominal threshold of the instrument was $10^{-4} \mu\text{mol quanta m}^{-2} \text{s}^{-1}$, but in order to avoid contamination by the dark current (electronic noise) of the instrument, no value below $10^{-2} \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ was used. Near-bottom PAR measurements were made (400–700 nm, Biospherical Instruments QCP-200) at the height of TAPS (1 m above the seabed) from September 25 to October 9, 2002, also recording continuous data, averaged over 1 min. Isolumes were modeled with Beer's law and inputs of measured surface PAR ($\text{PAR}_{0\text{m}}$) and $k = 0.5 \text{ m}^{-1}$ for 1-m intervals from just below the water surface to 10 m ($\text{PAR}_{10\text{m}}$), where k is the extinction coefficient. Absolute rate of change of irradiance over time and depth was modeled

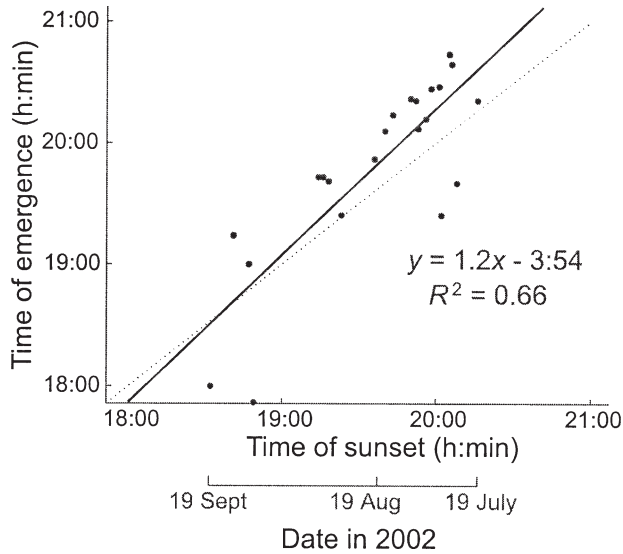


Fig. 3. Time of emergence versus time of sunset. As the sun set earlier (closer to the origin) during July–October 2002, emergence times trended similarly. The dotted line would indicate perfect coincidence and a slope of unity. Although the best-fit line (solid black) does not differ significantly in slope from the dotted line, a majority of emergence events falls above it; most—but not all—emergence events occurred after sunset. Note that the magnitude of the intercept in the equation (h:min) results from extrapolation of the solid line to a time of 0:00 on the abscissa and that x in the equation is measured in decimal hours after midnight (e.g., 18.3 h).

using a backward-difference approximation for the derivative, i.e., for each 1-m depth interval of data modeled as described above, the absolute rate of change was the difference in irradiance at time₂ – irradiance at time₁, divided by 1 min (60 s), in units of $\mu\text{mol quanta m}^{-2} \text{s}^{-2}$. The relative rate of change of irradiance was the absolute rate of change at each minute divided by the irradiance at time₁, in units of inverse seconds. Instantaneous comparisons were made between the time of emergence and the absolute irradiance, absolute rate of change of irradiance, and relative rate of change of irradiance. Rates of change at the time of emergence are generally negative, indicating decreasing irradiance. Reentry began much earlier than the same threshold of surface PAR was reached, so no correlation with absolute or relative rate of change was made.

Results

Daily emergence-trap samples from May to October 2001 were dominated by mysid shrimp, *N. americana*. In 2001, *N. americana* accounted for 93% of individuals of all species caught in the emergence traps. Both sexes of *N. americana* were present in the traps; at times, various females were present with all three distinct stages of brood pouches: eggs, eyeless

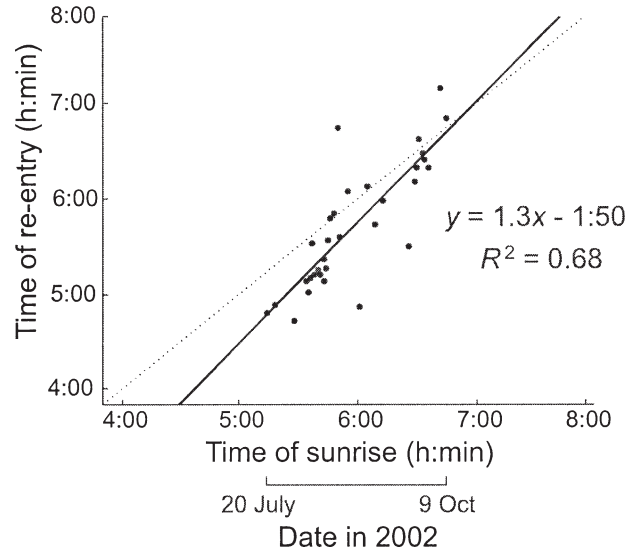


Fig. 4. Time of reentry versus time of sunrise. As sunrise trended later from July–October 2002, so did reentry. The dotted line would indicate perfect coincidence and a slope of unity. Although the dotted line approximately bisects the cloud of points, the best-fit line (solid black) has a significantly steeper slope; earlier in the season (closer to the origin), reentry more uniformly occurred before sunrise.

larvae, and eyed larvae. Juvenile *N. americana* (no secondary sexual characteristics) were always the most abundant; in 2001 juveniles composed 59% of the total number of *N. americana* individuals. Also present in the traps, but accounting for a total of only 7% of all individuals caught, were individuals of the larger mysid shrimp *Mysis mixta*, the seven-spined bay shrimp *Crangon septemspinosus*, cumaceans, amphipods, hydromedusae, and polychaetes. Although samples from 2002 have not been counted in their entirety, they also were clearly dominated by *N. americana* (Abello unpublished data). Initiation times of emergence events and times of sunset were correlated ($p^2 = 0.67$, $p < 0.001$; Fig. 3), as were times of reentry and sunrise ($p^2 = 0.74$, $p < 0.001$; Fig. 4). As determined by significant regressions, emerging populations left the seabed after sunset on only 68% of nights. Emergers left the seabed an average (± 1 SE; $n = 28$) of 2 (± 7) min after sunset throughout the study period (earliest = 1 h 17 min before sunset, latest = 39 min after sunset). Here and elsewhere in this paper, SE refers to the standard error of the mean. Migrators reached the surface an average of 15 (± 7) min after the end of nautical twilight (n.t.)—the time at which the sun is 12° below the horizon (earliest = 43 min before n.t., latest = 2 h 14 min after n.t.). In two cases where migrators reached the surface in excess of 1.5 h after the end

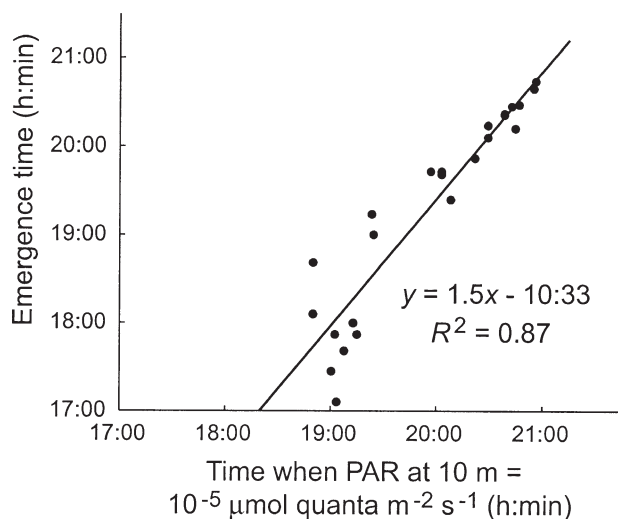


Fig. 5. Emergence time versus time when PAR 10 m below the surface reaches an irradiance of $10^{-5} \mu\text{mol quanta m}^{-2} \text{s}^{-1}$. Note the better fit to modeled irradiance than to time of sunset (Fig. 4); the latter does not account for local atmospheric conditions. Note that the magnitude of the intercept in the equation results from extrapolation of the line to a time of 0:00 on the abscissa.

of nautical twilight, moonset occurred at least 30 min after the end of nautical twilight.

Reentry times also bracketed sunrise but showed greater precision in timing relative to those of emergence times surrounding sunset. Reentering populations ($n = 34$) arrived at the seabed on average $15 (\pm 4)$ min before sunrise (earliest = 1 h 9 min before sunrise, latest = 55 min after sunrise). They arrived at the seabed before sunrise on 75% of days. Migrators left the surface an average of $27 (\pm 7)$ min before the beginning of nautical twilight.

The time at which $\text{PAR}_{10\text{m}}$ was estimated to equal $10^{-5} \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ was better correlated with time of emergence ($p^2 = 0.87$, $p < 0.001$; Fig. 5) than was time of sunset. The time at which $\text{PAR}_{10\text{m}}$ equaled $10^{-5} \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ took into account the relative daily irradiance incident upon the water surface and near the seabed. Atmospheric clouds resulted in a darker environment and prompted emergence earlier than on a clear day, suggesting that mysids were cued by actual light levels rather than endogenous rhythms alone. There was no better correlation between time at which calculated $\text{PAR}_{10\text{m}}$ equaled $10^{-5} \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ and time of reentry ($\rho = 0.55$, $p < 0.001$; Fig. 6) than between time of sunrise and time of reentry. There was no consistent threshold level for emergence; modeled instantaneous irradiance at 10 m using measured $\text{PAR}_{10\text{m}}$ at the algorithm-determined time of emergence varied widely, between 0.0002 and $2.58 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ (mean $\pm 1 \text{ SE} = 0.21 \pm 0.12$).

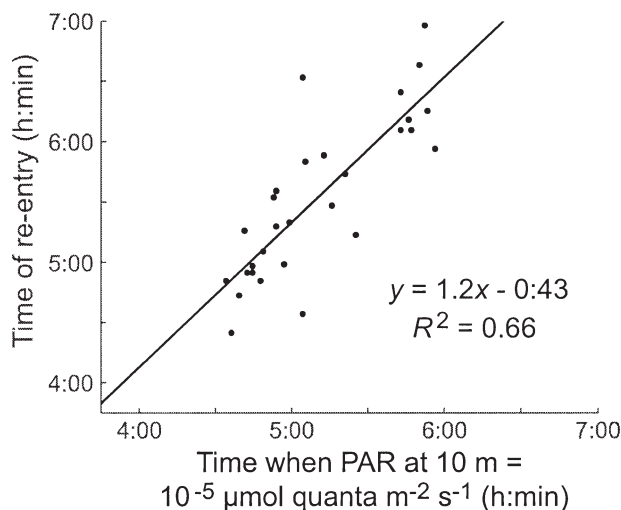


Fig. 6. Reentry time versus time when PAR 10 m below the surface reaches an irradiance of $10^{-5} \mu\text{mol quanta m}^{-2} \text{s}^{-1}$.

Mean instantaneous rate of change in absolute irradiance at 10 m at the time of calculated emergence was also variable, i.e., $-0.00034 \pm 0.0003 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$. Rate of relative change of irradiance at depth modeled from Beer's law and $\text{PAR}_{0\text{m}}$ must be the same as the relative rate of change in $\text{PAR}_{0\text{m}}$ itself. The instantaneous rate of relative change of irradiance at the time of calculated emergence was a much more precise predictor of emergence times, i.e., at a threshold level of $-0.0023 \pm 0.0002 \text{s}^{-1}$. Despite the highly derived nature of this estimate and the notorious spikiness of derivatives and second derivatives, it is the only one of the three irradiance parameters tested that showed a reasonably precise threshold for emergence.

The modeled shape of an isolume over time near dawn or dusk fit very closely a quadratic function for both direct ($0^\circ \leq \theta \leq 90^\circ$) and diffuse ($\theta > 90^\circ$) irradiance (where θ is the sun zenith angle), and was always concave upward (Fig. 7). If mysids were following an isolume, we would expect a concave upward quadratic function to be the best fit to the points at which there was a 20% increase in total biovolume. On only 26% of dates that showed significant linear fit with our algorithm did a quadratic function provide significantly better fit. Only 24% of those significant quadratic fits (or only 6% of significant fits to any line or curve) were concave upward, i.e., the same shape as an isolume (Fig. 7 and Table 1). Isoleths of relative rate of change also followed a quadratic, upward-concave form in the space of depth (ordinate) and time (abscissa).

Mean ascent speed of the emerging population was $0.29 (\pm 0.03) \text{ cm s}^{-1}$. Based on calculated ascent speed and acoustically determined, local tidal

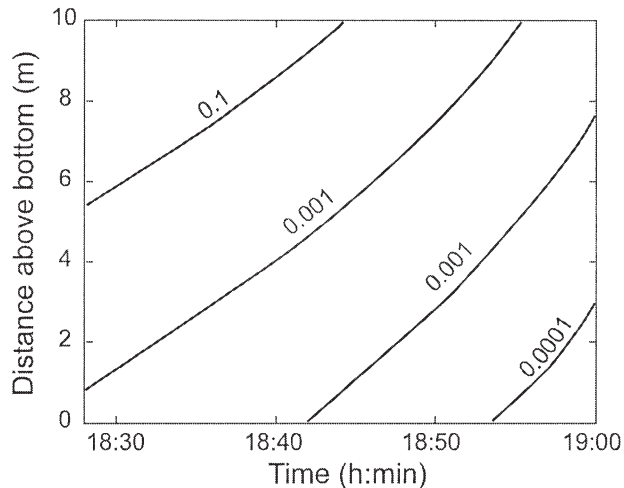


Fig. 7. Depth-versus-time contour plot of isolumes ($\mu\text{mol quanta m}^{-2} \text{s}^{-1}$) during twilight (diffuse irradiance) on September 26, 2002. Isolumes were modeled at 1-m increments from 0 to 10 m using measured surface PAR (400–700 nm) and Beer's law with $k = 0.5 \text{ m}^{-1}$.

height at the time of emergence, the average time it took the emerging population to reach the surface was 1 h 21 min (± 5 min). Ascent speed was positively correlated with the time lag between sunset and emergence ($p^2 = 0.55$, $p < 0.001$; Fig. 8). When emergence occurred before sunset (negative lag), ascent rate was slower than when emergence occurred after sunset (positive lag).

Mean descent speed of the reentering population was $-0.26 (\pm 0.02) \text{ cm s}^{-1}$. Based on this calculated descent speed and actual tidal height at time of reentry, the average time that it took the reentering population to reach the hyperbenthos was 1 h 22 min (± 8 min). Descent speed was positively correlated with time lag between the beginning of nautical twilight and leaving the surface ($p^2 = 0.59$, $p < 0.001$; Fig. 10); the closer to sunrise the animals began their descent, the more quickly they descended. As day length decreased, both ascent ($p^2 = 0.20$, $p = 0.009$) and descent ($p^2 = 0.22$, $p = 0.004$) speeds slowed (Figs. 10 and 11).

TABLE 1. Number of significant ($p < 0.05$) linear and quadratic fits for calculated emergence and reentry trajectories (height above bottom versus time).

Type of Curve	Emergence	Reentry	Total
Linear fit	29	37	66
Quadratic fit	8	9	17
Concave downward quadratic fit	6	7	13
Concave upward quadratic fit	2	2	4

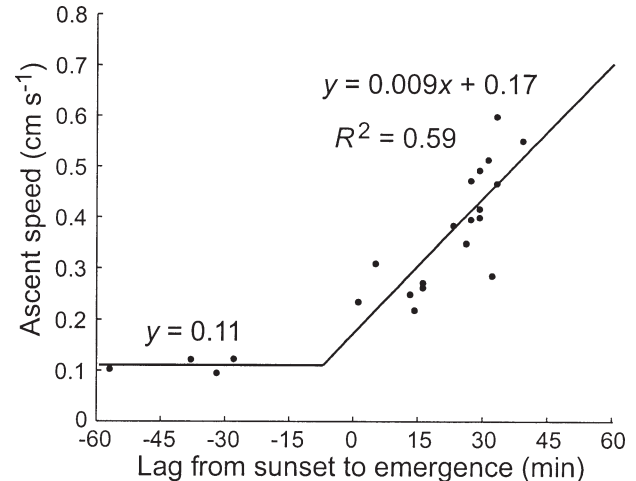


Fig. 8. Ascent speed versus lag in emergence time after sunset. There is no apparent relationship when emergence occurs before sunset (negative lags), but speeds increase when emergence occurs later after sunset.

Discussion

Given that the most abundant species caught in our emergence traps throughout the study was *N. americana*, we assume that this species contributed overwhelmingly to our signal, especially at the lower frequencies that best represent their size (Kringel et al. 2003). Since *N. americana* dwells in the hyperbenthic environment during the day and emerges

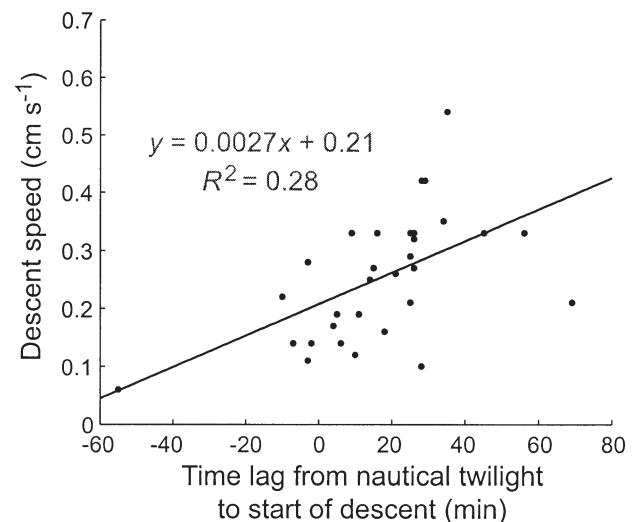


Fig. 9. Descent speed versus time lag from nautical twilight to start of descent with the least-squares, best-fit regression line. Although it is weak, the relationship is still statistically significant ($p < 0.002$ for the regression), and nonparametric correlation is also highly significant (see text), so the relation is not due to a few points with strong leverage. The longer the lag between nautical (dawn) twilight and the start of the mysids' return to the benthos, the faster their descent—evidence of the Dracula effect (see text).

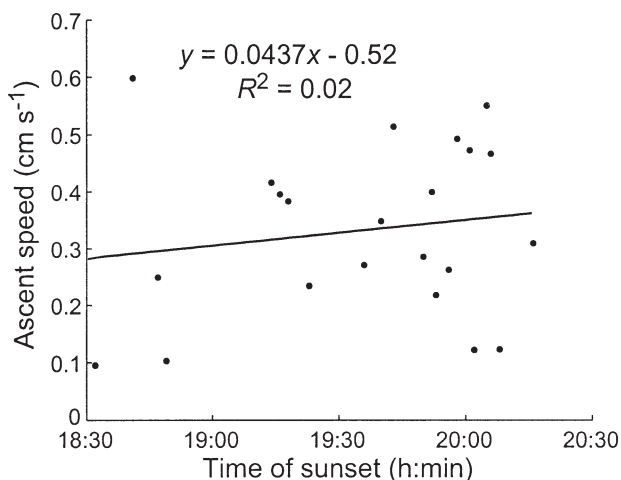


Fig. 10. Ascent speed versus time of sunset. Although the parametric coefficient of explanation for the best-fit line (solid black) is not statistically significant, the correlation proves significant nonparametrically ($p = 0.009$, see text). Note that x is measured in decimal hours after midnight (e.g., 18.3 h).

into the water column during the night (Corey 1988), this species is a link in benthic-pelagic coupling, although its relative or absolute contribution to this coupling is unknown. Divers involved with our study (Abello, Shellito, and Dorgan) observed that individuals during the day oriented into the current but otherwise remained quiescent. Our discussion focuses on this species, keeping in mind that traps may underestimate the diversity and abundance of emergent fauna in our acoustic signal. The sheer magnitude of the phenomenon (Fig. 1) and the fact that mysid shrimp are known to be abundant in demersal and pelagic fish diets (Mauchline 1982) suggests that emergence warrants serious attention as a pathway of energy and material flow.

Mysids are ubiquitous in estuaries and on continental shelves. *N. americana* is a common mysid on the East Coast from Canada to Georgia (e.g., Stickney and Knowles 1975; Winkler et al. 2003). Because most of the published studies are estuarine on account of accessibility for study, there is widespread perception that abundant stocks of mysids in general, and of *N. americana* in particular, are estuarine and not shelf characteristics. Mysids and *N. americana*, however, are abundant over most of the depth range of the continental shelf (Hulbert 1957; Wigley and Burns 1971; Pezzack and Corey 1979; Corey 1988; Grabe 1996). They are prominent components of groundfish diets, and because of high digestibility may represent much greater fractions of energetic demand than their proportions in gut contents would suggest (Lankford and Targett 1997). In samples from the Northeast shelf, mysids constituted over 80% of gut contents in cod,

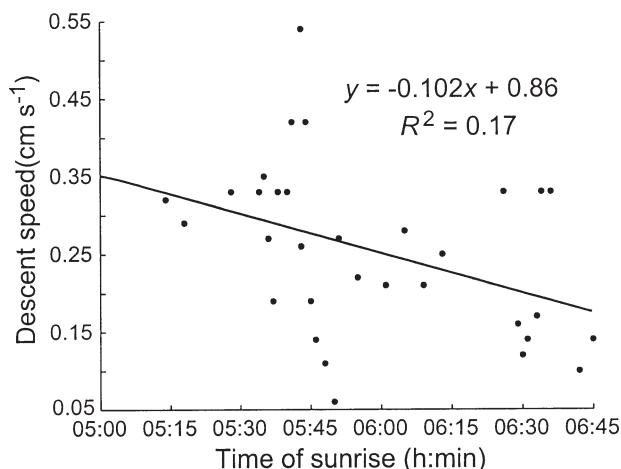


Fig. 11. Descent speed versus time of sunrise. Although the parametric regression is only weakly significant ($p = 0.02$), nonparametric correlation is stronger ($p = 0.004$, see text) because it is insensitive to outliers and lack of binormality in the data distribution. Note that x is measured in decimal hours after midnight (e.g., 18.3 h).

Gadus morhua, ≤ 10 cm long (Link and Garrison 2002). Preserved gut contents provide evidence of significant long-term changes in benthic foods of groundfishes over time (Link 2004). In the Gulf of St. Lawrence, euphausiids declined dramatically after 1987 in cod diets, replaced by mysids in small cod and Atlantic herring, *Clupea harengus*, in larger individuals (Hanson and Chouinard 2002). Whereas we focus on cod, mysids in general and *N. americana* in particular are important dietary components in a broad range of fishes of commercial and recreational interest including weakfish, *Cynoscion regalis* (Lankford and Targett 1997), smelt, *Osmerus mordax* (Dodson et al. 1989), drum, *Larimus fasciatus* (Ross 1989), hake, *Urophycis regia* (Rachin and Warkentine 1988), bluefish, *Pomatomus saltatrix* (Friedland et al. 1988), and tomcod, *Microgadus tomcod* (Grabe 1980). We hypothesize that the frequency of occurrence of mysids in diets and their emergence behaviors are closely linked. One specific prediction is that prevalence in fish diets will be related to the seasonal onset and termination of the emergence behavior.

Nocturnal vertical migration is thought to enable migrators to feed at a time when they experience reduced risk from visual predation (Zaret and Suffern 1976; Alldredge and King 1985; Frost and Bollens 1992; Lampert 1993; DeRobertis et al. 2000), but the risk is nonzero. Although this hypothesis has been well documented for midwater, daytime refuges in which food may be limited, but risk of visual predation is low (Stich and Lampert 1981), it raises additional questions in our shallow-water setting. Here, hyperbenthic animals that were performing

vertical migration may have had food sources available to them even during daylight, in the form of organic matter-covered sediments and detritus.

N. americana is an omnivore. Gut studies have shown mysid diets to consist of detritus, organic-matter-covered sediments, phytoplankton, and smaller animals (Mauchline 1980; Rudstam et al. 1989). Mysids' versatile thoracic appendages allow them both to generate currents in suspension feeding, and to pick up boluses of food and macerate them with mandibles, as we have observed in aquaria for *N. americana*. The presence of highly developed and stalked eyes also allows *N. americana* and other mysids to feed visually on smaller animal prey, at which in the laboratory they are not successful in the dark (Fulton 1982a; Ramcharan and Sprules 1986; Viherluoto and Viitasalo 2001). Field studies of *M. mixta* stomach contents indicated greater intake of zooplankton during the night and detritus during the day (Rudstam et al. 1989). We regularly observed copepod body parts in *N. americana* gut contents.

In 2002 it appeared that our acoustic record of abundance in the water column was bracketed by spring and fall diatom blooms on the bottom; i.e., diel vertical migration began after the conclusion of a benthic bloom in June and ended at commencement of a benthic bloom in late October at approximately 8 m depth near the location of TAPS (Abello and Shellito unpublished data). Other mysids (*Gastrosaccus psammodytes*) in a shallow surf zone have been associated with the presence of diatoms during the day, becoming carnivorous at night when diatoms migrate into the benthos (Wooldridge 1989). Because the quality of organic-matter-covered sediments or detritus is relatively low for the energy-intensive activities of egg production, migration in pursuit of richer food sources in the water column could provide metabolic advantage, particularly when benthic diatoms become scarce. Offshore migration of *N. americana* in the fall (Corey 1988) may also play a role in the seasonal initiation and conclusion of vertical migration seen in our acoustic record, and may be tied to a lack of food both in the hyperbenthos and water column. Whiteley (1948) observed *N. americana* on Georges Bank at depths less than 75 m throughout the year, but in greater abundance during winter. Our observations while diving indicate that this species is not at our study site in winter, and may move offshore to exploit a different food source or perhaps to further decrease risk from predation. To assess risk of predation versus gain from food, better quantification of spatial and temporal food sources of *N. americana* in our region is clearly needed.

Juvenile *N. americana* constituted the most abundant stages of this dominant migrator caught in our

emergence traps. Clutter (1969) found juvenile *Metamysidopsis elongata* dominant in surface waters at night. In the laboratory, he also observed copulation to occur only at night and to be correlated with molting of mature females. Herman (1963) also noted that juvenile *N. americana* migrated throughout the year, whereas mature animals migrated only during spawning. It is not known in our environment and of *N. americana* if juveniles, which have no secondary sexual characteristics, molt into a stage where sexual characteristics needed for mating are present, enabling the individual to copulate within the same night. If not, then the abundant juveniles caught in our traps have other reasons for emerging into the water column.

Whatever the ultimate or proximate driver, seasonal decrease of day length and corresponding increase of night length were reflected in timing of emergence and reentry, with emergence occurring earlier and reentry later as the season progressed after summer solstice. This result was not a simple artifact of our definition of emergence or reentry as occurring within a fixed time of sunset or sunrise, respectively. When we expanded our definition to include times further from sunset or sunrise, we were unable to find parallel events. Proximate cues may include seasonal changes in sun angle, water-column optical properties (e.g., turbidity), or food sources (or in two or more of these or other parameters).

It is less clear what might cause populations sometimes to migrate before sunset or after sunrise, especially if the risk of being preyed upon is greater in light than dark. One possibility is that relative rate of change in irradiance, when averaged by the animal over a suitable period, is a lower-risk, but yet imperfect, indicator that it is safe to emerge than are either absolute irradiance or rate of irradiance change. Relative rate of change may be least sensitive to surface irradiance variations due to atmospheric clouds and subsurface irradiance variations due to turbidity. It would be especially detrimental to an individual or population to be at the surface when light intensities are too great. Migrators sometimes began their ascent before sunset (36% of the time), but less frequently began their descent after dawn (25% of the time). The asymmetry of risk in delayed emergence (low) versus delayed reentry (high) we call the Dracula effect, and the greater organization and concentration of reentering groups is evident in some acoustic records (e.g., Kringel et al. 2003). On 64% of dates, migrators arrived at the surface after darkness (here defined as the end of nautical twilight); on 75% of dates, migrators left the surface before the beginning of first light (defined as the beginning of

nautical twilight). Although being at the surface when it is light seems counter to the predator-avoidance hypothesis (Zaret and Suffern 1976), our results are not unique; Clutter (1969) found that mysids were caught in surface waters from one hour after sunset to one hour after sunrise. Factors other than absolute irradiance may reduce capabilities of visual predators and risk during twilight, or the associated risk may be outweighed by fitness benefits of other activities such as feeding, mating, or dispersal.

Despite the better correlation of calculated PAR_{10m} than time of sunset with emergence time, a large range and standard deviation surrounded the mean in absolute irradiance at the calculated time of emergence. Rate of change in irradiance also provided imprecise prediction of emergence time. Our results best support the hypothesis, proposed by Clarke (1930), that the relative rate of change in irradiance is the cue to emerge. Our observations of behavior in the field bear remarkable similarity to Stearns and Forward's (1984) laboratory observations of copepod (*Acartia tonsa*) migrations under simulated light conditions in the laboratory, including sensitivity to rate of relative change in light intensity. Rate-of-change hypotheses have traditionally been applied to such laboratory experiments involving measured phototaxes in response to a light source (Ringelberg 1964), but prior to high-resolution acoustic measurements there have not been reliable means to estimate onset times of emergence in the field for correlation with estimated light cues. Future acoustic measures coupled with more precise in situ measures of spectral irradiance would seem worthwhile.

Measured swimming speeds for mysids with body lengths in the range of 5–10 mm are as high as 20 cm s^{-1} (Mauchline 1980). Clutter (1969) found that mysids (*M. elongata*) in the same size range as juvenile *N. americana*, i.e., 4–7 mm, did not swim slower than 3 cm s^{-1} , and their swimming speeds were lower in dim than bright light. Group swimming speeds derived from our acoustic data are at least one order of magnitude lower than individual swimming speeds reported in these two studies and suggest that we observed a consequence of schooling behavior rather than individual swimming speed. Indeed it is remarkable that concentrations of mysids in our study were able to maintain such a relatively constant and low group swimming speed in a turbulent water column that has such fast horizontal currents. We examined 12.5-cm range bins once each minute. In that minute at the characteristic tidal velocity of 25 cm s^{-1} , mysids would be carried 15 m horizontally. We by no means tracked individuals up and down but

observed advection of impressively choreographed and coherent behaviors of clouds of mysids carried rapidly through the ensonified region over TAPS-6. On ascent or descent, feeding on reverse-migrating copepods (Fulton 1982b; Ohman et al. 1983) or on emergent copepods may be facilitated by the schooling detected by our algorithm. Similarities of the calculated swimming speeds in ascent and descent do suggest that similar mechanisms govern their vertical movement during both upward and downward migration.

We could explain some night-to-night variation in ascent and descent speeds (Figs. 7 and 8) through irradiance levels. Swimming speed increased when emergence occurred after sunset and decreased when populations left the surface before the beginning of nautical twilight. When populations emerged early relative to sunset, they apparently slowed their speeds on ascent in accordance with some property of the light regime to remain better concealed from visual predators. When populations emerged after they were effectively concealed, their swimming speeds were less restricted. It should be noted that isolumes travel much slower in our turbid-water setting than they do in clear, open-ocean waters (e.g., Widder and Frank 2001).

Richards et al. (1996) calculated effective (relative) isolumes as the temporal change in light intensity divided by the attenuation coefficient and the adaptation light intensity (the light intensity at time₁) ($dz/dt = (1/kE) \times dE/dt$). Factoring in the attenuation coefficient and adaptation light intensity to our calculation of speeds of isolumes yields magnitudes on the order of our calculated ascent and descent speeds. Although our results generally suggest some inconsistency in the form of a roughly constant vertical migration speed of the population in a nonlinearly changing light regime, the estimated nonlinearities in the time-depth distribution of isolumes are not large.

In terms of potentially important nonlinearities, the rate of relative change of irradiance is small for some time after sunset before accelerating. The time at which this rapid decrease in irradiance begins varies daily, depending on atmospheric and water-column properties, but may serve as a primary signal to emerge. The rapid decrease in relative light intensity near sunset coincides with onset of migration in several marine and freshwater species (Ringelberg 1995). In our environment, this theory is supported by the relatively low standard error of the mean ($-0.0023 \pm 0.0002 \text{ s}^{-1}$) in relative rate of change of irradiance at the time of calculated emergence and the small range of this parameter (minimum = -0.00012 , maximum = -0.004 s^{-1}).

A decided shortcoming of our approach is the use of broadband PAR. A regular and important aspect of twilight under water is its spectral shift in wavelength of maximal transmission from shorter, blue, to longer, blue-green, wavelengths (Forward 1988). Zooplankton spectral sensitivity has been shown to match that of wavelengths prevalent during twilight, 475 to 525 nm (Forward 1988) in coastal and estuarine waters. *N. americana* has reported in vitro peak sensitivity at 515 nm (Herman 1962). This match between the ambient spectrum and zooplankton sensitivity at twilight lends credence to the sensitivity hypothesis. Spectral sensitivity of many fishes is not adapted to the spectral shift that occurs at twilight; wavelength of maximal sensitivity in fishes is generally above 600 nm (Cronin 1986). The advantage of migrating zooplankton having a spectral sensitivity matched to the wavelength of maximal transmission during twilight may be twofold. It may serve as a cue to initiate migration after predation pressure from fishes is lifted, and it may then be used to feed visually.

Principal properties of light that remain to be explored as mechanisms governing migration in coastal environments are the timing of the spectral shift in irradiance during twilight as a cue to emerge or reenter and underwater changes in polarization (Forward 1988) as a mechanism governing orientation during navigation. Orientation perpendicular to the plane of polarization has been shown both for terrestrial arthropods (Jander and Waterman 1960) and for a marine mysid (Bainbridge and Waterman 1958) in turbid water, and homing behavior has been demonstrated in a reef species of mysid (Twining et al. 2000). Investigation of both of these aspects of the light field would likely be profitable, but will require very sensitive and not yet commercially available instrumentation.

Perhaps the most exciting potential of high-resolution acoustics in understanding emergence is nearly within grasp. It is to connect physiological measurements in the laboratory with important, ecosystem-changing behaviors in the field. Light influences emergence, which substantially influences benthic-pelagic coupling and flow of material to ecologically and economically important populations. Realizing this potential is an important impetus to observatory science.

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