Ecosystem response to a temporary sea ice retreat in the Bering Sea: Winter 2009

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1. Introduction

The seasonal advance and retreat of sea ice in the Bering Sea is a dynamic physical process that influences the entire marine ecosystem. During summer the Bering Sea is ice free, but starting in late March is usually associated with an early bloom which occurs in cold water. This pattern favors conditions which may ultimately result in fluxes of energy to the Bering Sea benthic community (Walsh and McRoy, 1986; Stabeno et al., 1998; Hunt and Stabeno, 2002). Alternatively, when sea ice retreats early (before mid-March), the spring phytoplankton bloom is delayed until the surface waters become thermally stratified. This late spring bloom occurs in warmer water, supporting the transfer of energy to a pelagic food web via grazing by proto- and metazoans. These differences in the flow of energy from phytoplankton to zooplankton of the eastern Bering Sea shelf are known to have a significant impact on survival of feeding fish larvae and migratory species of marine mammals.
The Bering Sea experienced significant warming (−3 °C) during the early 2000s that was closely associated with marked decreases in sea ice concentration, ice duration, maximum ice extent, and recruitment of walleye pollock (Theragra chalcogramma) and Pacific cod (Gadus macrocephalus) (Stabeno et al., 2007, 2010, 2012b; Wang and Overland, 2009; Hunt et al., 2011). This was then followed by a series of cold years from 2007 to 2011 that were characterized by high ice extent, increases in large copepods and euphausiids, and improved recruitment for pollock and cod (Stabeno et al., 2012a,b). The pattern of summer sea ice melt-back in the high Arctic is already shifting to earlier in the season compared to the trend observed in the 1970s (Stabeno and Overland, 2001). The two most extreme summer minimum sea ice cover years were observed in 2007 and 2008 (Wang and Overland, 2009). The details relating to the speed and extent to which the changing conditions in the Arctic will impact the sub-Arctic dynamics of the Bering Sea are largely unknown, but models predictions and time series of observed temperature from the Bering Sea middle shelf suggest general warming south of 60°N with the uncommon possibility of extreme cold years with extensive sea ice over the southern shelf (Stabeno et al., 2012a,b). It is also expected that the Bering Sea shelf north of 60°N will continue to have extensive ice during March and April, but a reduction of ice during May (Stabeno et al., 2012a). These reductions in ice would likely strongly impact apex predators and the economies they support (Coyle et al., 2008, 2011; Stabeno et al., 2010; Mueter et al., 2011).

Predicting how climate change will eventually affect the eastern Bering Sea ecosystem requires a detailed understanding of the physical processes and biological responses associated with sea ice presence throughout the winter and spring. Early spring phytoplankton blooms observed under the ice may be the critical factor in predicting ecosystem dynamics in the late spring and summer (Hunt and Stabeno, 2002). It is during the ice covered periods that critical events between the shelf and adjacent waters are likely to occur, and it is during this period, because of the very limited number of ice-strengthened ships, that there is a void in observation of upper and lower trophic level dynamics. The use of acoustic technology on moorings is playing a vital role in the investigation of biophysical and predator–prey interactions during this time period, as acoustic sensors operate year round to record environmental signals (physical and biological) when the area is typically inaccessible to traditional ship-based sampling methodologies (Miksis-Olds et al., 2010; Stafford et al., 2010).

A suite of active and passive acoustic sensors were deployed on a National Oceanic and Atmospheric Administration (NOAA) oceanographic mooring (MS) on the middle shelf in the central Bering Sea and provide a time series of physical and biological measurements relating to the seasonal patterns of ice advance and spring retreat prior to and following a rapid, 2-week winter retreat in March 2009. The temporary winter retreat occurred within an overall heavy ice year compared to the 30-year averages with near record maximum sea ice extent on the southeastern shelf (Stabeno et al., 2012b). The objectives of this study were to: (1) describe the ecosystem response to the temporary winter retreat, (2) compare patterns observed during the open water period in March to patterns observed before and after the seasonal ice advance and spring retreat, and (3) determine whether the patterns observed during the temporary winter retreat resemble typical patterns associated with the spring ice retreat in cold, high ice extent years. This work also illustrates the value of incorporating acoustic instrumentation into ocean observing platforms for detecting, measuring, and tracking ecosystem response to changing environmental conditions in remote areas (e.g. Stafford et al., 2010).

2. Methods
2.1. Moorings

Two subsurface moorings (acoustic and oceanographic) were deployed on the 70-m isobath of the eastern Bering Sea shelf south of St. Matthew Island starting in 2005 (Stabeno et al., 2010). The mooring location corresponds to Mooring Site M5 of the NOAA Ecosystems and Fisheries-Oceanography Coordinated Investigations (EcoFOCI) Program (Stabeno et al., 2010) (Fig. 1). The acoustic (59°54.285′N, 171°42.285′W) and oceanographic (59°54.585′N, 171°42.649′W) moorings were located less than one kilometer apart. Acoustic sensors were deployed on a separate, short mooring to minimize the recording of transient sounds or interference produced by the long sequence of chain and sensors in the oceanographic mooring. Data obtained during a 2-week, temporary ice retreat in the middle of the winter season were recorded on instruments deployed on the moorings from September 25, 2008 to May 29, 2009.

The moorings were constructed of heavy chain to help protect them from loss due to sea ice and heavy fishing pressure in the region. Data collected by instruments on the moorings included temperature (miniature temperature recorders, SBE-37 and SBE-39), salinity (SBE-37), nitrate (Satlantic MBARI-ISUS V1), and chlorophyll fluorescence (WET Labs DLSB ECO Fluorometer). Temperature sensors were located at 21, 25, 33, 45, 50, 60, and 67 m. Salinity sensors made measurements at 19, 30, and 55 m, and fluorescence was measured at 20 m. During the winter, sensors shallower than 19 m run significant risk of being caught by ice. The factory calibration was used to convert chlorophyll fluorescence to chlorophyll. We recognize that these are only estimates of chlorophyll, especially since the only chlorophyll samples taken at the site were on deployment and recovery. Data were collected at least hourly, and all instruments were calibrated prior to deployment. The data were processed according to manufacturers’ specifications. A low pass filter (35-h Lanczos squared) was applied to each series and the series were averaged over 6 h intervals.

Sensors on the acoustic mooring consisted of an upward-looking 300 kHz RDI ADCP at 56 m, a three-frequency (125 kHz, 200 kHz, and 460 kHz) scientific echosounder system of Acoustic Water Column Profilers (AWCPs: ASL Environmental Sciences, Inc, Sidney, BC) at 63 m, and a Passive Aquatic Listener (PAL) recorder at 65 m. The AWCP system was mounted in an upward-looking direction 15° off vertical. The vertical offset eliminated interference from flotation and instruments in the mooring line directly above the active acoustic system. AWCPs monitor the presence and location of acoustic scatterers such as zooplankton and fish within the water column (Brierley et al., 2006; Kunze et al., 2006). The transducers of the three different frequencies were positioned in the mooring cage so that the beam patterns were aligned to sample the same parcel of water nearly simultaneously. All three echosounders sampled the water column for 5 min each half hour. During each 5 min sampling period, acoustic backscatter measurements were recorded every 2 s with 25 cm range bins from approximately 0.75 m above the transducer face to the water surface.

The PAL is an adaptive subsampling instrument that recorded at 2 or 5 min intervals depending on the sound sources and level of acoustic activity detected in the area. Acoustic activity in this work refers to the occurrence of acoustic events (e.g. animal vocalizations, passing ships, rain, etc.) attributed to identifiable sources, as opposed to the combination of distant sounds that creates the background sound level. The default sampling strategy was to record a 4.5 s time series, or soundbite, at 100 kHz every 5 min. This
corresponded to a 1.5% duty cycle. Eight spectra were computed from 1024 point samples of the 4.5 s time series and used to identify acoustic events in the time series. When real-time processing algorithms detected a transient sound or signal of interest in the soundbite, the interval between samples was decreased to 2 min, resulting in a duty cycle of 4% during periods of high acoustic activity. The sampling period of 4.5 s remained the same. A transient sound is defined in this context as a sound lasting less than the length of a single soundbite (4.5 s). When operating in default (or low duty cycle mode), the average spectrum calculated from each soundbite was saved, and the raw time series was discarded. Data saved during the high duty cycle mode included the raw time series and eight individual power spectra. The soundbites were used in the post-processing analysis to verify the identity of the sound source triggering the transition from low to high duty cycle sampling. A daily limit of 20 soundbites restricted the number of soundbites saved each day to ensure adequate data storage over each deployment, but eight individual spectra continued to be saved every 2 or 5 min, depending on sampling mode, throughout the duration of the deployment, which provided a quasi-continuous record of the background acoustic environment with a temporal resolution of 2–5 min. The low-noise wideband hydrophone of the PAL (0–50 kHz; instrument noise less than sea state zero) was calibrated prior to deployment using the comparison method with a calibrated hydrophone to produce absolute sound levels (Urick, 1983). Details related to the PAL sub-sampling strategy, detection thresholds, and probability of detection for marine mammals in the Bering Sea is found in Miksis-Olds et al. (2010).

2.2. Zooplankton sampling

Zooplankton net tows were conducted at and around the moorings to identify dominant species, species composition, and numerical density during mooring deployments and recoveries, as well as on separate research cruises in the area. Samples obtained closest in time to the winter retreat and closest in proximity to the mooring location were four zooplankton samples collected from April 8–9, 2009. These samples were collected between 10 and 75 miles (16 and 120 km) from the mooring location. Small zooplankters were sampled with a 25-cm diameter CalVET system (CalCOFI Vertical Egg Tow; Smith et al., 1985) having 0.15 mm mesh nets. Each net was equipped with General Oceanics flowmeters in the mouth of the net to monitor the volume filtered. The flowmeters were attached to the net frame with an elastic cord to keep the flowmeter inside the nets during descent. The nets were fished vertically during the day from 100 m depth to the surface or from the bottom to the surface at depths less than 100 m. It was not possible to conduct oblique tows during this period due to the presence of ice and the operating characteristics of the research vessel.

Each zooplankton sample was poured into a sorting tray and large organisms, primarily shrimp and jellyfish, were removed and enumerated. The sample then was split sequentially using a Folsom splitter until the smallest subsample contained about 100 specimens of the most abundant taxa. The most abundant taxa were identified, staged, enumerated and weighed. Each larger subsample was examined to identify, enumerate and weigh the larger, less abundant taxa. Blotted, preserved wet weights of all specimens of each taxa and stage initially were taken on each sample, and the coefficient of variation in average wet weight was computed. If, as subsequent samples were analyzed, the coefficient of variation for any given taxa and stage changed by less than 5%, wet weights were no longer measured for that taxon for that cruise, and the wet weight biomass was estimated by multiplying the specimen count by the mean wet weight. In practice, only calanoid copepods had consistent wet weights after weighing each
taxon and stage in about 10–15 samples. Therefore, wet weights on euphausiids, shrimp and other larger taxa were measured and recorded individually for each sample. Wet weight measurements were done on a Cahn Electrobalance or Mettler top loading balance, depending on the size of the animal. All animals in the samples were identified to the lowest taxonomic category possible. Copepodid stages were identified and recorded.

Additional zooplankton samples were obtained during the mooring maintenance cruises at the mooring site. Mesozooplankton samples were obtained at the mooring location on 27 August–2 September 2008 and 22 June–24 July 2009. Samples were collected with double-oblique tows of bongo frames (60-cm frame with 0.333 mm mesh and 20-cm frame with 0.150 mm mesh). Tows extended from the surface to within 5 m of the bottom. A Sea-Bird SBE 19 plus was attached above the bottom bongo frame and telemetered net depth in real time to the operator. Each net mouth contained a calibrated General Oceanics mechanical flow meter. The samples were preserved in a sodium borate-buffered 5% formalin-seawater solution and then sent to the Polish Plankton Sorting and Identification Center (Szczecin, Poland) for processing. Organisms were identified to the lowest possible taxonomic level and then enumerated. All enumerated organisms were returned to the Alaska Fisheries Science Center (AFSC) in Seattle, Washington, for quality control. The mean and variance of the number of organisms per cubic meter (concentration) were calculated from fourth root-transformed data. The transform was used to stabilize the variance.

2.3. Sea ice

Several ice products are used in this paper. The source of ice extent and concentration was the Advanced Microwave Scanning Radiometer EOS (AMSR-E), which has data available from 2002 to 2010. The AMSR-E is flown aboard NASA’s Modis Aqua satellite. AMSR data consist of daily ice concentrations at 12.5 km resolution, which are available from the National Snow and Ice Data Center (NSIDC) website (http://pafc.arh.noaa.gov/ice.php). Daily ice cover (or percent cover in this specific region) was calculated in a box, 20 km on a side, centered on the location of M5. Since the AMSR resolution is 12.5 km, there were only four points within the box.

We also show “true-color” images from the Modis Aqua satellite (Fig. 2). True-color images are composites of data from three wavelengths measured by the satellite: a red band centered at 645 nm, a green band centered at 555 nm, and a blue band centered at 469 nm. To create the images, we obtained level 0 files from NASA’s Ocean Color website and processed them with the SeaDAS suite of programs, provided and maintained by NASA. Data on ice thickness were obtained from the images produced by the NOAA ice desk at the National Weather Service in Anchorage, Alaska. The images are posted on http://pafc.arh.noaa.gov/ice.php.

2.4. Analytical methods

Analysis of the passive acoustic dataset recorded by the PAL was divided based on the data type: soundbites and spectra. Soundbites were processed to detect and classify transient signals. Each soundbite was reviewed by a human classifier and verified by a second independent human classifier blind to the results of the first reviewer. Sound sources detected in the soundbites were identified from spectrograms (1024 point FFT, Hamming window, 87.5% overlap) made from the original 100 kHz recordings down-sampled to 48 kHz using Adobe Audition 3.0 (Adobe Systems Incorporated). These settings provided a frequency resolution of 47 Hz and a time resolution of 2.7 ms (Miksis-Olds and Parks, 2011). Biological signals were classified aurally and visually from the spectrograms by species (bowhead whale (Balaena mysticetus), humpback whale (Megaptera novaeangliae), gray whale (Eschrichtius robustus), killer whale (Orcinus Orca), beluga whale (Delphinapterus leucas), walrus (Odobenus rosmarus), ribbon seal (Histriophoca fasciata), and bearded seal (Erignathus barbatus)).

Analysis of PAL spectra included examination of the hourly rate of transient signals detected over time, as well as the spectral content (shape) and levels. Sea ice produces sound underwater via several different physical mechanisms including freezing, floe banging and melting. These sounds are distinctive, often invariant for tens of minutes to hours, allowing surface ice conditions to be identified from the time series of PAL spectral data. Temporal clusters of distinctive sound spectra lasting tens of minutes to hours were manually identified and classified. This process identified five general sea surface conditions (open water, freeze up, retreat, solid ice, seasonal melting). These time periods are identified in Figs. 3–6.

Variation of sea ice conditions from the passive acoustic data was inferred from the satellite ice thickness and mean ice cover calculations, seasonality, and recorded soundbites of physical processes.

Sound levels were computed from the time series of spectra. Each of the 8 PAL spectra were computed from 1024 point samples of the 4.5 s time series. This resulted in a 513 point power spectral density with each of the bins covering 97 Hz of the 50 kHz usable bandwidth. The spectra were then reduced from 513 points to 64 points by averaging spectra levels over two bins below 3 kHz and over ten bins from 3 to 50 kHz. The resulting power spectral density, relative to 1 μPa2/Hz, represents energy from the complete 50 kHz bandwidth with variable frequency resolution. To compute the sound level from these spectra, the values were converted to linear power spectral density and multiplied by the frequency resolution of the bins and then summed. The unit of the full bandwidth average is a sound pressure level, re 1 μPa.

Initial processing of power spectral density from the PAL spectra were conducted for each of three frequencies (low – 800 Hz, mid – 2 kHz, and high – 30 kHz) with the assumption that the sound levels relating to these frequencies were associated with different and independent sources (e.g. low frequency whale vocalizations, mid-frequency pinniped vocalizations, or high frequency wind components). Although the power spectral density levels differed between the frequency categories with high levels occurring at low frequencies (Table 1), regression tests of collinearity showed a strong level of dependence between the three frequencies. Therefore, subsequent analysis of sound level over the deployment used full bandwidth averages (50 kHz).

To assess patterns and variability of physical and biological parameters in different regions of the water column, the water column was divided into horizontal layers based on depth: surface (2–4 m), upper water column (15–17 m), and bottom water (45–47 m). The AWCP data were processed in 2 m vertical depth bins within each of the water column regions. Mean volume backscatter coefficient (mean S, in units m2/m3) was calculated from integrations in 24 h bins over each 2 m depth layer and from identified region subsets within individual aggregations using EchoView software (Myriax, Tasmania). The visually identified aggregations were then classified as to the likely source of the scattering based on differences in scattering amplitude between the three frequencies. Analyses using this dB-difference approach (Watkins and Brierley, 2002; Reiss et al., 2008; De Robertis et al., 2010) are typically groundtruthed with information from net tows or video observations. However, given the paucity of direct sampling of the water column in this study, a different approach was used. If scattering assemblages were monospecific, then the dB-difference
for a single scatterer type and an aggregation of scatterers of this type would be identical, although the volume backscattering at each frequency would be different.

Theoretical scattering curves for four different types of individual scatterers were generated and dB-differences at the three acoustic frequencies used in this study were calculated. Scattering amplitudes (and the subsequent dB differences at 125, 200, and 460 kHz) were generated using a Stochastic Distorted Wave Born Approximation model (Demer and Conti, 2003) for the following scatterers: (1) small scatterers such as copepods (lengths of 1–5 mm), (2) medium scatterers (lengths of 5–15 mm) which includes juvenile krill, chaetognaths, and amphipods, (3) large scatterers such as adult euphausiids (lengths of 15–30 mm), (4) resonant scatterers, and (5) unknown. The acoustic system was not able to detect the weak scattering strengths of scatterers less than approximately 5 mm in length unless they were present in extremely dense aggregations. Neritic copepod species typically found over the middle shelf (Pseudocalanus spp., Acartia longigrevis, Oithona spp. and Calanus) are less than 5 mm (Gardner and Szabo, 1982; Coyle and Pinchuk, 2002) and comprised the small scatterer category. The resonant scatterer type represents an organism with a gas-inclusion such as a swim-bladdered fish or siphonophore which has a strong resonant peak in the scattering spectra (Stanton, 1998). Two theoretical resonant scattering spectra were generated: weak (<3 dB increase in $S_v$ at 200 kHz) and strong (>20 dB increase in $S_v$ at 200 kHz). Aggregations were classified as belonging to one of the five categories (small, medium, or large scatterer; resonant; or unknown) by determining the shortest

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**Figure 2.** Satellite image photo series of ice cover and corresponding 24-h echogram (200 kHz) over mooring M5 in winter 2009. The mooring location is denoted by the black point with a red circle (included only to highlight visibility of the mooring location). The solid and dashed lines on echograms denote sunrise and sunset, respectively.

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**Figure 3.** Time series of ice presence over the M5 mooring during the 2008–2009 winter season. A temporary ice retreat was observed in March 2009 that persisted for approximately 2 weeks. Acoustic presence of species does not correspond to a numerical value on the y axis. The species-specific symbols reflect daily acoustic presence and are separated spatially for easy visualization. The horizontal bar running across the top indicates overall ice activity above the mooring based on the passive PAL spectral data. The period marked "Complex" included rapid transitions between distinctive ambient sound backgrounds, suggesting that a complex variety of ice activity was present. During other periods persistent (invariant) spectra lasted for hours to days.
Fig. 4. Time series of temperature (A), salinity and estimated chlorophyll concentration at 20 m (B), and 460 kHz volume backscatter (C) from December 2008–May 2009. There is a 0.5 °C offset between the temperature time series at each depth in panel (A). The true values from which all other depths are offset are the temperatures from 21 m depth. Temperature, salinity, estimated chlorophyll, and volume backscatter values represent daily averages. The horizontal bar running across the top of the panel indicates general sea ice surface conditions.

Fig. 5. Time series of rate (number/hour) of transient signal detections by the PAL. Open water and the five periods of general ice conditions are indicated with the color bar running along the top of the figure. Ice screeching was only detected during the freeze-up period.
geometric distance between the three dB differences calculated for the aggregation and that of the theoretical scatterers. If the closest geometric distance was more than 12 dB (an arbitrarily chosen value), then the aggregation was classified as unknown.

Periodicity of acoustic backscatter patterns was assessed with an autocorrelation technique. Mean volume backscatter values were calculated for 2 min periods (corresponding to the bi-hourly sampling duration) over 4 m depth increments offset from the surface. This resulted in 15 depth layers and 48 samples per day. The data were linearized and grouped into periods of 14 days for analysis. Each 14 day period was zero-meaned and normalized. Zero-meaning shifts the mean from an arbitrary positive value to zero; values that were all positive now oscillate around zero. Normalizing prevents bias due to increased volume backscatter not associated with periodicity. The autocorrelation value with a 24 h lag was computed for each 14 day period. This value represents the relatedness of the mean volume backscatter to the successive 24 h period.

![Graph](image.png)

**Fig. 6.** (A) Time series of sound levels at 800 Hz (blue), 2000 Hz (green) and 30,000 Hz (red) during the winter ice season at mooring location M5. Open water and five periods of general ice conditions are indicated with color bars running along the top of the figure. (B) Within each time period, distinctive ambient sound spectra (shape and level) were temporally invariant for tens of minutes to hours. Examples of these spectra are shown for physical process [open water – solid; melting ice – dashed; solid ice – dotted; storm – dash/dot] with the color coordinated to the periods identified in (A). These are mean spectra averaged over time periods when the spectra were invariant (tens of minutes to hours).

**Table 1**
Comparison of average daily spectrum levels for the seasonal (ice advance, winter retreat, and spring retreat periods) and short-term (before, during and after the winter retreat) analyses. All values are in dB re 1 μPa²/Hz. Values in parentheses reflect the standard deviation for each associated average.

<table>
<thead>
<tr>
<th>Period (# samples)</th>
<th>Dates</th>
<th>Low frequency sound level</th>
<th>Mid-frequency sound level</th>
<th>High frequency sound level</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ice advance (10)</td>
<td>18–28 December 2008</td>
<td>75.6 (5.6)</td>
<td>67.6 (6.7)</td>
<td>41.2 (2.6)</td>
</tr>
<tr>
<td>Winter retreat (10)</td>
<td>4–14 Mar 2009</td>
<td>72.1 (1.9)</td>
<td>61.5 (5.7)</td>
<td>44.3 (3.6)</td>
</tr>
<tr>
<td>Spring retreat (10)</td>
<td>18–28 May 2009</td>
<td>69.5 (5.8)</td>
<td>62.6 (6.1)</td>
<td>47.2 (2.0)</td>
</tr>
<tr>
<td>Before (10)</td>
<td>17–27 February 2009</td>
<td>67.4 (2.2)</td>
<td>56.5 (5.5)</td>
<td>34.4 (4.6)</td>
</tr>
<tr>
<td>During (10)</td>
<td>4–14 March 2009</td>
<td>72.1 (1.9)</td>
<td>61.5 (5.7)</td>
<td>44.3 (3.6)</td>
</tr>
<tr>
<td>After (10)</td>
<td>19–29 March 2009</td>
<td>67.3 (3.4)</td>
<td>55.3 (3.9)</td>
<td>33.2 (2.0)</td>
</tr>
</tbody>
</table>
Changes in ecosystem parameters in response to the temporary ice retreat were statistically compared over two different time scales. First, a short-term analysis compared parameter observations from 10 day periods immediately before (17–27 February), during (4–14 March), and immediately after (19–29 March) the mid-winter ice retreat. The 30 days of measurements used in the short-term analyses were not consecutive because 4 days of transition between each analysis period were omitted to reduce confounding data related to rapidly changing surface conditions. The short-term analyses were conducted to quantify the immediate ecosystem changes related to the rapid ice retreat. The specific hypothesis tested was that the mean of the daily averages of each measurement parameter over a 10 day period was equal before, during, and after the retreat. The longer term, or seasonal, comparison of ecosystem parameters compared observations from 10 day periods prior to the ice advance (18–28 December 2008), during the winter retreat (4–14 March 2009), and after the spring retreat (18–28 May 2009). These analyses were conducted to determine how similar or different the conditions observed during the winter retreat were from conditions associated with the ice advance and spring retreat. The specific hypothesis tested for each parameter in the seasonal analyses was that the mean of daily averages over 10 days was equal prior to the ice advance, during the retreat, and after the spring retreat.

For parameters with datasets meeting the assumption of normality as tested by the Shapiro–Wilkinson test, an analysis of variance (ANOVA) was performed to compare means across the time periods of analysis. Datasets not meeting the assumption of normality indicated in the Shapiro–Wilkinson test were tested using the Kruskal–Wallis test, a non-parametric generalization of the ANOVA test for non-uniformly distributed data (Glass et al., 1972; Lix et al., 1996), to compare means across time periods. An ANOVA was used to compare the average number of acoustic transients detected in each of the three analysis periods for the short-term and seasonal analysis. Average sound level comparisons were conducted using the Kruskal–Wallis test, as ambient sound data is logistically rather than normally distributed (Aminov, 2012). Primary and secondary biomass proxies have been shown to be tightly coupled during spring ice retreats (Stafford et al., 2010), but it could not be assumed that the same ecological relationships would be associated with the rapid, mid-season retreat; therefore, a linear regression analysis was performed to test for significant collinearity between the chlorophyll and acoustic backscatter ($S_b$) estimates. The results of a linear regression analysis from 40 days centered on the middle of the winter retreat showed no significant correlation between these variables ($F = 2.67, p = 0.11, r^2 = 0.062, df = 41$), so each parameter was assumed to be independent and examined separately. Separate single factor Kruskal–Wallis and ANOVA tests were conducted with the acoustic backscatter ($S_b$) and chlorophyll measurements, respectively. The Tukey–Kramer method was used to conduct post hoc multiple comparisons in all significant ANOVA analyses, and Wilcoxon rank sum tests were used for the multiple comparisons of significant Kruskal–Wallis tests.

### 3. Results

#### 3.1. Physical processes

Ice cover over the mooring site (M5) was first detected on 2 January, 2009. The extent of ice cover and ice thickness gradually increased until 20 January and reached a plateau near 100% ice cover in the vicinity of the mooring with ~50 cm thickness (Fig. 3). A short period of very low ice cover was observed from 2 to 14 March (Figs. 2 and 3). After 15 March, sea ice returned and ice cover neared 100%, with a ~1 m thickness. This persisted until 30 April when the spring ice retreat began. Ice over the mooring was not observed after 20 May.

The southward advection of sea ice that began in early January cooled the water column to ~1.74 °C by 10 January, 2009. The rapidly moving sea-ice was effective in stirring the water column resulting in vertical temperatures being relatively uniform until early May when the uppermost instrument (21 m depth) detected increasing temperatures in the surface mixed layer (Fig. 4A). During the winter retreat in March, there was a slight temperature perturbation throughout the water column. The temperature warmed approximately 0.1 °C during the retreat and cooled again with the return of the ice. These changes were seen uniformly throughout the water column because the relatively strong winds kept the water column well mixed. There was a gradual increase in salinity from the end of January to mid-April (Fig. 4B), as a result of either the nearby polynya to the southwest of St. Matthew Island or possibly advection of more saline water from west (Stabeno et al., 2012a). A decrease in surface salinity was associated with the spring ice retreat and temperature increase in May. The freshening of the water column was likely a result of melting sea ice. Overall, the rapid winter ice retreat in March did not appear to be associated with large deviations in temperature, salinity, or chlorophyll, nor did they have lasting effects on the physical properties of the water column at any depth.

#### 3.1.1. Ambient sound and acoustic activity

The ambient background sound levels and overall acoustic activity of the area were highly dependent on ice conditions (Figs. 5 and 6). One measure of acoustic activity was the number of hourly transient signal detections (Fig. 5). Most of the transient detections at M5 were attributed to ice movement and animal vocalizations, as geophysical sounds (e.g. wind, rain, melting ice) generally have time scales longer than 4.5 s. Two types of ice-generated sounds were associated with movement: (1) very loud harmonic screeching/squeaking sounds of ice floes grazing together (Fig. 6B), and (2) broadband, rapid rise time signals of ice floe cracking and bumping. During periods of open water very few transients were recorded. During periods of ice presence, high numbers of transients were recorded; thus, periods with sea ice are easily detected in the ambient sound record based on transient sound triggers alone (Fig. 5).

There was an overall difference between conditions immediately before, during, and after the winter ice retreat (short-term: $F = 14.1, p < 0.001, df = 29$; seasonal: $F = 8.4, p = 0.001, df = 29$). Post-hoc multiple comparisons showed significant differences between the retreat and all other analysis periods in both analyses. The seasonal comparison showed a high level of hourly transient detections compared to the corresponding low level of detections during the ice advance and spring retreat open water periods (Table 2). Ice advance and spring retreat values were not significantly different. Post-hoc multiple comparisons of the short-term

<table>
<thead>
<tr>
<th>Period (# samples)</th>
<th>Dates</th>
<th>Hourly transient detections</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ice advance (10)</td>
<td>18–28 December 2008</td>
<td>0.2 (0.2)</td>
</tr>
<tr>
<td>Winter retreat (10)</td>
<td>4–14 March 2009</td>
<td>2.7 (2.1)</td>
</tr>
<tr>
<td>Spring retreat (10)</td>
<td>18–28 May 2009</td>
<td>0.8 (1.8)</td>
</tr>
<tr>
<td>Before (10)</td>
<td>17–27 February 2009</td>
<td>5.3 (3.1)</td>
</tr>
<tr>
<td>During (10)</td>
<td>4–14 March 2009</td>
<td>2.7 (2.1)</td>
</tr>
<tr>
<td>After (10)</td>
<td>19–29 March 2009</td>
<td>9.5 (3.4)</td>
</tr>
</tbody>
</table>
transient analysis showed the opposite relationship of transient detection patterns compared to the seasonal analysis. There were fewer transients detected during the retreat compared to the two periods of ice cover immediately before and following the retreat (Table 2). The decrease in the number of transient detections during the retreat corresponded to a decrease in the detection of marine mammal species over the same time period (see Section 3.2).

The seasonal comparison of sound levels from the open water periods prior to ice advance, during the winter retreat, and after the spring retreat showed no significant difference (means: prior to advance = 109 dB re 1 µPa; winter retreat = 112 dB re 1 µPa; spring retreat = 109 dB re 1 µPa) ($\chi^2 = 4.98$, $p = 0.08$, $df = 29$). This indicates that the detectability of transient signals during the retreat was not inversely related to sound level during the open water periods because the sound levels were not significantly different across the three analysis periods. The short-term comparison of sound levels in open water during the winter retreat and under ice before and after the winter retreat did show a significant difference in mean daily sound levels (before = 108 dB re 1 µPa; during = 113 dB re 1 µPa; after = 114 dB re 1 µPa) ($\chi^2 = 12.42$, $p = 0.002$, $df = 29$). Post-hoc multiple comparisons identified that sound levels recorded under the ice prior to the retreat were significantly lower than the sound levels during and after the retreat. There was no significant difference in the sound levels during or after the retreat. The increase in sound levels during the winter retreat was observed in association with a decrease in transient detections most likely related to a decrease in detected marine mammal vocalizations, as an inverse relationship between noise level and detectability was not supported by the data in this analysis. The sound levels after the retreat were not significantly different from those during the retreat, yet the number of transient detections increased significantly.

In Figs. 2 and 4–6, the 2009 ice season was partitioned into five periods based on the general surface conditions above the mooring as interpreted from the acoustic record and groundtruthed by satellite imagery. The first ice period is an initial freeze up starting on 5 January and lasting until 24 January. It is marked by the screeching sound of sea flos squeezing together, triggering the transient sound detection algorithm of the PAL. Bowhead whale calls became prevalent and also triggered the transient sound detection algorithm during this period. Following this initial ice coverage over the mooring, ice cover decreased and rapid transitions between distinctive background ambient sound conditions were observed indicating a “complex” sequence of sea ice processes, including some open water spectra. Starting on 25 January, the ice cover became mostly solid, as indicated by very low spectral levels at high frequency (over 20 kHz) lasting for hours to days. The number of transients per hour increased from less than two detections per hour to over 10 detections per hour. The trigger spectra were consistent with bowhead whales and walrus, and trigger spectra due to ice movements were not detected. The period from 25 January to 24 February is acoustically complex. It includes periods of solid ice cover (25 January–4 February), open leads, ice plate cracking (5 February), and the first occurrence of ice melting (12 February). All of these processes were distinctive from open water which produces its own unique sound via wind wave breaking (Medwin and Beaky, 1989).

The acoustic detection of the rapid winter retreat period started on 24 February and lasted until 16 March. This is indicated in the transient record by an overall drop in the number of transients per hour and a complete absence of solid ice spectra (characterized by very low 30 kHz levels – see Fig. 6). Spectra of transient signals consistent with marine mammal vocalizations decreased, whereas transient detections of ice movements associated with flos banging together were detected. A strong storm was detected on 5 March (Fig. 6B) with very high sound levels. The loudest overall sound spectra were recorded during the beginning of the winter retreat period when ice floe interactions were detected most often. Spectra recorded during the winter retreat also indicated periods of open water (Fig. 6B) and melting ice, based on the acoustic spectral shape. There were no detections of the screeching sounds generated by grating ice during the winter retreat period.

The winter retreat period ended abruptly on 16 March when solid ice cover returned. Sound levels were lowest during solid ice cover above the mooring, especially for frequencies above 20 kHz. The transient count increased in conjunction with the ice return over the mooring. Spectral characteristics were consistent with the presence of marine mammal vocalizations. There were no triggers associated with floe screeching in contrast to the initial freeze up in early January. The ice became thick (up to 1 m) and persistent, with small leads opening occasionally, generating a fissing sound at high frequency associated with ice melting. The solid ice period lasted from 16 March to 25 April. The seasonal ice breakup was from 25 April to 16 May, and is marked by a drop in transient counts per hour and by an increase in sound levels. The ambient sound spectra during the spring retreat were predominantly composed of melting ice, with most of the transient sounds identified as ribbon seal calls. Triggers due to flow banging were not recorded during the spring break up. When the ice was completely absent, starting on 17 May, the transient count per hour dropped to near zero, consistent with open water.

3.2. Biological response

Chlorophyll concentration was consistently low until the last week of February, just prior to the winter retreat of ice over the mooring (Fig. 4B). The increase in chlorophyll concentration from near zero to 0.4 µg/l preceded the actual ice disappearance by approximately a week and remained at this level throughout the retreat. When the ice returned to the mooring location in mid-March, the chlorophyll concentration doubled and remained stable until the spring ice break-up, which was then followed by a mid-May bloom. The increases immediately prior to and following the March retreat were gradual and small compared to the increase in chlorophyll concentration associated with the spring bloom in May, which was most likely a water column bloom concentrated in the upper 20 m of the stratified water column. Both short-term and seasonal analyses of estimated chlorophyll concentrations showed significant differences between analysis periods (short-term: $F = 175$, $p < 0.001$, $df = 29$; seasonal: $F = 26.6$, $p = 0.001$, $df = 29$). Post-hoc multiple comparisons between each analysis period within the two ANOVAs showed significant increases in chlorophyll concentrations over time consistent with the pattern in Fig. 4B.

Time series of daily averaged acoustic backscatter over the full water column and in 2 m depth bins was calculated at three frequencies (125 kHz, 200 kHz, 460 kHz) (Fig. 4C). Just prior to the open water period of the March retreat, there was a dramatic increase in the depth averaged volume backscatter, with the greatest increase observed at the deeper depths (Fig. 4C). The short-term analysis of acoustic backscatter strength averaged over the full depth of the water column showed a significant increase in scattering amplitude during the retreat compared with almost identical values prior to and immediately following the retreat (before: $-63.6$ dB, during: $-59.4$ dB, after: $-63.4$ dB; $\chi^2 = 7.99$, $p = 0.02$, $df = 29$). Acoustic classification of the scattering at deeper depths showed the presence of resonant, medium, and large-sized scatterers, listed in decreasing order of observed number of classified aggregations (Table 3). The peak in acoustic backscatter in the deeper layers lagged slightly behind that of the initial chlorophyll increase in late February. Acoustic backscatter decreased during
the initial days of the winter retreat, corresponding to the second increase in chlorophyll concentration at this time. Following the winter retreat, the acoustic backscatter values in the upper water column continued to increase, peaking in early April. Conversely, the lower water column values continued to decrease reaching a minimum in mid-April. The spring phytoplankton bloom is coincident with increases in acoustic backscatter at all depths of the water column, although the magnitude of the bloom decreased with depth. The comparison of the 200 kHz acoustic backscatter strength over the season showed that the levels observed during the retreat were similar to those observed prior to the seasonal ice advance, which were greater than those observed following the spring ice retreat (ice advance: $-60.8$ dB, winter retreat: $-59.4$ dB, spring retreat: $-63.3$ dB; $\chi^2 = 10.04, p = 0.006, df = 29$). Post-hoc multiple comparisons showed no difference in the ice advance and winter retreat values, and both of these periods had stronger backscatter measurements than the spring retreat period.

We quantified daily migration patterns for zooplankton taxa (i.e. chaetognaths, Calanus and euphausiids) and fish from December 2008 through May 2009 with an autocorrelation analysis designed to measure periodicity in the acoustic backscatter signals over 14 day periods. Diel vertical migration (DVM) patterns were observed throughout the season with the exception of the 2 week period directly preceding the temporary ice retreat in March 2009 (24 h autocorrelation = 0.00) and following the return of the ice in April 2009 (24 h autocorrelation = 0.00). Stronger DVM patterns were present prior to the ice advance in December at the surface (24 h autocorrelation = 0.35) and mid-water column depths (24 h autocorrelation = 0.22). The strength of the DVM periodicity decreased with the advance of ice over the mooring, but was still evident in the mid-water column prior to March (24 h autocorrelation = 0.14). Two weeks prior to the temporary winter ice retreat, no DVM was observed at any depth in the water column. During the winter retreat period, strong periodicity was observed throughout the water column (24 h autocorrelation = 0.14). Periodicity of zooplankton and/or fish behavior again weakened following the re-establishment of ice over the mooring for the remainder of the winter/spring season.

Potential biological aggregations, defined as concentrated areas of increased backscatter compared to background levels, were identified in the backscatter data during the 2 weeks prior to the ice advance in December, the 2 weeks during the winter retreat in March, and the 2 weeks in May immediately following the spring ice retreat. The majority of aggregations in each period were classified as having scattering consistent with that of a resonant scatterer or medium sized scatterer (5–15 mm) (Table 3). The resonant scatterer category may include scattering from turbulence, microstructure, or other physical mixing processes as these scattering processes have similar scattering spectra (and dB differences) to resonant biologies (Lavery et al., 2003; Warren et al., 2003; Ross et al., 2007). Aggregations classified as small scatterers were least abundant in the acoustic record. Medium and resonant scatterer proportions were almost identical prior to the ice advance in December and during the temporary winter retreat in March. There was an increase in the proportion of medium-sized scatters, and a corresponding decrease in the proportion of resonant scatterers, in the 2 weeks following the spring ice retreat.

Zooplankton net sampling conducted closest in time and space to the seasonal ice advance, winter retreat, and spring retreat generally supported the relative community composition of medium scatterers estimated from the acoustic data over the winter/spring time period. Medium-sized scatterers observed in the acoustic record consisted predominantly of Sagitta elegans, which were found to represent a greater species-specific biomass in the April 2009 net tow samples despite the smaller crustacean species (Pseudocalanus spp., A. longiremis, and Calanus) having greater numerical abundance and combined biomass (Fig. 7). While large crustaceans represented by euphausiids Thysanoessa raschii were found in the samples, net avoidance by euphausiids is a well-known phenomenon, thus making a direct comparison of the net collected euphausiids and acoustic records impossible.

Marine mammal species detected in 2008–2009 followed the general seasonal pattern of species observed in this area over the past decade (Moore et al., 2000, 2002; Miksis-Olds et al., 2010) (Fig. 8). Gray whales, humpbacks, and killer whales were detected in the fall. Ice-dependent and ice-associated marine mammals (bowhead whales, bearded seals, walrus, ribbon seals, and beluga) were detected throughout the winter and spring. The pattern of marine mammal presence during the month of the winter ice retreat differed from the pattern observed in the winter of 2008 when there was consistent ice cover in the region throughout the winter and spring (Fig. 8) (Miksis-Olds et al., 2010). The major differences observed in conjunction with the winter retreat were a later peak in bowhead detections, an increase in gray whale detections, a decrease in bearded and ribbon seal detections, and a decrease in beluga detections in March 2009. There was a shift in the solid ice spectra for frequencies of 300 Hz–10 kHz from 26 January compared to 8 April (Fig. 6B). This is most likely attributed to the shift in peak vocal activity of the different marine mammal species detected in the area. Early in the winter season, the low frequency vocalizations of bowhead whales and walrus dominated the soundscapes where higher frequency vocalizations of bearded and ribbon seals occurred during the solid ice period following the winter retreat.

Examination of the daily detection patterns in March 2009 revealed that bearded and ribbon seal detections were tightly coupled to the presence of sea ice (Fig. 3). The bearded seal detections disappeared with the temporary winter retreat of ice and immediately returned following the return of ice to the area. Ribbon seal vocal detections also disappeared with the winter retreat of ice in early March, but unlike the immediate return of the bearded seal vocalizations, ribbon seal vocalizations were not consistently detected again in the area until the ice thickness reached 100 cm. The presence of gray whale detections was closely associated with the absence of ice. Gray whale vocalizations were not detected at all in February when ambient sound levels were low; gray whale vocalizations were detected on 5 days during the open water period of the winter retreat when sound levels were comparatively higher. Bowhead whales and walrus were detected consistently before, during, and after the winter retreat, although consistent walrus detections ended around 31 March. Beluga vocalizations were only detected on March 16, 2009, the day after ice moved back into the area (Fig. 8).
4. Discussion

Integration of active and passive acoustic sensors into an oceanographic mooring created an observation system that was able to document a previously unobserved coupling of physical and biological processes associated with a rapid, short-term change in ice cover during a mid-winter ice retreat. Seasonal and short-term comparisons of the conditions observed during the temporary retreat provide information for interpreting retreat conditions in comparison to ice advance and spring retreat conditions, as well as to under-ice conditions immediately prior to and following the winter retreat. Acoustically, the winter retreat period differed from the ice covered periods before and after the retreat with less transient detections and louder overall sound levels compared to levels before the retreat. The sound levels observed during the retreat were similar to that of open water periods prior to the seasonal ice advance and following the spring retreat. The acoustic soundscape during the winter retreat was a combination of open water and melting conditions. The elevated sound levels at high frequencies (>20 kHz) were consistent with melting ice, and the elevated sound levels at lower frequencies coupled with a marked reduction in the number of transient signal detections was consistent with open water characteristics and an attendant change in the composition and number of marine mammals species in the vicinity.

Physically, the water column remained stable with no abrupt changes in temperature during the winter retreat compared to immediately before or after. Salinity and chlorophyll increased
slowly over the course of the season, but there were no sudden increases or spikes associated with the winter retreat period. Overall, the hydrographic parameters observed at the mooring location during the temporary retreat were very similar to the conditions immediately preceding the spring ice retreat in early May. The water temperature was cold (\(-1.5\) °C) and there was a short-term salinity decrease most likely associated with melting ice. Synoptic records of hydrography and acoustics confirmed the presence of melting ice during the winter retreat, which was consistent with the salinity and spectral characteristics observed during the melting period of the spring ice retreat.

Compared to the degree of change in physical parameters typically associated with retreating ice in May and resulting phytoplankton bloom (i.e. temperatures increasing to above freezing, decreasing salinity associated with the ice melt, and water column stratification), the conditions during the temporary winter retreat period were not conducive to a phytoplankton bloom. There was a small increase in chlorophyll (0.2 μg/l) 1 week prior to the winter retreat of ice over the mooring, but the magnitude of the increase was within the range of variability observed over the 6 weeks prior to the winter retreat. The small increase could have indicated some level of ice-melt, as there is chlorophyll associated with the ice that enters the water column as it melts. Chlorophyll associated with the ice often sinks to the bottom, but can remain within the water column (Stabeno et al., 2010). Since the water column remained well mixed, the slight chlorophyll increase was most likely associated with phytoplankton that was distributed throughout the water column. The mixing and low light levels typical of this time of year make it unlikely that the system could support a water column bloom (that is the phytoplankton would spend too much time out of the euphotic zone). The spring phytoplankton bloom was a late bloom that occurred in May–June as the water column stratified. Ice cover during the month of April prevented the bloom from happening any earlier in the season.

The level of acoustic backscatter in the upper portion of the water column prior to and during the winter retreat was relatively consistent. The uniform levels of acoustic backscatter in the upper water column may have been due to a combination of under-ice algae and maintenance of position by zooplankton in the upper water column. A dense community of microalgae forms on the underside of the ice from late winter through breakup in the Bering Sea, and may be substantial enough to support a minimal zooplankton community (Saito and Taniguchi, 1978; Schandelmeier and Alexander, 1981). The increase in acoustic backscatter intensity was by over an order of magnitude over the full water column and in the lower portion of the water column at the beginning of the winter retreat period was unexpected and inconsistent with patterns reported for the spring ice retreat (i.e. an absence of thermal or salinity induced stratification, initiation of a spring phytoplankton bloom with elevated chlorophyll, and corresponding increases in secondary production) (Niebauer et al., 1999; Stabeno et al., 2012a).

Backscatter throughout the water column was estimated to consist of medium-sized scatterers representative of chaetognaths and resonant scatterers indicative of fish in approximately equal amounts. Community structure observed during the winter retreat was almost identical to the community structure observed in December 2008 prior to the ice advance, and very different from the community structure following the spring retreat which was dominated by medium-sized scatterers. Results of net tows conducted a month after the winter retreat showed that chaetognaths (Sagitta elegans) were indeed a large proportion of the biomass in the 5–15 mm size category even though small copepods (<5 mm; Pseudocalanus spp., etc.) were numerically dominant. The lack of corresponding estimates from our acoustic data for the smaller crustaceans was most likely due to the fact that the weak scattering levels of the smaller animals using our three frequencies was not sufficient enough to be detected acoustically unless they were encountered in extremely high numerical densities. Acoustic instruments utilizing higher frequencies (e.g. Holliday et al., 2009) would have been necessary to better resolve the biomass of these smaller crustaceans.

Diel vertical migration (DVM) behavior was observed throughout the acoustic time series both under ice and in open water. Adult Calanus in the Bering Sea and North Pacific are known to perform diel vertical migrations (e.g. Schabetsberger et al., 2000; Lamb and Peterson, 2005), while A. longiremis remains in the upper layer both day and night (Mackas and Galbraith, 2002). The DVM behavior of Pseudocalanus spp. is more complex, since both positive and negative migration and lack of migration in relation to the presence of predators have been observed (Turner and Dagg, 1983; Sameoto, 1984; Ohman, 1990; Bollens and Frost, 1991). Therefore, the increase in DVM detected during the winter retreat provides support for the presence of Calanus, assuming that the early life history stages of T. raschii were not yet present (Smith, 1991). The combination of multi-frequency acoustic analysis and net tow information acquired as close as possible to the mooring location at the time of the winter retreat suggests that the large increase in volume backscatter observed in the lower portion of the water column during the retreat was due to an increase in chaetognath and copepod abundance, as well as potential predatory fish indicated by the presence of resonant scatterers. The backscatter at depth was not considered to be resuspended sediment, as resuspended particles are strong scatterers with different acoustic properties. Additionally, the echosounders were approximately 10 m above the seafloor and oriented towards the surface making detection of any resuspended particles by bottom currents unlikely. The sharp increase could be attributed to: (1) advection of a new water mass into the region, (2) a change in vertical distribution of scatterers from below the deepest depth ensnored by the acoustic to a new shallower depth, or (3) a rapid increase in their abundance during the ice retreat. Increase in deeper water column backscatter may also be indicative of carbon export towards the benthos during the retreat period.

If the observed increase in deep water backscatter during the temporary ice retreat was due to a local increase in small copepod numerical density, and not due to advection or repositioning of zooplankton in the water column, then it is inconsistent with the hypothesis that temperature is the most important variable influencing small copepod production in the Bering Sea and in other oceans (Smith and Vidal, 1986; Hirst et al., 2003). In this study, the increase in backscatter was not accompanied by an increase in temperature prior to or at the beginning of the temporary retreat period. The overall backscatter increase throughout the water column during the winter retreat also indicated that the observed deep layer increase in volume backscatter was not due to a simple repositioning of animals from shallower depths. What caused the increase in deep water backscatter coincident with the temporary ice retreat is unknown and requires further investigation of under-ice dynamics over the winter.

The interpretation of which species are present and performing vertical migrations during the winter retreat period is also complicated by the emerging knowledge that the Calanus captured in the Bering Sea are a mixture of two closely related and difficult to identify species (Calanus glacialis and Calanus marshallae; R. Campbell, personal communication). Our data are, however, consistent with the described life cycle of Bering Sea Calanus spp., which includes a diapause phase during winter followed by one or two periods of reproduction; the first and main period occurs in early spring and takes place well in advance of the second period, in conjunction with the spring bloom of diatoms (Naumenko, 1979). Results of Smith and Vidal (1984) suggest the first spawning is in March which corresponds with our observations of increased backscatter.
and DVM patterns. Baier and Napp (2003) calculated that the individuals they captured in late spring were those whose metamorphosis from the naupliar to copepodid stages was synchronous with the spring bloom.

Following the increase in lower water column acoustic backscatter at the beginning of the temporary retreat period, there was a sharp decline in the backscatter signal across the entire water column in mid-March (Fig. 4C). This was most likely due to advection of new, plankton-poor waters to the vicinity of the mooring. By early April, the backscatter signal in the upper water column increased to levels observed prior to the temporary winter retreat, whereas the levels in the lower water column continued to decrease until the start of the spring ice retreat. An alternative explanation to in situ processes (bottom-up control) or advection is predation (i.e. top-down control by fish, seabirds, and whales). However, the acoustic backscatter data does not support the theory of top-down control by fish because there was not a substantial increase in the proportion of resonant scatterers representative of fish during the winter retreat compared to values prior to the ice advance. Possible predation by marine mammals is not clear. Bowhead whales migrate from the Beaufort and Chukchi Seas to the Bering Sea during the winter breeding season, and there is evidence of opportunistic feeding by the whales during this time (Hazard and Lowry, 1984). Gray whales feed in the productive waters of the Bering Sea and Arctic waters, and gray whale calls have been recorded in the western Beaufort Sea in every month during a study from Oct 2003 through May 2004 (Moore et al., 2006). It is highly likely that the increase in gray whale detections during the winter retreat was associated with an opportunistic feeding window related to the open water conditions and prey increase during the winter retreat.

Passive acoustic recordings in the study showed three distinct changes in vocalization patterns during the 2009 winter retreat compared to the winter of the previous year. First, both years had a peak in bowhead vocal detections in January, but in winter 2009, a second peak in bowhead whale detections was observed in March that coincided with the temporary winter retreat. Second, a strong peak in gray whale detections was observed during the winter retreat of 2009. No gray whale vocalizations were detected during the winter of 2008 when ice covered the region throughout the season. Bowhead and gray whales feed on a wide variety of crustacean zooplankton, including copepods and euphausiids (Lowry, 1993), so it is not unreasonable to attribute the increase in bowhead and gray whale detections to an increase in whale presence and predation pressure on the plankton.

During the winter retreat there was a marked decrease in the detection of bearded and ribbon seal vocalizations in March 2009 compared to the previous year. Underwater vocal displays in aquatic-mating phocid species such as the bearded and ribbon seal are typically associated with mating behaviors during the winter/spring breeding season (Van Parijs, 2003; Van Opzeeland et al., 2008). Without concurrent visual observations or GPS tag locations, it was not possible to know whether the seals left the area in conjunction with the ice or whether vocal activity ceased while the animals remained in the area but engaged in behaviors other than mating displays. The decrease in vocal detections does indicate that local mating behaviors were disrupted by the temporary winter retreat. If the seals did leave the area, it is not known whether they did so passively by drifting on the ice or actively followed the ice edge.

5. Conclusions

The incorporation of active and passive acoustic sensors into ocean moorings created the opportunity to observe a never before witnessed, full-scale ecosystem response to a temporary, midwinter ice retreat in the central Bering Sea. Synoptic measurements of hydrography and acoustics have provided the necessary information to begin to understand how perturbations in ice cover are manifested through different levels of the ecosystem. During the winter retreat there was very little change in the physical properties of the water column often seen in conjunction with the spring ice retreat and ensuing phytoplankton bloom (i.e. temperature, salinity, fluorescence), yet there was a striking change in zooplankton and marine mammal dynamics. These results demonstrate how rapidly upper trophic-level dynamics can change in what appears to be a relatively consistent physical environment. Although there is more than one explanation to account for the non-uniform increase in epipelagic acoustic backscatter, observation of these rapidly changing signals would not have been possible without the integration of acoustic technology into the ocean mooring. Ice is the defining characteristic of the Bering Sea shelf ecosystem, with advance and retreat of sea ice resulting in quick and quantifiable changes in the biological portion of the ecosystem. Acoustic technology provides the mechanism to observe the tight biophysical coupling that would be otherwise undetected under ice during the winter season.

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References
