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The Use of Acoustics to Resolve Nightly Excursions of Hyperbenthos

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THE USE OF ACOUSTICS TO RESOLVE

NIGHTLY EXCURSIONS

OF HYPERBENTHOS

By

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Thesis Advisor: Dr. Peter A. Jumars

Acoustic analysis of diel vertical migration in the Damariscotta River estuary, Maine, showed a fairly regular nightly increase in biovolume (mm^3 m^{-3}) of organisms in the water column, presumed to be due to emergence, the entry of hyperbenthic organisms into the water column. Timing of these events was significantly correlated with time of sunset and time of sunrise for more than 50% of the dates where emergence and re-entry could be identified, between June and October 2002. Emergence traps indicate that the mysid shrimp, *Neomysis americana*, is the predominant migrator. Daily fluctuations in irradiance influence the timing of emergence from the hyperbenthos. Local variability in irradiance that may cause populations to emerge before sunset or leave the surface after the beginning of nautical twilight is accommodated in speed of ascent or descent. Emergence before sunset is marked by a slow ascent rate, and leaving the surface after the initiation of nautical twilight is marked by a fast descent rate. This pattern would be

expected for populations avoiding visual predators by concealing themselves in dark waters. Mean ascent ($\pm$ 1 SE) (0.29 $\pm$ 0.03 cm s^{-1}) and descent (-0.26 $\pm$ 0.02 cm s^{-1}) rates show little difference, suggesting that a similar mechanism controls both. Variations in the light regime as both a cue and mechanism for migration under the isolume hypothesis and rate of change hypothesis are discussed.

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Vertical migration is common in aquatic environments. It is characterized by an active vertical movement of organisms, on scales from several hundreds of meters (Frank and Widder, 1997; Tarling et al., 2001; Luo et al., 2000) to only a few meters (Akiyama and Yoshida, 1990) or less. Benthic, hyperbenthic, and pelagic zooplankters may perform this migration, usually on a diel cycle (Bollens et al., 1994; Herman, 1963; Kringel et al., 2003; Roe, 1984; Rudstam et al., 1989). Types of diel vertical migration are nocturnal, twilight, and reverse (Hutchinson, 1967). In the most frequently observed pattern, nocturnal migration, maximal abundance occurs near the surface during the night; reverse vertical migration is defined by a maximum in abundance near the surface during the day; twilight migration is defined as two daily maxima near the surface associated with sunset and sunrise, and a component known as "midnight (or nocturnal) sinking," where zooplankters descend in the water column, either to subsequently rise again or to stay down for the night (Forward, 1988). It is hypothesized that the benefits of migrating are avoidance of visual predators such as fishes (Alldredge and King, 1985), access to food (Lasenby and Langford, 1973), avoidance of high light intensities (Herman, 1962), and facilitation of reproductive behavior and molting (Clutter, 1969).

The correlation of vertical migration with irradiance and its time variation is well known (Alldredge and King, 1980; Bainbridge et al., 1966; Forward 1976, 1988; Foxon, 1939; Frank and Widder, 1997; Gal, 1999; Herman, 1962; McFarland, 1986). Several hypotheses address the specific light-mediated mechanism that cues emergence. Three hypotheses involve the changing characteristics of light during twilight: the preferendum or isolume hypothesis, the rate of change hypothesis, and the relative rate of change

1

hypothesis. The preferendum or isolume hypothesis (Russell, 1927) postulates that there is a specific light intensity, or isolume, that migrating organisms follow in their movement in the water column. The rate of change hypothesis (Clarke, 1930) postulates that the rate and duration of the change in light intensity from the ambient intensity (the adaptation intensity) serves as the cue to emerge, or given that organisms may undergo some level of adaptation to the ambient intensity, the cue may better be described by the relative rate of change of light intensity ($\Delta I/I$). Two hypotheses stemming from fish vision research also may play an important role. The sensitivity hypothesis (Munz, 1958) postulates that the spectral sensitivity of an organism is matched to that of the environment in which they live. The contrast hypothesis (Lythgoe, 1968) postulates that the visual sensitivity of an organism is set to maximize the contrast between the object viewed and its background. These latter two hypotheses may be true for zooplankton with complex eyes (Cronin, 1986), such as mysid shrimp, and certainly can be used to infer a great a deal about the migrators from their predators.

Optical properties of the water also contribute to the mechanisms (Han and Straskraba, 2001) and timing (DeRobertis, 2002) of vertical migration. A higher attenuation coefficient (k (m^{-1})) may lower the effect of predation pressure, which lowers migration velocity (Han and Straskraba, 2001). A higher attenuation coefficient may also increase the difference in time of emergence between smaller (10 mm) and larger (20 mm) euphausiids (DeRobertis, 2002).

Diel vertical migration has been studied in the lab and in the field. Lab studies have generally focused on phototaxes in response to directional light (Ringelberg, 1964) in a column, where flow properties and food preferences are not introduced or measured.

2

Field studies have included many net trawls and subsequent enumeration of organisms caught at various depths and times (Clutter, 1969). Some acoustic measurements of DVM have been conducted, but have been limited to single-frequency instruments measuring Doppler shift (Liljebladh and Thomasson, 2001; Luo et al., 2000; Tarling et al., 2001; Fischer and Visbeck, 1993), and measuring backscatter intensity (Kringel et al., 2003). Although initial acoustic methods were able to characterize the deep scattering layer in depth and time, single-frequency measurements have the disadvantage of sampling only those particles within the size range resolved by the acoustic frequency of the instrument, thus underestimating the actual abundance of particles in the area of the acoustic beam.

One disadvantage of using acoustics is the inability to discern the type of particles constituting the signal. Here, the concurrent use of a method to trap particles becomes vital. Kringel et al. (2003) observed acoustically the presence of a regular DVM at West Sound, Orcas Island, which was discerned by emergence traps as a mysid shrimp-dominated population. Mysid shrimp are very abundant in coastal waters and are a very important food source to economically valuable fish species. They are a potentially important vector for coupling between the benthic and pelagic environment, as they dwell on the surface of bottom sediments (the hyperbenthos) or in the sediments during the day. The dynamic nature of mysids in space and time places an importance upon gathering information related to their behavior.

This study is novel in that an acoustic instrument with six frequencies is used to observe and characterize DVM in a relatively shallow (~ 10m), tidally well-mixed, turbid (k = 0.5 m-1) estuary with little freshwater input. The use of a multi-frequency, high

temporal- and spatial-resolution acoustic instrument allows a large range of particle sizes to be represented in the signal, thus more accurately sampling the total volume and abundance of particles.

The objectives of this study are to observe and quantify vertical migration using this multi-frequency acoustic instrument, to characterize daily and seasonal patterns of emergence of local fauna, to characterize the underwater light field at the study site, and to relate the timing of vertical migration of local fauna to the underwater light field, specifically targeting above-mentioned prevailing hypotheses on properties of light as cues for initiation of vertical migration.

METHODS

Study site

     This study was conducted in the Damariscotta River, at the University of Maine's

Darling Marine Center campus in Walpole, Maine (Figure 1). The Damariscotta River

estuary is a unique environment in which to study vertical migration. The water

properties more closely resemble coastal oceanic water because of the strong tides (height

= 3 m) and little freshwater input (0.63×10^5 m^3 per tidal period in mid-summer,

McAlice, 1993). Tidal velocities are 25 cm s^{-1} on average (Mayer et al., 1996). The

strong tidal currents and relatively shallow depth (~ 10 m) at the study site promote a

tidally-mixed, fairly homogenous water column. Generally, the water is very turbid (k =

0.51 m^{-1} at 10 m, Mayer et al., 1996). Bottom type varies along the 29-km length of the

river, from rock and gravel to primarily sand and silt. The bottom type at the study site is

classified as silty sand (McAlice, 1993). Water temperatures range from 1°C in February

to 18°C in September. Diatom blooms occur on the bottom (~10 m) in the spring and fall

(observed while diving).

Acoustic measurements and data processing

     Acoustic records were collected using TAPS (Tracor Acoustic Profiling System,

BAE Systems). TAPS was mounted in a frame, moored 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, 1100, 1800, 3000 kHz) ping simultaneously twenty-four

times and integrate backscatter (S_v, in dB) over either one- or two-minute intervals, at

each 12.5-cm depth bin in the water column above. As the height of the water column

changes with tidal height, so does the number of depth bins recording backscatter. Due
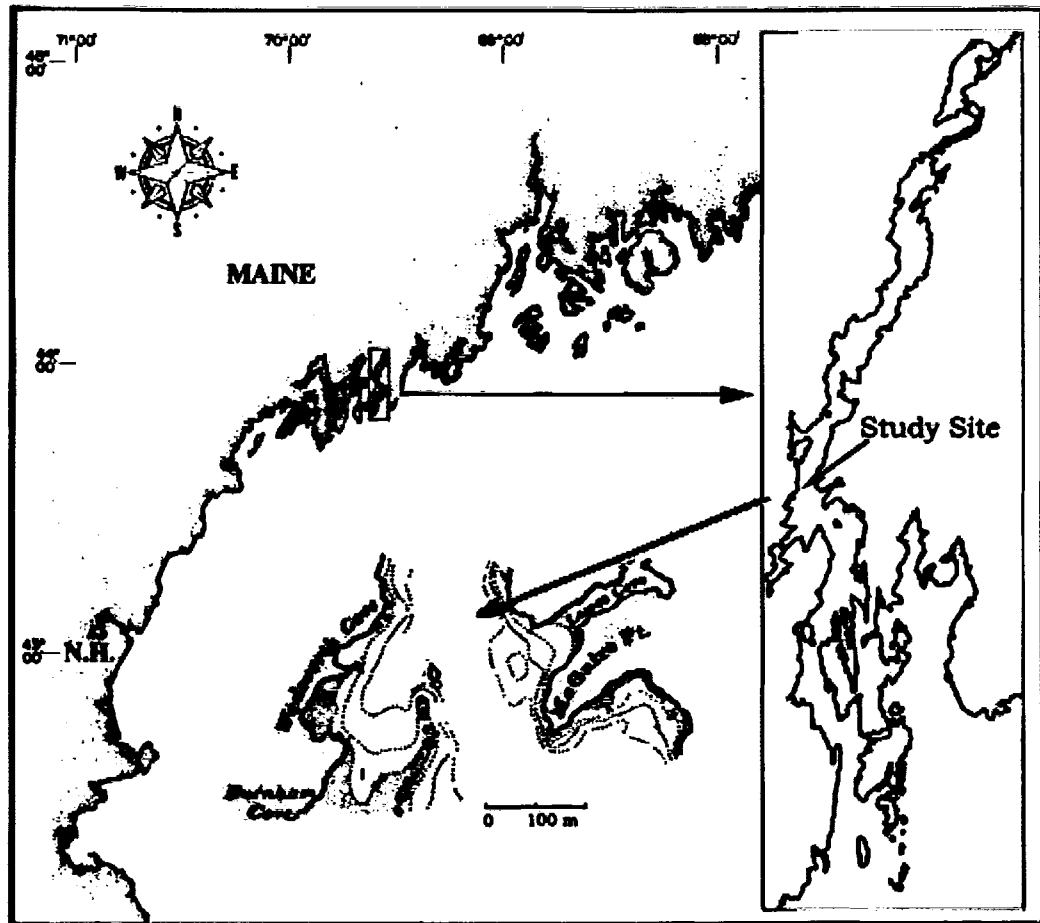
Figure 1. Study site at the Darling Marine Center, on the Damariscotta River, Maine. (Modified from Watling et al. 2001). Tidal velocities are 25 cm s^{-1} on average. Bottom type is classified as silty sand. Average water depth is 10m.

to the position of TAPS in the frame, the transducers were approximately 1m above the seafloor, and the average height of the water column above the transducers was 9m.

Raw backscatter matrices are processed using Matlab (Appendix, makermtlh.m). Calibration constants and beam spreading functions are applied in the first steps of processing, but underestimate the vertical extent of beam spreading. To correct for this problem, an additional algorithm is applied (Appendix, nospread.m). Due to the effect of ringing of the frame, backscatter data within 2 m above the transducers (3 m above the seafloor) were eliminated. Backscatter data from 3m off the bottom to the surface were smoothed in time using a nineteen-point median smoother (Appendix, smoothdata.m). Smoothed backscatter data are inverted to biovolume ($mm^{-3}m^3$) using an equivalent spherical radius model based on the temperature and salinity of the water (Appendix, makets.m, invsndr.m). Using an under-determination factor of 5, six frequencies yields thirty size classes in the inversion. In this analysis, only the sum of the biovolume across all size classes, or total biovolume, is used (Figure 2).

Analysis of Total Biovolume: Finding emergence and re-entry

The algorithm created for finding time of emergence and re-entry involved fitting a line to points generated by finding the difference between each one- or two-minute interval of total biovolume at each depth bin (Appendix 1, findfirstpm.m, findlastam.m). For each depth bin, backward differences ($time_2 - time_1$) was calculated per time period and translated to percent differences. For emergence, increases of at least 20% from the previous minute were noted. For re-entry, decreases of at least 20% from the previous minute were recorded. For both emergence and re-entry, this method yielded a cluster of points during the night and few points during the day (Figure 3). Using the time of sunset
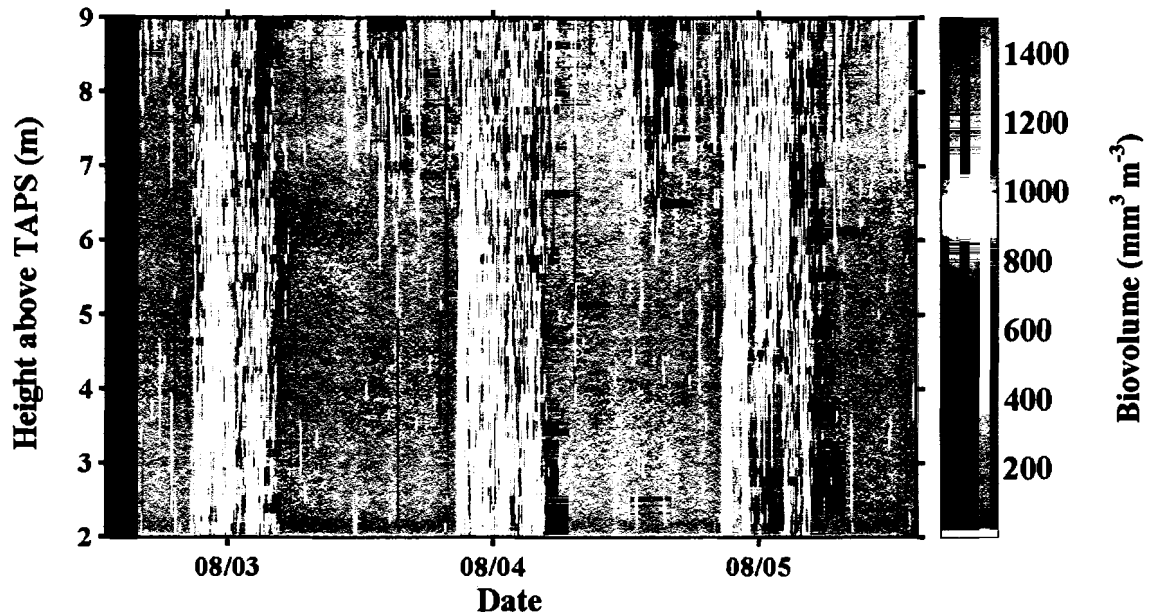
Figure 2. Total biovolume ($mm^3 \, m^{-3}$) for August 2 to 5, 2002. Due to ringing of the frame, the first reliable measurement above the bottom is at 2 m above TAPS, or 3 m above the bottom. The height of the surface is dynamic due to tides, but has been cut at 9 m. Ticks indicating dates signify midnight. Biovolume increases during the night from the background level ($\sim 200 \, mm^3 \, m^{-3}$) during the day. Red streaks near the surface during the day may be fishes. Note the variability in the night- time signal over the three dates.
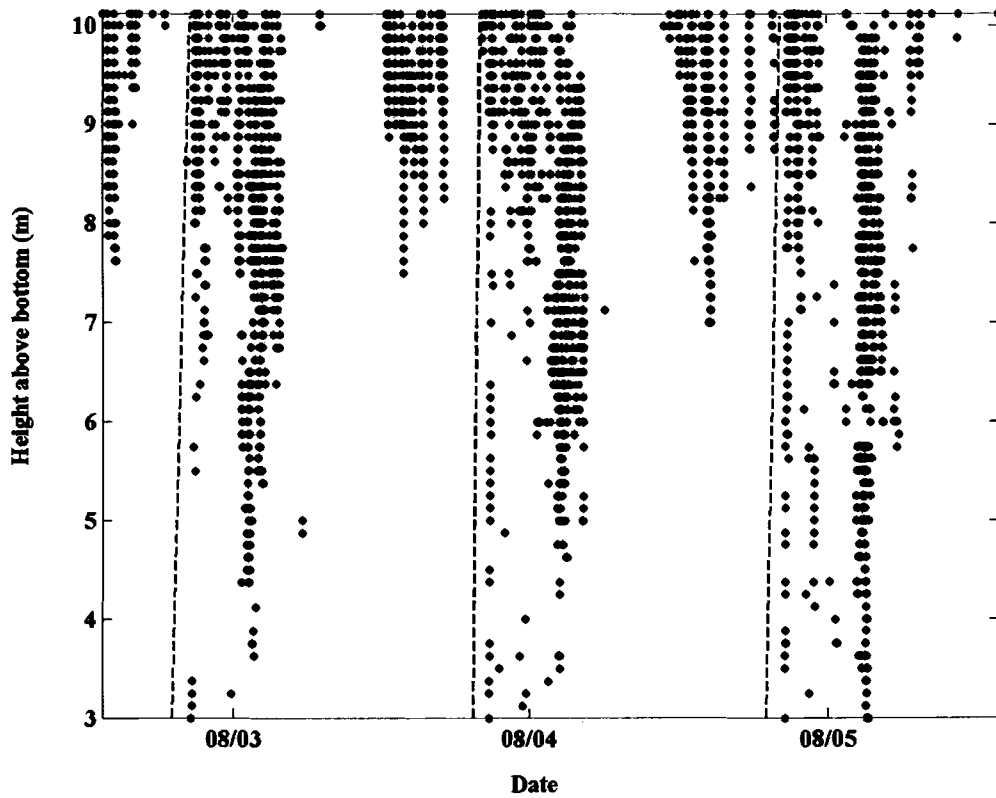
Figure 3. Index of total biovolume ($mm^3 \ m^{-3}$) where the percent change is at least 20%

greater than the minute before, for August 2 to 5, 2002. Tick indicating dates signify

midnight. Black dashed lines parallel the rate of 20% increase for emergence, and are for

visualization purposes only.

for emergence and the time of morning civil twilight (the time at which the sun is 6°

below the horizon) for re-entry, all points within an hour of this time were plotted as a

scatterplot, with time as the independent variable and height above TAPS as the

dependent variable. A line was fitted to the resulting points; only days with at least three

points were considered. If the fit was significant, the line was extrapolated to its intercept

with the bottom (0 m) to yield either time of emergence or time of re-entry, and ascent or

descent rate (cm s^{-1}) was calculated from the slope of the fitted line (Figure 4). This

process was iterated for all of the days for which there were data, from July to October,

2002. Descent rates are indicated by a negative sign, while the magnitude of the descent

rate is the absolute value. For emergence, this method yielded n = 28 points; for re-entry

it yielded n = 34 points.

The first date in 2002 for which the emergence and re-entry algorithms yielded

points was July 19. Due to instrument failure, the last day of the study was October 9,

2002. Data from another TAPS instrument suggests that vertical migration may have

continued past this date, and in 2001, vertical migration could be seen in November. In

July to October 2002 there were 55 d in which enough emergence points could be found

to fit a line; for re-entry there were 64 total days in which a line could be fitted.

However, only those days in which the fit of the line was significant at α = 0.05 were

used in subsequent analyses. Using only those days that were significant disqualified

slightly fewer than 50% of the days from analysis, for both emergence and re-entry.

While this sample-size reduction may seem disastrous, the algorithm worked well given

the high complexity of the acoustic record. Acoustic data from the period September 26

10
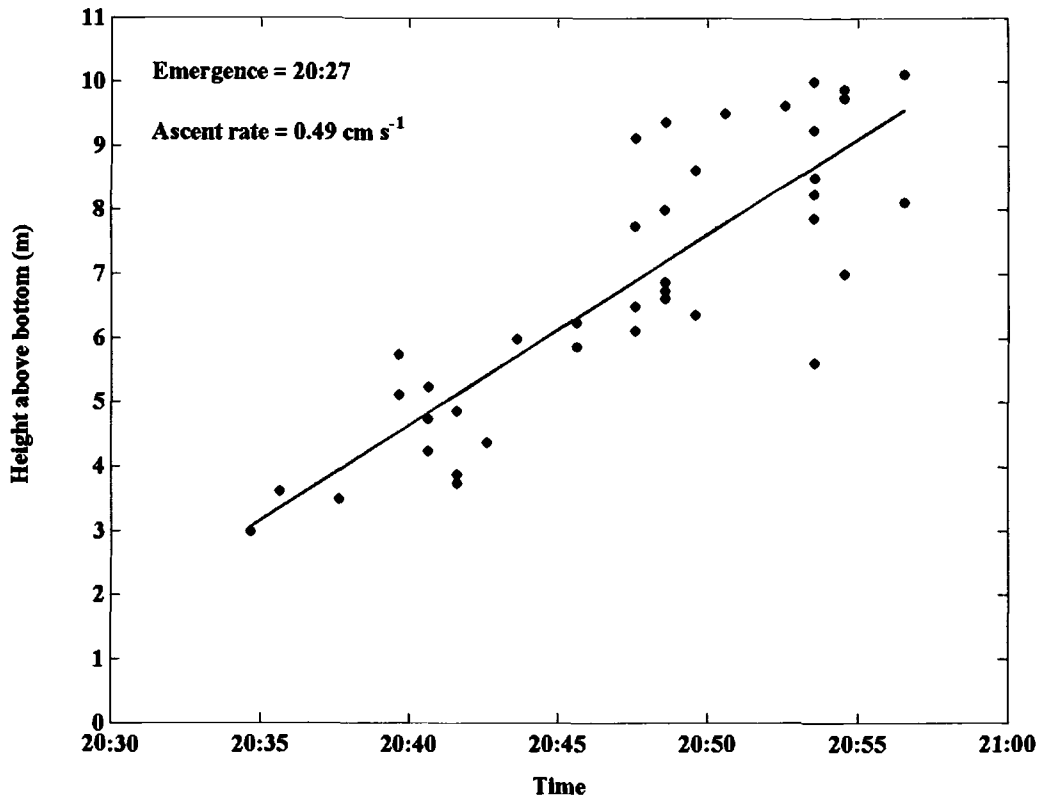
Figure 4. Example of finding emergence and ascent rate, for August 4, 2002. Points

mark depth and time indices where total biovolume ($mm^3 m^{-3}$) is at least 20% greater than

the minute before, as shown in Figure 3 (n = 39). The line is a least-squares linear

regression fit to the points. The slope of the line is the ascent rate (cm s^{-1}) and the

intercept of the line with the bottom is the start time of emergence.

to October 8, and September 15, 2002 were recorded at 2-min intervals, and the

remainder of the days in the period were recorded at 1-min intervals.

Light measurements

Surface PAR (photosynthetically available radiation, 400-700 nm, Licor 190SA)

was averaged from continuous data over 1-min intervals. The threshold of the instrument

was 10^{-4} μmol quanta m^{-2} s^{-1}, but no value lower than 10^{-2} μmol quanta m^{-2} s^{-1} was used

due to the realization that the raw voltage of the datalogger may have been confounding

the readings. Bottom PAR (400-700 nm, Biospherical Instruments QCP-200)

measurements were made at the height of TAPS (1m above the seabed) from September

25 to October 9, 2002, also recording continuous data, averaged over one- minute. The

light attenuation coefficient, k (m^{-1}), was calculated using Beer's Law (Kirk, 1983).

Isolumes were modeled using Beer's Law with inputs of measured surface PAR

(PAR$_{0m}$) data and k = 0.5 m^{-1} for 1-m intervals from just below the water surface to 10 m

(PAR$_{10m}$). The shape of an isolume (0.01 μmol quanta m^{-2} s^{-1}, chosen from the resulting

plot) was modeled best by a quadratic polynomial for both direct ($0° < \theta < 90°$) and

diffuse ($\theta > 90°$) irradiance, where theta (θ) is the sun zenith angle.

The rate of absolute change of irradiance over time and depth was modeled using

a backward difference approximation for the derivative, i.e. for each 1 m depth interval of

data modeled as described above, the rate of absolute change was the difference in

irradiance at time$_2$ – irradiance at time$_1$, divided by 1 min (60 s), in units of μmol quanta

m^{-2} s^{-2}. The rate of relative change of irradiance was the rate of absolute change at each

minute divided by the irradiance at time$_1$, in units of s^{-1}. Instantaneous comparisons were

made between the time of emergence and the absolute irradiance, rate of change of

absolute irradiance, and rate of relative change of absolute irradiance. Rates of change at the time of emergence are negative to indicate a decrease in irradiance in time; magnitudes are the absolute value. Re-entry began much earlier than the threshold of surface PAR was reached, and thus no correlation with the rate of absolute or relative change was made.

Emergence traps

Four emergence traps were placed in the vicinity of the study site from June to December 2001, and June to November 2002. Aluminum-framed traps were pyramidal with a 1 m^2 base and 1 mm mesh walls. The traps were topped with inverted clear 1 L collection bottles, with clear tubes extending from the neck to three-fourths of the height of the bottle. A hole was drilled in the top of the inverted collection bottle and replaced with 1mm mesh to allow water exchange. Traps were lowered by hand with the base perpendicular to the seafloor, and pulled upright upon reaching the bottom, the to allow the base to sit flush with the sediment. Collection bottles were changed daily, and emergent animals placed in 4% formaldehyde, followed by 70% ethanol. *Neomysis americana* was divided into stages following work by Mauchline (1980). Males were classified by elongated fourth pleopods, females were classified by the presence of a brood pouch, either empty or containing various stages of young, and juveniles were classified by having none of these sexual characteristics.

RESULTS

Analysis of acoustic data

Testing the hypothesis that diel vertical migration is modulated by a light cue during twilight, calculated emergence and re-entry times were compared with times of sunset and sunrise, respectively, for July to October, 2002. To avoid assumptions of binormality, Spearman's rho (ρ) was used as a measure of correlation (Conover, 1999). Rho squared 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.

The timing of emergence and re-entry is correlated with setting and rising of the sun, respectively. There is a significant correlation between the timing of emergence and sunset ($\rho^2 = 0.67$, $p < 0.001$, Figure 5), and between the timing of re-entry and sunrise ($\rho^2 = 0.74$, $p < 0.001$, Figure 6). Seasonal decrease of day- length and corresponding increase of night- length is reflected in the timing of emergence and re-entry, with emergence occurring earlier and re-entry later as the season progresses. Night- length (time of sunset to time of sunrise, USNO Astronomical Tables) in the earliest 24-h period of the acoustic study, July 19 –20, 2002, was 7 h 55 min; the time between emergence and re-entry was 8 h 27 min. On the last day of the study, October 8-9, 2002, night-length was 12 h 40 min; the time between emergence and re-entry was 12 h 10 min.

Emerging populations did not always leave the hyperbenthos after sunset (68%), although this behavior was more common than leaving before sunset (32%). Emergers left the seabed an average ($\pm$ 1 SE; n = 28) of 2 ($\pm$ 7) min after sunset throughout the study period (earliest = 1 h 17 min before sunset; latest = 39 min after sunset). Migrators

14

Figure 5. Time of sunset versus time of emergence, for July to October 2002. There is a significant positive correlation at $\alpha = 0.05$ ($\rho^2 = 0.67$, $p < 0.001$) (n = 28). The date corresponding to the time of sunset is shown on the lower x-axis.
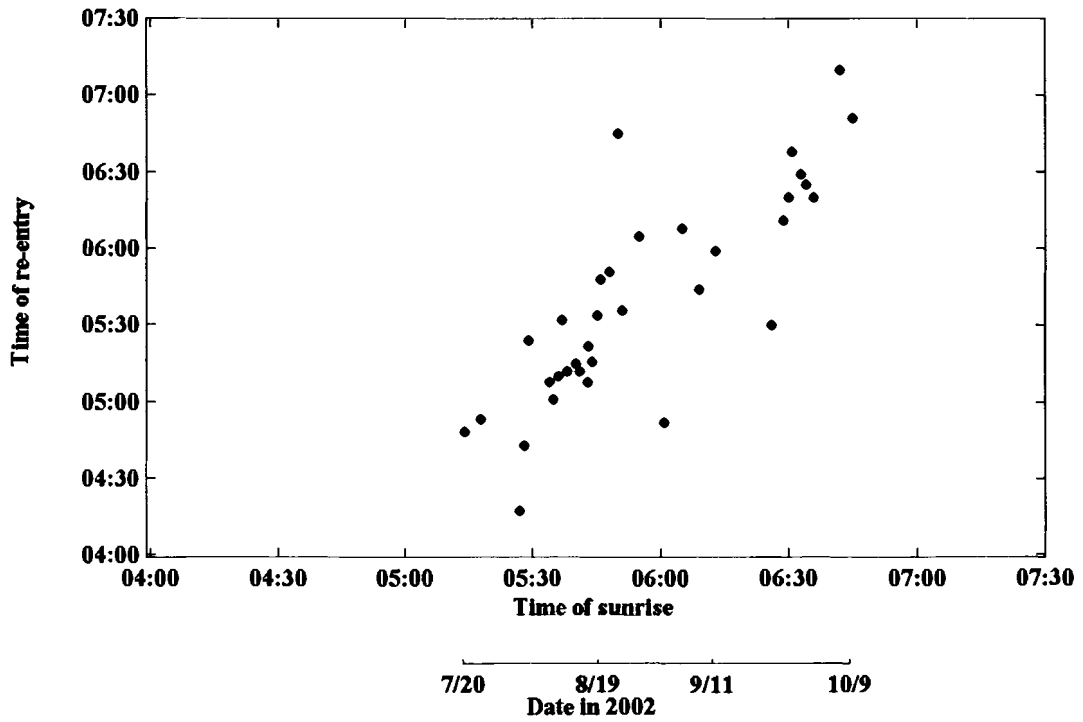
Figure 6. Time of sunrise versus time of re-entry, for July to October 2002. There is a

significant positive correlation at $\alpha = 0.05$ ($\rho^2 = 0.74$, p < 0.001) (n = 34). The date

corresponding to the time of sunrise is shown on the lower x-axis.

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 of nautical twilight, moonset occurred at least 30 min after the end of nautical twilight. The mean ascent rate of the emerging population was 0.29 (± 0.03) cm s^{-1}. Using this calculated ascent rate and the actual tidal height at the time of emergence, the average length of time it took the emerging population to reach the surface was 1 h 21 min (± 5min). The time lag between sunset and emergence was significantly correlated with the ascent rate ($\rho^2 = 0.55$, p < 0.001, Figure 7). When emergence occurred before sunset (negative lag), the ascent rate was slower than when emergence occurred after sunset (positive lag).

Re-entry times also bracketed sunrise. Re-entering populations arrived at the seabed on average (n = 34) 15 (± 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 the days, and arrived at the seabed after sunrise on 25% of the days. Migrators left the surface an average of 27 (± 7) min before the beginning of nautical twilight. The mean descent rate of the re-entering population was -0.26 (± 0.02) cm s^{-1}. Using this calculated descent rate and the actual tidal height at the time of re-entry, the average length of time it took the re-entering population to reach the hyperbenthos was 1 h 22 min (± 8 min). The time lag between the beginning of nautical twilight and leaving the surface was correlated significantly with descent rate ($\rho^2 = 0.59$, p < 0.001, Figure 8). When populations left the surface before the beginning of nautical twilight (negative lag), the
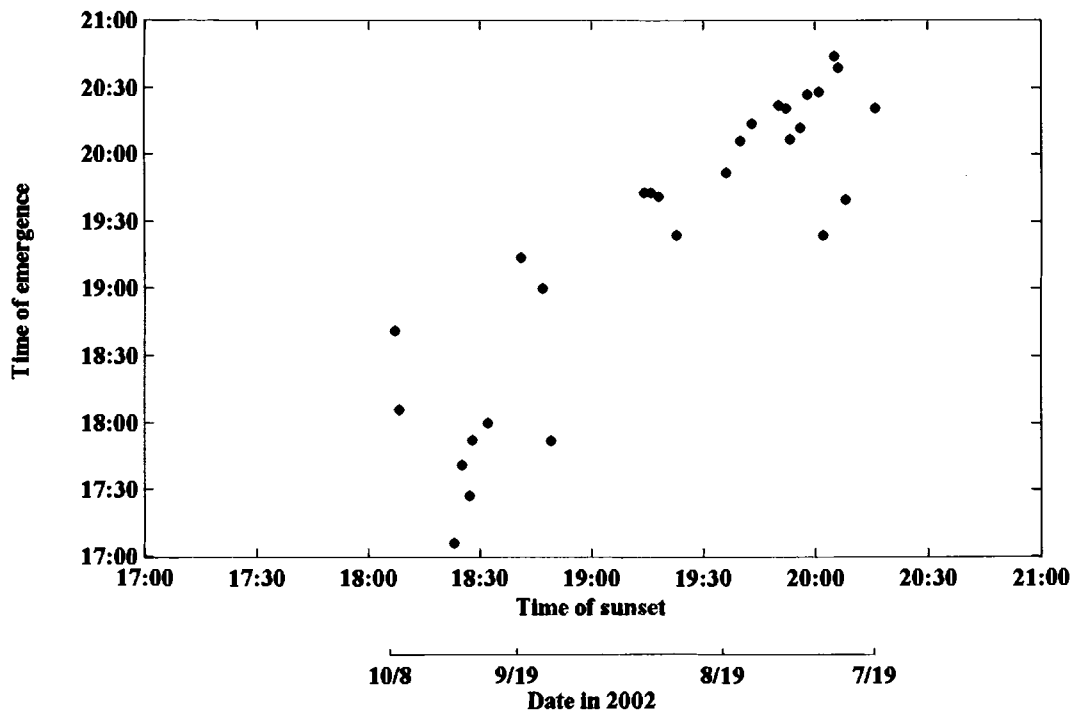
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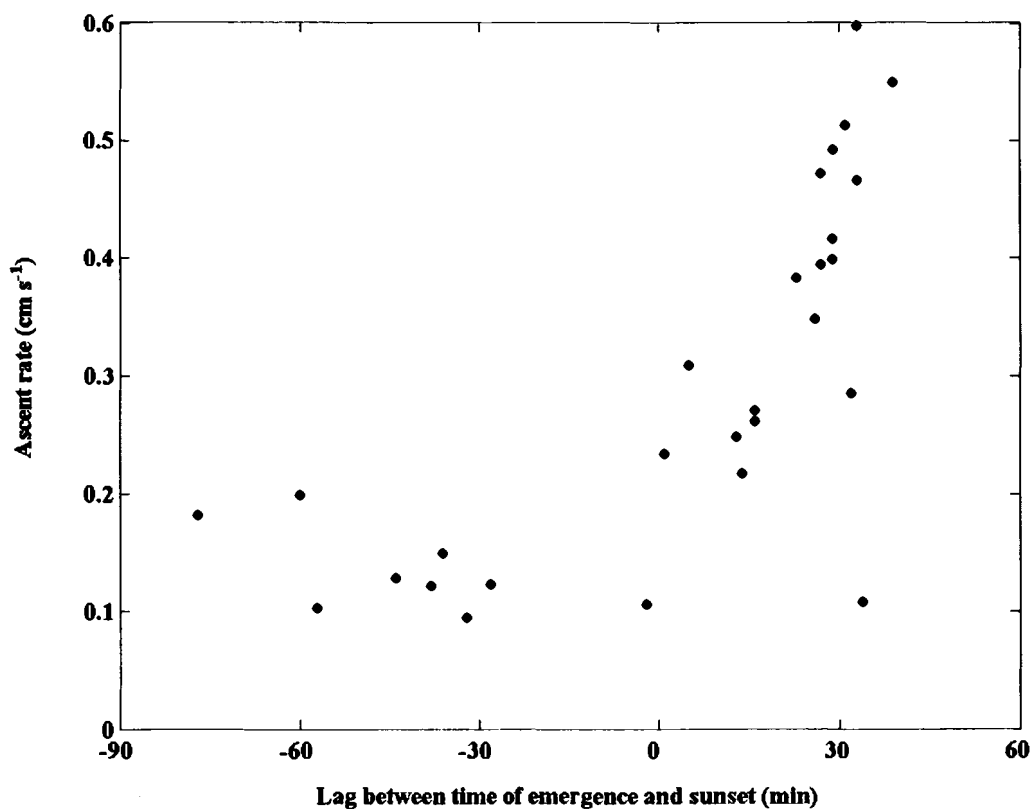
Figure 7. Lag between time of emergence and sunset versus ascent rate, for July to October 2002. There is a significant positive correlation at $\alpha = 0.05$ ($\rho^2 = 0.55$, $p < 0.001$) ($n = 28$). Sunset is used as an indicator of the initiation of evening twilight, as irradiance is no longer direct, but diffuse. A negative lag indicates emergence from the seabed before sunset; a positive lag indicates emergence after sunset.
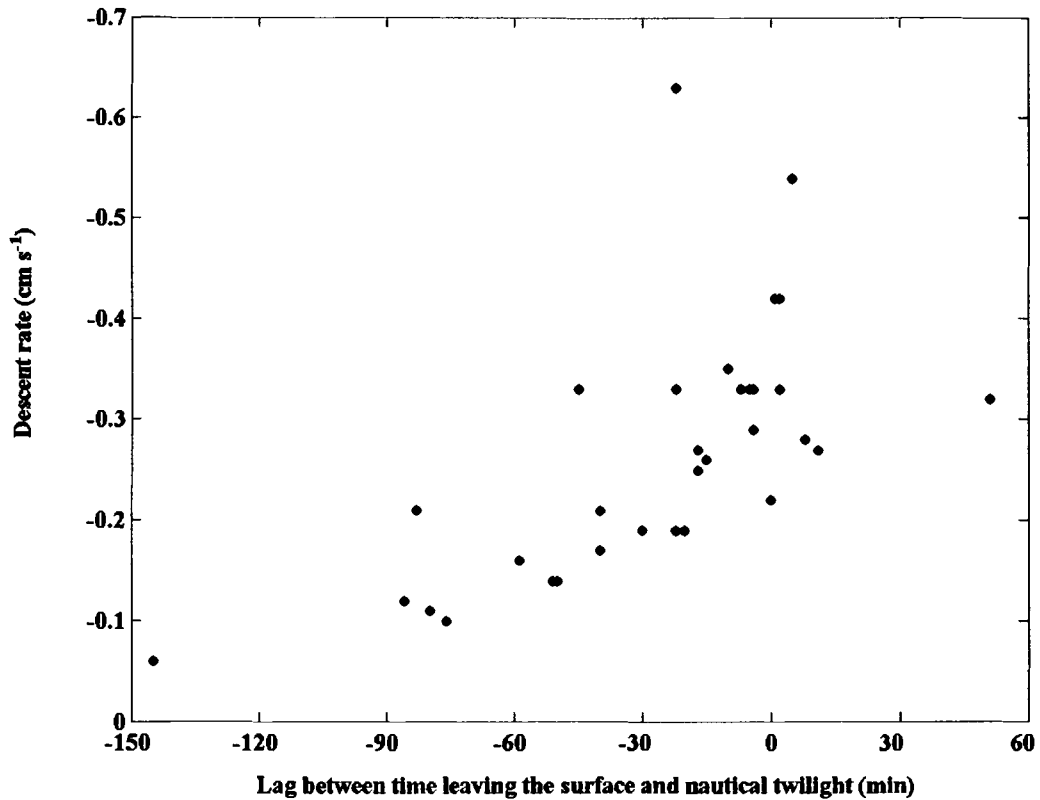
Figure 8. Lag between time at which migrating populations leave the surface and nautical twilight versus descent rate, for July to October 2002. There is a significant positive correlation at $\alpha = 0.05$ ($\rho^2 = 0.59$, $p < 0.001$) ($n = 34$). Time of nautical twilight is used as an indicator of the initiation of morning twilight. Descent rates are negative merely to indicate downward direction of migration; magnitudes of descent are read as absolute values. A negative lag indicates populations left the surface before the beginning of nautical twilight; a positive lag indicates that populations left the surface after the beginning of nautical twilight.

descent rate was slower than when populations left the surface after nautical twilight (positive lag).

There was a significant positive seasonal trend in both ascent ($\rho^2 = 0.20$, p = 0.009) and descent ($\rho^2 = 0.22$, p = 0.004) rates (Figures 9, 10). As day- length became shorter, both ascent and descent rates slowed, but the variability was large.

The temperature measured by TAPS, at a distance of approximately 10 cm from the sediment, fluctuated throughout the study period. On the first day on which emergence and re-entry could be found using the algorithm, July 19 – 20, 2002, the mean temperature was 15°C (min = 14.33°C, max = 16.33°C). On the last day that emergence and re-entry could be found, October 8 – 9, 2002, the mean temperature was 14.75°C (min = 14.15°C, max = 15.32°C). At the middle of the study period, August 14 – 15, 2002, when the water temperature was roughly at its peak, the mean temperature was 17.56°C (min = 16.7°C, max = 18.95°C). Since diel vertical migration was observed throughout the study period, no attempt was made to correlate emergence and re-entry with water temperatures at that time. It is therefore clear that the most abundant migrator, *N. americana*, will migrate in water temperatures of at least 14°C.

Correlation of measured irradiance and acoustic data

A significantly better correlation exists between the time at which PAR_{10m} is estimated to equal 10^{-5} µmol quanta m^{-2} s^{-1} and the time of emergence ($\rho^2 = 0.87$, p < 0.001, Figure 11). The time at which PAR_{10m} equals 10^{-5} µmol quanta m^{-2} s^{-1} takes into account the relative daily irradiance incident upon the water surface, and thus available in the hyperbenthic environment. Atmospheric clouds result in a darker hyperbenthic environment and prompt migrators to emerge earlier than on a clear day. There is no
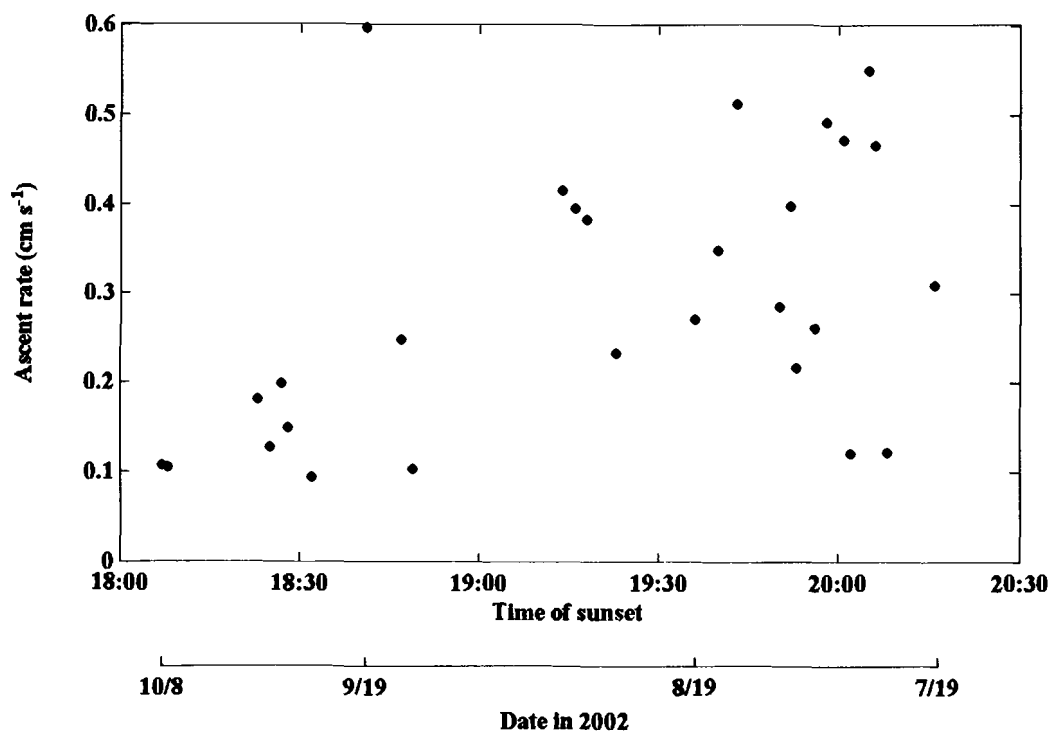
Figure 9. Seasonal trend in ascent rate, for July to October 2002. There is a significant positive correlation between the time of sunset and the ascent rate at $\alpha = 0.05$ ($\rho^2 = 0.20$, $p = 0.009$) ($n = 28$). The date corresponding to the time of sunset is shown on the lower x-axis.
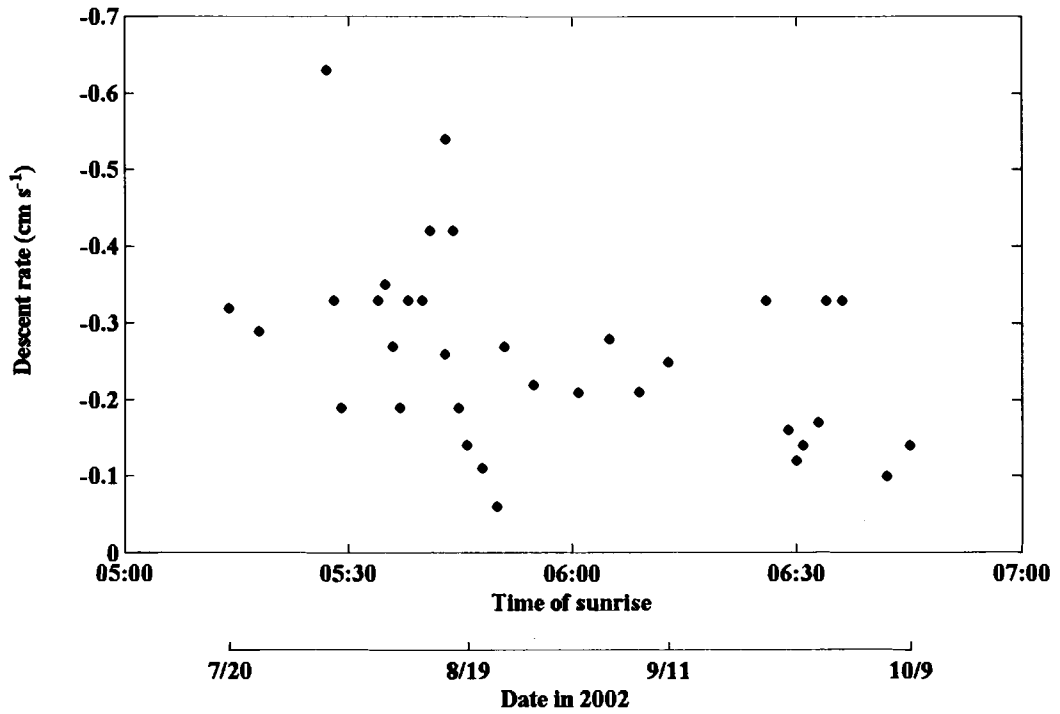
Figure 10. Seasonal trend in descent rate, for July to October 2002. There is a significant positive correlation between the time of sunrise and the descent rate at $\alpha = 0.05$ ($\rho^2 = 0.22$, p = 0.004) (n = 34). The date corresponding to the time of sunrise is shown on the lower x-axis.
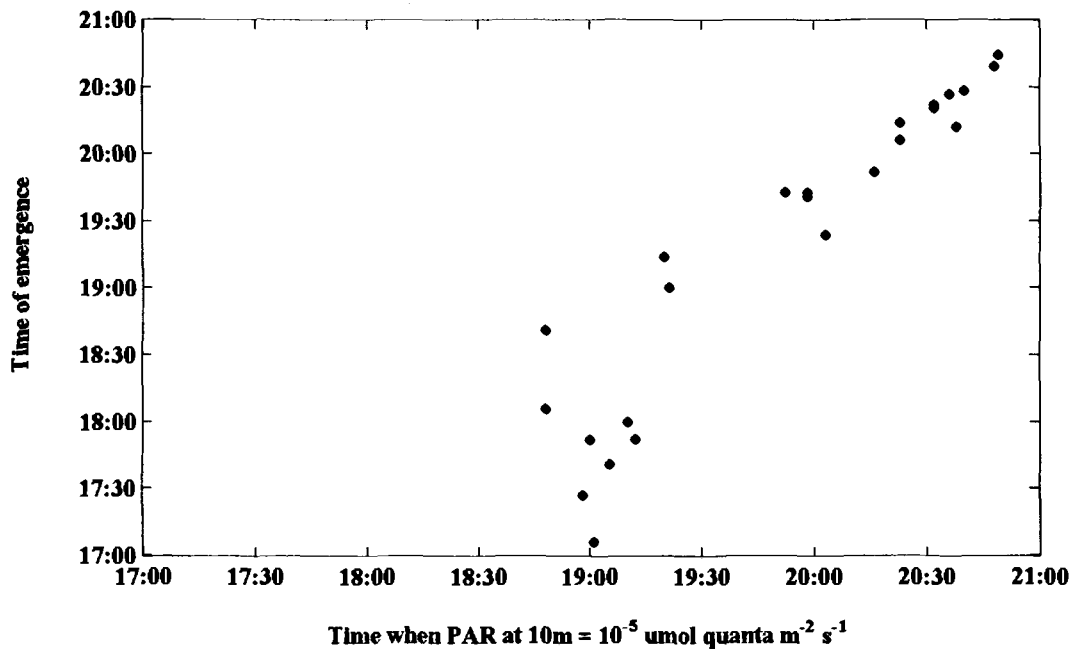
Figure 11. Time when modeled $PAR_{10m} = 10^{-5}$ μmol quanta m^{-2} s^{-1} versus time of

emergence, for July to October 2002. There is a significant positive correlation at α =

0.05 ($\rho^2 = 87$, $p < 0.001$) ($n = 28$). This suggests that daily changes in irradiance due to

atmospheric variation influences the time of re-entry more than the time of sunset (i.e.

time of iniation of twilight).

better correlation between the time at which PAR_{10m} equals 10^{-5} µmol quanta m^{-2} s^{-1} and the time of re-entry ($\rho^2 = 0.55$, $p < 0.001$, Figure 12), presumably due to the many factors affecting timing of return to the hyperbenthos once the migrators have been at or near the surface for some portion of the night (e.g. satiation, presence of predators, completion of molting or copulation, release of brood).

The modeled shape of an isolume over time was found to fit very closely to a quadratic polynomial, for both direct ($0° \leq \theta \leq 90°$) and diffuse ($\theta > 90°$) irradiance, and was always concave upward (Figure 13). For 26% of the dates that could be described significantly by a linear fit, a quadratic fit could significantly better describe the points. Further analysis of the concavity showed that 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 (Figure 14 and Table 1). Mysids do not appear to be tracking an isolume.

The modeled shape of the rate of change in absolute irradiance after sunset in time and depth was also closely approximated by a quadratic fit. No further analyses were performed using this parameter, since it was already demonstrated that emergence and re-entry is not well described by a quadratic fit. The mean instantaneous rate of change in absolute irradiance at 10 m at the time of calculated emergence was -0.00034 ± 0.0003 µmol quanta m^{-2} s^{-2}.

The disadvantage of modeling the rate of relative change of irradiance at 1 m intervals to the bottom from PAR_{0m} was that there was no change in this property of light with depth, as it mirrored the relative change of PAR_{0m}. However, the instantaneous rate of relative change of irradiance at 10 m at the time of calculated emergence was -0.0023
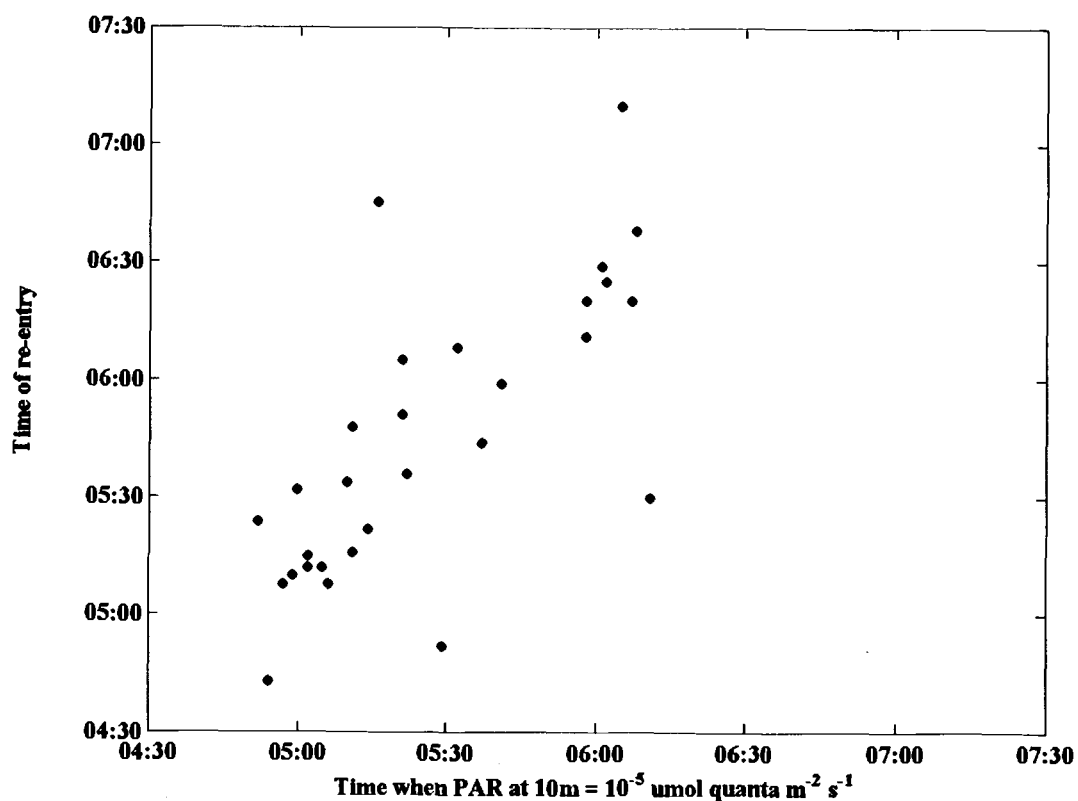
Figure 12. Time at which modeled $PAR_{10m} = 10^{-5}$ µmol quanta m^{-2} s^{-1} versus time of re-entry, for July to October 2002. There is a significant positive correlation at $\alpha = 0.05$ (ρ^2 = 0.55, p < 0.001) (n = 34). This suggests that daily changes in irradiance due to atmospheric variation influences the time of re-entry less than the time of sunset, as migrators generally leave the surface before the initiation of nautical twilight (see Figure 8).
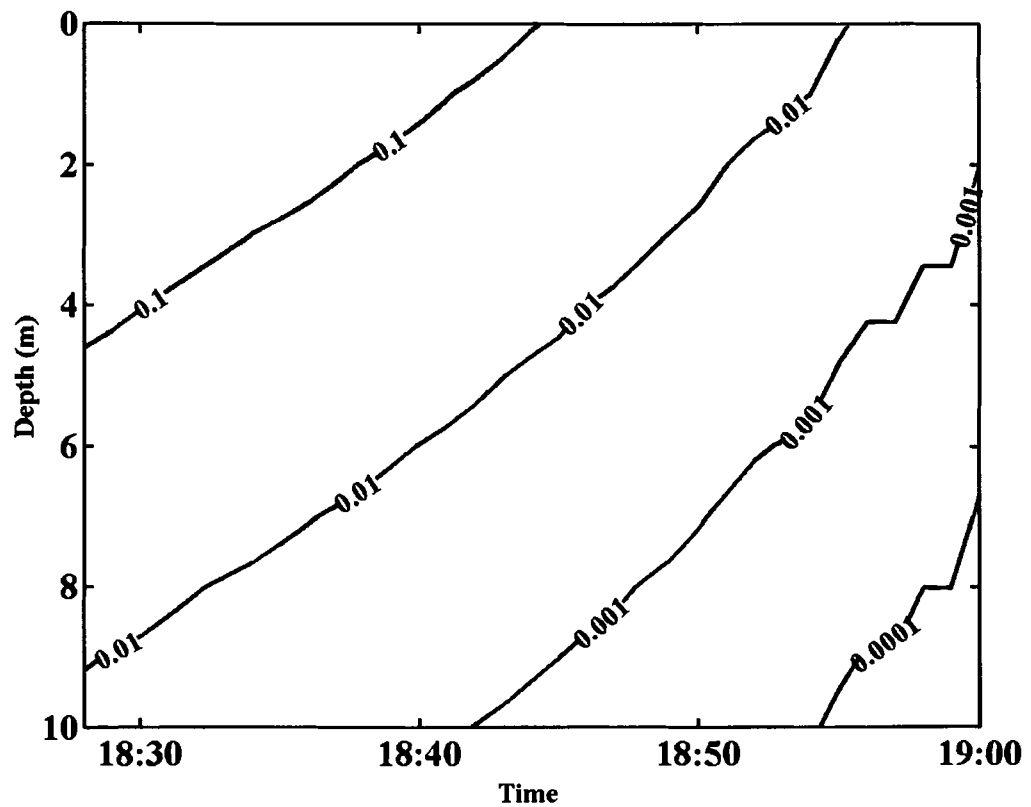
Figure 13. Shape of an isolume during twilight (diffuse irradiance) on September 26,

2002. Isolumes were modeled at 1m increments from 0 m (surface) to 10 m (bottom)

using measured surface PAR (400-700 nm) and Beer's Law with a k = 0.5 m^{-1}. The

shape of an isolume for both direct (θ < 90°) and diffuse (θ < 90°) irradiance closely fit a

quadratic polynomial (fit not shown).
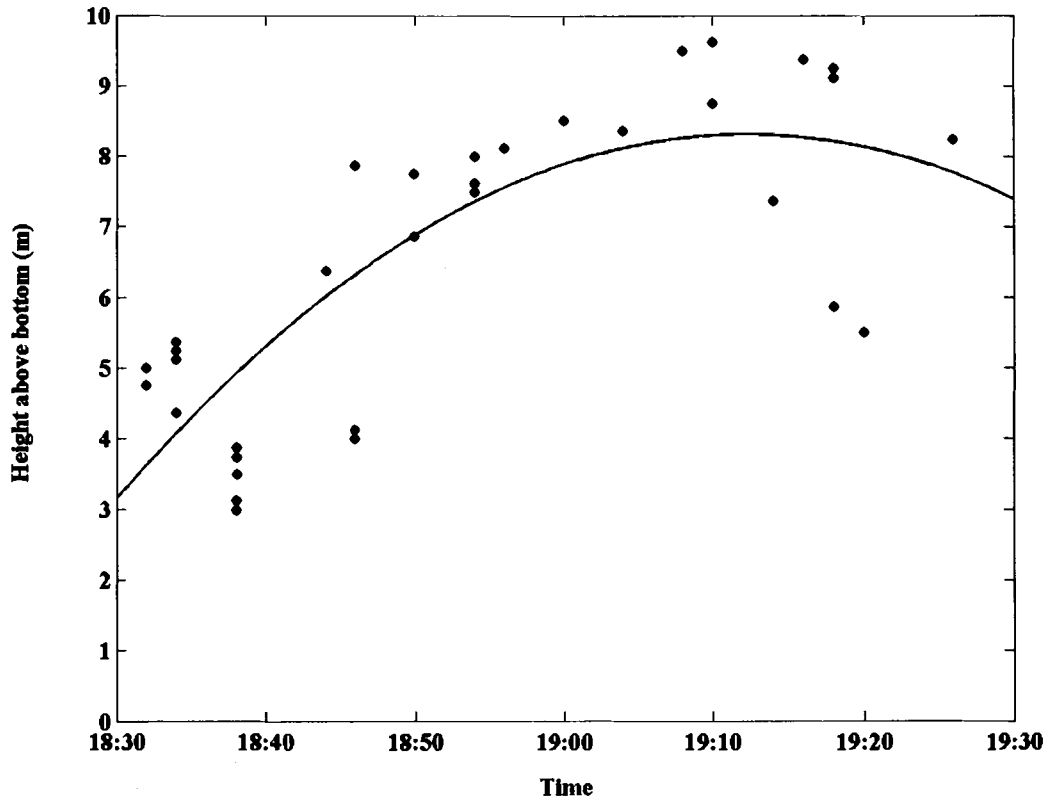
Figure 14. Second-order fit to emergence points on September 26, 2002. In this case, and several others (see Table 1) a second order polynomial fits better than a line (r^2 = 0.63, n = 33), but given that the concavity of the majority of quadratic polynomials is opposite of that for an isolume, it does not show support for the isolume hypothesis.

	Emergence	Re-entry	Total
Days with significant 1st order fit	29	37	66
Days with significant 2nd order fit	8	9	17
Concave down	6	7	13
Concave up	2	2	4

Table 1. Comparison of linear and quadratic fit for calculated emergence and re-entry points. Of the 66 days that a linear fit is significant ($p < 0.05$), a quadratic fit is also significant ($p < 0.05$) for 17 (or 26%) of the days. Of the 17 days that a quadratic fit is significant, only 4 (or 24%) are the concave up, i.e. the same shape as an isolume.

$\pm$ 0.0002 s^{-1}. The modeled instantaneous irradiance at 10 m using measured PAR$_{0m}$ at the calculated time of emergence varied between 0.0002 and 2.58 μmol quanta m^{-2} s^{-1} (mean $\pm$ 1 SE = 0.21 $\pm$ 0.12).

Emergence trap samples

Emergence traps deployed daily from May to October 2001 showed a predominance of the mysid shrimp, *Neomysis americana*. In 2001, *N. americana* composed 93% of the 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 three distinct stages of brood pouches: eggs, eyeless 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-spine bay shrimp, *Crangon septemspinosa*, cumaceans, amphipods, hydromedusae, and polychaetes.

DISCUSSION

Given that the most abundant species caught in our emergence traps throughout the study was *Neomysis americana,* an assumption is that they contribute overwhelmingly to our signal, especially at the lower frequencies which represent their size well (Kringel et al., 2003). Mysid shrimp are known to be abundant in demersal and pelagic fish diets (Mauchline, 1982). Since *N. americana* dwells in the hyperbenthic environment during the day and emerges into the water column during the night (Corey, 1988), this species is a link in benthic-pelagic coupling, although its relative contribution to this coupling is not known. My further discussion focuses on this species, keeping in mind that traps may underestimate the diversity and abundance of emergent fauna to our acoustic signal.

Reduced risk from visual predation is a leading hypothesis for the fitness benefit of vertical migration (Zaret and Suffern, 1976; Alldredge and King, 1985; Lampert, 1993; DeRobertis et al., 2000; Frost and Bollens, 1992). Although this hypothesis has been well documented for deep-water environments 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 environment. Here, hyperbenthic animals that are performing vertical migration may have a food source available to them even during daylight, in the form of organic matter-covered sediments and detritus. *Neomysis americana* is an omnivore. Gut studies have shown mysid diets to consist of detritus, organic-matter covered sediments, phytoplankton, and smaller zooplankton (Mauchline, 1980; Rudstam et al., 1989). Their versatile thoracic appendages allow mysids to both generate feeding currents and filter feed, and to pick up a bolus of food and macerate it with mandibles, as

30

we have observed in an aquarium. The presence of highly developed and stalked eyes allows *Neomysis americana* to feed visually on smaller zooplankton prey, at which in the laboratory they are not successful in the dark (Fulton, 1982a; Ramcharan and Sprules, 1986; Viherluoto and Viitasalo, 2001). Conversely, field studies (Rudstam et al., 1989) found that *Mysis mixta* stomach contents indicated a greater intake of zooplankton during the night, and detritus during the day.

It seems that in 2002, our acoustic record of abundance in the water column is correlated with spring and fall diatom blooms on the bottom, i.e., diel vertical migration begins after the conclusion of a benthic bloom in June and ends at the commencement of a benthic bloom in late October at approximately 8 m near the location of TAPS (observed while diving). Mysids (*Gastrosaccus psammodytes*) in a shallow surfzone have been correlated with the presence of diatoms during the day, becoming carnivorous during the night when diatoms migrate into the benthos (Wooldridge, 1989). Since the quality of organic-matter covered sediments or detritus is low for the energy-intensive activities of reproducing and egg production, richer food sources in the water column would provide a metabolic advantage. The seasonal offshore migration of *Neomysis 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 the lack of food availability both in the hyperbenthos and water column. Whitley (1948) observed *N. americana* on Georges Bank at depths less than 75 m throughout the year, but in greater abundance during winter. My observations while diving indicate this species is not at our study site in winter, and they may move offshore to exploit a different food source.

In terms of proximate causes, diel vertical migration is modulated by light, as seen by the significant positive correlation of emergence and re-entry with sunset and sunrise, respectively. It is less clear what might cause populations to migrate before sunset or after sunrise, especially if the risk of being preyed upon is greater in light than dark. On most occasions migrating populations moved under cover of relative darkness, indicated by the larger percentages of days where emergence occurred after sunset (68%) and re-entry occurred before sunrise (75%). It would be especially detrimental to an individual or population to be at the surface when light intensities are too great. Again, on 64% of the dates, migrators arrived at the surface after darkness (here defined as the end of nautical twilight); on 75% of the 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), these results are not unique; Clutter (1969) found that mysids were caught in surface waters from one hour after sunset to one hour after sunrise. Since calculated emergence and re-entry times did not correlate with a specific irradiance at that time, it is probable that factors other than absolute irradiance reduce the capabilities of visual predators during twilight or that the associated risk was balanced by fitness benefits of other activities such as feeding, mating, or dispersal.

Given that variability in the light regime due to clouds affects the time of emergence, it also suggests dependence of emergence on water- column properties such as turbidity. If emergence were tied to an endogenous rhythm only, there would be no effect of short-term factors on the timing of emergence. Emerging earlier in more turbid

conditions might be a response to reduced predation pressure. Aksnes and Giske (1993) showed that the visual range of aquatic predators decreases with increasing turbidity.

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 (*Metamysidopsis elongata*) in the same size range as juvenile *N. americana* - 4-7 mm, did not swim slower than 3 cm s^{-1}, and the swimming rate was slower in dim than bright light. Swimming speeds derived from our acoustic data are at least one order of magnitude lower than in both of these studies. Horizontal tidal currents (25 cm s^{-1} on average) in our region may influence the amount of time it takes for a school of vertically migrating mysids to ascend or descend through the water column. Alternatively, feeding, on reverse- migrating copepods, for example (Fulton, 1982b; Ohman, Frost, and Cohen, 1983) on ascent or descent may slow progress. Furthermore, there is evidence that not all members of a population migrate to the same depth, and some may not migrate at all (Mauchline, 1980; Rudstam et.al., 1989). The algorithm is most likely to detect distinct patches of animals, and thus the swimming speeds that I estimate are group velocities. The similarities of the calculated swimming speeds (mean ± 1 SE) upon ascent (0.29 ± 0.03 cm s^{-1}) and descent (-0.26 ± 0.02 cm s^{-1}) - do suggest that a similar mechanism is governing their vertical movement during emergence and re-entry.

Variation in ascent and descent rates with lags between time of initiation of vertical movement and time of atmospheric increase or decrease in light (Figure 9, 10) suggests a feedback mechanism controlling vertical movement of populations during migration. When local variability (i.e., passing atmospheric clouds, turbidity events) in the light regime prompt populations to emerge before they might otherwise do so in clear

conditions, they may slow their speed on ascent in accordance with some property of the light regime to remain concealed from visual predators. Likewise, when populations emerge after they are effectively concealed, it is expected that their rate of vertical movement would be less restricted. This inference is supported by an increase in swimming speed if emergence occurs after sunset and if populations leave the surface before the beginning of nautical twilight.

The same seasonal trend is observed in both ascent and descent rates. As day-length shortens, both ascent and descent rates decrease. While the correlation coefficients are not high, the correlation is significant. Some ideas driving this result might be seasonal changes in water- column properties (.e.g. turbidity) or food sources.

Literature dating to the early 1900s on diel vertical migration focuses on two different aspects of migration – the cue to migrate and the controlling mechanism by which animals migrate. Prominent hypotheses addressing the former are the rate of absolute change (of irradiance) and the rate of relative change, proposed by Clarke in 1930. The preferendum or isolume hypothesis (Russell, 1927) addresses the latter. In most instances in the literature, these hypotheses have been tested one at a time. Largely this approach has stemmed from the variation in study habitat – the isolume hypothesis is generally applied to depths on the order of one hundred to several hundred meters, where migrating populations are not necessarily associated with the benthos (Frank and Widder, 1997; Widder and Frank, 2001). Rate of change hypotheses have traditionally been applied to laboratory experiments involving measured phototaxes in response to a light source (Ringelberg, 1964).

The isolume hypothesis prevails as a mechanism controlling rates of vertical migration in water on the order of hundreds of meters in deep. This has been demonstrated both by submersible (Frank and Widder, 1997), by acoustic Doppler current profilers (Liljebladh and Thomasson, 2001; Luo et al., 2000; Tarling et al., 2001; Fischer and Visbeck, 1993), and by net sampling methods (Roe, 1984). Rudstam et al. (1989) observed *Mysis mixta* migrating in avoidance of light levels above approximately 10^{-4} lux, in water < 100 m deep.

In some cases, the isolume hypothesis has not been supported merely because the data did not show that a constant intensity surrounded migrating zooplankton (Roe, 1984). Richards et al. (1996) address this misconception in their model of isolumes and zooplankton vertical distribution by assuming that if a migrating animal can detect a specific light intensity, it can also detect the magnitude of the difference between a preferred light level and the actual light level. Use of a threshold difference in actual versus preferred intensity to elicit a swimming response in their model suggested that zooplankton can catch and maintain a depth distribution on or near a preferred isolume for the duration of the day.

Due to the high spatial and temporal resolution of our acoustic record, the results supporting a significant linear fit to the points representing emergence and re-entry for 75% of the days in which vertical migration could be found give great strength to the argument against the tracking of an isolume by migrating populations at our study site. Calculations of the speed of an isolume (i.e. the derivative of the quadratic that models the shape of an isolume) at points near the beginning, middle, and end of the study show that isolumes travel through the water with average speeds at least one order of

magnitude lower than the calculated ascent and descent rates for vertical migration. This result contrasts with deeper- water measurements of the speed of an isolume (Frank and Widder, 1997). The difference is largely due to the high attenuation coefficient in the Damariscotta River estuary. In clearer water isolumes move more quickly.

Richards et al. (1996) calculated isolumes as the temporal change in light intensity divided by the attenuation coefficient and the adaptation light intensity (the light intensity at $time_1$) ($dz/dt = 1/kE * dE/dt$). Using this formula for an isolume of 0.005 (unitless) in intensity yielded maximum speeds of 0.6 cm s^{-1} for this isolume at sunset and sunrise. Factoring in the attenuation coefficient and adaptation light intensity to our calculation of speeds of isolumes yields magnitudes on the order of the calculated ascent and descent rates.

The isolumes modeled by Richards et al. (1996) in time and depth (20 m) were also parabolic, and calculated isolume velocities reached a maximum of 0.6 cm s^{-1} during sunrise and sunset. As our calculated daily ascent and descent rates were never higher than this theoretical value (max. descent= 0.63 cm s^{-1}; max. ascent = 0.6 cm s^{-1}), this result seems to lend support to the isolume hypothesis in our environment. Although our results generally support a constant vertical migration speed of the population in a non-linearly changing light regime, the estimated nonlinearities in the time- depth distribution of isolumes are not large.

The rate of change of irradiance over time is also approximated by a quadratic equation. I have already been shown that a quadratic fit did not describe the distribution of emergence or re-entry points better than a straight line, and the large standard error of

the mean (-0.00034 ± 0.0003 μmol quanta m^{-2} s^{-2}) and range (min = 0.00001; max = -0.006 μmol quanta m^{-2} s^{-2}) also do not support the rate of change hypothesis.

The rate of relative change of irradiance changes over time, being small for some time after sunset, before accelerating at some point after sunset. The time at which this rapid decrease begins varies daily, depending on atmospheric and water- column properties, but may serve as a signal to emerge. The maximum rate of relative decrease of light intensity at sunset coincides with onset of migration in several marine and freshwater species (Ringelberg, 1995). In our environment, this theory may be supported by the relatively low standard error of the mean (-0.0023 ± 0.0002 s^{-1}) about the instantaneous rate of relative change of irradiance at the time of calculated emergence (minimum = 0.00012; maximum = -0.004 s^{-1}). Whether this mechanism also plays a role in controlling vertical migration needs further investigation. The large range (minimum = 0.0002; maximum = 2.58 μmol quanta m^{-2} s^{-1}) and variance (0.21 ± 0.12 μmol quanta m^{-2} s^{-1}) around the absolute irradiance at the calculated time of emergence does not lend support to a particular light level as a cue for emergence or re-entry.

Juveniles of *N. americana* were 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. However, 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* migrate throughout the year, while 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.

A regular and important aspect of twilight underwater is the spectral shift in the wavelength of maximum transmission from longer blue wavelengths to shorter blue-green wavelengths (Forward, 1988, Fig. 2). 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. *Neomysis americana* has a peak sensitivity at 515 nm (Herman 1962). This match between the spectrum and zooplankton sensitivity to that spectrum at twilight lend credence to the sensitivity hypothesis. The spectral sensitivity of many fishes is not adapted to the spectral shift that occurs at twilight; wavelength of maximum sensitivity in fishes is generally above 600 nm (Cronin, 1986). Thus, the advantage of migrating zooplankton having a spectral sensitivity matched to the wavelength of maximum transmission during twilight may be twofold. It may serve as a cue to initiate migration after predation pressure from fishes is lifted, and to then utilize the maximum transmission at that wavelength to feed visually.

Shape of isolumes and their rates of relative change modeled from surface PAR serve as proxies for the shapes and rates of isolumes of smaller bandwidths. The extinction of irradiance from the surface to some depth follows an exponential decay, at both broadband and individual wavelengths. The shape of an isolume of any wavelength, modeled in time and depth, would also be closely approximated by a quadratic equation. Thus the only properties of light which remain to be explored as mechanisms governing migration in our environment are the timing of the spectral shift in irradiance during

twilight as a cue to emerge or re-enter, and the changes in polarization underwater

(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. Investigation of both of these aspects of the light field would involve

very sensitive and not-yet commercially available instrumentation.

Given that acoustically-observed diel vertical migration did not directly support

the isolume hypothesis, and only weakly supported the rate of relative change hypothesis

using broadband PAR, the strength of the argument for a spectral cue is enhanced. It

seems unlikely that migrating populations respond to one property of light for emergence

from the hyperbenthos, and a second for control of their ascent toward the surface.

Future research should be directed toward spectral properties of light during twilight and

their correlation with diel vertical migration observed acoustically.

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Matlab m-files

```
% findfirstpm.m
% this program uses the same algorithm as findemergence2.m
% but instead of finding all the points within a specified time frame,
% it finds the first points after sunset, civil twilight, or whatever
% time you specify
% use after loading smoothed data
% HUA 1-21-03

% compute first difference and convert to percent difference
for i=1:min(c)
   diffrow(i,:)=diff(smooth(i,:));
   xm(i,:)=(diffrow(i,:)*100)./smooth(i,2:end);
end

[r,col]=find(xm(15:min(c),:)>=20); % take data above 2m
r=r+14;                                        % add 14 to r will represent the correct depth
zcol=zdatenew(col);
depr=dep(r);
d1=datestr(zdatenew(1),2);
d2=datestr(zdatenew(end),2);
figure
plot(zcol,depr,'.','markersize',11)
set(gca,'fontname','timesnewroman','fontweight','bold','fontsize',12)
datetick('x',6)
grid on
t1=['Index of BVT w/ >= 20% difference between minutes'];
title(t1)
ylabel('Height above TAPS (m)')
xlabel('Date')
axis tight
hold on

%filename=input('Enter filename for saved plot: ','s');
%[img,cmap]=capture;
%imwrite(img,cmap,filename,'tif')
%disp('Plot saved')

[rbot,colbot]=find(xm(15:min(c),:)>=20);
rbot=rbot+14;
zcolbot=zdatenew(colbot);
deprbot=dep(rbot);

n=input('How many re-entry events (i.e. days) are there in this file? ');
for i=1:n
   if i==1
      disp('Finding first emergence event...');
   elseif i==2
      disp('Finding second emergence event...');
   elseif i==3
```

```
    disp('Finding third emergence event...');
elseif i==4
    disp('Finding fourth emergence event...');
elseif i==5
    disp('Finding fifth emergence event...');
end

da=input('Enter DAY: ');
h=input('Enter HH: ');
m=input('Enter MM: ');
se=0;
[yr,mo] = datevec(zcolbot(1));
t=datenum(yr,mo,da,h,m,se);
[ztime]=find(zcolbot>=t);
e1=zcolbot(ztime(1));
h2=h+1;                                       % restrict point to those within an hour of the
t2=datenum(yr,mo,da,h2,m,se);                 % time specified
[ztime2]=find(zcolbot<=t2);
e2=zcolbot(ztime2(end));

for j=15:min(c)
    begall=find(rbot==j);
    [first]=find(begall>=ztime(1) & begall<=ztime2(end));
    if isempty(first)
        beginning(j)=0;
    else
        beginning(j)=begall(first(1));
    end
end

[notzer]=find(beginning>0);
enddep=deprbot(beginning(notzer));
endtime=zcolbot(beginning(notzer));
sorttime=sort(endtime);

% eliminate all points above 6m that occur earlier than the first point
%  below 6m and
% eliminate all points below 5m that occur later than the last point
%  above 5m
[below]=find(enddep<=5);
[above]=find(enddep>=6);
belowtime=endtime(below);
abovetime=endtime(above);
sortbelow=sort(belowtime);
sortabove=sort(abovetime);

if isempty(above) | isempty(below)
    newtime=endtime;
    newdep=enddep;
    sorttimenew=sort(newtime);
elseif sortbelow(1)>sortabove(end)
    [f]=find(endtime>=sortbelow(1));
    newtime=endtime(f);
    newdep=enddep(f);
    sorttimenew=sort(newtime);
elseif sortabove>sortbelow(1) & sortabove<sortbelow(end)
```

```
    newtime=endtime;
    newdep=enddep;
    sorttimenew=sort(newtime);
else
    [f]=find(endtime>=sortbelow(1) & endtime<=sortabove(end));
    newtime=endtime(f);
    newdep=enddep(f);
    sorttimenew=sort(newtime);
end

[yr,mo,da,h3,m3,se] = datevec(sorttimenew(1));
[yr,mo,da,h4,m4,se] = datevec(sorttimenew(end));

if size(newtime,1)>2

    for i=1:length(sorttimenew)-1            % chop any times that are greater than 15 min
        if sorttimenew(i+1)-sorttimenew(i)>=0.0105    % away from the rest of the points
            fl(i,:)=1;
        else fl(i,:)=0;
        end
    end

    if sum(fl)==0
        newtimeu=newtime;
        newdepu=newdep;
        sorttimeu=sorttimenew;
        [yr,mo,da,h3,m3,se] = datevec(sorttimeu(1));
        [yr,mo,da,h4,m4,se] = datevec(sorttimeu(end));
    end

    if sum(fl)>0
        [fx]=find(fl==1);
        v=size(fl,1);
        if size(fx,1)==1
            if fx/v > 0.75 & fx/v < 1
                u=find(sorttimenew(fx)==newtime);
                newtimeu=newtime;
                newdepu=newdep;
                newtimeu(u)=[];
                newdepu(u)=[];
                sorttimeu=sort(newtimeu);
                [yr,mo,da,h3,m3,se] = datevec(sorttimeu(1));
                [yr,mo,da,h4,m4,se] = datevec(sorttimeu(end));
            elseif fx/v < 0.25
                u=find(sorttimenew(fx)==newtime);
                newtimeu=newtime;
                newdepu=newdep;
                newtimeu(u)=[];
                newdepu(u)=[];
                sorttimeu=sort(newtimeu);
                [yr,mo,da,h3,m3,se] = datevec(sorttimeu(1));
                [yr,mo,da,h4,m4,se] = datevec(sorttimeu(end));
            elseif fx/v == 1
                u=find(sorttimenew(fx+1)==newtime);
                newtimeu=newtime;
                newdepu=newdep;
```

```
            newtimeu(u)=[];
            newdepu(u)=[];
            sorttimeu=sort(newtimeu);
            [yr,mo,da,h3,m3,se] = datevec(sorttimeu(1));
            [yr,mo,da,h4,m4,se] = datevec(sorttimeu(end));
          else
            newtimeu=newtime;
            newdepu=newdep;
            sorttimeu=sorttimenew;
            [yr,mo,da,h3,m3,se] = datevec(sorttimeu(1));
            [yr,mo,da,h4,m4,se] = datevec(sorttimeu(end));
          end
      elseif size(fx,1)>1
        if fx(end)/v > 0.75 | fx(end)/v < 0.25
          for k=fx(1:end)
            u(k)=find(sorttimenew(k)==newtime);
          end
          newtimeu=newtime;
          newdepu=newdep;
          newtimeu(u)=[];
          newdepu(u)=[];
          sorttimeu=sort(newtimeu);
          [yr,mo,da,h3,m3,se] = datevec(sorttimeu(1));
          [yr,mo,da,h4,m4,se] = datevec(sorttimeu(end));
        else
          newtimeu=newtime;
          newdepu=newdep;
          sorttimeu=sorttimenew;
          [yr,mo,da,h3,m3,se] = datevec(sorttimeu(1));
          [yr,mo,da,h4,m4,se] = datevec(sorttimeu(end));
        end
      end
      if size(newtimeu,1)<=1
        disp('No emergence to be found')
      end
  end

if h4-h3>0
  space=(60-m3)+m4;
elseif h4-h3==0
  space=m4-m3;
end

newdepu=newdepu';
d=datestr(e1,2);
p=polyfit(newtimeu,newdepu,1);          % fit a line to just the minutes
xi=linspace(sorttimeu(1),sorttimeu(end),space);
figure
yi=polyval(p,xi);
plot(newtimeu,newdepu,'b.','markersize',10)
hold on
plot(xi,yi,'r-')
grid on
datetick('x',15)
t1=['Emergence - ' d];
title(t1)
```

```
ylabel('Depth (m)');
xlabel('Time')
hold on

slope=(yi(end)-yi(1))/(xi(end)-xi(1));
slopem=(yi(end)-yi(1))/space;   % in m/min

b=yi(1)-slope*xi(1);                    % y-intercept
xeq=(0-b)/slope;
rate=slopem*1.6667;             % change units to cm/s
txt1=datestr(xeq,15);
txt2=num2str(rate);
cor=corrcoef(newtimeu,newdepu);
r2=cor(1,2)^2;
txt3=num2str(r2);
g2=['R2 = ' txt3];
g=['Emergence begins at ' txt1]  % x-value at y=0 (depth=0m)
g1=['Ascent rate is ' txt2(1,1:5) ' cm/s'];
text(xi(1),max(newdepu),g);
text(xi(1),max(newdepu)-0.5,g1);
text(xi(end),max(newdepu),g2);

filename=input('Enter filename for saved variables: ','s');
folder=('c:\Taps\efiles_pm');
cmd=['cd ' folder];
eval(cmd);
cmd=['save ' filename ' newdepu newtimeu slopem slope b txt1 rate xi yi r2'];
eval(cmd)
fprintf('Data saved to disk\n')

clear f1 newtimeu newdepu newtime newdep endtime enddep sorttimenew sorttime

elseif size(newtime,1)<=2
    disp('No emergence to be found')
  end
end
```

```matlab
% findlastam.m
% this program uses the same algorithm as findentry.m
% but instead of finding all the points within a specified time frame,
% it finds the last points before sunrise, civil twilight, or whatever
% time you specify
% use after loading smoothed data
% HUA 1-21-03

% compute first difference and convert to percent difference
for i=1:min(c)
  diffrow(i,:)=diff(smooth(i,:));
  xm(i,:)=(diffrow(i,:)*100)./smooth(i,2:end);
end

[r,col]=find(xm(15:min(c),:)<=-20);           % take data above 2m
r=r+14;                                        % add 14 so r will represent the correct depth
zcol=zdatenew(col);
depr=dep(r);
d1=datestr(zdatenew(1),2);
d2=datestr(zdatenew(end),2);
figure
plot(zcol,depr,'.','markersize',10)
datetick('x',15)
grid on
t1=['Index of BVT w/ <= -20% difference between minutes, ' d1 ' - ' d2];
title(t1)
ylabel('Depth (m)')
xlabel('Time')
hold on

%filename=input('Enter filename for saved plot: ','s');
%[img,cmap]=capture;
%imwrite(img,cmap,filename,'tif')
%disp('Plot saved')

[rbot,colbot]=find(xm(15:min(c),:)<=-20);
rbot=rbot+14;
zcolbot=zdatenew(colbot);
deprbot=dep(rbot);

n=input('How many re-entry events (i.e. days) are there in this file? ');
for i=1:n
  if i==1
    disp('Finding first re-entry event...');
  elseif i==2
    disp('Finding second re-entry event...');
  elseif i==3
    disp('Finding third re-entry event...');
  elseif i==4
    disp('Finding fourth re-entry event...');
  elseif i==5
    disp('Finding fifth re-entry event...');
  end

  da=input('Enter DAY: ');          % for re-entry, it seems that time of am
  h=input('Enter HH: ');            % civil twilight works well
```

```
m=input('Enter MM: ');
se=0;
[yr,mo] = datevec(zcolbot(1));
t=datenum(yr,mo,da,h,m,se);
[ztime]=find(zcolbot<=t);
e1=zcolbot(ztime(end));
h2=h+1;                                          % restrict point to those within an hour of
the
t2=datenum(yr,mo,da,h2,m,se);    % time specified
[ztime2]=find(zcolbot<=t2);
e2=zcolbot(ztime2(end));

for j=15:min(c)
   lastall=find(rbot==j);
   [last]=find(lastall>=ztime(end) & lastall<=ztime2(end));
   if isempty(last)
      ending(j)=0;
   else
      ending(j)=lastall(last(end));
   end
end

[notzer]=find(ending>0);
enddep=deprbot(ending(notzer));
endtime=zcolbot(ending(notzer));
sorttime=sort(endtime);

% eliminate all points below 6m that occur earlier than the first point
% above 6m and
% eliminate all points above 5m that occur later than the last point
% below 5m
[above]=find(enddep>6);
[below]=find(enddep<5);
abovetime=endtime(above);
belowtime=endtime(below);
sortabove=sort(abovetime);
sortbelow=sort(belowtime);
if isempty(above)
   [f]=find(endtime<sortbelow(end));
elseif isempty(below)
   [f]=find(endtime<sortabove(1));
else
   [f]=find(endtime>=sortabove(1) & endtime<=sortbelow(end));
end
newtime=endtime(f);
newdep=enddep(f);
sorttimenew=sort(newtime);

[yr,mo,da,h3,m3,se] = datevec(sorttimenew(1));
[yr,mo,da,h4,m4,se] = datevec(sorttimenew(end));

if size(newtime,1)>2

   for i=1:length(sorttimenew)-1                 % chop any times that are greater than 15 min
      if sorttimenew(i+1)-sorttimenew(i)>=0.0105  % away from the rest of the points
         f1(i,:)=1;
```

```
      else fl(i,:)=0;
      end
end

if sum(fl)==0
  newtimeu=newtime;
  newdepu=newdep;
  sorttimeu=sorttimenew;
  [yr,mo,da,h3,m3,se] = datevec(sorttimeu(1));
  [yr,mo,da,h4,m4,se] = datevec(sorttimeu(end));
end

if sum(fl)>0
  [fx]=find(fl==1);
  v=size(fl,1);
  if size(fx,1)==1
    if fx/v > 0.75 | fx/v < 0.25
      u=find(sorttimenew(fx)==newtime);
      newtimeu=newtime;
      newdepu=newdep;
      newtimeu(u)=[];
      newdepu(u)=[];
      sorttimeu=sort(newtimeu);
      [yr,mo,da,h3,m3,se] = datevec(sorttimeu(1));
      [yr,mo,da,h4,m4,se] = datevec(sorttimeu(end));
    else
      newtimeu=newtime;
      newdepu=newdep;
      sorttimeu=sorttimenew;
      [yr,mo,da,h3,m3,se] = datevec(sorttimeu(1));
      [yr,mo,da,h4,m4,se] = datevec(sorttimeu(end));
    end
  elseif size(fx,1)>1
    if fx(end)/v > 0.75 | fx(end)/v < 0.25
      for k=fx(1:end)
        u(k)=find(sorttimenew(k)==newtime);
      end
      newtimeu=newtime;
      newdepu=newdep;
      newtimeu(u)=[];
      newdepu(u)=[];
      sorttimeu=sort(newtimeu);
      [yr,mo,da,h3,m3,se] = datevec(sorttimeu(1));
      [yr,mo,da,h4,m4,se] = datevec(sorttimeu(end));
    else
      newtimeu=newtime;
      newdepu=newdep;
      sorttimeu=sorttimenew;
      [yr,mo,da,h3,m3,se] = datevec(sorttimeu(1));
      [yr,mo,da,h4,m4,se] = datevec(sorttimeu(end));
    end
  end
  if size(newtimeu,1)<=1
    disp('No re-entry to be found')
  end
end
```

```matlab
if h4-h3>0
    space=(60-m3)+m4;
elseif h4-h3==0
    space=m4-m3;
end

newdepu=newdepu';
d=datestr(e1,2);
p=polyfit(newtimeu,newdepu,1);                          % fit a line to just the minutes
xi=linspace(sorttimeu(1),sorttimeu(end),space);
figure
yi=polyval(p,xi);
plot(newtimeu,newdepu,'b.','markersize',10)
hold on
plot(xi,yi,'r-')
grid on
datetick('x',15)
t1=['Re-entry - ' d];
title(t1)
ylabel('Depth (m)');
xlabel('Time')
hold on

slope=(yi(end)-yi(1))/(xi(end)-xi(1));
slopem=(yi(end)-yi(1))/space;   % in m/min

b=yi(1)-slope*xi(1);                                    % y-intercept
xeq=(0-b)/slope;
rate=slopem*1.6667;                                     % change units to cm/s
txt1=datestr(xeq,15);
txt2=num2str(rate);
cor=corrcoef(newtimeu,newdepu);
r2=cor(1,2)^2;
txt3=num2str(r2);
g2=['R2 = ' txt3];
g=['Re-entry begins at ' txt1]     % x-value at y=0 (depth=0m)
g1=['Descent rate is ' txt2(1,1:5) ' cm/s'];
text(xi(1),max(newdepu),g);
text(xi(1),max(newdepu)-0.5,g1);
text(xi(end),max(newdepu),g2);

filename=input('Enter filename for saved variables: ','s');
folder=('c:\Taps\efiles_am');
cmd=['cd ' folder];
eval(cmd);
cmd=['save ' filename ' newdepu newtimeu slopem slope b txt1 rate xi yi r2'];
eval(cmd)
fprintf('Data saved to disk\n')
clear f1

elseif size(newtime,1)<=2
    disp('No re-entry to be found')
end
                                                        end
```

BIOGRAPHY OF THE AUTHOR

Heather Uhden Abello was born in Point Pleasant, New Jersey on February 6, 1976. She was raised in Sea Girt, New Jersey and graduated from Saint Rose High School in 1994. She attended Fordham University and graduated in 1998 with a Bachelor's degree in Biological Sciences. She taught Algebra I and General Science at the Academy of Mount Saint Ursula, Bronx, New York, from 1998 to 2000. She then moved to Maine and entered the Oceanography graduate program at The University of Maine in the summer of 2000.

Heather is a candidate for the Master of Science degree in Oceanography from The University of Maine in May, 2003.