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Acoustic observations of vertical and horizontal swimming velocities of a diel migrator

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ABSTRACT

A strong sound scattering layer which underwent diel vertical migration was observed over 176 days using a bottom-mounted 600 kHz ADCP at a depth of approximately 285 m on the upper continental slope. Average observed descent times of the scatterers were within 12 minutes of sunrise and average ascent times were within 13 minutes of sunset. Average ascent speeds progressively increased away from the bed and approached 6 cm/s. Average descent speeds similarly reached a maximum of ∼6 cm/s. Horizontal velocities of the scatterers during vertical migration were found to be smaller than ambient velocities (by up to 3 cm/s), and it is inferred that the migrators were swimming horizontally against the flow. Horizontal velocities of the scatterers during time intervals when the layer was near the seafloor were found to be southwest (up to 3 cm/s), and onshelf (up to 1.7 cm/s) relative to the flow above the layer. Swimming velocities were independent of alongshelf flow direction, counter to the hypothesis that the scatterers sought to maintain their position by swimming against the flow.

1. Introduction

In water depths of several hundred meters along the Earth's continental margins, stratified ocean waters impinge on continental slopes. This region is characterized by interesting and complex physical processes (Huthnance, 1995). A topic of ongoing research is the propagation of internal tides and waves over sloping bottoms, a process that can intensify nearbed currents, leading to sediment transport and to enhanced turbulent mixing (Ribbe and Holloway, 2001; Raaphorst *et al.*, 2001; Cacchione *et al.*, 2002; Davies and Xing, 2004, 2005).

As part of a project intended to investigate the effects of internal tides on sediment transport, an instrumented bottom pod was deployed on the upper slope of the Nova Scotian continental margin in the late summer and early autumn months of 2002 and 2003. The bottom pod was equipped with an upward-looking Acoustic Doppler Current Profiler (ADCP) to monitor flow velocity as a function of height above bottom. ADCPs measure flow velocity by recording the Doppler shift of transmitted acoustic pulses that return to the sensor after encountering scatterers in the water column.

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Ideally, scatterers move at the same velocity as the fluid. In practice, swimming organisms can be the dominant scatterers, and they do not move at the same velocity as the fluid. Under these circumstances, estimates of velocity can be biased by the behavior of the swimming organisms (Wilson and Firing, 1992; Ott, 2005). Numerous studies have shown that diel vertical migrations by zooplankton and micronekton (small fishes, shrimps, and squids) affect estimates of vertical velocity obtained by ADCPs, particularly near times of ascent in the evening and descent in the morning (Plueddemann and Pinkel, 1989; Buchholz *et al.*, 1995; Ashjian *et al.*, 1998; Rippeth and Simpson, 1998; Robinson and Gomez-Gutierrez, 1998; Luo *et al.*, 2000; Tarling *et al.*, 2001; Valle-Levinson *et al.*, 2004; Ott, 2005). In contrast, bias in horizontal velocities arising from directional swimming is generally absent from ADCP data (Geyer and Signell, 1990; Ott, 2005). The absence of horizontal bias is attributed to uncorrelated horizontal motions among the scattering organisms. In short, zooplankton and micronekton generally do not migrate horizontally.

On the other hand, observations near boundaries indicate that horizontal migrations of mesopelagic micronekton do occur (Wilson and Firing, 1992; Benoit-Bird *et al.*, 2001; Benoit-Bird and Au, 2004; Wilson and Boehlert, 2004). The mesopelagic realm extends from approximately 200 to 1000 m, and is a region of low light. The reasons for horizontal migrations are not known but may include food foraging (Benoit-Bird *et al.*, 2001), position maintenance (Wilson and Firing, 1992; Wilson and Boehlert, 2004) or predator avoidance (Wilson and Firing, 1992; Benoit-Bird *et al.*, 2001).

Initial analysis of the ADCP data in this study revealed a pronounced diel signal in the vertical velocity data and in the backscatter data. We began our analysis in part to investigate the day/night differences in backscatter as a means of identifying backscatter from sediment in suspension. It was through this line of investigation that velocity bias was identified. The goal of this study, therefore, is to assess velocities arising from vertical and horizontal migrations of micronekton. The present observations were continuous over several months and have a high temporal resolution (ca. 1.5-min sample interval). With these data we could accurately monitor the seasonal changes in the descent-ascent times and quantify the day/night differences in mean velocity.

A description of the experiment is presented in Section 2, followed by observations of near-bottom currents in Section 3. Section 4 includes descent and ascent velocities of the scatterers and documents arrival and departure times. Section 5 presents scattering layer velocities which were estimated by removing ambient flows and by comparing velocities during time intervals when scatterers were present and when they were absent. The discussion presents potential hypotheses for horizontal swimming direction, and is followed by the summary and conclusions.

2. Experiment description

The experiment included two deployments at a site located on the upper slope of the Scotian margin (Fig. 1) at a depth of approximately 285 m. This site is on a cross-shelf profile

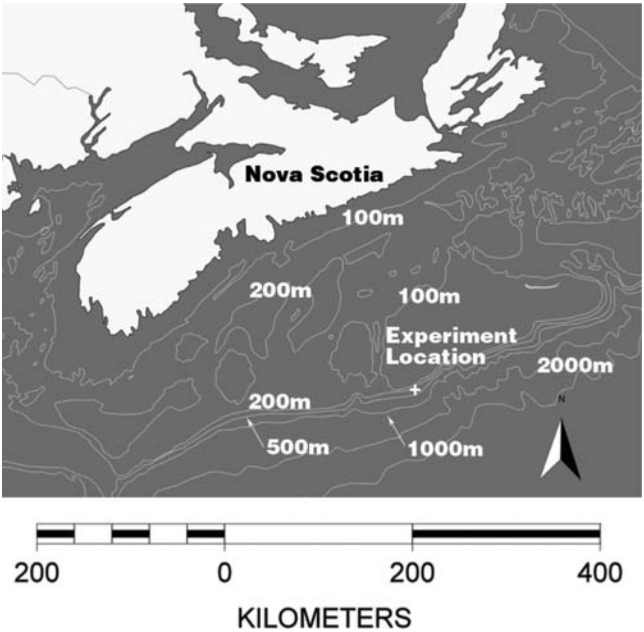

Figure 1. Scotian shelf bathymetry showing the experiment location.

called the Halifax section, for which the shelf-break occurs at a depth of approximately 100 m (see for example Loder *et al.*, 2003). Table 1 lists summary information for both deployments.

Profiles of velocity were measured with an RD Instruments Acoustic Doppler Current Profiler (600 kHz Broadband Workhorse Sentinel) equipped with 4 transducers inclined at

Table 1. Experiment summary information. Experiment-averaged values of depth, temperature, pitch, roll and heading are listed, along with the standard deviation.

Quantity	2002	2003
Latitude	42°59.5’ N	42°59.5’ W
Longitude	61°44.7’ N	61°44.7’ W
Deployment Date	Aug. 17	Jul. 14
Recovery Date	Oct. 20	Nov. 3
Duration	64 days	112 days
Mean Depth	285.7 ±0.4 m	283.2 ±0.4 m
Mean Temperature	8.5 ±0.7 °C	8.7 ±0.8 °C
Mean Pitch	2.4 ±0.04°	−0.7 ± 0.1°
Mean Roll	0.1 ±0.1°	−2.5 ± 0.3°
Mean Heading	318.9 ±0.1° MN	18.1 ±0.2° MN
Mag. Declination	19.0°W	19.1°W

20° from the vertical. The ADCP was located ∼1.8 m above the seafloor and was attached to an instrumented 2.6 m × 3.3 m × 2 m quad frame, which has been discussed in some detail by Heffler (1996) and Smyth and Li (2005).

In 2002, 64 days of good quality data were collected using 60 1-m range bins, with a 30-ping ensemble-average profile taken every 90 s. In 2003, there were 112 days of data with 100 1-m range bins, and a 30-ping ensemble-average profile taken every 105 s. For both data sets, the first bin was 2.9 m away from the transducer. Velocities were collected in the East/North/Up coordinate system relative to magnetic North, and were rotated into an alongshelf/cross-shelf system based on the shelf-break bathymetry. The rotation angle was estimated as −20°. Magnetic declinations for 2002 and 2003 at the experiment location were 19.7° and 19.1°, and thus the applied rotation was less than 1 degree. The rotated coordinate system was defined as U positive alongshelf to the northeast and V positive onshelf. Vertical velocities were defined as positive upwards. Pressure and temperature were also measured by the ADCP.

Backscatter amplitudes were converted from counts to dB/m using manufacturer scale-factors. Corrections were applied for spherical spreading, freshwater attenuation and attenuation caused by ionic relaxation of magnesium sulfate and boric acid (Clay and Medwin, 1977). To prevent noise from biasing the backscatter amplitude at larger distances from the transducer, a threshold was defined for each beam, and data below the threshold were not considered. Noise thresholds were selected from histograms of the backscatter amplitude which clearly showed two distinct peaks about the median value. The noise threshold was selected for each beam as the minimum between the two peaks. Most of the data after bin 50 was below the noise threshold, and only data in the first 50 bins were included in this analysis.

The 4-beam ADCP estimated the error velocity as the difference in vertical velocities from the two pairs of two beams. Error velocity profiles averaged over the experiment were small, ∼0.2 ± 0.2 cm/s, and did not change significantly when scatterers were present. The error velocity is expected to be zero on average for homogenous flows. Horizontal homogeneity was assessed using criteria by Lu and Lueck (1999). The mean error velocity was smaller than its standard deviation (ratio < 0.1), which satisfied the first criterion for horizontal homogeneity. The average error velocity was 5% of the mean flow during the day when scatterers were present and 3% at night, which was considered acceptable for the second criterion of horizontal homogeneity. Thus, the effect of the scattering layer on horizontal heterogeneity was found to be small.

Also attached to the frame was a 5 MHz Acoustic Doppler Velocimeter (ADV-Ocean, Sontek/YSI) which collected single-point, three-component estimates of particle velocity nominally 0.52 m above the seafloor at an ensemble-averaged rate of 12.5 Hz. Data were collected for 5 minutes every hour for a total of 52 days, starting on July 14th, 2003. ADV data were used to identify flow disturbance effects, and were compared with ADCP velocities. No ADV data were available for 2002.

3. Mean and tidal velocities

Time series of near-bottom velocities were analyzed to determine tidal currents and velocity variability during the deployments. These analyses documented the ambient flow field and assessed if the scattering layer presence was linked to the lunar-day or the solar-day.

Velocities were filtered with a third-order Butterworth low-pass filter with a 0.5 cycles/day cutoff frequency and were vertically averaged over a 10 m range (30–40 m above bottom). Time series of the low-pass filtered horizontal velocities showed large alongshelf currents to the northeast with some reversals (Fig. 2). Experiment-averaged velocities from the bottom-mounted ADCP were ~3 cm/s alongshelf to the northeast and ~3 cm/s offshelf in 2002. Averaged near-bottom currents were larger in 2003, ~14 cm/s alongshelf to the northeast and ~4 cm/s offshelf. Surficial alongshelf currents in 2002 were southwest on average, but exhibited flow reversals. At times the bottom currents were opposite in sign to surficial currents (J. W. Loder, Person commun.).

There are few predictions of near-bottom upper slope currents available for comparison with the present measurements. Han *et al.* (1997) modeled seasonal-mean circulation over the Scotian Shelf using a 3D nonlinear diagnostic model. In winter months, a strong southwest surface current over the shelf-break was predicted. In summer months, the southwest

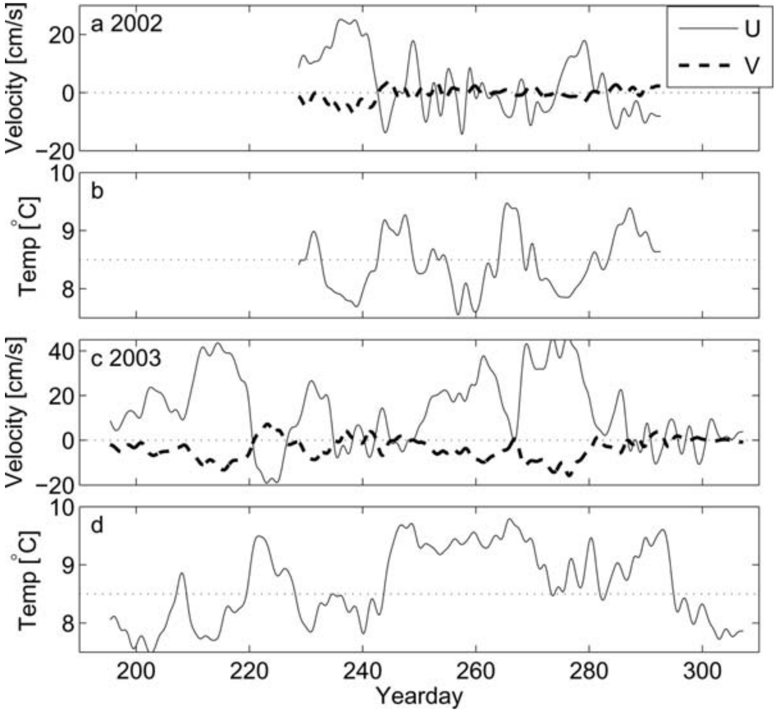

Figure 2. Time series of low-pass filtered alongshelf (U) velocity, cross-shelf (V) velocity and temperature for 2002 (a,b) and 2003 (c,d). Velocities were averaged over 10 m at 35 m height.

flow was predicted to weaken, allowing a northeast continental slope current to reach the shelf-break. Han and Loder (2003) also predicted near-bottom eastward currents that were assumed to be due to local anomalies in the baroclinic and/or barotropic pressure gradients.

Near-bed temperatures measured by the ADCP varied between 7.5 and 9.5°C with an average of 8.5°C in 2002 and 8.7°C in 2003 (Fig. 2). Previous observations of the vertical structure of the upper continental slope-water have described a wedge of relatively fresh upper-layer shelf water, a middle layer of warm slope water centered at 200–300 m (temperature of 9–12°C, salinities above 35), and a bottom layer of Labrador slope water (4–9° C, 34–35) (Loder *et al.*, 2003, and references therein).

Tidal analysis was performed on the sea-surface elevation time series (from the ADCP pressure data) using T_tide (Pawlowicz *et al.*, 2002). For 2003 data, 96.5% of the variance was explained by five constituents M2,S2,N2,O1,K1 with amplitudes 0.47, 0.11, 0.10, 0.06, 0.06 m respectively, and a form number of 0.21 (semidiurnal). For 2002 data, the results were similar: 98.3% of the variance was explained by the same five constituents which had similar amplitudes (0.48, 0.14, 0.13, 0.06, 0.06 m) and a form number of 0.19.

Tidal analysis of the near-bottom velocities was not successful as the tidal velocities were intermittent, likely caused by variability in the strength of the internal tide (Wunsch, 1976). Harmonic analysis of the internal tidal velocities was unsuccessful over the entire time series, but could be used over short time windows. To determine the average tidal velocities, the data were averaged over a lunar and solar day.

Lunar-day averaging (24 hrs, 50 min) of the data over the entire experiment showed the currents had a lunar semidiurnal signal (M2 12.42 hr period) with a modest average amplitude of ~5 cm/s. Backscatter amplitude was strong near the bed, but did not have any lunar-day variation which suggests the migrators were not linked to the lunar tidal cycle. Solar-day averaging of the data showed a weak solar semidiurnal (S2 12 hr period) contribution to the currents of ~3 cm/s.

4. Swimming velocities during migration

ADCP vertical velocities showed evidence of a diel vertical migrator. A large downward velocity just before sunrise coincided with the appearance of a near-bottom strong scattering layer, and a large upward velocity just before sunset coincided with the disappearance of the scattering layer (Fig. 3). Maximum vertical migration velocities in this figure are ~8 cm/s.

Diel migration times were estimated from velocity peaks which were visually correlated with the arrival/departure of the scatterers within a 2.5 hr window of sunrise/sunset in the upper half of the data (30–54 m above the seafloor). Selected velocity peaks had to exceed a threshold of twice the standard deviation of the daily velocity excluding the 5-hr time window. Median arrival time of the scattering layer at the seabed was 11.5 ± 3.8 min (standard error) after sunrise in 2002 and 10.5 ± 1.3 min before sunrise in 2003. Median departure times were similar: 13 ± 5 min before sunset in 2002 and 9.5 ± 1.6 min after sunset in 2003. Time series of descent and ascent times are shown in Figure 4. Inter-annual

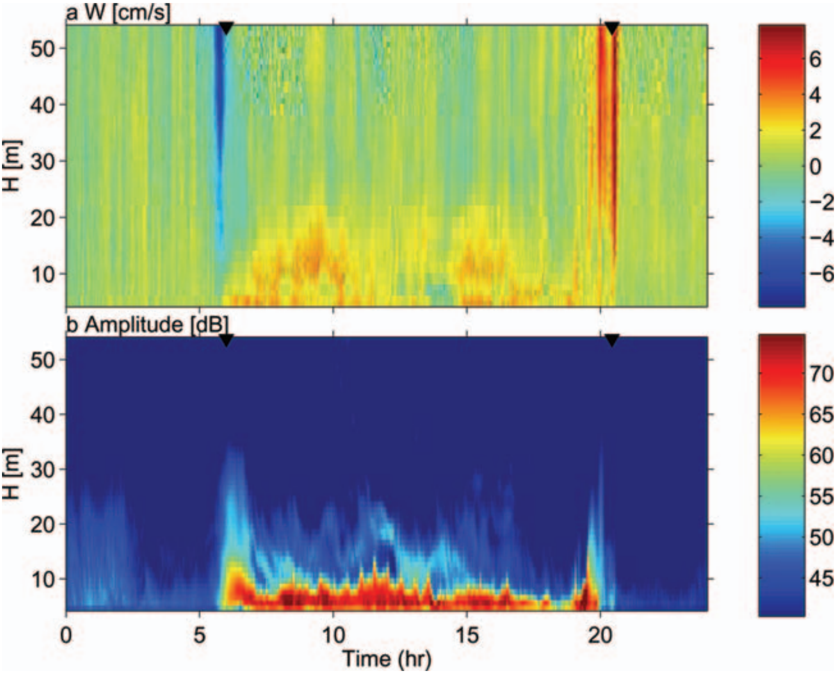

Figure 3. Time series of (a) vertical velocity and (b) backscatter amplitude for yearday 220. Black triangle symbols indicate sunrise and sunset, and H is the distance above the seafloor.

differences in descent and ascent times were likely related to differences in migration speeds. Median descent times were based on 47 and 105 days for 2002 and 2003 respectively, and median ascent times were based on 55 and 109 days in 2002 and 2003 respectively.

These migration time estimates are consistent with other studies. Rippeth and Simpson (1998) observed migration (likely of euphausiids) coincident with sunrise/sunset at a depth of 77 m and Thomson and Allen (2000) observed a rapid descent (likely of *Euphausia Pacifica* and *Thysanoessa Spinifera*) 25 minutes before sunrise at 100–150 depth.

Average vertical migration velocities at 50 m above bottom approached 6 cm/s in 2003 and 3 cm/s in 2002. Previous results have found vertical migration velocities range from 2–8 cm/s, and are affected by travel distance, migrator size, fish presence and swarm dynamics (Heywood, 1996; Buchholz *et al.*, 1995; Rippeth and Simpson, 1998; Thomson and Allen, 2000; Tarling *et al.*, 2001).

Upward and downward migration velocity profiles were fairly symmetric, and speeds increased with distance away from the bed (Fig. 5). Smaller swimming velocities were observed in the 2002 data which suggests travel time to the near-surface layers would take longer and thus a shorter amount of time would be spent at depth. This is consistent with the observed descent and ascent times (Fig. 4).

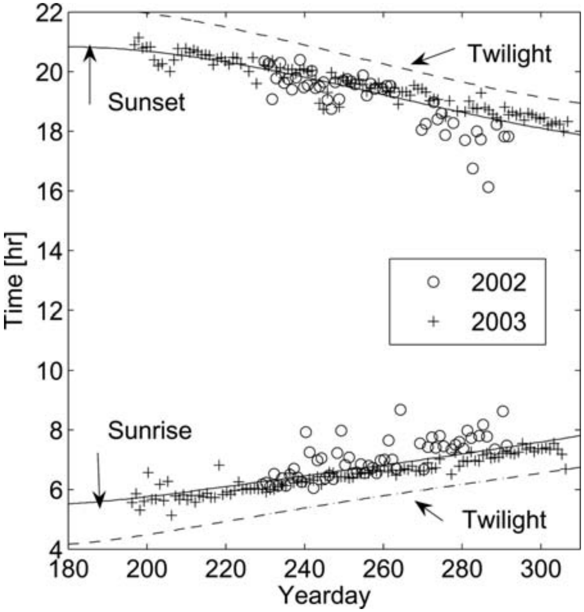

Figure 4. Migration times compared to sunrise, sunset and nautical twilight.

To determine if there was horizontal swimming during migration, daily data were averaged according to migration times (Fig. 6). Averaging the data in this way clearly shows the appearance of the near-bed strong scattering layer following descent, and the absence of the layer after ascent. In Figure 6, timing of descent was shifted to hour 0, and ascent to hour 12. The averaged horizontal velocities exhibit vertical bands coincident with the ascent and descent vertical migration velocities. These bands indicate that horizontal migration occurred during ascent and descent and tended to oppose the background flow.

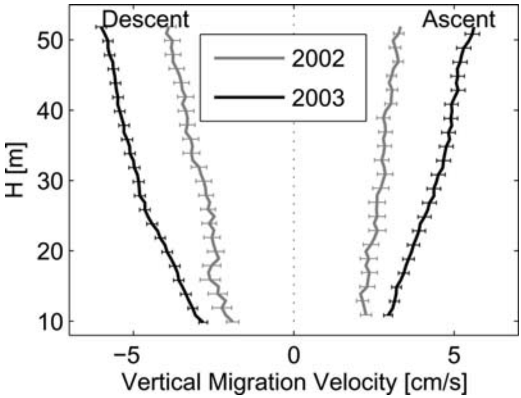

Figure 5. Vertical migration velocity profiles for 2002 and 2003. Errorbars indicate standard error.

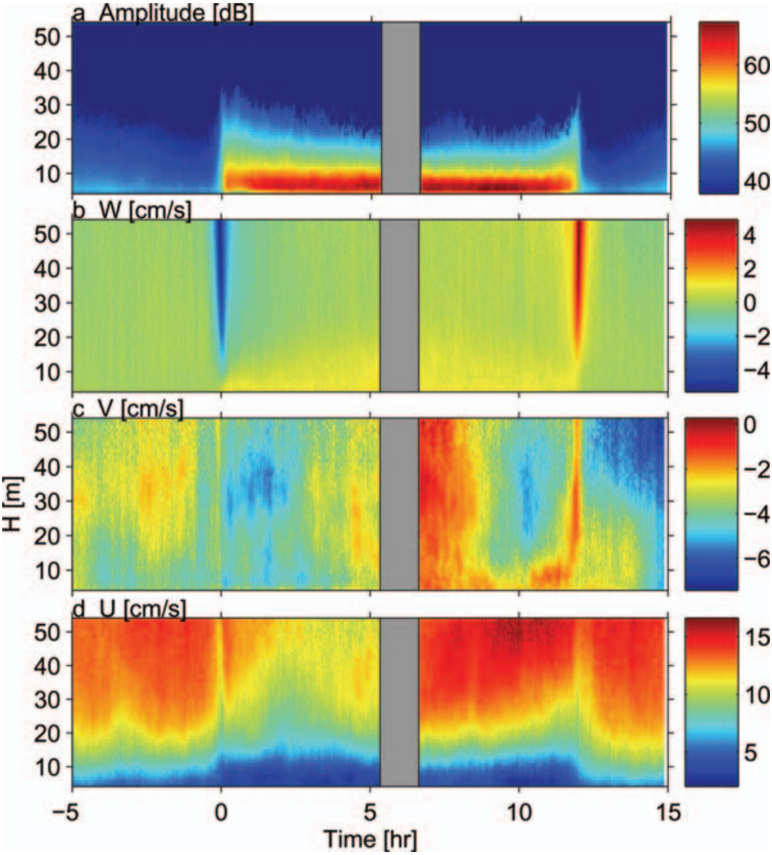

Figure 6. Experiment-averaged day based on migration times of (a) backscatter amplitude, (b) vertical (c) onshelf and (d) alongshelf velocities. Time series were shifted according to migration times, and the gap results from the varying daylight hours.

Horizontal swimming speeds during migration were quantified by comparing the velocity during migration to background velocities just before descent and just after ascent. Data windows were defined by the vertical migration times, and were averaged over the entire deployment. Data were further spatially-averaged over 3 m in the vertical (3 bins). A 3rd-order polynomial was fit over a 3.5 hr window, and the background velocity was chosen as the value at the edge of the window (25 minutes before descent or 25 minutes after ascent). Horizontal speeds during descent/ascent were typically smaller than the background speed (Fig. 7). Smaller speeds indicate that the scatterers were swimming against the flow during ascent and descent. Maximum horizontal swimming velocities for descent and ascent were estimated to be 2.2 cm/s to the southwest and 3 cm/s onshelf for 2003. These values are much larger than the horizontal velocity uncertainty which was estimated to be 0.17 cm/s. Horizontal swimming speeds were slightly smaller in 2002: 1.7 cm/s to

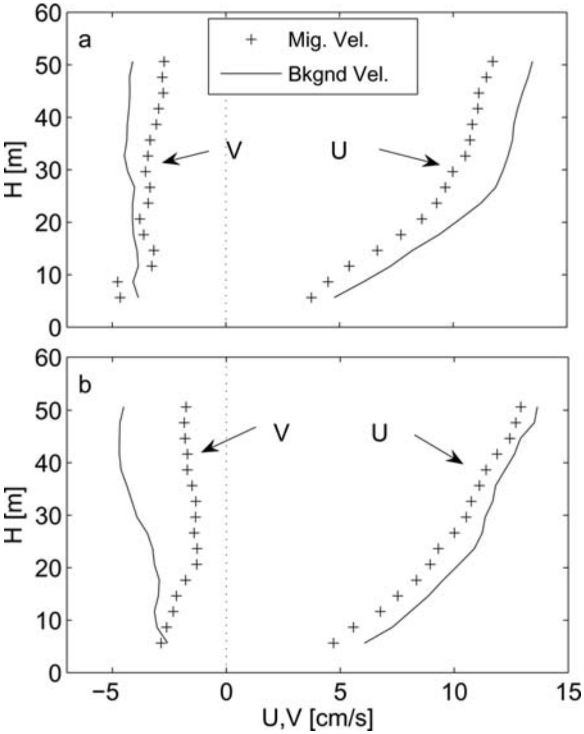

Figure 7. Profiles of experiment-averaged alongshelf and cross-shelf velocities during (a) descent and (b) ascent for 2003. Ambient velocity profiles are also shown.

the southwest and 1.5 cm/s onshelf. The smaller horizontal swimming speeds in 2002 were consistent with the smaller observed vertical migration speeds.

A second method was used to obtain estimates of average horizontal swimming speeds during ascent/descent, and to estimate the variability in the migration velocities. In this method, ADCP velocity time series were fit with a four term Fourier series to remove background currents and tides. Horizontal velocities were fit in a least-squares sense at each height, over a lunar day, for each velocity component. For example, the alongshelf component was fit as:

$$U(t, z) = \sum_{i=1}^{4} a_i \sin\left(\frac{2\pi t}{b_i} + c_i\right) \tag{1}$$

where a_i is the amplitude, b_i is the period, and c_i is the phase. All Fourier coefficients were estimated using Matlab's curve-fitting toolbox, with the only restriction that the minimum period allowed was 1 hr so as not to remove velocity changes associated with migration.

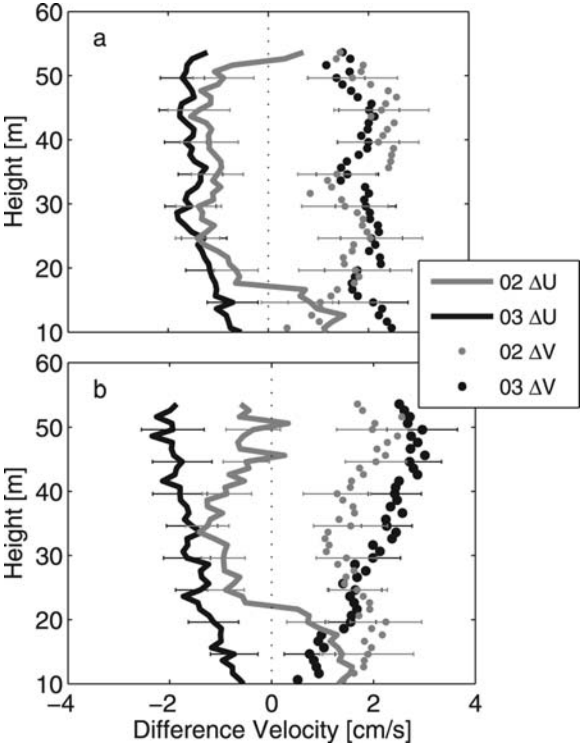

Figure 8. Profiles of alongshelf and offshelf velocity differences during (a) descent and (b) ascent. Error bars indicate the standard deviation. Fitted velocities (Fourier method) were subtracted from measured velocities.

For fits with a high squared-correlation coefficient ($r^2 > 0.6$), the fitted velocity was subtracted from the measured velocity, and the swimming velocities were estimated as the difference velocity at the time of migration.

Horizontal swimming velocities obtained from the Fourier series method were also alongshelf to the southwest and onshelf, with a maximum of 2 cm/s (Fig. 8). This result is consistent with the results from the previous method. Averaged alongshelf profiles included 50 days for 2002 and 83 days for 2003. Averaged cross-shelf profiles included 31 days for 2002 and 66 days for 2003. An attempt was made to separate the data by alongshelf flow direction (southwest versus northeast) to determine if the migrators were swimming in a particular direction or swimming against the flow, but there was limited data for the southwest flow case and not enough of the fits had high squared-correlation coefficients.

In summary, during ascent and descent the scatterers were migrating horizontally at a speed of approximately 2 cm/s against the background flow.

5. Near-bottom swimming velocities

Swimming velocities were also determined during daytime intervals when the scattering layer was located near the seafloor. Two methods were used to estimate scatterer velocity. The first used the velocity difference between upper-level flow and near-bed flow. Velocity differences were compared for daytimes when the scatterers were present near the bed, and for night-times, when the scatterers were generally absent. The second method compared the velocity above the boundary of the strong scattering layer to the velocity within the layer.

In the first method, the velocity difference was estimated between velocities averaged over the upper-half of the data (29.6 to 53.6 m) and the lower-half of the data (4.6 to 28.6 m). Velocity differences were separated by scattering layer absence/presence based on the migration times, excluding a 40 minute window about the migration time. As the migration times were so closely related to sunrise and sunset, this essentially separated the data into daytime and night-time.

Generally the magnitude of the velocity difference increased with upper-layer flow due to bed friction reducing the near-bed flows (Fig. 9). However, there were differences between day and night which appear to indicate a preferred swimming direction. When alongshelf velocities were to the northeast, the daytime velocity differences were large (up to 8 cm/s), suggesting scatterers were swimming against the flow. This was not the case for flow to the southwest as the velocity difference was small, suggesting the scatterers were not swimming against the flow. The average of the alongshelf day/night difference was 3 cm/s to the southwest. Cross-shelf velocity differences suggest the scatterers were swimming onshelf, but the average rate was small $\sim$1 cm/s. Vertical velocity differences suggest the scatterers were swimming upwards, and these velocities are discussed further in Section 5a.

These swimming velocities may also include S2 tidal currents which have day/night differences. However, the results show an asymmetry in the velocity differences and offsets from zero which suggests the scatterers had a preferred swimming direction and were not simply swimming against the flow.

Velocities measured by the Acoustic Doppler Velocimeter ($\sim$0.5 m above bottom) would contain S2 tidal currents, but would not include swimming velocities as the sampling volume was likely too small to contain scatterers. Bin-averaged velocity differences (estimated from upper level ADCP velocities minus ADV velocities) did not exhibit large day/night differences (Fig. 9d).

The second method for estimating the swimming velocity used the amplitude data to identify the upper boundary of the strong scattering layer and compared the velocity within the layer to the ambient flow above. The boundary height was determined from large jumps in amplitude ($>$3dB in all 4 beam-wise amplitudes) with the constraint that there must be high scattering amplitudes within the layer ($>$90% of the maximum experiment-averaged amplitude profile). Once the boundary was identified, short vertical sections 9 m above and 6 m within the scattering layer were selected from the velocity time series, (Fig. 10).

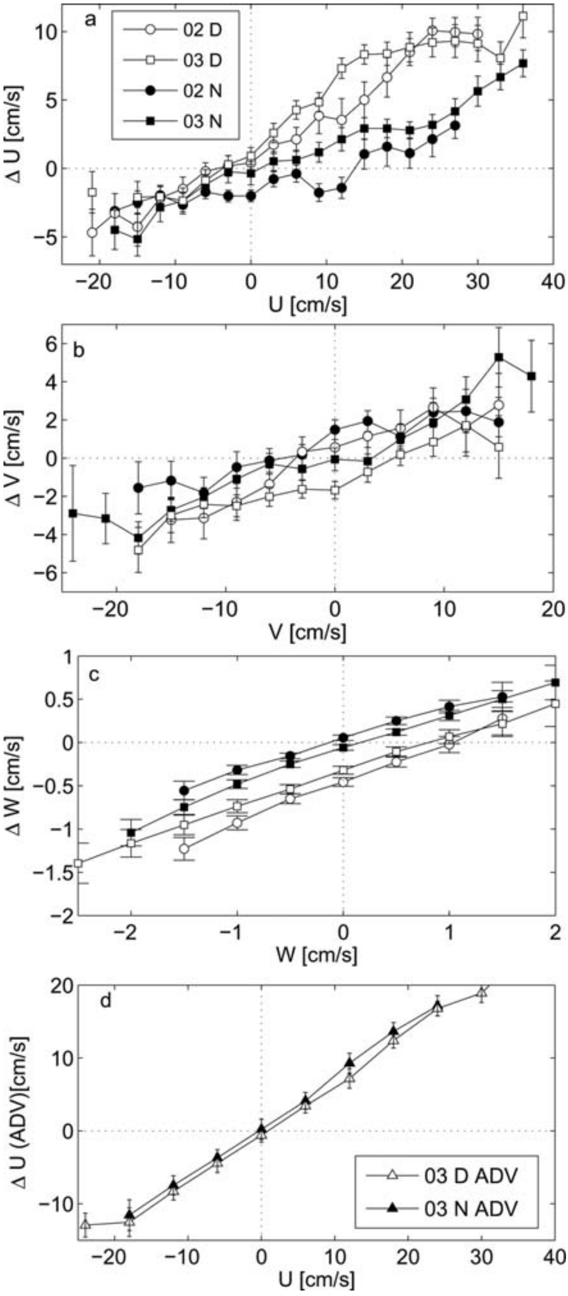

Figure 9. Upper minus lower (a) alongshelf (b) cross-shelf and (c) vertical velocities as a function of bin-averaged upper velocities for day (D) and night (N). Errorbars indicate 5 times the standard error. (d) Upper ADCP flow minus ADV alongshelf velocity as a function of bin-averaged upper velocities. Errorbars indicate twice the standard error.

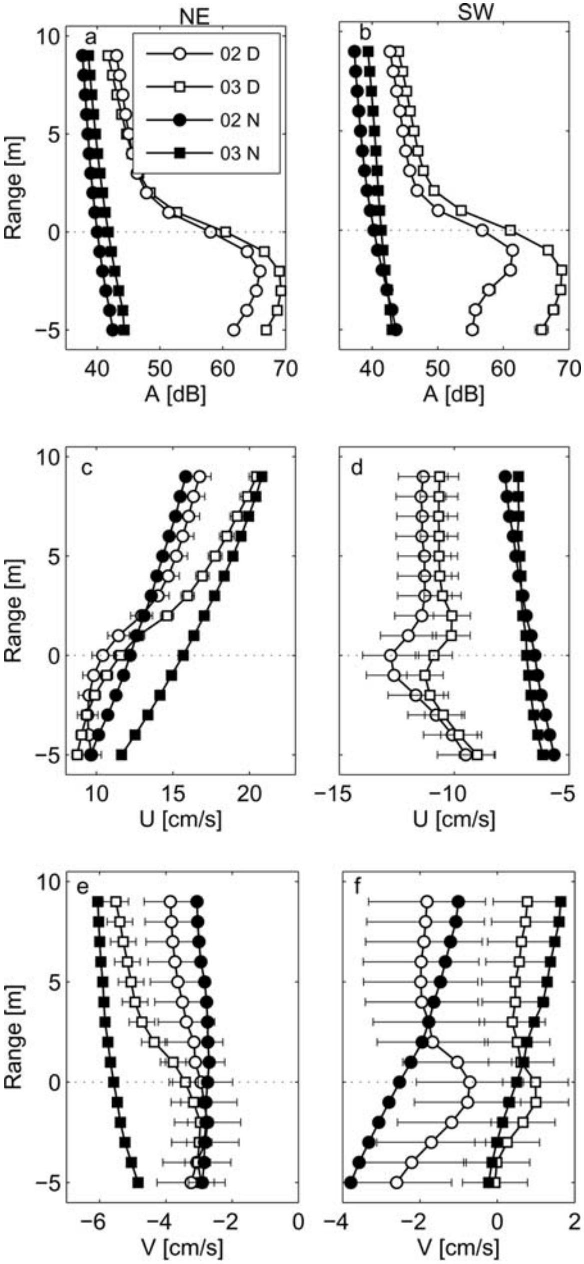

Figure 10. Profiles of amplitude, alongshelf, and cross-shelf velocity profiles and averaged background profiles half a lunar period away for northeast flow(a,c,e) and southwest flow (b,d,f). The upper boundary of the scattering layer is at a range of 0. Errobars indicate twice the standard error.

These velocity profiles likely included small effects from tidal currents and bottom friction, and these effects were quantified by estimating velocity profiles half a lunar period earlier. To determine if inferred swimming velocities were affected by flow direction, data were separated by alongshelf flow direction (northeast: a,b,c versus southwest: b,d,e). Small velocities (<5 cm/s averaged 14 to 24 m above the seafloor) were omitted from the analysis.

Alongshelf northeast velocity profiles (Fig. 10c) showed a marked velocity decrease within the layer which was not present in the background profiles. This suggests the scatterers were moving against the flow, to the southwest, at speeds up to 3.3 cm/s. For alongshelf flow to the southwest (Fig. 10d), velocity profiles also suggest the scatterers were swimming southwest, up to 2.8 cm/s. Average cross-shelf velocity profiles (Fig. 10e, f) suggest the scatterers were moving onshelf, up to 1.7 cm/s. These results confirm the conclusion of the first method, although they are based on a small percentage of the data: 1.3 to 3.5% of the southwest and northeast flows (respectively) met amplitude and velocity criteria in 2002, and 1.7 to 9% of the data in 2003.

In summary, swimming velocities estimated using two methods suggest the scatterers had a preferred onshelf and southwest swimming direction, and were not simply swimming against the flow. Potential reasons for a preferred swimming direction are considered in the discussion.

a. Upward velocities

Upward swimming velocities were found in the time series in Figure 3, and in the results presented in Figure 9. How is it that near-bed velocities are upwards during the day, and yet the scattering layer does not leave the near-bed region? It is possible the upward vertical velocities were caused by scatterers swimming up over the frame only to swim or sink back down outside the sampling region, or they were due to flow disturbance caused by the frame.

Some flow disturbance was expected due to the presence of the space-frame, the ACDP, and other instruments and pressure cases ($\sim$1.7 m above bottom). Potential flow would have caused upward vertical velocities in the ADCP data, and downward velocities in ADV data ($\sim$0.5 m above bottom), both of which would have increased with ambient flow speed. Mean downward velocities measured by the ADV show the expected correlation with flow speed (Fig. 11). However, the ADCP data show near-zero vertical velocities at all horizontal flow speeds when scatterers were not present (i.e. at night). Average absolute error velocities were comparable to the maximum vertical velocities (0.8–0.9 cm/s for 2002 and 1.4–1.6 cm/s for 2003).

These results demonstrate that flow disturbance due to the frame did not contribute significantly to the observed near-bed upward velocities, and that they were probably caused by scatterers swimming over the frame. It is possible that frame avoidance behavior generated horizontal velocities as well, but the observations show the same horizontal swimming

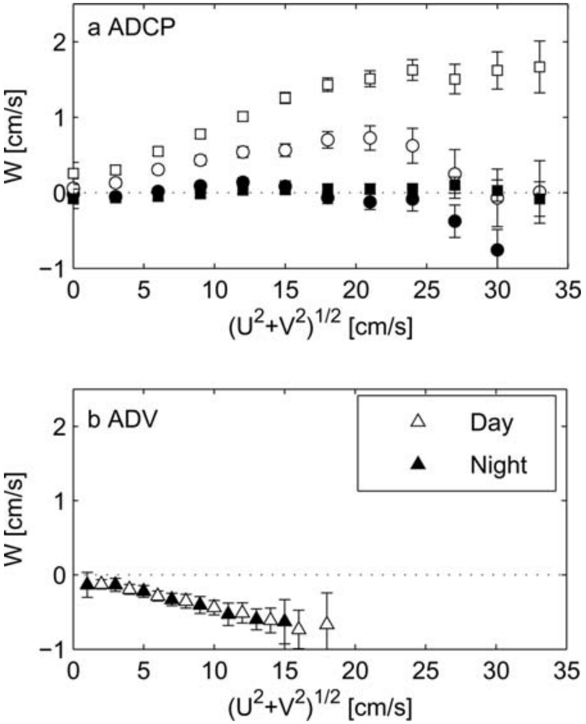

Figure 11. Mean vertical velocities as a function of horizontal speed for (a) ADCP data at 6.7 m height and (b) ADV data at 0.5 m height. ADCP symbols are the same as Figure 10. Errobars indicate five times the standard error.

direction while migrating vertically, suggesting horizontal swimming velocities were not associated with frame avoidance.

Avoidance behavior was observed in response to a light that was used in conjunction with a video camera to take images of the seafloor for ~50 days in 2003. The light was oriented towards the seafloor (~0.6 m above bottom) and was turned on for 8 s approximately every half hour. The scatterers responded strongly to the light, by moving several meters upward (and away) from the light (Fig. 12). It is possible that light avoidance could have affected horizontal swimming velocities, but observations for 2002 and 2003 were similar, and the light only functioned for 52 out of 112 days in 2003, and did not function in 2002.

6. Discussion

There are several hypotheses as to why the scatterers were swimming onshelf and alongshelf toward the southwest. Evaluation of these hypotheses would be easier if the identity of the scatterers was known. The available literature on the species structure of the zooplankton community on the Scotian shelf (Sameoto, 1982), and the 5–6 cm/s vertical migration

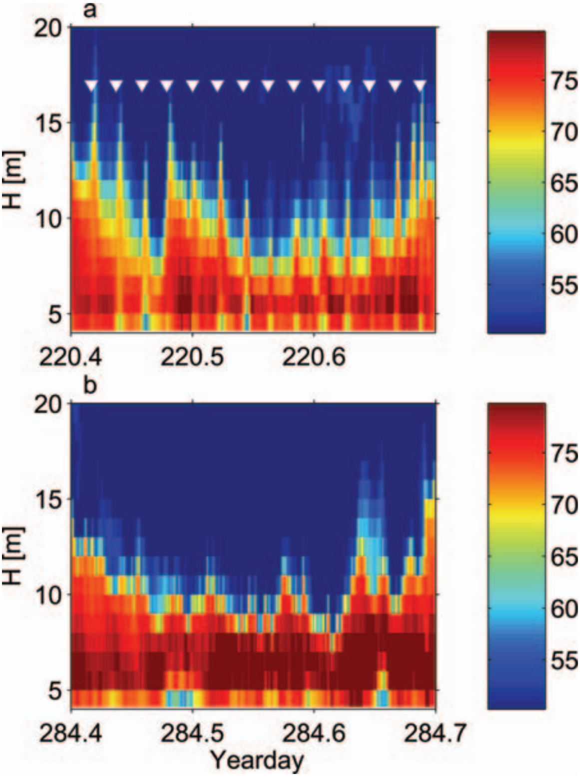

Figure 12. Backscatter amplitude for 2003, yeardays 220 and 284. White symbols indicate times when the light was briefly turned on.

speeds (Rippeth and Simpson, 1998; Tarling *et al.*, 2001), suggest that euphausiids are a likely candidate.

Onshelf swimming might be related to a preferred depth and feeding environment, in this case the shallower and more productive waters at the shelf break. Onshelf swimming could be guided by obvious cues such as depth and light intensity. Recalling however that the mean flow in the bottom boundary layer was offshelf and ca. 4 cm/s, the horizontal swimming speed of ca. 3 cm/s indicates that the animals would barely be able to hold position during their daytime period near the bottom.

Swimming alongshelf to the southwest is more problematic, both with regard to identifying possible directional cues and possible reasons for the behavior itself. A possible directional cue is the Earth's magnetic field. Possible reasons might include higher predator densities to the northeast, which the scatterers were attempting to avoid. Dense aggregations of older silver hake form on the shelf break where the temperature front comes in contact with the slope or enters on the shelf (Rikhter *et al.*, 2001). However, the experiment-averaged near-bed alongshelf velocities in 2003 were larger than the estimated swimming velocity.

There are some hypotheses that the results do not support. The migrators were probably not traveling onshelf to shallow food-rich regions during the night only to return to deeper waters during the day to avoid predation. If this were the case, the horizontal swimming velocity would have been onshelf during ascent and offshelf during descent. However, the data indicate that the swimming velocity was onshelf during both ascent and descent. Additionally, Benoit-Bird *et al.* (2001) found that the horizontal migration velocity of scatterers on the Hawaii shelf was relatively large (i.e. 0.5 m/s). Their inferred migration speed is much larger than the present observations of ca. 3 cm/s.

The scatterers were probably not attempting to maintain their position by swimming against the flow. As mentioned above, the mean offshelf flow in the bottom boundary layer was comparable to and exceeded the apparent onshelf swimming speed, based on the day-night differences. Also, the experiment-averaged near-bed alongshelf velocities in 2003 were larger than the estimated swimming velocity. Thus, both alongshelf and across-shelf position maintainance would have been difficult. Furthermore, the results indicate that when the alongshelf flow was toward the northeast the organisms were swimming against the flow, whereas when the alongshelf flow was southwestward they were swimming with it.

Thus, the behaviors underlying the inferred swimming velocities remain enigmatic. Resolving them would require knowledge of the identity and spatial distribution of the scatterers as well as some knowledge of the spatial distribution of predators and prey.

7. Summary and conclusions

This paper reports on 176 days of data from two deployments of a bottom-mounted ADCP on the Scotian upper slope. The ADCP data show evidence of a diel migrator, with large downward velocities at sunrise, large upward velocities at sunset, and high backscatter amplitudes near the bed during the day. The particular migrator was not identified, but the 6 cm/s vertical migration speeds are consistent with larger zooplankton like euphausiids, which are known to be abundant in this area (Sameoto, 1982). Near-bed currents were variable in direction and magnitude, but average flows were alongshelf to the northeast and offshelf. Tidal velocities were intermittently large, but average lunar semi-diurnal and solar semi-diurnal velocities were small.

Maximum vertical migration speeds during ascent and descent approached 6 cm/s, and were found to increase away from the bed. Median descent time was 11.5 ± 3.8 min (standard error) after sunrise in 2002 and 10.5 ± 1.3 min before sunrise in 2003. Median ascent times were 13 ± 5 min before sunset in 2002 and 9.5 ± 1.6 min after sunset in 2003. These estimates of vertical migration velocity and timing are not unique, but these observations were continuous over several months, which was long enough to follow the seasonal changes in the descent/ascent times. In addition, the high temporal resolution of the data (ca. 1.5-min sample interval) enabled accurate monitoring of the migration times and quantitative estimates of day/night differences in mean velocity.

During the day, scatterers congregated near the bed had a mean upward vertical velocity of approximately 1 cm/s. The upward velocity of the scattering layer was interpreted to be upward swimming to avoid the frame. The scattering layer also moved rapidly away from a near-bed light that was briefly turned on every half hour during part of the second experiment.

Averaging the data by migration times revealed the scatterers had a smaller horizontal velocity than the ambient flow velocity during ascent and descent. Experiment-averaged data revealed the scatterers induced a velocity bias of up to 2 cm/s alongshelf to the southwest and up to 3 cm/s onshelf. A second method of estimating the velocity bias by curve-fitting daily data also found a swimming velocity was alongshelf to the southwest and onshelf up to 2 cm/s.

Velocity bias also occurred in the horizontal velocity during the day when the scattering layer was located near the seabed. Experiment-averaged data showed the velocity differences between the upper half (30–54 m) and the lower half (5–29 m) of the profile were larger during the day and were affected by flow direction, which suggested a preferred swimming direction. Further investigation into horizontal velocities during the day identified velocity bias as a function of flow direction. When the alongshelf flow was to the northeast, the estimated swimming velocities were up to 3 cm/s to the southwest, and up to 1.7 cm/s onshelf. When the alongshelf flow was to the southwest, the estimates were similar: ∼3 cm/s to the southwest and onshelf. It is suggested that the scatterers were swimming in a preferred direction, and not simply swimming against the flow.

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