Patterns of diel vertical migration of zooplankton in acoustic Doppler velocity and backscatter data on the Newfoundland Shelf

Nicholas R. Record and Brad de Young

Abstract: Backscatter data from moored acoustic Doppler current profilers (ADCPs) are analysed to quantify the diel vertical migration patterns of zooplankton on the Newfoundland Shelf, Canada. Data from 11 moorings provide long time series (~100 days each) for in-depth statistical analysis. For one deployment, dry weight measurements of zooplankton are used to calibrate the acoustic backscatter. Quantification methods are developed and applied to the backscatter and vertical velocity time series to determine the characteristics of the observed diel migration. We show that the migration responds to changes in light intensity and water column temperature structure. We have sufficient spatial data to show high correlation of migration characteristics over spatial scales of up to tens of kilometres.

Résumé : Nous analysons les données de rétrodiffusion recueillies par des enregistreurs acoustiques de profils de courants Doppler (ADCP) amarrés sur la plate-forme de Terre-Neuve, Canada, afin de déterminer quantitativement les patrons de migration du zooplancton. Les données provenant de 11 points d'amarrage forment de longues séries (chacune d'environ 100 jours), ce qui rend possible une analyse statistique détaillée. Pour une des séries, des déterminations des masses sèches du zooplancton permettent de calibrer la rétrodiffusion acoustique. Nous mettons au point des méthodes de quantification que nous utilisons pour déterminer les caractéristiques de la migration journalière observée à partir des séries temporelles de rétrodiffusion et de vitesse verticale. Nous démontrons que la migration réagit aux changements d'intensité lumineuse et à la structure thermique de la colonne d'eau. Nous possédons suffisamment de données spatiales pour mettre en évidence une forte corrélation entre les caractéristiques de la migration sur des échelles spatiales pouvant atteindre des dizaines de kilomètres.

[Traduit par la Rédaction]

Introduction

Many species of oceanic zooplankton exhibit patterns of diel vertical migration (DVM). Migration is typically nocturnal; the zooplankton is near the surface at night and at depth during the day. Migration occurs during twilight hours. DVM is of interest for many reasons, including population dynamics, predator–prey interactions (Clark and Levy 1988; Lampert 1989), and contributions to biogeochemical processes, such as transport of dissolved inorganic carbon and nitrogen to deep water (Madin et al. 2001; Hays 2003). Off the northeastern coast of Newfoundland, Canada, zooplankton play a key role in the marine ecosystem as prey for capelin, a major forage and commercial species in the Northwest Atlantic (Carscadden et al. 2001). Recent experimental work (Kunze et al. 2006) supports earlier theoretical calculations (Huntley and Zhou 2004) that zooplankton migration may provide an important source of energy for mixing in coastal waters.

Despite many decades of study, much debate remains regarding both the evolutionary mechanisms behind DVM and the cues influencing it (cf. Lampert 1989; Hays 2003). Predator evasion is currently the most favoured evolutionary hypothesis, i.e., nocturnal zooplankton migration is a result of balancing a need to graze in phytoplankton-rich surface waters with a need to avoid visually orienting predators (Zaret and Suffern 1976). Cues including light, temperature, food availability, predation, and endogenous rhythms (Forward 1988) are believed to influence migration, though the relative importance of each is unresolved. Zooplankton has been observed in the laboratory to respond to changes in light intensity (Clarke 1930). In situ, the synchronisation of migration times to the day–night cycle is further evidence of this relationship (Ashjian et al. 2002), though Lorke et al. (2004) found migration timing in *Chaoborus flavicans* larvae to be unaffected by changes in cloud cover, suggesting an endogenous rhythm. Not surprisingly, water temperature is also important because of its influence on the development and metabolism of zooplankton (McLaren 1963, 1974; Enright 1977). Sea water temperature is highly stratified in the vertical, and this stratification can have a substantial effect on DVM. Isotherms have been observed to define upper

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and lower migration boundaries (Geller 1986). Many types of zooplankton have also been observed to alter their migration behaviour in response to the presence of predators (Dodson 1988; Neill 1990) and the availability of food (Mauchline 1998).

Bioacoustic techniques provide certain advantages for studying zooplankton DVM in situ. Acoustic instrumentation offers a higher temporal resolution than towed nets, as well as information on the entire water column, without any invasive effects (Brierley et al. 1998). The acoustic Doppler current profiler (ADCP), an instrument designed to measure water velocities, has been shown to have value as a bioacoustic tool, in particular for observing zooplankton DVM (Flagg and Smith 1989; Heywood 1996; Tarling et al. 1998). The ADCP measures three-dimensional velocity vectors of acoustic scatterers in the water column by using the Doppler shift in reflected acoustic signals (at least three beams oriented at different angles to produce a three-dimensional vector). With a high enough concentration of migrating zooplankton in the water column, both the measured velocity and the intensity of the backscattered signal are dominated by zooplankton signal. If enough zooplankton are present, then it should be possible to detect both the presence of zooplankton and its vertical velocity, if large enough (Sindlinger et al. 2005).

There are two facets to the application of acoustic data to zooplankton studies. The first is the need to calibrate the backscatter by correlation of the backscatter with zooplankton abundance, taxonomy, and size. This can be approached as either the "forward problem" of mathematically modelling scattering based on assumptions about the properties of the animal (Stanton and Chu 2000) or the "inverse problem" of determining the properties of the animal based on measured backscatter (Holliday and Pieper 1995). These problems can be very difficult in complex multispecies zooplankton communities requiring multiple frequencies, directed tow studies, and very high-resolution acoustic data, as well as specialised calibration of the instrument (Brierley et al. 1998). The second facet is the common use of backscatter to provide descriptive information regarding spatial and temporal patterns of scattering layers. Use of ADCPs for bioacoustic data in surveys and moorings has become quite common (Thomson and Allen 2000), and calibration and directed tow data are often not available for conversion to zooplankton abundance, taxonomy, and size. This need not limit assessments of these data to the qualitative type. Because of the ease and regularity of collecting such data, it is valuable to develop quantitative techniques for their analysis. These techniques are used here with historical ADCP data to (*i*) examine the vertical swimming velocities of zooplankton measured by the ADCP, (*ii*) assess the influence of light and temperature stratification the observed DVM pattern, and (*iii*) address the issue of horizontal homogeneity at spatial scales from tens of metres to tens of kilometres using data from multiple simultaneous moorings.

Materials and methods

There are several different techniques found in the literature for quantifying the migration of zooplankton, each suited to a different purpose. Ashjian et al. (2002) calculate the biomass median depth from the backscatter field, i.e., the depth that divides the biomass profile in half. Such an approach is valuable provided that there are not multiple simultaneous layers, and it gives a better representation of the layer depth than other quantification techniques, e.g., the depth of maximum backscatter. Rippeth and Simpson (1998) use the velocity field measured by the ADCP to model the path of a hypothetical Lagrangian particle to examine the spatial and temporal dynamics of the zooplankton population.

One advantage of Doppler profilers over other bioacoustic instruments is that information is also provided on the speed of acoustic scatterers. Vertical velocities of water in the ocean are generally on the same order of magnitude as the error in averaged velocity measurements by the ADCP, of the order of several millimetres per second, so that the velocity of migrating zooplankton can be easily discerned, depending on the speed of migration. In addition to resolving swimming velocities, quantification methods allow assessment of how accurately the velocities measured by the ADCP represent actual zooplankton velocities.

Heywood (1996) uses a numerical simulation whereby scatterer distribution in the water column is modelled as a function of time, t, and depth, z, based on the measured vertical velocities, w, according to

$$(1)\qquad \frac{\partial S}{\partial t} = \frac{\partial (wS)}{\partial z}$$

where S is a measure of scatter abundance logarithmically related to relative volume backscatter strength, S_v. This model is used to demonstrate that vertical velocities measured by the ADCP accurately represent migration velocities, though the possibility of a small bias is suggested.

In addition to these techniques, the vertical velocities can also be modelled by applying a velocimetry algorithm to the backscatter array. The technique used here relies on the assumptions that (*i*) the surface (or bottom) provides a closed boundary through which migrators do not pass and (*ii*) the backscatter array represents an essentially one-dimensional phenomenon. The flux of scatterers through any depth z_1 and through time step n is given by

$$(2)\qquad F_S(z_1) = \frac{1}{\Delta t} \sum_{z=z_1}^{\text{surface}} [S(z)_{n+1} - S(z)_n]$$

and the velocity is then given by

$$(3)\qquad w(z_1) = \left(\frac{\Delta z}{\Delta t}\right) \frac{\sum_{z=z_1}^{\text{surface}} [S(z)_{n+1} - S(z)_n]}{S(z_1)}$$

This calculation models the full velocity field based on the backscatter field.

The above quantification techniques, with the exception of the Lagrangian particle path, all rely on an intermediate conversion from S_v to S. Converting backscatter intensity to equivalent zooplankton biomass or some measure of abundance is a tricky process with many parameters to take into account (Stanton et al. 1994; Martin et al. 1996; Fielding et al. 2004). To formulate a reliable conversion, precalibration

Fig. 1. Locations of moorings for 1999, 2001, 2002, and 2004 deployments and automated weather observation system (AWOS) station. Inset map of Canada shows the location of Newfoundland.

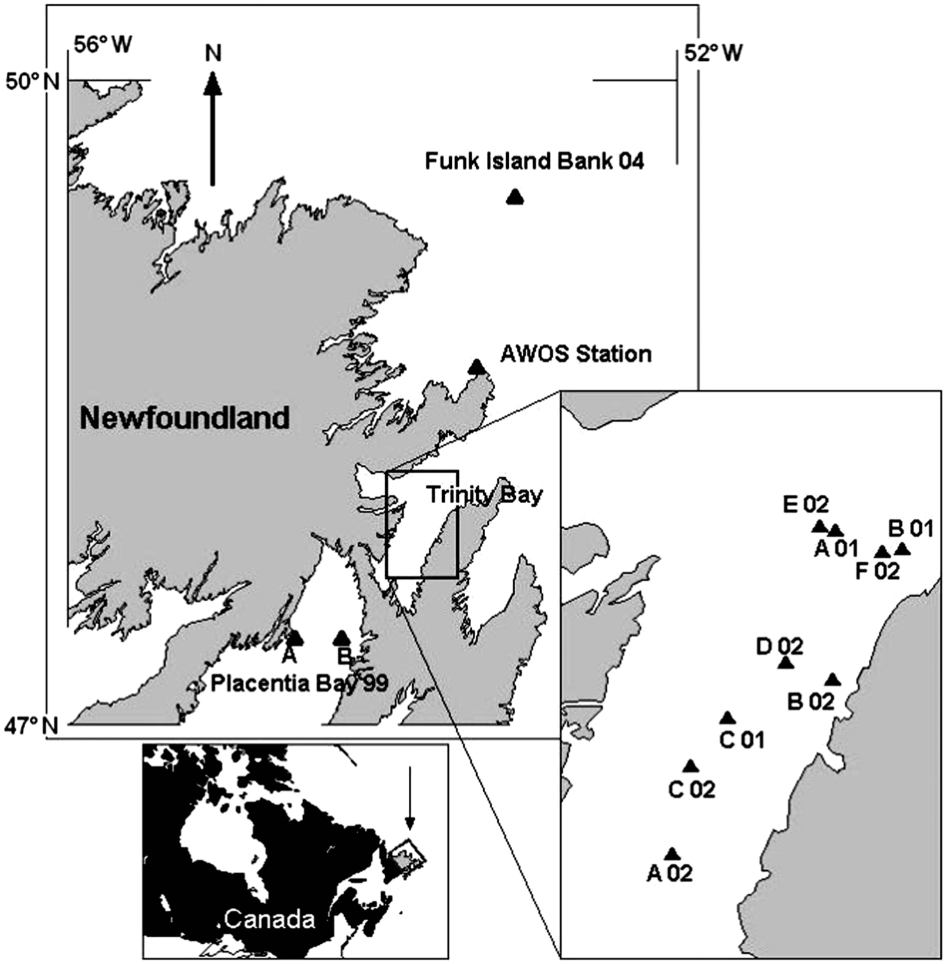


Table 1. Mooring information.

Mooring	Latitude (N)	Longitude (W)	Water depth (m)	Thermistor and ADCP depths (m)	Pings per ensemble	Year days
Placentia Bay 1999						
A	47°24.63′	54°24.17′	428	110 (ADCP)	70	107–180
B	47°24.56′	54°04.27′	304	110 (ADCP)	70	107–180
Trinity Bay 2001						
A	48°04.83′	53°24.53′	240	55, 105 (ADCP), 155, 200, 233	50	140–234
B	48°03.59′	53°17.98′	244	51, 101 (ADCP), 151, 201, 238	50	140–234
C	47°54.68′	53°31.74′	301	50, 100 (ADCP), 150, 200, 294	50	140–234
Trinity Bay 2002						
A	47°47.53′	53°36.17′	340	20, 30, 40, 50, 75 (ADCP), 100, 200	50	126–240
B	47°56.72′	53°23.47′	400	20, 30, 40, 50, 75 (ADCP), 100, 200, 383	50	126–187
C	47°52.16′	53°34.69′	350	20, 30, 40, 50, 75 (ADCP), 100, 200, 338	50	126–240
D	47°57.67′	53°27.19′	449	20, 30, 40, 50, 75 (ADCP), 200, 432	50	126–240
E	48°04.57′	53°23.31′	239	20, 30, 40, 50, 74 (ADCP), 100, 200	50	126–240
F	48°03.47′	53°19.60′	300	20, 30, 40, 50, 75 (ADCP), 100, 200	50	126–240
Funk Island Bank 2004						
	49°27.85′	52°51.30′	327	15, 20, 30, 40, 50, 60, 70, 80, 110 (ADCP), 150, 250, 300	100	219–233

Note: ADCPs operated at 307.2 kHz with bin size 4 m. Time interval of ensemble averaging was 1200 s, with the exception of the Funk Island Bank mooring, which was 600 s.

Fig. 2. Averaged backscatter and vertical velocity data from mooring C, Trinity Bay 2001: (*a*) diel average of measured volume backscatter and (*b*) associated standard deviation; (*c*) diel average of measured vertical velocity and (*d*) associated standard deviation. Averages include year days 141–230. This plot is characteristic of all moorings.

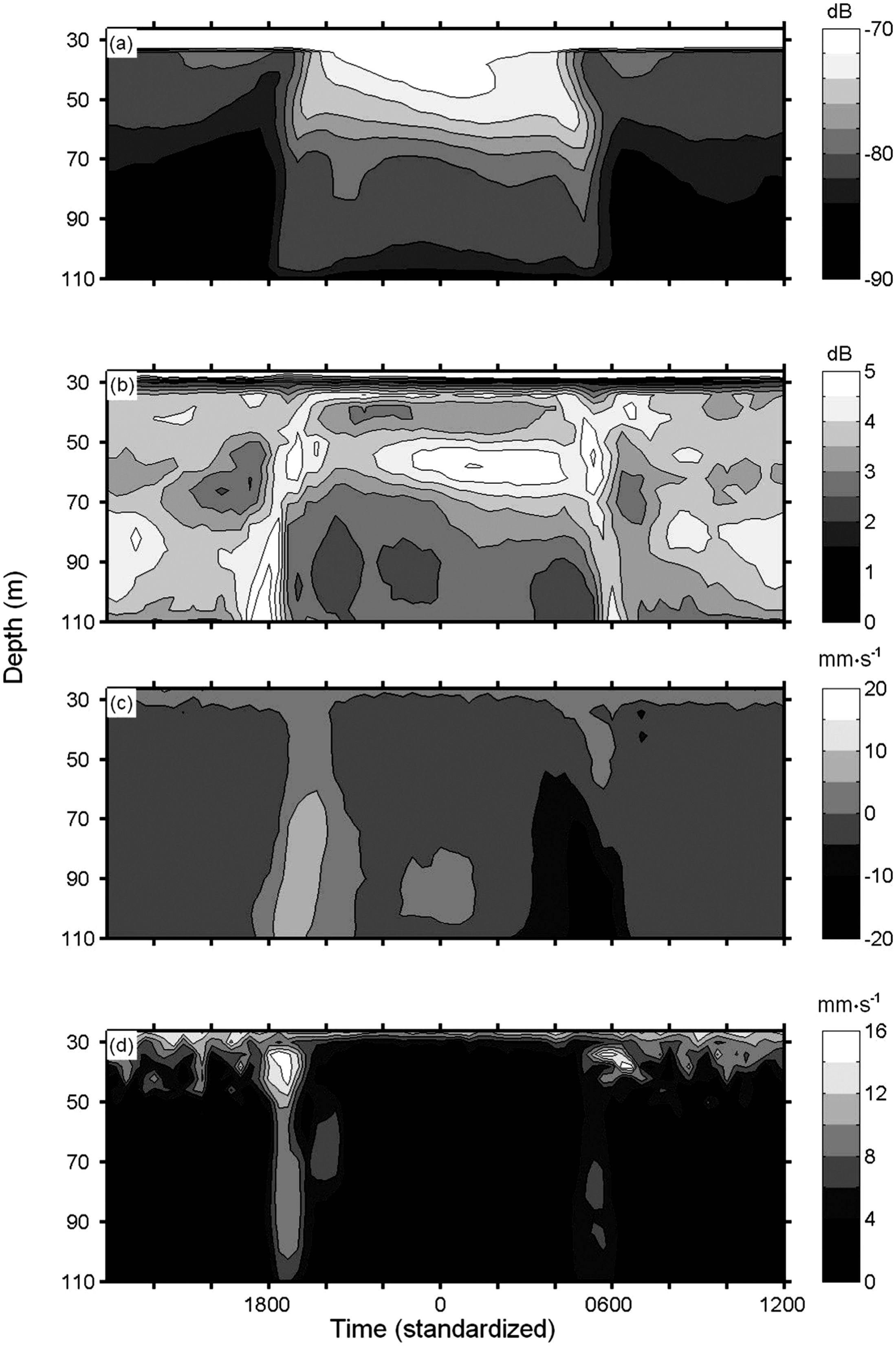
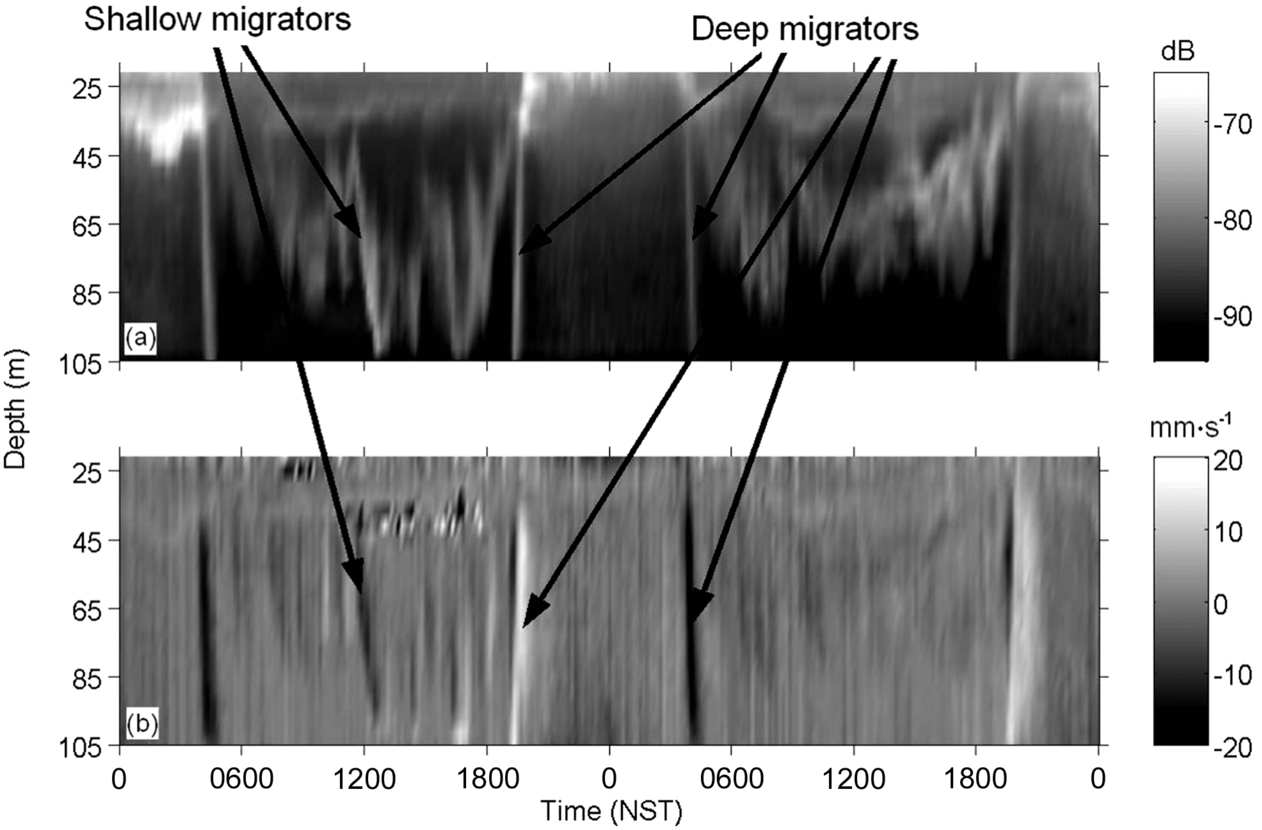


Fig. 3. A 2-day sample of (*a*) backscatter and (*b*) vertical velocity data from the Funk Island Bank 2004 mooring showing the presence of two distinct groups of migrators. Time is shown in Newfoundland Standard Time (NST).



of the ADCP is optimal (Flagg and Smith 1989), and tow data should be directed to this purpose for taxonomic differentiation (Wiebe et al. 1996). Such conversions are typically viewed only as estimates of biomass because many acoustic scatterers in the water column are not captured in zooplankton nets (Ashjian et al. 2002). Because volume backscatter is logarithmically related to measures of abundance, a biomass estimate can be a useful tool for determining relative abundance. Heywood (1996) uses a simple log–antilog relationship, but when tow data are available, better estimates improve the output of the quantification algorithms.

Timing of migration is also of interest. Lorke et al. (2004) determined the timing of migration from the temporal derivative of S_v at a given depth; Ashjian et al. (2002) used peak velocity times.

We applied these techniques to the ADCP data from the Newfoundland Shelf, with a focus on the Northeast Newfoundland Shelf and the coastal embayments (Colbourne et al. 1997; Davidson et al. 2001), and the significant results are presented here. Results of the analysis are used to answer the questions put forth in the introduction of vertical swimming velocity, horizontal homogeneity of the migrating layer over Trinity Bay, and migrator response to light and temperature stratification.

Historical data

We use mooring data primarily from bay circulation studies (e.g., Tittensor et al. 2002). ADCPs that have been moored for studies on physical characteristics of the ocean also collect backscatter data that are in many cases seen to contain valuable information on the DVM patterns of zooplankton. Deployments took place in 1999, 2001, 2002, and 2004; the moorings were located off the eastern coast of Newfoundland (Fig. 1; Table 1).

The Funk Island Bank mooring was deployed as part of a study exploring the relationship between capelin (*Mallotus villosus*), seabirds, and zooplankton. This mooring recorded at a higher temporal resolution and had better thermistor coverage through the water column. It also included a downward-looking ADCP to view the lower portion of the water column, but this ADCP malfunctioned and did not collect data.

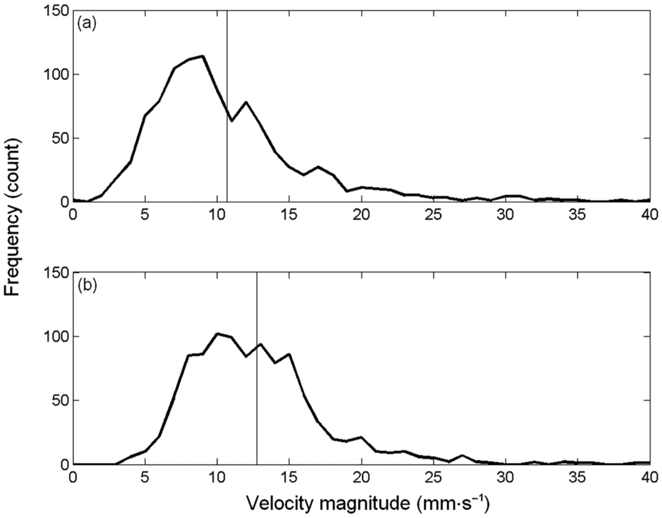
ADCP configuration

Each mooring contained an upward-facing 307.2 kHz RDI Workhorse ADCP (Teledyne RD Instruments USA, Poway, California), using a four-beam Janus configuration with a beam angle of 21°. The vertical bin size was 4 m, and ensemble intervals were either 10 or 20 min (Table 1). Relative volume backscatter strength (S_v) was calculated from backscatter (the average of four beams) according to Deines (1999) and is given in decibels (dB) referenced to $(4\pi m)^{-1}$.

Biological sampling

The 2004 data were complimented with oblique bongo net tows (mesh sizes 333 and 232 µm, depths to 100 m) collected as part of a large-scale survey that covered a 100 nautical mile (185 km) grid surrounding the mooring. Mesh

Fig. 4. Distribution of (*a*) upward and (*b*) downward migration velocities (magnitude) for all data. Vertical lines indicate average.



sizes and depths were determined based on zooplankton known to inhabit this area (Dalley et al. 2001). Dry weight was determined after filtering by three sieve sizes (2, 1, and 0.232 mm). The samples were heated at 60 °C for 24 h and weighed. Use of dry weight to calibrate backscatter follows Ashjian et al. (2002).

Additional physical data

Most moorings had thermistors spaced at intervals to collect temperature data over the water column for the duration of the deployment (Table 1). Thermistors were generally arranged to give a higher spatial resolution over the thermocline, and data were linearly interpolated into 4 m bins. Ensemble intervals corresponded to those of the ADCPs.

Cloud opacity data were obtained from Environment Canada, collected at a land-based automated weather observation system (AWOS) at the tip of Bonavista Peninsula (48.68°N, 53.12°W, 27 m elevation) (Fig. 1), to be used as a proxy for light intensity for the 2001 and 2002 deployments. Cloud opacity is calculated from laser ceilometer measurements. The weather station's location at the tip of a peninsula in close proximity to the study area minimises the effect of land on cloud coverage. The 1999 deployment was not considered in light calculations because of the large distance between the moorings and the weather station. The 2004 deployment was not considered because of the short deployment duration.

Results

Migration behaviour is highly persistent at all moorings throughout the deployments. The persistence can be illustrated by taking "diel averages", i.e., averaging each 10 or 20 min time bin over many days to determine the average diel rhythm (Fig. 2). The typical nocturnal migration pattern is easily recognisable in both the volume backscatter and vertical velocity data. The average signal near the surface is 10 dB higher at night than during the day. Because deployments spanned about 3 months, during which twilight times varied a great deal, the data were "time-standardised" following Ashjian et al. (2002) so that sunrise corresponds to 0600 and sunset corresponds to 1800.

Table 2. Mean and extremum ascent and descent velocities of migrating scatterers.

	Ascent velocity (mm·s^{-1})		Descent velocity (mm·s^{-1})	
Mooring	Mean	Maximum	Mean	Minimum
Placentia Bay 1999				
A	10.1	18.6	–10.8	–19.4
B	9.4	21.0	–10.0	–19.7
Trinity Bay 2001				
A	8.4	14.9	–14.1	–22.2
B	12.7	21.1	–15.5	–26.4
C	10.4	18.8	–13.8	–22.6
Trinity Bay 2002				
A	6.7	15.0	–10.2	–19.5
B	5.9	11.1	–10.0	–18.6
C	7.0	14.2	–10.3	–17.5
D	8.9	16.1	–10.7	–18.6
E	9.3	15.3	–8.7	–14.6
F	12.1	22.1	–8.9	–17.0
Funk Island Bank 2004				
	25.2	37.7	–22.5	–13.2

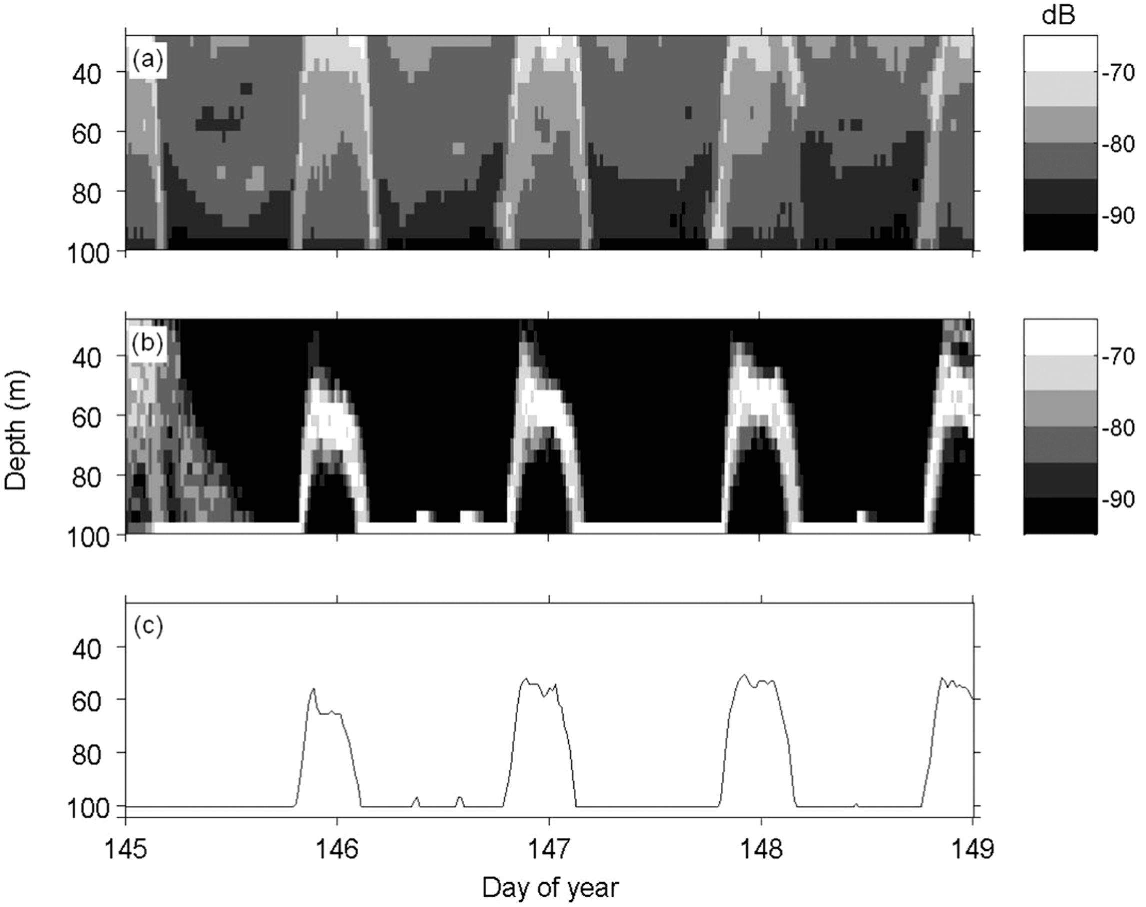
Examination of the time series typically reveals two distinct groups of migrators (Fig. 3). Both occupy the shallow waters at night, yielding a strong scattering layer. In the morning, a group of "deep migrators" travels abruptly to below ADCP depths, out of range, re-emerging as abruptly in the evening. This migration is marked by very large vertical velocities, typically 10–40 mm·s^{-1}. A group of "shallow migrators" descends for the daytime but remains at depths within ADCP range most of the time, visible as a scattering layer at 50–100 m. This latter group is not always detectable in the vertical velocity data, i.e., the migration velocities are often indistinguishable from the background velocities. Shallow migrators are most apparent in the Funk Island Bank and Trinity Bay data sets; they are less apparent in the Placentia Bay data set.

Historical data offer a speculative interpretation of these two groups. Copepods are the most numerous zooplankton in this part of the ocean, and in terms of biomass, *Calanus finmarchicus* is dominant (Dalley et al. 2001). *Calanus finmarchicus* is known to be a shallow migrator relative to other zooplankton (Cushing 1951), suggesting that they are likely to contribute significantly to the shallow migrators seen in the ADCP signal. Indeed, the majority of zooplankton sampled during our net tows was comprised of copepods. The deep migrators are likely composed of other vertical migrators known to be abundant in this region, including amphipods and euphausiids (Dalley et al. 2001), which generally have greater swimming speeds than calanoid zooplankton.

Migration velocity

Migration velocity calculations suggest that descent is more rapid than ascent. The migration velocity was calculated as

Fig. 5. A 4-day sample of (*a*) backscatter data from mooring C, Trinity Bay 2001, and (*b* and *c*) output from quantification algorithms: (*b*) redistribution of scatters based on measured vertical velocities and (*c*) Lagrangian particle path modelled using measured vertical velocities.



follows. For each day, the maximum velocity was found for each 4 m depth bin within a 20 m interval (the interval from 50 m to 70 m depth was used to maintain consistency between all moorings). These five values were averaged, omitting the two outliers, to give an ascent velocity for that day. Descent velocities were determined analogously using minima. An immediate result of this calculation is that descent velocities are greater in magnitude than ascent velocities (Fig. 4; Table 2).

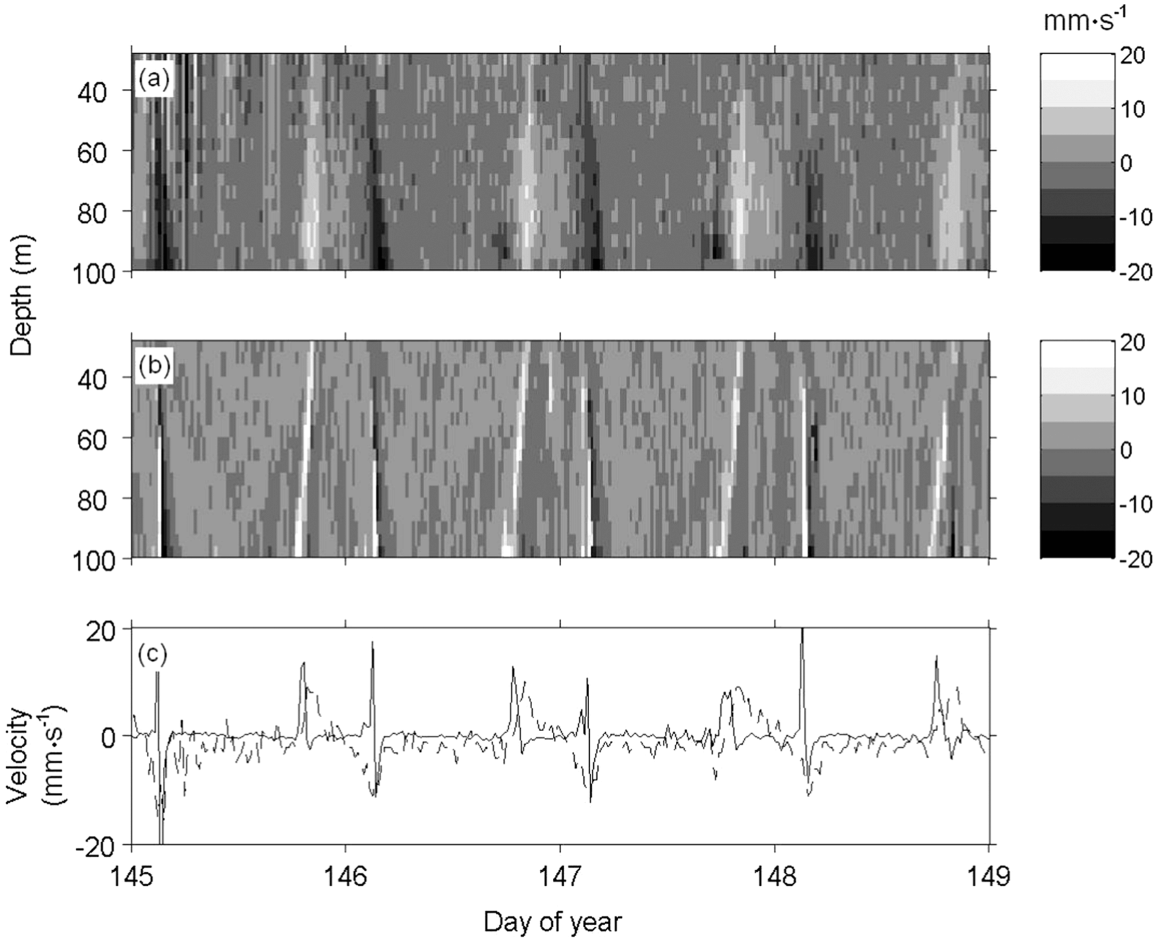
Each individual velocity measurement represents an ensemble average over many pings. The presence of non-migrating acoustic scatterers throughout the water column is likely to bias the velocity measurement. The measurements themselves suggest a low bias: zooplankton migrating at a mean velocity of only 10 $\mathrm{mm \cdot s^{-1}}$ would require almost 3 h to migrate the 100 m viewed by the ADCP. Three aforementioned models were applied to test for this bias: (*i*) Lagrangian particle path (Rippeth and Simpson 1998), (*ii*) redistributing scatterer concentration based on measured velocity according to eq. 1 (Heywood 1996), and (*iii*) velocimetry from backscatter data according to eq. 3. The first two models yield migrating layers that are consistently deeper than the measured scattering layer (Fig. 5), suggesting that measured velocities do not account for the full magnitude of migration. The velocimetry analysis also supports this conclusion, yielding migration velocities that are larger than measured velocities (Fig. 6). The velocimetry algorithm has the added benefit that only migration velocities are modelled, while background velocities are filtered out. That the surface is not a true closed boundary causes some error in velocimetry calculations, which could be reduced by using a downward-looking ADCP, with the bottom as a closed boundary. Patchiness of drifting zooplankton also contributes to the uncertainty of this calculation.

Light

The data from the two Trinity Bay deployments reveal a response by migrators to differences in atmospheric light conditions. The timings of ascent and descent are determined by the maximum and minimum temporal derivatives of backscatter, respectively, for each day. For dusk ascent on a given day, the maximum temporal derivative of backscatter is found for each depth bin (up to 50 m), yielding a time for each depth. These times are averaged, omitting two outliers, to give the timing of ascent. The timing of decent is determined analogously. Some subjectivity exists in choosing the depth interval over which to determine timing. Using a different depth interval alters the resulting values, but the dominant trend, described below, remains.

Cloud opacity data are taken from a land-based weather station at the tip of Bonavista Peninsula (Fig. 1). There is some uncertainty associated with using cloud data as a proxy

Fig. 6. A 4-day sample of (*a*) vertical velocity data from mooring C, Trinity Bay 2001, and (*b*) output from velocimetry algorithm. (*c*) Cross sections of (*a*) and (*b*) at 75 m are shown, indicated by the broken line and the solid line, respectively.



for light, as well as using land-based measurements, and therefore a direct functional relationship between light and migration timing is not apparent, but with large enough data sets, a statistically significant effect becomes clear. Mornings and evenings are classified as "overcast" if cloud opacity is 10/10 during migration (i.e., during 1 h centred at migration timing) and "clear" if cloud opacity is 0/10 during migration. These two cases make up the majority of the data set, and days with intermediate cloud cover are disregarded. Migration timing on clear days is then compared with that on overcast days using *t* tests.

The result is a statistically significant difference in timing between clear days and overcast days, with sample sizes $62 \leq n \leq 85$. For 10 of the 16 tests, $p \leq 0.07$, and for 13 of the 16 of tests, $p \leq 0.2$. Migrators leave the surface 10–20 min later on overcast mornings and arrive at the surface 10–20 min earlier on overcast evenings (Fig. 7; Table 3). This indicates that migrators modify their behaviour to increase their time spent near the surface under darkness. The descent timing shows slightly more statistical significance than that of ascent, suggesting that zooplankton may be more likely to respond to different light conditions while near the surface. Additional tests were performed with artificial cloud data to check for numerical biases, and no statistically significant results were found.

Biomass estimate

Tow data were sufficient for acoustic backscatter calibration, yielding an estimate of relative biomass based on backscatter data (cf. Ashjian et al. 2002). The only mooring for which coincident tow data exist is the Funk Island Bank 2004 mooring, because the other deployments were not explicitly designed for bioacoustic studies. Backscatter data from the 2004 mooring are correlated with tow data from a survey that took place while the ADCP was moored. The biological data collected during this deployment covered a region around the mooring approximately 100 nautical miles (185 km) across. Estimations of biomass based on backscatter intensity at the location of the mooring therefore contain large uncertainties, but a relative index of biomass can be developed as a tool for analysing the diel pattern.

Over a 2-week interval, 50 oblique tows were performed to a depth of 100 m, randomly distributed with respect to time of day. Tow samples consisted almost entirely of copepods, which are historically the most abundant zooplankton on the Newfoundland Shelf, comprising over 80% of sampled zooplankton (Dalley et al. 2001). Other zooplankton included amphipods and euphausiids, comprised less than 20% of the dry weight, and fell entirely within the largest size class, with the exception of one tow. Because of the uncertainty associated with the large spatial scale, we could not

Fig. 7. Frequency of migration times for clear and overcast days — composite of all Trinity Bay 2002 moorings: distributions for (*a* and *b*) overcast days and (*c* and *d*) clear days. Vertical line indicates average time of migration.

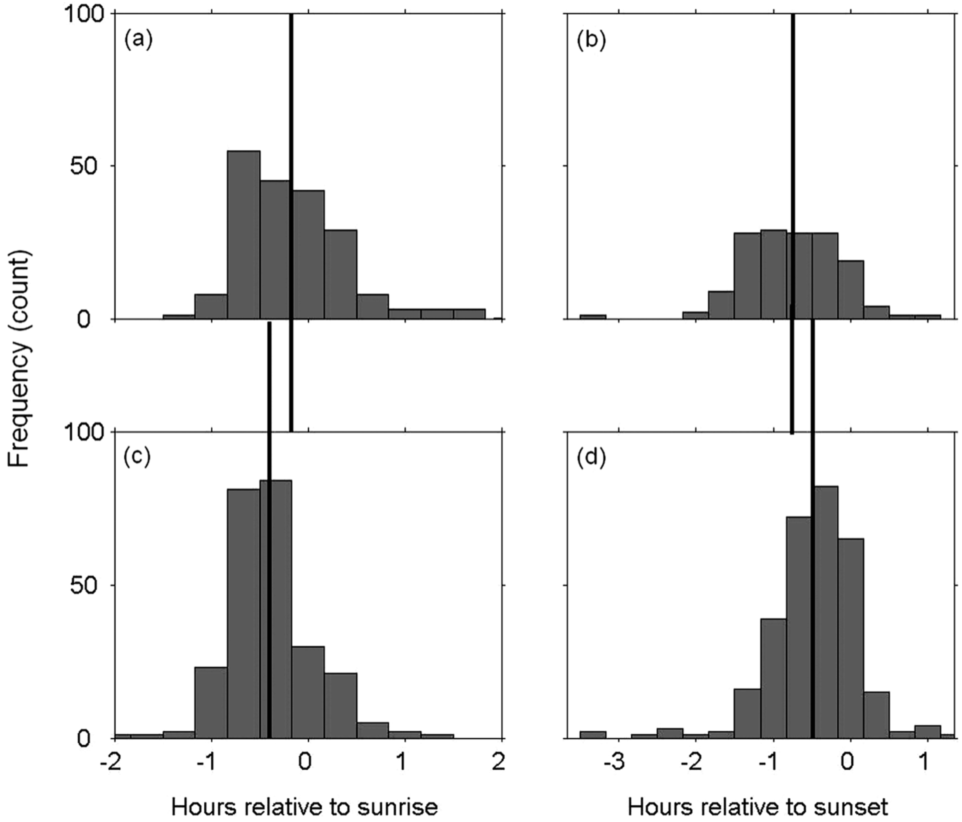


Table 3. Average ascent and descent times of the deep scattering layer on clear days (cloud opacity = 0/10), with the timing difference for overcast days (cloud opacity = 10/10), the *p* value (null hypothesis probability), and the sample size, *n*.

Mooring	Ascent time on clear days	Difference to overcast (min)	*p*	*n*	Descent time on clear days	Difference to overcast (min)	*p*	*n*
Trinity Bay 2001								
A	1829	–14	0.07	73	0553	2	0.80	62
B	1807	–18	0.11	70	0542	16	0.04	70
C	1822	–15	0.07	69	0536	18	0.01	67
Trinity Bay 2002								
A	1811	–13	0.13	83	0523	17	0.03	85
C	1813	–12	0.17	81	0535	13	0.06	85
D	1813	–27	0.00	84	0538	18	0.00	82
E	1810	2	0.70	79	0536	14	0.07	83
F	1818	–22	0.00	81	0541	6	0.46	84

Note: A p value of 0.00 indicates that $p < 0.005$. Times are standardised so that 0600 corresponds to sunrise and 1800 corresponds to sunset.

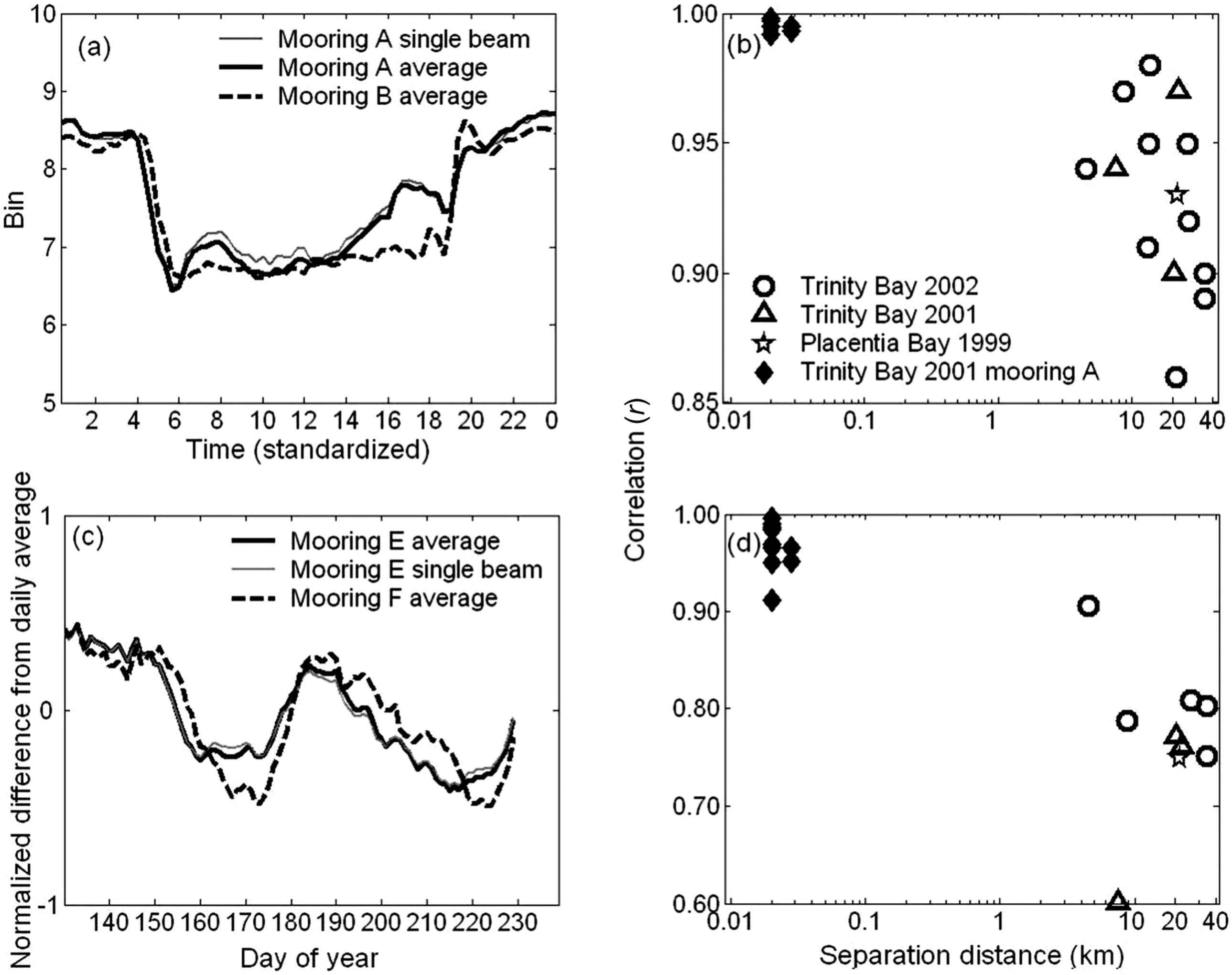
distinguish different types of zooplankton in the acoustic signal. Therefore our analysis is limited to treating the scattering layer as a whole.

The diel average of depth-averaged backscatter is correlated with diel-averaged dry weight from oblique bongo net tows. Depth averaging and oblique tows are both to 100 m. Daily-averaging tow data from an area 100 nautical miles (185 km) across relies on the assumption that variations in the horizontal are small compared with the dominant diel pattern. This question of horizontal homogeneity is addressed in a later section. A log-linear relationship is used because of the logarithmic relationship between backscatter intensity and scatterer abundance ($r^2 = 0.77$):

$$(4) \qquad \log(S) = 0.07\, S_v + 5.01$$

where S gives a relative index of biomass or scatterer abundance. Because of the assumptions made in the calculation, no absolute biomass estimates are attempted. The relationship is used only in calculations where a relative index of biomass is sufficient, such as in calculating the biomass median depth.

Fig. 8. Horizontal correlations. Diel average of biomass median depth: (*a*) three example time series taken from the Trinity Bay 2001 deployment, and (*b*) correlations of such time series between pairs of moorings taken from the same deployment (all moorings) and pairs of individual beams (Trinity Bay 2001 mooring A), plotted as a function of separation distance between moorings or beams. Seasonal index of migration depth: (*c*) three example time series taken from Trinity Bay 2002 deployment, and (*d*) correlations of such time series between pairs of moorings taken from the same deployment and pairs of individual beams (Trinity Bay 2001 mooring A), plotted as a function of separation distance between moorings or beams. Trinity Bay 2001 mooring A is the only mooring shown for beam-to-beam correlation in (*b*) and (*d*) because all moorings show essentially the same beam-to-beam correlation and separation distance.



Horizontal homogeneity

High correlations between migration patterns were found across various spatial scales. A general problem in oceanography is that the ocean is large compared with our resources for collecting data. In the case of a single mooring that is to represent a large horizontal area, some assumption of horizontal homogeneity must be made. The Trinity Bay deployments contain multiple moorings separated by tens of kilometres that can be used to assess this assumption. In addition, each ADCP has four beams angled at 21° from the vertical. The beams converge at the ADCP, but for the upper portion of the data, they are separated by distances of tens of metres. The horizontal correlation is found as a function of separation distance, with distances spanning both of these spatial scales. This analysis is performed both for daily-averaged time series and for seasonal time series.

The diel average of biomass median depths for four beams on the same mooring are more highly correlated with each other than with the same series calculated for a nearby mooring (Fig. 8*a*). This calculation excludes the 40 m closest to the ADCP so that the beams reach a separation distance of tens of metres. Correlations are found for this time series between every pair of moorings that were part of the same deployment. There is a trend of decreasing correlation with increasing separation distance (Fig. 8*b*). For time series separated by tens of metres, $r \approx 0.99$. For time series separated by tens of kilometres, r ranges from approximately 0.9 to 0.95.

The same analysis is performed for seasonal time series. The example shown here is a normalised index of DVM. For each day, the index indicates whether the biomass median depth is shallower or deeper than the diel average for the whole time series. The same trend of decreasing correlation with increasing separation distance is apparent (Figs. 8*c*, 8*d*). Seasonal time series show a lower horizontal correlation than daily-averaged time series. The correlation is still good,

Fig. 9. Biomass median depth and 0 °C isotherm overlaid on volume backscatter for Trinity Bay 2002 mooring A. Each column of data is the average of 6 h centred at midnight for the indicated day. The broken line indicates the biomass median depth, and the solid line indicates the 0 °C isotherm. This plot is characteristic of all moorings.

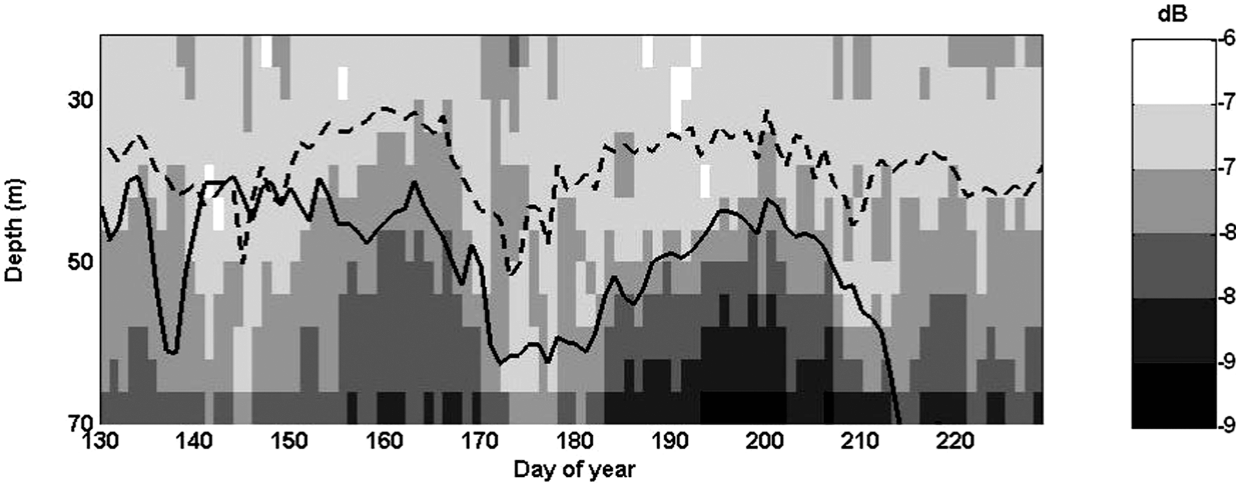
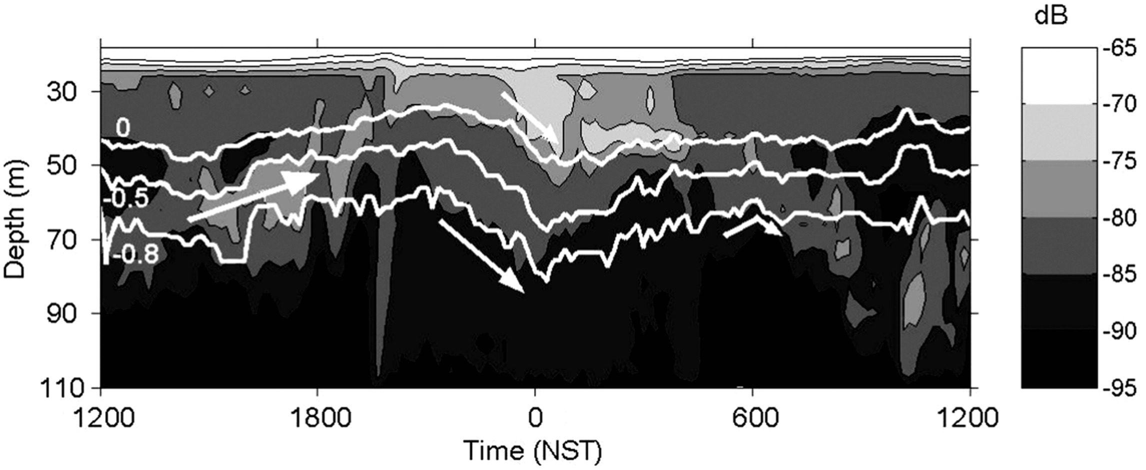


Fig. 10. Isotherms (°C) overlaid on one day of volume backscatter for the Funk Island Bank 2004 mooring showing examples of high-frequency (period << 1 day) response to temperature, as indicated by arrows. Time is shown in Newfoundland Standard Time (NST).



with $r \approx 0.95$ at scales of tens of metres, and $r \approx 0.8$ at scales of tens of kilometres.

Temperature

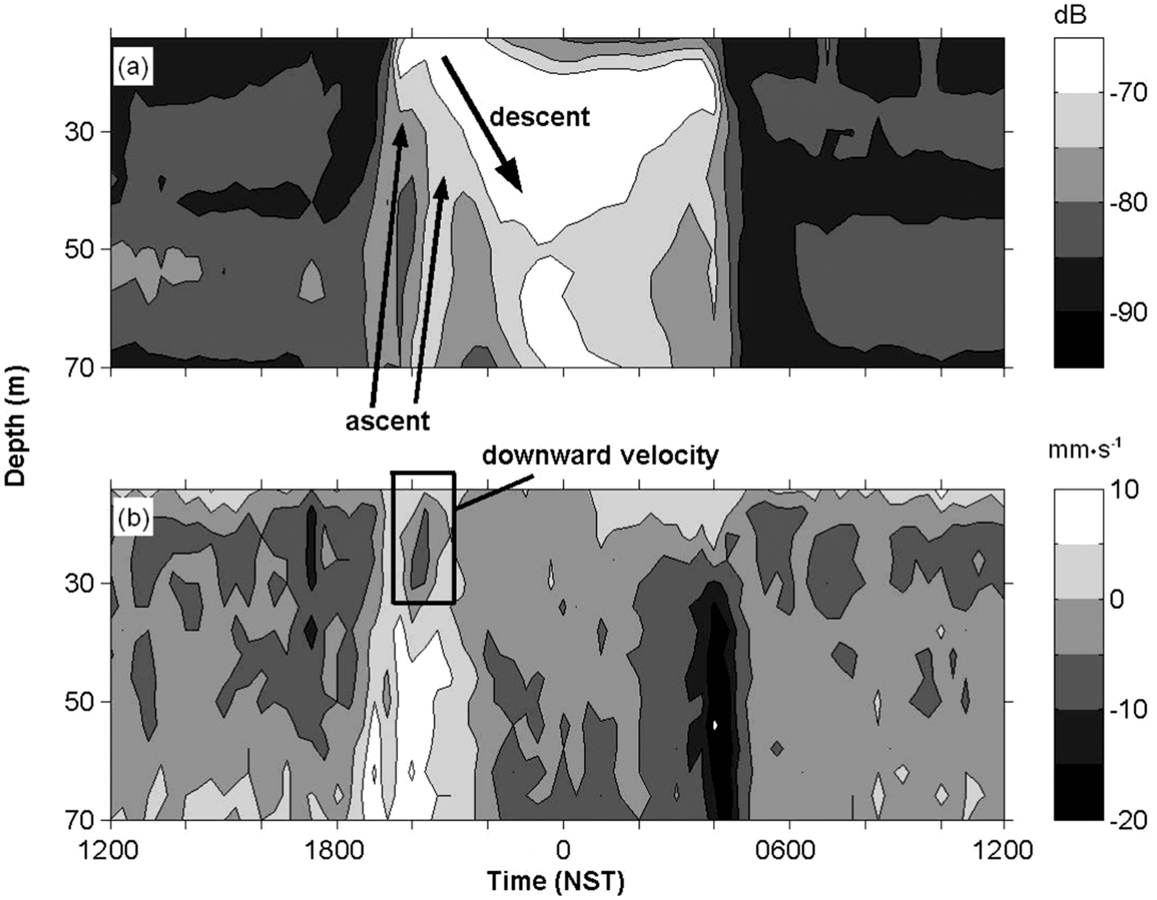
A migratory response to temperature stratification is seen to occur at both large and small time scales. The composition of zooplankton seen during the day is different from that seen at night because of the truncation of data below the ADCP depth, so the following analysis is performed separately for day and night. For day time series, biomass median depth is averaged over 6 h centred at 1200 to give a single depth per day. The same averaging is performed for night at 2400 (Fig. 9). Coherence analysis on the resulting time series shows a high correlation ($r > 0.9$) to isotherm depth (averaged in the same manner) on frequencies less than 0.05 day^{-1} for all moorings. Coherence at higher frequencies varies from mooring to mooring.

There is also a clear response by migrators to abrupt changes in temperature stratification. For most of the moorings, there is substantial surface warming around year day 170, and the 0 °C isotherm deepens abruptly. The biomass median depth deepens in response. A higher-frequency response by migrators to changing temperature stratification can be identified visually in some short stretches in the backscatter data. The response is quite clear for some brief intervals (Fig. 10), but for most of the data, the response is less clear.

Complex migration patterns

Migration patterns other than the typical nocturnal migration are often seen in the ADCP data. In addition to the two aforementioned groups of migrators, other scattering layers often exist, and other migration behaviours are exhibited. Twilight migration (also termed “midnight sinking,” where zooplankton ascend to the surface for both dusk and dawn twilight hours, sinking in between (cf. Cushing 1951)) can be identified on occasion, particularly after year day 200. The sinking that occurs following dusk ascent can be seen in the vertical velocity as well (Fig. 11). There are also sometimes multiple distinct scattering layers that ascend at differ-

Fig. 11. One day of (*a*) backscatter and (*b*) vertical velocity data from Trinity Bay 2002 mooring D showing an example of "midnight sinking" and multiple migrating layers. Time is shown in Newfoundland Standard Time (NST).



ent times during dusk. These layers can be identified in both the backscatter and velocity data (Fig. 11).

Discussion

ADCPs are powerful bioacoustic tools, particularly when accompanied with detailed taxonomic data. Even in the absence of such data, however, analysis techniques can yield valuable information on the DVM of zooplankton.

In Trinity Bay, zooplankton migrates in a manner that is mostly homogeneous throughout the bay, in terms of both the diel average and the seasonal variation. A single mooring may therefore be appropriate for representing a horizontal area tens of kilometres across. Spatial correlations between seasonal time series were lower than those for diel averages, implying an effect of temporally and spatially local phenomena on migration behaviour.

On the Newfoundland Shelf, a marked difference is seen between upward and downward migration velocities, suggesting that passive sinking plays a role in downward migration. Quantification techniques indicate that velocity measurements are biased low, likely because of ensemble averaging and the presence of nonmigrating acoustic scatterers.

The response by migrators to cloud cover is promising but requires further examination. Reliance on land-based historical cloud cover data as a proxy for light intensity perceived by zooplankton carries a high degree of uncertainty. However, the observed response was persistent and found with high statistical significance. Migrating zooplankton appear to be maximising time spent near the surface under darkness. This supports the predator-avoidance hypothesis of DVM and suggests that a threshold light level, rather than an endogenous rhythm, cues migration. By coordinating ADCP data with light data collected at the mooring location and by obtaining backscatter data from the entire water column, it is possible to examine the response to changes in light intensity in greater detail.

The migration pattern can be viewed with respect to three different time scales. Low-frequency signals within the migration pattern, corresponding to time scales of many days, can be attributed to changes in temperature stratification of the water column. The dominant daily cycle is seen to be driven by light to the extent that cloud cover appears to influence migration timing. In some cases, the higher-frequency variation appears to be driven by changes in temperature stratification, but in many cases, higher-frequency variation remains unexplained. Many possibilities exist. A direct measure of light intensity in close vicinity to a mooring may show that higher-frequency changes in light caused by clouds have a direct effect on the behaviour of shallow migrators. The presence of predators and the local availability of food may also function as important high-frequency cues.

It should also be noted that there are at least two possible explanations for high-frequency responses to changes in temperature stratification: zooplankton may be either actively swimming to remain at a constant temperature or passively transported by some water mass movement such as internal waves. In the former case, one would expect the vertical swimming velocity to be measured by the ADCP. In the latter case, a measured vertical velocity may or may not be associated with change in stratification, depending on the cause of the change in stratification. Because both these cases occur in the data, a more detailed analysis is required to address this question.

The ADCP can record more complex migration patterns when they are present, including reverse migration, twilight migration, and multiple distinct groups of migrators. In complex zooplankton communities, taxonomic identification remains difficult based on acoustic data alone. In conjunction with taxonomic data, the ADCP offers the potential to map multiple simultaneous migration patterns to high temporal and spatial resolution.

Many aspects of zooplankton migration may have implications for higher trophic levels. On the Newfoundland Shelf, capelin preying on zooplankton also undergo a nocturnal diel vertical migration, which likely indicates a dependence on the vertical distribution of their prey (cf. Clark and Levy 1988). Northern gannets (*Morus bassanus*) preying on capelin have been observed to have a distribution of feeding times with peaks during dawn and dusk twilight hours corresponding to the timing of migration (Garthe et al. 2003), suggesting the possibility that capelin are too deep during the day and invisible at night. If this is the case, then the environmental factors that influence timing and depth of zooplankton migration are of importance to ecosystem-scale studies.

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