

Diel periodicity in both sei whale vocalization rates and the vertical migration of their copepod prey observed from ocean gliders

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Abstract

The daily activity cycles of marine predators may be dictated in large part by the timing of prey availability. For example, recent studies have observed diel periodicity in baleen whale vocalization rates that are thought to be governed by the diel vertical migration of their zooplanktonic prey. We addressed this hypothesis by studying associations between sei whale (*Balaenoptera borealis*) vocalization rates, oceanographic conditions, and the vertical distribution of the whales' prey, the calanoid copepod *Calanus finmarchicus*, during May 2005 in the southwestern Gulf of Maine using an array of autonomous ocean gliders. Each of the four gliders was equipped with sensors to measure temperature, salinity, and chlorophyll fluorescence. Three of the four gliders carried a digital acoustic recorder and the fourth carried a 1-MHz acoustic Doppler current profiler. We observed strong diel periodicity in the acoustic backscatter measured by the current profiler that we attribute (based on a corroborating shipboard study) to the diel vertical migration of *C. finmarchicus*. Sei whale vocalization rates also exhibited diel periodicity, with more calls detected during the daytime when *C. finmarchicus* was observed at depth. We found no evidence to suggest that the observed patterns in sei whale calling rates were attributable to diel periodicity in background noise or acoustic propagation conditions. Sei whales are adept at foraging on near-surface aggregations of *C. finmarchicus*; therefore we expect that the whales were feeding at night. We hypothesize that calling rates are reduced at night while the whales are feeding, but increase with social activity during the day when copepods are either more difficult or less efficient to capture at depth. The gliders' persistence during adverse weather conditions experienced during the study allowed continuous collocated observations of whale vocalization behavior and oceanographic conditions that have not been previously possible with traditional shipboard techniques.

Both whalers and scientists have observed diel patterns in baleen whale feeding behavior for decades. Ingebrigtsen (1929) described sei whale (*Balaenoptera borealis*) skim feeding on copepods by noting, "it is especially in the evening and early in the morning, when the copepods are most at the surface, that 'skimming' takes place." Likewise, Nishiwaki and Oye (1951), Nemoto (1957), and Kawamura (1974) observed diel patterns in stomach fullness of blue (*Balaenoptera musculus*), fin (*Balaenoptera physalus*), humpback (*Megaptera novaeangliae*), and sei whales

harvested in the North Pacific and the Southern Ocean that suggested many prey species are not captured during the daytime. These authors speculated that the diel vertical migration of copepods and euphausiids governed the availability of prey for relatively shallow-diving baleen whales, and that the whales fed primarily during the evening and early morning when their prey was near the surface (interestingly, nighttime feeding was not considered by these authors, perhaps because whales could neither be observed nor harvested at night). Diel vertical migration in herbivorous zooplankton is a well-studied phenomenon that is classically described as zooplankton migrating from depth to the surface at night to feed on phytoplankton and then returning to depth at dawn to escape visual predators (Lampert 1993). This behavior has been documented in a wide variety of marine zooplankton, including those considered important prey species for baleen whales, such as *Calanus finmarchicus* (Durbin et al. 1995; Dale and Kaartvedt 2000; Baumgartner et al. 2003), *Meganctiphanes norvegica* (Kulka et al. 1982; Tarling et al. 1999; Tarling 2003), *Euphausia superba* (Kalinowski and Witek 1980; Demer and Hewitt 1995), and *Euphausia pacifica* (Bollens et al. 1992; De Robertis et al. 2000).

Recent long-term acoustic recordings of blue whales have revealed diel variability in vocalization behavior that may be related to diel feeding patterns established by the vertical migration of prey (Stafford et al. 2005; Wiggins et al. 2005). These studies raise the interesting possibility that

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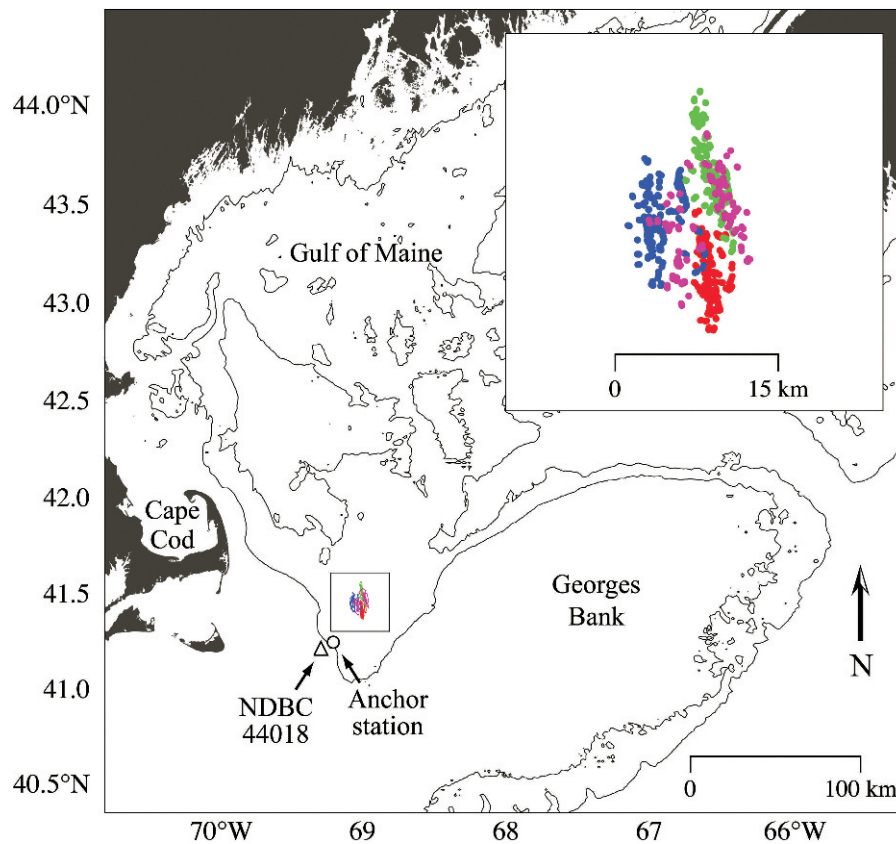


Fig. 1. Study area in the Great South Channel between Cape Cod and Georges Bank. Glider movements are shown as colored dots (WE04, red; WE06, green; WE07, blue; WE08, magenta). The triangle indicates the location of National Data Buoy Center meteorological buoy 44018 from which the wind and wave height observations were collected, and the open circle indicates the anchor station at which the corroborating study of ADCP acoustic backscatter was conducted.

prey distribution strongly regulates the daily timing of baleen whale behavior, including feeding behavior, acoustic behavior, and perhaps social and reproductive behaviors as well. Although these diel patterns have been observed separately, no studies to date have attempted to measure vocalization rates and prey distribution simultaneously to determine whether an association between the two actually exists. The long timescales over which simultaneous measurements must be made to adequately characterize diel variability (several days to weeks) have proved a major impediment to studying these relationships. Moored acoustic recorders are easily capable of collecting vocalization rates over the required timescales, but measuring prey throughout the water column over similar timescales at a temporal resolution of minutes to hours and a vertical resolution of meters to tens of meters (to adequately document migration events) is not trivial. While ship-based studies lack persistence because of storms and cost and profiling moorings are complicated, expensive, and inflexible, autonomous underwater vehicles (Rudnick et al. 2004) have considerable promise to provide a robust, adaptable cost-effective platform from which both acoustic recordings and high-resolution oceanographic measurements can be collected for the study of marine mammal ecology (Moore et al. 2007).

We deployed an array of four ocean gliders in the Great South Channel between Cape Cod, Massachusetts, and Georges Bank to simultaneously monitor both oceanographic conditions and the vocalization behavior of nearby baleen whales (Fig. 1). Our immediate goals were, first, to test the feasibility of making high-quality acoustic recordings from mobile autonomous platforms and, second, to examine potential relationships between baleen whale vocalization behavior and relevant environmental factors. The Great South Channel is probably best known as a major springtime habitat of the highly endangered North Atlantic right whale (*Eubalaena glacialis*; Kenney et al. 1995), but the area is also visited in the spring by sei, fin, and humpback whales. Right and sei whales forage on aggregations of late-stage *C. finmarchicus* (Payne et al. 1990; Schilling et al. 1992; Wishner et al. 1995) that are likely advected into the Great South Channel from the western Gulf of Maine during the spring (Chen et al. 1995; Wishner et al. 1995). *C. finmarchicus* is a 2–3-mm long calanoid copepod that is a vital constituent of both the neritic and oceanic ecosystems of the North Atlantic (Marshall and Orr 1955). The high abundance of both *C. finmarchicus* and sei whales makes this region ideal for examining the relationship between vocalization rates and prey availability from an autonomous platform. This paper

reports on the first use of ocean gliders for the study of marine mammal acoustic behavior and ecology.

Methods

Gliders—Autonomous observations of temperature, salinity, chlorophyll fluorescence, optical backscatter, photosynthetically active radiation (PAR), acoustic backscatter, and baleen whale vocalizations were collected by four Slocum coastal gliders (Webb Research Corp.; Rudnick et al. 2004). The gliders profile in the water column by adjusting their buoyancy to become alternately heavier and lighter than the surrounding seawater. Short wings provide lift during both descent and ascent, allowing the glider to move laterally at relatively slow speeds ($\sim 0.5 \text{ m s}^{-1}$). Each glider is equipped with a global positioning system (GPS) receiver to provide the vehicle's location when it is at the surface. Two-way communication with the glider is accomplished with an Iridium satellite modem. The gliders periodically surface to telemeter position, sensor, and diagnostic information so that the status of the vehicles can be monitored from land.

Sensors—Each of the gliders was equipped with a Sea-Bird Instruments SBE-41cp conductivity–temperature–depth (CTD) sensor to provide profiles of temperature and salinity. Each glider also carried a Wet Labs bb2f sensor (chlorophyll fluorescence and red and blue optical backscatter) and a custom photodiode-based PAR sensor. One glider carried a prototype fast-response CTD (Schmitt and Petitt 2007) to investigate centimeter-scale physical fine structure; both types of CTD instruments were mounted near the vehicle's midsection under the wing root. The bb2f was located in a flooded section of the vehicle's tail assembly. The Sea-Bird CTD measured at a rate of 0.5 Hz, the bb2f and PAR sensors at approximately 1 Hz, and the fast CTD at 10 Hz. All data were logged internally at full resolution. Subsampled data were telemetered to shore at regular intervals.

One of the gliders (serial WE04) was equipped with a 1-MHz acoustic Doppler current profiler (ADCP; Nortek Aquadopp) from which measurements of velocity and acoustic backscatter were derived. The ADCP was affixed to the top surface of the glider, and a custom angled transducer head was used so that the acoustic beams were directed straight up when the glider was descending in the water column. Acoustic backscatter was measured in 1-m vertical bins at a rate of 1 Hz with a resolution of 0.45 dB and a dynamic range of 90 dB. We used the ADCP primarily as an uncalibrated echosounder for this study to estimate the distribution and abundance of *C. finmarchicus*. We conducted an independent shipboard study of the ADCP to verify that *C. finmarchicus* was the dominant contributor to the observed acoustic backscatter (see below).

Digital acoustic recorders were custom built and installed on the remaining three gliders (serials WE06, WE07, and WE08). The recorders consisted of a hydrophone, an analog front end, analog-to-digital (A/D) converter, data logger, and a compact flash memory card (Fucile et al. 2006). The hydrophone (HTI-96-MIN; 2-Hz–

30-kHz frequency response, $-165 \text{ dB re } 1 \text{ V } \mu\text{Pa}^{-1}$ sensitivity) was potted in a faired housing and mounted on the underside of the glider. The analog front end provided preamplification and an antialias high-pass filter. The conditioned signal from this front end was digitized at 2048 Hz by a 16-bit A/D converter, temporarily stored to internal random access memory in the data logger (CF2, Persistor Instruments), and ultimately written to individual 3-min long data files on a removable 4 gigabyte compact flash card. To facilitate accurate localization of detected baleen whale calls by time difference of arrival, a high-precision real-time clock (Dallas Semiconductor) was also incorporated into the recorder. The acoustic recorder clocks were synchronized by introducing impulsive sounds simultaneously to all of the glider recorders at known times both before deployment and after recovery.

Data processing—The physical and optical profile measurements were extracted from the glider data, checked for outliers, and vertically averaged into 1-m bins. Raw acoustic backscatter data from the 1-MHz ADCP deployed on glider WE04 were extracted and converted to engineering units using the Nortek AquaPro software. Only data from a fixed range, 4 m away from the vehicle, were extracted and used in the analysis. Since the glider continuously profiled, this provided vertical profiles of acoustic backscatter at similar space and timescales as observed by the other physical and biological sensors. Sound levels recorded on glider WE08 were measured every 2 s as the root mean square of the waveform (in volts), which were converted to units of dB re $1 \mu\text{Pa}$ using the preamp gain and factory calibration of the hydrophone. Background noise was estimated as the quietest 2-s sound level each hour.

We employed an automated detection algorithm to assist in isolating occurrences of sei whale vocalizations in the acoustic data from gliders WE06, WE07, and WE08 (Baumgartner et al. 2008). The detection method is adapted from the spectrogram correlation approach of Mellinger and Clark (2000). Briefly, a synthetic kernel (a mathematical representation of a particular vocalization in frequency-time space) is cross-correlated with a spectrogram of the recorded audio data to produce a detection function. Peaks in the detection function above a specified threshold indicate the occurrence of a call. This method is particularly useful for identifying stereotypical calls despite varying noise conditions (including impulsive sounds, white noise, and transient background noise, e.g., ship noise). Whereas Mellinger and Clark (2000) used a synthetic kernel constructed from sections of linear frequency-modulated (FM) sweeps, we designed a synthetic kernel from amplitude contours of averaged exemplar vocalizations, thereby accurately incorporating the shape of nonlinear FM sweeps in the synthetic kernel. The sei whale detector was constructed and validated using a 25.5-h acoustic dataset collected in the Great South Channel during the spring of 2006 near several baleen whale species, including sei whales (see Baumgartner et al. 2008). The detector was designed to capture 30–85-Hz downsweeps lasting roughly 1.5 s (Fig. 2) produced by sei whales (Rankin and Barlow

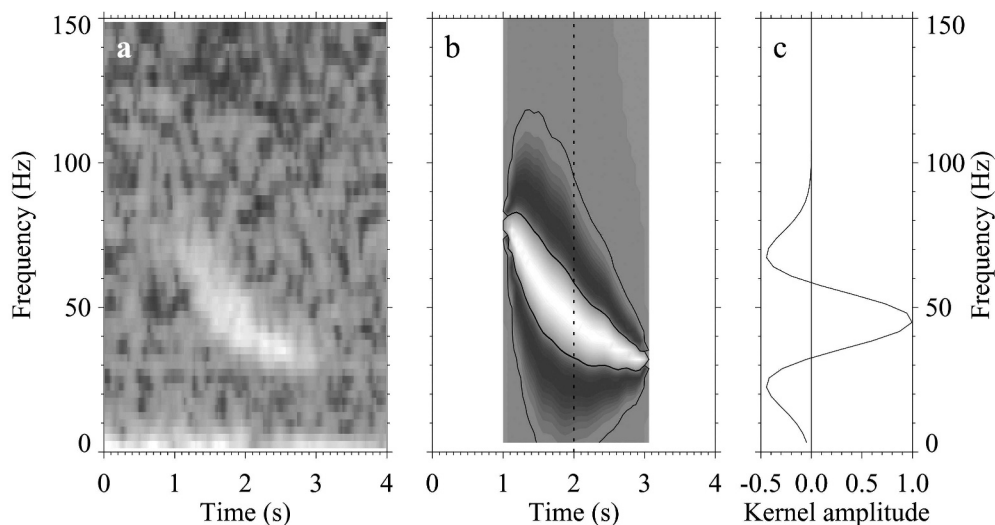


Fig. 2. (a) Spectrogram of a sei whale downsweep call. (b) Synthetic kernel used in automated detection (Baumgartner et al. 2008); light areas correspond to high positive kernel amplitude and dark areas correspond to high negative kernel amplitude. (c) Kernel amplitude as a function of frequency for the time indicated by the dotted line in (b).

2007; Baumgartner et al. 2008). Independent validation tests indicated that the kernel produced false detections 4% of the time, while missing 27% of calls at a threshold of $r = 0.3$ (Baumgartner et al. 2008). We used this same threshold for automatically detecting sei whale calls in the glider acoustic data; however, we found that the time series of relative call rates (i.e., hourly call rates as a percentage of the total number of calls) was insensitive to modest changes in the detection threshold. No adjustment was made to the relative call rates to account for missing calls. Call rates were computed as the sum of all calls detected on all three gliders for a given hour divided by the total amount of time monitored by the gliders during that hour; time when noise was produced by the glider at the top or bottom of a dive or during satellite communications was therefore taken into account in the calculations.

Corroborating study of ADCP backscatter—Acoustic backscatter at a single frequency can be used to assess zooplankton abundance under particular circumstances (Holliday and Pieper 1995), including dominance by a single organism. Late-stage *C. finmarchicus* dominates the zooplankton community in the Great South Channel during the spring (Wishner et al. 1988, 1995); therefore we conducted an independent shipboard study to determine whether the 1-MHz ADCP acoustic backscatter could be used to detect changes in *C. finmarchicus* vertical distribution. Collocated observations of ADCP acoustic backscatter and zooplankton abundance were collected with a vertical profiling package that housed an identical ADCP to that used on glider WE04 (Nortek Aquadopp), an optical plankton counter (OPC-1T), a video plankton recorder (AutoVPR) and a CTD (Seabird model SBE19-plus). The instrument package was profiled every half hour at an anchor station occupied by the NOAA Ship *Albatross IV* for 26.5 h. The station was located 25 km to the southeast of the glider operation area in 98 m water depth

(Fig. 1) and was occupied 1 week after glider recovery. Abundance of late-stage *C. finmarchicus* was estimated from the OPC data using the calibration equation of Baumgartner (2003), and zooplankton taxonomic composition and abundance was estimated by manually classifying images of zooplankton acquired in situ by the VPR.

Results

Glider deployments—Four gliders were deployed in the Great South Channel on 06 May 2005 in an array configuration (Fig. 1). The deployment site was chosen in an area where several sei and a few right whales were encountered. The gliders were programmed to remain within 5 km of a predetermined station but were allowed to advect with the tide. Tidal currents in this region (principally north-south and parallel to the topography) are comparable in magnitude with the vehicle's top speed ($\sim 0.5 \text{ m s}^{-1}$). The gliders were able to counteract lower frequency currents (i.e., the subtidal drift through the Great South Channel from the Gulf of Maine to the northern flank of Georges Bank; Chen et al. 1995) and remained in an area approximately 250 km². This vehicle movement pattern was acceptable for this study, since baleen whales and the zooplankton patches upon which they feed are also advected by the tide. The gliders repeatedly profiled between 5 and 100 m (local water depths were 110–150 m) for a period of 2 h before returning to the surface to obtain a GPS-derived position and to telemeter sensor and diagnostic information to shore via the Iridium satellite communication link. Approximately six descent-ascent cycles were completed during each 2-h dive period, and each dive period was separated by a 5–10-min surface communication interval. Recovery of the gliders occurred on 11 May 2005, 5 d after deployment.

Physical observations—Shortly after the gliders were deployed, a strong storm (northeaster) moved through the

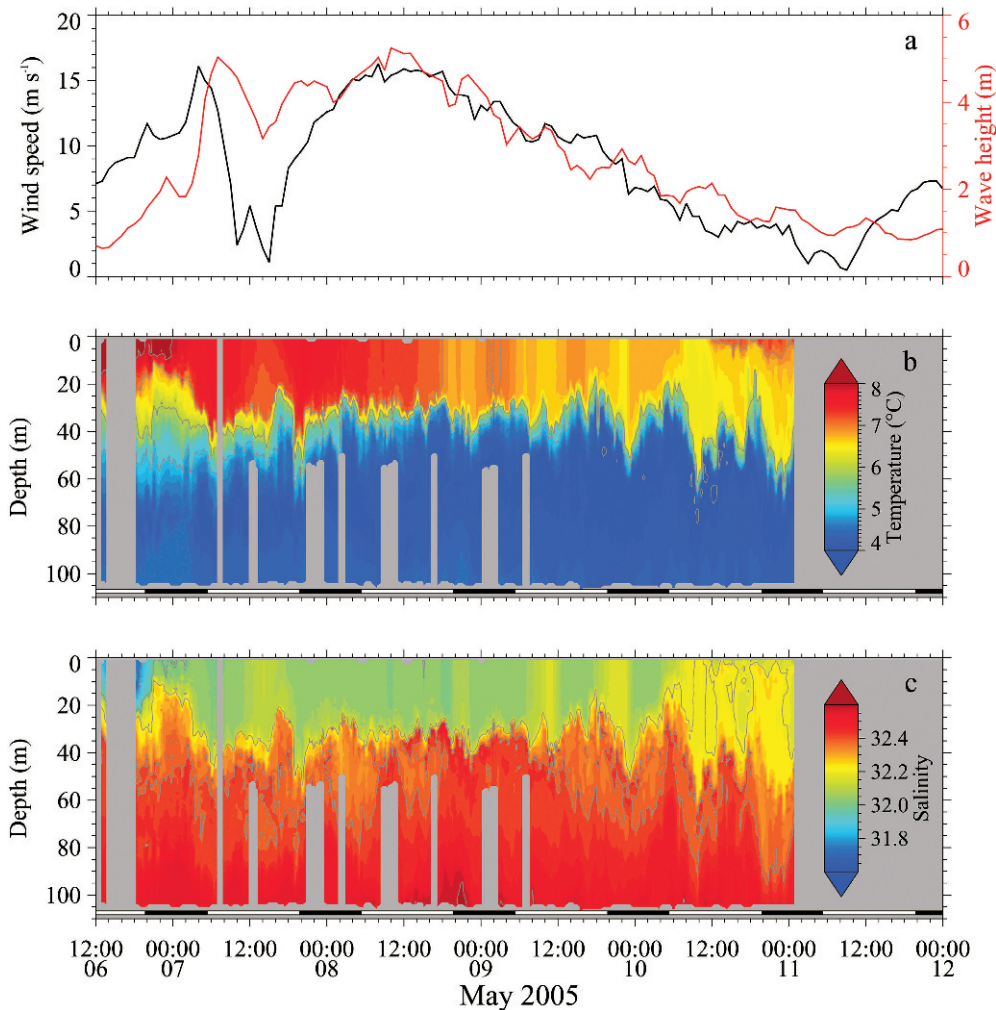


Fig. 3. (a) Wind speed (black) and wave height (red) measured at NDBC buoy 44018 (see Fig. 1) during the glider deployments. (b) Temperature and (c) salinity observed by glider WE04. Gray areas indicate periods when glider was in diagnostic mode and was not collecting data. Times on the abscissa are local. Bar at bottom of (b) and (c) indicates day (white) and night (black).

region. Sustained wind speeds exceeded 16 m s^{-1} and wave heights reached 5.25 m (Fig. 3a; measured nearby at the National Data Buoy Center meteorological buoy 44018; see Fig. 1). The water column was initially stratified with a strong thermocline near 20-m depth; however, the storm mixed the surface waters to a depth of 40 m (Fig. 3b). Despite sustained strong winds lasting over 3 d, mixing was limited to the upper 40 m during much of the storm because of a strong halocline at 40 m (Fig. 3c). Surface waters steadily cooled by nearly 2°C as the storm progressed, and stratification did not begin again until the 12 h prior to glider recovery. The higher salinities observed from 20- to 50-m depth to the surface during this late period of stratification were not likely to have been caused by local air–sea interactions but instead are suggestive of an advective event that brought a different water mass into the region. Changes in the upper ocean sound speed data reflected storm-driven variability in temperature and salinity; however, sound speed profiles at depth provided evidence of a sound channel that rose

from 80-m depth at the beginning of the study to 55 m at the end (Fig. 4a).

Biological observations—We observed high chlorophyll fluorescence in the upper 40 m, particularly during the first 2 d of the time series (Fig. 4b). While high fluorescence was generally restricted to the mixed layer, we observed a patch of very high fluorescence in the thermocline during the night of 06–07 May that appears to have been entrained in the mixed layer during the morning of 07 May. Near-surface fluorescence varied on a diel timescale, with less fluorescence observed in the upper 5 m during local noon than at any other time. Reduction in chlorophyll fluorescence during periods of strongest insolation is consistent with photoadaptation (e.g., increases in photoprotective pigments) and closing of photosynthetic reaction centers (Dandonneau and Neveux 1997; Laney et al. 2005).

We observed high acoustic backscatter from the ADCP in the upper 5 m during periods of high winds (correlation between hourly wind speed and acoustic backscatter at 2-m

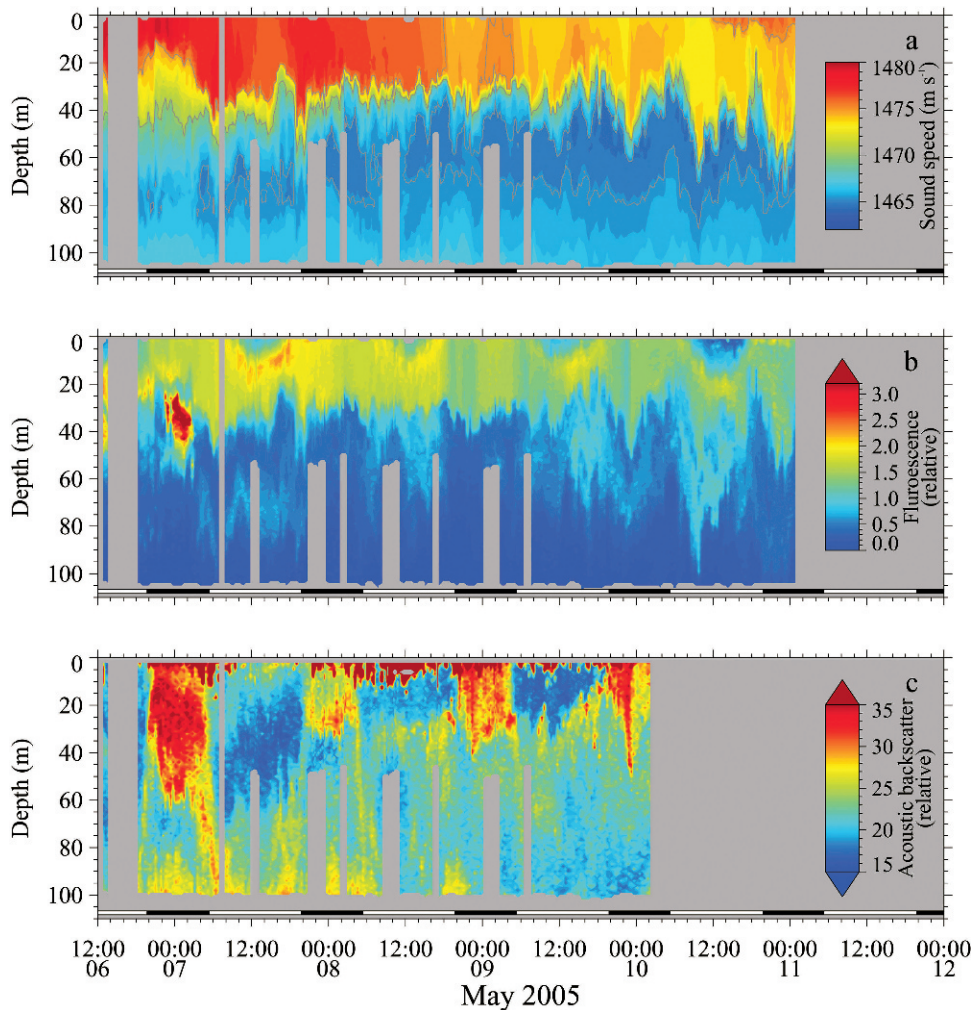


Fig. 4. (a) Sound speed, (b) chlorophyll fluorescence, and (c) acoustic backscatter observed by glider WE04. The time series of acoustic backscatter is shorter than other observations because of an expected early depletion of the ADCP batteries. Gray areas indicate periods when glider was in diagnostic mode and was not collecting data. Times on the abscissa are local. Bar at bottom of each panel indicates day (white) and night (black).

depth: $r = 0.696$, $p < 0.0001$) that was likely caused by bubbles from breaking surface waves (Fig. 4c). We also observed high acoustic backscatter in the upper 30–40 m each night but low acoustic backscatter in this same depth stratum during the day. Moreover, peaks in scattering moved up toward the surface at dusk and down toward the seafloor at dawn. This pattern is consistent with the diel vertical migration of *C. finmarchicus*, the dominant contributor to the 1-MHz ADCP backscatter (see corroborating study results below). The observed vertical migration rates of backscatter peaks (Table 1) are comparable with (albeit slightly faster than) the migration speeds reported for *C. finmarchicus* by Baumgartner et al. (2003; they measured upward migration speeds of 0.50 and 0.67 cm s^{-1} , downward speeds of 0.60 cm s^{-1}).

Acoustic observations—Because the gliders move slowly, the acoustic recordings were of superb quality with no detectable flow noise while profiling up or down. At the top and bottom of each profile, however, brief periods of noise

were produced by the glider as a displacement piston was activated to alter the vehicle's buoyancy and thus provide propulsive force (Fig. 5). The glider also generated motor (air pump) and electronic noise while at the surface during periods of radio communication. Detection of whale vocalizations was impossible during these periods.

Rates of sei whale vocalizations were highly variable and ranged between 0 and over 500 calls per hour (Fig. 6). Vocalization rates were highest within the first 24 h of the study, likely because the gliders were initially deployed in an area with relatively high sei whale abundance. Sei whale vocalizations were detected throughout the study, however, indicating that sei whales remained in proximity to the gliders. Vocalization rates were significantly higher during the day than at night when rates for each day were compared with those of the succeeding night (log-transformed paired t -test, $n = 4$, $t = 4.16$, $df = 3$, $p = 0.025$): daytime rates were an average 2.91 (95% confidence interval [CI] 1.29–6.59) times higher than the succeeding nighttime vocalization rates (Table 2; note that days and

Table 1. Vertical migration rates for *Calanus finmarchicus* inferred from migration of peaks in ADCP acoustic backscatter at dawn and dusk.

Date	Time	Vertical migration rate (cm s ⁻¹)	95% CI
06 May 2005	dusk	1.15	1.00–1.29
07 May 2005	dusk	0.81	0.40–1.22
07 May 2005	dawn	0.89	0.44–1.33
08 May 2005	dawn	1.51	0.61–2.40
09 May 2005	dawn	0.81	0.48–1.15

succeeding nights with incomplete acoustic coverage were not included in these comparisons). Although vocalization rates for the first night of the study (06–07 May) were quite high, the preceding day was only monitored during the

afternoon and a valid comparison was not possible. Hourly vocalization rates were weakly, yet significantly, correlated with the wind speed ($r = 0.211$, $p = 0.022$); daytime vocalization rates tended to decrease as winds associated with the storm diminished.

Corroborating study of ADCP backscatter—During the shipboard study of the 1-MHz ADCP acoustic backscatter conducted 1 week after the gliders were recovered, diel vertical migration by late-stage *C. finmarchicus* was observed in both the OPC and VPR data (Fig. 7). Interestingly, a portion of the copepod population stayed in the upper 20 m throughout the study; however, the remaining *C. finmarchicus* migrated to the surface at night and returned to depth (near bottom) during the day. This pattern of diel vertical migration was clearly observable in

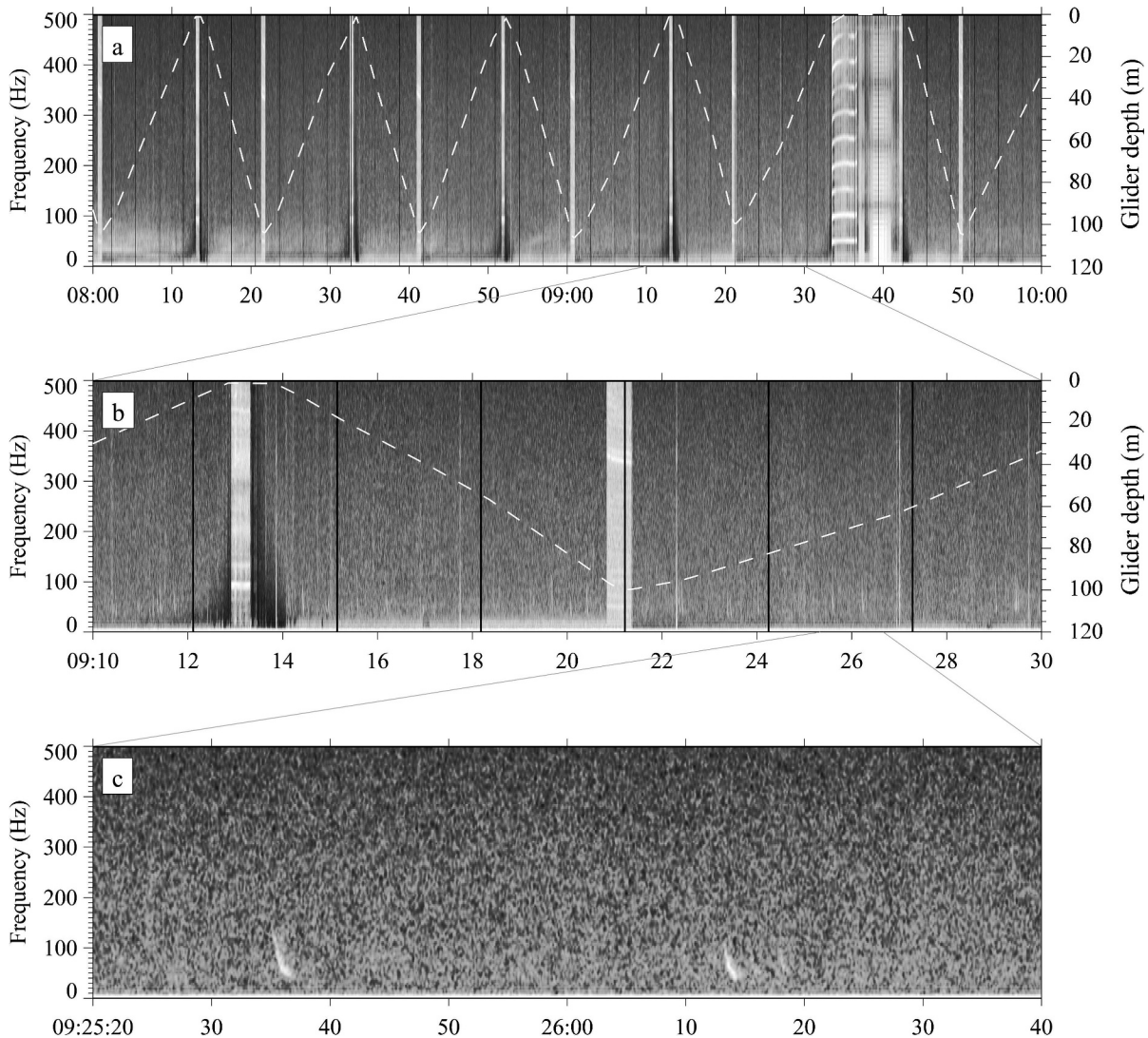


Fig. 5. Spectrograms of recordings collected by glider WE07 on 09 May 2005 0800–1000 h local time. Spectrograms are shown in (b) and (c) at successively finer temporal resolutions. The glider's dive profile is shown as a broken line in (a) and (b). Noise is produced by the displacement piston at the top and bottom of each dive, as well as by the Iridium satellite modem when the glider surfaces to communicate with computers on land (between 0933 and 0942). Gaps lasting 2–3 s are also apparent between each 3-min recording during which data are transferred from internal memory to compact flash memory in the acoustic recorder. Two sei whale calls with high signal-to-noise ratios can be seen clearly in (c).

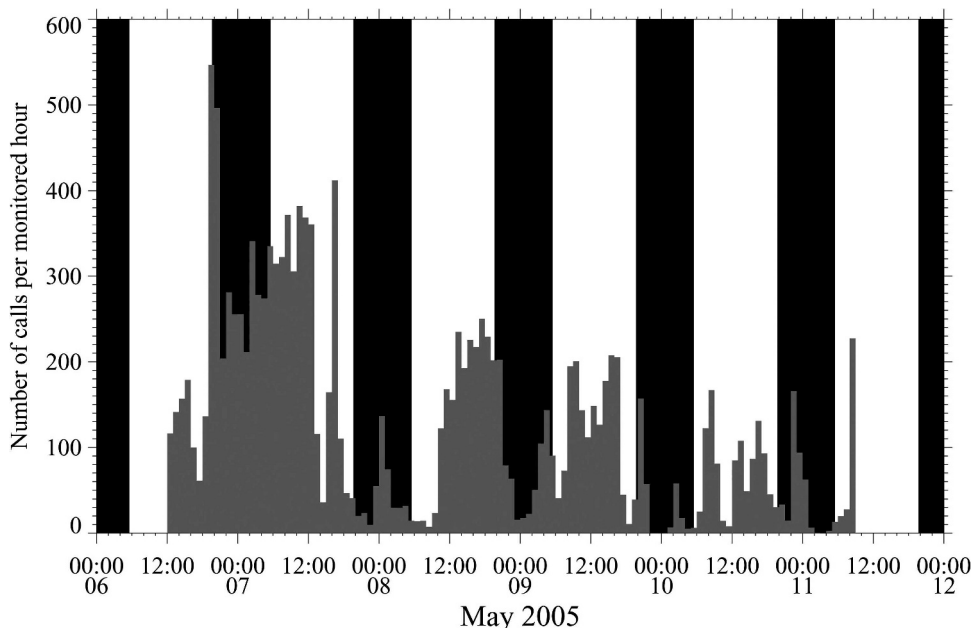


Fig. 6. Hourly sei whale call rates observed by the gliders. Times on the abscissa are local, and dark background bands indicate nighttime.

the 1-MHz ADCP backscatter. The agreement between the OPC, VPR, and ADCP was good, which suggests that late-stage *C. finmarchicus* was the dominant contributor to the 1-MHz acoustic backscatter.

Discussion

Observations of diel periodicity in sei whale vocalization rates could be caused by several processes: first, diel periodicity in background noise; second, diel periodicity in propagation conditions; and, third, diel periodicity in the production of calls by sei whales. Diel changes in both background noise and propagation conditions would alternately increase and decrease the range at which sei whale calls were detected by the gliders; if the production of calls was constant over both space and time, then this variability in the acoustic environment would be observed

Table 2. Average number of calls per monitored hour observed each day and night by the gliders. Data only shown for day and night pairs if the entire day and night were monitored. Daytime call rates were significantly higher than nighttime call rates (log-transformed paired *t*-test: $n = 4$, $t = 4.16$, $df = 3$, $p = 0.025$) by an average factor of 2.91 (95% CI: 1.29–6.59).

Date		Average number of calls per hour	Day : night call ratio
07 May 2005	day	122.9	5.44
	night	22.6	
08 May 2005	day	73.3	1.78
	night	41.2	
09 May 2005	day	63.8	3.59
	night	17.8	
10 May 2005	day	39.0	2.07
	night	18.8	

as diel variability in calling rates. Background noise was correlated with wind speed (hourly observations, $r = 0.726$, $p < 0.0001$), and we observed strong tidal periodicity likely caused by flooding and ebbing tidal currents (Fig. 8a); however, there was no evidence of diel periodicity in the background noise (Table 3). There was also no evidence of diel periodicity in propagation conditions estimated from the observed glider sound speed profiles and the range-dependent acoustic model (RAM; Collins 1993) for a 50-Hz signal produced at various source depths (Fig. 8b, Table 3). This model did not account for refraction or attenuation of sound due to wave-induced bubbles; however, there was no evidence of diel periodicity in the amplitude of the near-surface ADCP measurements, a crude proxy for the abundance of bubbles (Table 3). While there was variability in both background noise and propagation conditions that undoubtedly influenced the range at which sei whale calls could be detected by the gliders, there was no evidence to suggest that the diel periodicity observed in sei whale call rates was caused by diel periodicity in the acoustic environment. We therefore conclude that our observations were caused by diel periodicity in the production of calls by sei whales.

Sei whale calls were more numerous during the day when *C. finmarchicus* was at depth than during the night when *C. finmarchicus* was observed near the surface. These observations suggest that the availability of *C. finmarchicus* in the surface waters influences sei whale vocalization behavior. The assertion that diel periodicity in sei whale vocalizations is governed by the availability of prey presumes that feeding at night on *C. finmarchicus* entails a reduction in vocalizations. No evidence exists to suggest that zooplanktivorous whales use sound to locate prey patches (unlike echolocating odontocetes and perhaps piscivorous humpback whales; Stimpert et al. 2007);

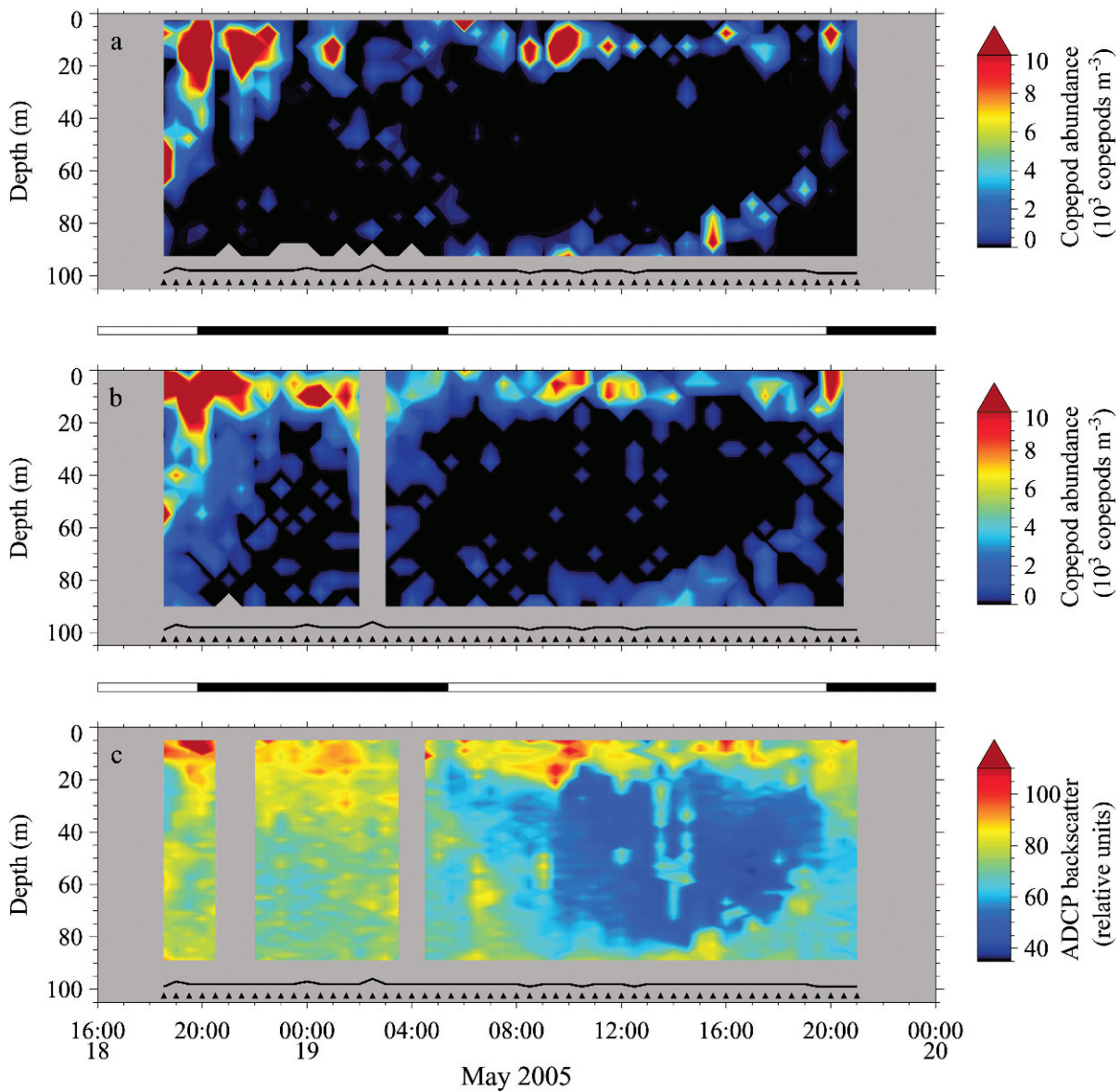


Fig. 7. Collocated observations of copepod abundance and acoustic backscatter at an anchor station in the Great South Channel during the corroborating study conducted aboard the NOAA ship *Albatross IV*. (a) Late-stage *Calanus finmarchicus* abundance estimated with an optical plankton counter using the calibration equation of Baumgartner (2003). (b) Large copepod abundance estimated with a video plankton recorder. (c) Acoustic backscatter from an identical 1-MHz acoustic Doppler current profiler to that deployed on glider WE04. Triangles denote profile times, and the dark black line at the bottom of each plot indicates the seafloor. Times on the abscissa are local. The bars between each panel indicate day (white) and night (black). Missing data attributable to instrument malfunction.

therefore, we assume that vocalizations are produced in a social context (e.g., maintaining contact with conspecifics, agonistic displays, attracting a mate). The effort required to find and filter zooplankton patches would seemingly leave little time for social activity, thus vocalization rates would be reduced while feeding. Indeed, Matthews et al. (2001) report that a tagged traveling North Atlantic right whale vocalized (moaned) more often than tagged foraging right whales. However, Croll et al. (2002) suggested that male fin whales vocally advertise prey resources to attract females; thus social displays could be intimately linked to the availability of prey. It is conceivable that sei whales that find high concentrations of *C. finmarchicus* at night

similarly advertise the presence of these patches by day. Interestingly, sei whale vocalization rates were highest during and after the highest concentrations of *C. finmarchicus* were observed in the upper ocean on the night of 06–07 May (Fig. 4c). The reduction in vocalization rates over the course of the study could also be attributed to a decrease in the abundance of sei whales in proximity to the gliders or a decrease in wind-generated background noise (Fig. 8a), which might reduce the need for individuals to repeat calls to be distinctly heard by other whales.

We speculate that sei whales maximize foraging efficiency by feeding on near-surface aggregations of *C. finmarchicus* at night. Foraging near the surface for an air-breathing

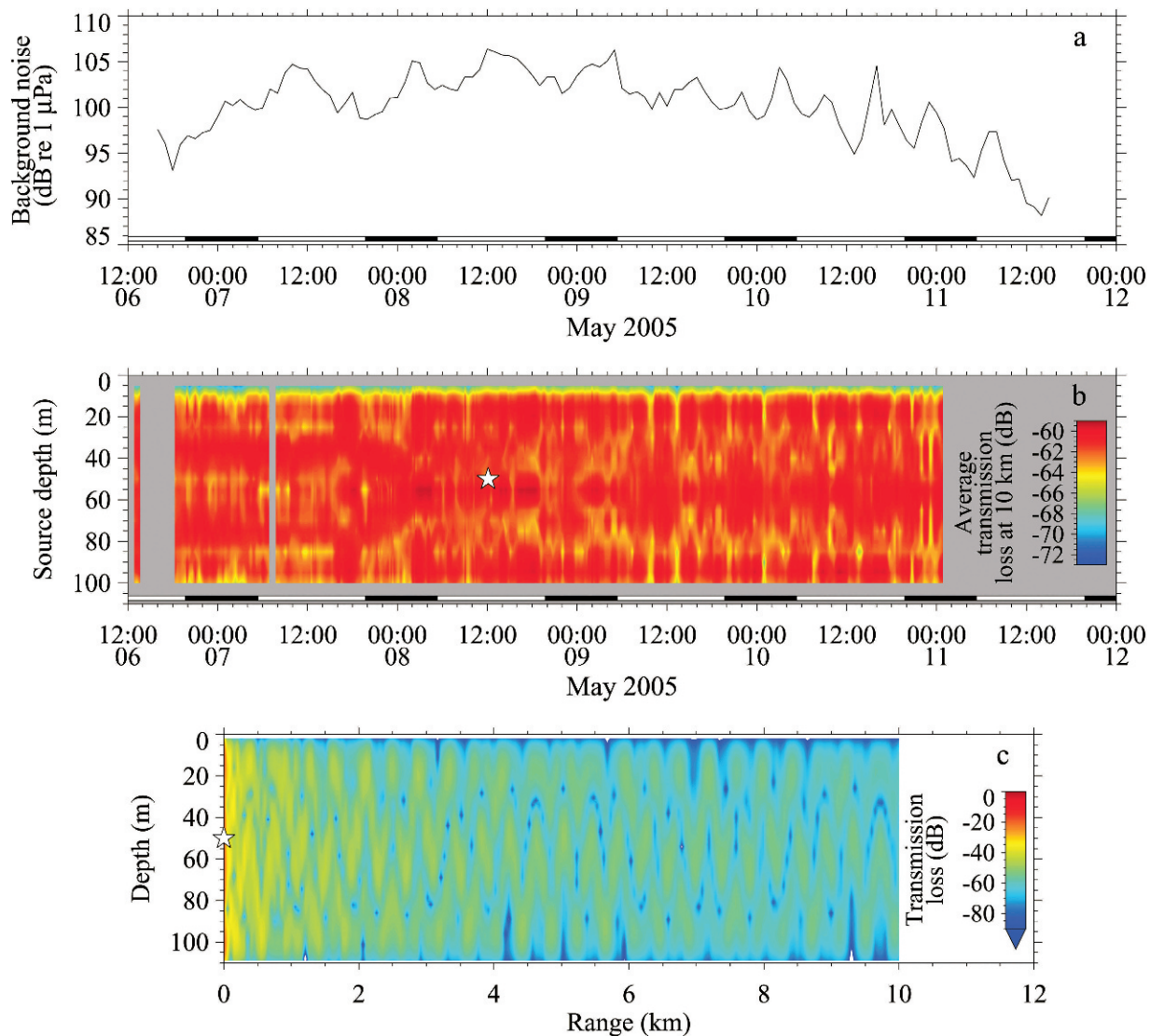


Fig. 8. (a) Background noise measured by glider WE08 as the sound level of the quietest 2-s period during each hour of the time series. (b) Depth-averaged transmission loss for a 50-Hz signal over a sandy substrate at a range of 10 km as estimated by the range-dependent acoustic model (RAM; Collins 1993). A separate model was run for each sound speed profile collected by glider WE04 (Fig. 4a) and for sources placed at 5-m intervals from 5- to 100-m depth. (c) An example of one model run showing range-dependent transmission loss from a source at 50 m depth at local noon on 08 May 2005 (time and source depth indicated with a star in b and c).

Table 3. Results of tests for diel periodicity in processes potentially influencing the acoustic environment (i.e., the acoustic detection range of sei whale calls). Statistics shown for paired one-sample *t*-tests on arithmetic differences between day and night observations ($n = 3$ for acoustic backscatter, $n = 4$ for all other variables). Tests are identical to that used to test for day–night differences in sei whale call rates; results of the sei whale call rate test are shown for comparison (from Table 2).

Variable	Hypothesized diel process	Mean Day: night difference	<i>t</i> statistic	<i>p</i> value
Noise (dB re 1 μ Pa)	background noise	0.617	0.689	0.540
Transmission loss at 10 km (dB), source = 5 m	propagation	0.090	0.291	0.790
Transmission loss at 10 km (dB), source = 25 m	propagation	0.067	0.398	0.718
Transmission loss at 10 km (dB), source = 50 m	propagation	-0.077	-0.271	0.804
Transmission loss at 10 km (dB), source = 75 m	propagation	0.057	0.341	0.756
Transmission loss at 10 km (dB), source = 100 m	propagation	0.144	0.548	0.622
Acoustic backscatter at 2 m (relative units)	bubbles	-1.146	-0.248	0.827
Sei whale call rate (calls h^{-1})	diel calling rates	2.913*	4.165	0.025

* Day:night ratio.

marine predator is more efficient than foraging at depth, since the transit time from the surface to a shallow layer of food is short and therefore the time spent actually feeding in the layer is maximized for a constant submergence time (Kooyman et al. 1992). It is possible that sei whales continued to feed on deep layers of *C. finmarchicus* during the day; after all, the North Atlantic right whale, another zooplanktivorous baleen whale that feeds primarily on *C. finmarchicus*, is capable of feeding deep in the water column (Baumgartner and Mate 2003) and even near the bottom during the day in the Great South Channel (Baumgartner unpubl.). However, the observed diel change in vocalization rates likely implies a corresponding change in behavior. The increase in vocalization rates during the day might be attributed to either reduced feeding and increased socializing (which may be accompanied by more acoustic activity to facilitate interactions between individuals) or switching to another prey species (which may be accompanied by increased vocalization rates to either coordinate activities among individuals or to agonistically maintain control over patchy prey resources).

The diet of sei whales, the most catholic of all the baleen whales, ranges in size from copepods to small schooling fish (Hjort and Ruud 1929; Kawamura 1974; Flinn et al. 2002). Baleen has evolved as an adaptation to capture large quantities of small prey, either by continuously filtering water while swimming forward (ram filter feeding) or by engulfing large quantities of seawater and prey in a single mouthful, and then straining this water as it exits the mouth (lunge feeding). Specific baleen morphology has evolved in concert with target prey taxa and these two feeding strategies. Ram filter feeders (right and bowhead whales; *Balaena mysticetus*) have long baleen plates, two distinct racks of baleen on either side of the mouth separated by the subrostral gap (a space between the racks of baleen at the front of the upper jaw), and fine baleen fringes for feeding on copepods and euphausiids, whereas lunge filter feeders (e.g., blue, fin, and humpback whales) have short baleen plates, no subrostral gap, and coarse baleen fringes for feeding on relatively larger euphausiids and small schooling fish (e.g., capelin, herring, and pollack). Sei whales have the seemingly unique ability among baleen whales to both ram filter feed on copepods and euphausiids and to lunge feed on euphausiids and fish (Ingebrigtsen 1929; Nemoto 1957; Flinn et al. 2002). While sei whales have the same general mouth morphology as other rorquals such as blue, fin, and humpback whales, they have very fine baleen fringes and have developed a surface skim-feeding behavior reminiscent of skim feeding in right and bowhead whales (Ingebrigtsen 1929). Switching between different prey taxa is undoubtedly an advantage in times of fluctuating prey abundance, but it perhaps comes at a cost of specialization for capturing particular prey under a variety of circumstances.

Our understanding of the foraging behavior of sei whales when feeding on copepods is limited to surface observations of skim feeding (Ingebrigtsen 1929); therefore, we are ignorant of their ability to forage on copepods at depth. If sei whales forego feeding on *C. finmarchicus* at depth during the day, do they do so because it is inefficient or are

they somehow incapable of foraging on copepods at depth? If the latter, then is their inability to forage a result of insufficient sensory capabilities or do the mechanics of prey capture for sei whales simply not work at depth? Other rorquals are capable of lunge feeding at depths of 100–200 m (Croll et al. 2001; Acevedo-Gutiérrez et al. 2002) and perhaps even as deep as nearly 500 m (Panigada et al. 1999); therefore it seems unlikely that sei whales lack the sensory capabilities to detect prey at depth. However, different sensory modalities may be required to detect layers of copepods than to detect swarms of euphausiids or schools of fish. Watkins and Schevill (1979) reported aerial observations of a multispecies aggregation of feeding whales that included a few right whales and a single sei whale feeding in proximity to one another (sometimes only meters apart) on a concentrated patch of zooplankton. While the right whales “remarkably demonstrated their ability to select and continue to feed in the densest patches of plankton,” the sei whale “often moved past the edge of a patch and then abruptly turned and swam back into it” and generally “appeared to be less adept than the right whales at staying in the dense portions of the plankton patches” (Watkins and Schevill 1979). These observations suggest that sei whales have inferior sensory capabilities to detect zooplankton aggregations in comparison with those of right whales. Perhaps sei whales rely to a great extent on light to find zooplankton patches visually, which could explain why their foraging may be restricted to near-surface waters, whereas right whales may rely on sensory hairs to monitor zooplankton concentration (Kenney et al. 2001). The sensory modalities used in baleen whale foraging are very poorly understood, so we can only speculate on this matter.

In addition to potential sensory inefficiencies, sei whale mouth morphology may also severely reduce the effectiveness of ram filter feeding when submerged. Sei whales raise the tip of their rostrum above the sea surface while skim feeding, which allows seawater to continuously move into the mouth as they swim forward. At depth, the lack of a subrostral gap in the baleen may impede the smooth flow of water into the mouth, perhaps creating turbulence that could alert zooplankton to the presence of the oncoming whale. Capture avoidance behavior in copepods is well known, and any disturbance at the front of a whale’s mouth could evoke an escape response. Flow into a balaenid mouth (i.e., that of right and bowhead whales) is likely laminar because of the subrostral gap, thus reducing this escape response (Werth 2004). Moreover, the large lips and curved surface of the baleen racks that promote accelerated flow (Bernoulli effect) and enhanced filtering through the baleen (Venturi effect) in the balaenid mouth (Werth 2004; Lambertsen et al. 2005) are completely absent in the sei whale. While the balaenid mouth seems elegantly adapted for filtering copepods and small euphausiids from seawater, the sei whale seems to have converged on only the fine baleen fringe and the surface skim-feeding behavior of the balaenids, presumably to retain the ability to successfully lunge feed on larger prey. Therefore, it is plausible that both their filtering apparatus and foraging behavior make sei whales far less efficient than balaenids while feeding at depth.

There is currently great interest in assessing the occurrence, abundance, and spatial distribution of marine mammals from vocalization rates obtained from moored and moving platforms. While it remains to be seen whether vocalization rates can reliably indicate either occurrence or abundance for particular species, diel periodicity in vocalization rates has important implications for determining the spatial distribution of animals from moving platforms (e.g., towed hydrophones, gliders, drifting profilers). During our study, sei whale acoustic detectability was higher during the day than at night; diel differences such as these can confound realizations of sei whale spatial distribution based on measured vocalization rates alone. Without a complete understanding of this diel variability, areas surveyed at night will be judged to have fewer or no animals compared with areas surveyed during the day. For very slow moving platforms (e.g., ocean gliders or drifting profilers), diel variability poses less of a problem because the areas surveyed by day and by night likely overlap to a great extent; however, this is not the case for most towed hydrophone applications. If diel variability can be parameterized, however, then measured vocalization rates can be adjusted to a baseline rate. Just as diving studies have helped to refine detectability estimates for visual abundance surveys, studies of diel periodicity in vocalization rates will ultimately help improve estimates of abundance or occurrence from acoustic data.

The quality of the acoustic recordings from the ocean gliders was superb; our initial concerns about flow noise were mitigated by the faired design of the hydrophone housing and the slow speed of the vehicle. Although the pump and communication system created noise during particular operations, the gliders were silent on descent and ascent. For all but the most rare of biological sounds, the duty cycle imposed by these vehicle noises is acceptable. While the glider's silence makes high-quality acoustic recordings possible, this comes at the expense of speed; the glider can only move at $\sim 0.5 \text{ m s}^{-1}$ relative to the background currents. Although this speed is too slow for tracking applications, the glider can plod along for very long periods of time (days to weeks) over long distances (hundreds of kilometers) since the buoyancy pump does not consume much power. Higher speeds can be obtained using propeller-driven vehicles, but with a commensurate and potentially unacceptable increase in noise and reduction in endurance.

Autonomous profiling platforms equipped with passive acoustic instrumentation have the potential to provide persistent observations of not only marine mammal occurrence and vocalization behavior, but also prey distribution and oceanographic conditions throughout the water column over vertical spatial scales as small as centimeters, and in the case of ocean gliders, horizontal spatial scales of hundreds of meters or more. The timescales over which marine mammal ecology studies can be conducted with traditional methods (shipboard studies with human observers) is limited to hours to days because of visibility (e.g., fog, rain, night), observer fatigue, sea state, and expense. Stormy conditions (such as those encountered during our study) preclude traditional observ-

er-based ecological studies altogether. In contrast, autonomous platforms are robust in poor sea conditions and their low power requirements allow them to remain at sea for weeks to even months. We anticipate that this new observing capability will enable unmanned marine mammal surveys, distribution and habitat studies, and long-term ecological monitoring over finer spatial scales and longer temporal scales than previously possible.

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