

## Relationship Between the Distribution of Gray Whales (*Eschrichtius robustus*) and Two Types of Prey in the Northern Bering and Chukchi Seas

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**ABSTRACT.** We examined the distributional relationship between gray whales and their prey, benthic amphipods and euphausiids, using data collected from shipboard surveys in the Pacific Arctic. We conducted four survey cruises (in 2007, 2008, 2012, and 2013) in the northern Bering Sea, Chukchi Sea, and adjacent waters, and collected data on cetacean sightings, including gray whales, benthic amphipods by benthic grabs, and euphausiids using plankton nets. We observed a total of 160 gray whales from 55 groups during the four surveys. Statistical analysis across the study area using a generalized linear model indicated that gray whale distribution was related to benthic amphipods, whereas their relationship with euphausiids was unclear. The Distributed Biological Observatory 3 (DBO3) area off Point Hope, Alaska, had the highest density of gray whales (0.035 individuals/km<sup>2</sup>, hereafter referred to as ind./km<sup>2</sup>) in the fall of 2012 compared with the densities of the other surveys (0.00 – 0.006 ind./km<sup>2</sup>). Higher biomass of euphausiids and higher average wet weight of a single euphausiid were also observed in the fall of 2012, which may have contributed to the high density of gray whales. Aligning with previous direct confirmation by visual whale surveys and prey sampling in the fall of 2003, the present study confirmed that, in the fall of 2012, the DBO3 area was an area where gray whales could feed on both benthic amphipods and euphausiids.

**Keywords:** gray whales; euphausiids; distribution; amphipods

**RÉSUMÉ.** Nous avons examiné la relation de distribution entre les baleines grises et leurs proies, les amphipodes benthiques et les euphausiacés, à l'aide de données prélevées à partir de navires dans la région arctique du Pacifique. Nous avons effectué quatre expéditions de recensement (en 2007, 2008, 2012 et 2013) dans le nord de la mer de Béring, dans la mer des Tchouktches et dans les eaux avoisinantes. Cela nous a permis d'acquérir des données d'observation sur les cétacés, y compris les baleines grises, ainsi que sur les amphipodes benthiques saisis par bennes benthiques et les euphausiacés capturés à l'aide de filets à plancton. Nous avons dénombré un total de 160 baleines grises appartenant à 55 groupes lors de nos quatre expéditions de recensement. L'analyse statistique de la zone d'étude, réalisée à l'aide d'un modèle linéaire généralisé, a révélé que la distribution des baleines grises était liée aux amphipodes benthiques, mais que leur relation avec les euphausiacés restait floue. La zone visée par l'observatoire biologique distribué 3 (Distributed Biological Observatory 3 – DOB3) situé à Point Hope, en Alaska, a enregistré la plus forte densité de baleines grises (0,035 individu/km<sup>2</sup>, ci-après indiqués sous la forme de ind./km<sup>2</sup>) à l'automne 2012, par rapport aux autres recensements (de 0,00 à 0,006 ind./km<sup>2</sup>). Une plus grande biomasse d'euphausiacés ainsi que le poids moyen plus élevé d'un seul euphausiacé ont également été observés durant l'automne 2012, ce qui pourrait avoir contribué à la grande densité de baleines grises. En conformité avec la confirmation préalable directe des dénombrements visuels de baleines et de l'échantillonnage de proies effectués à l'automne 2003, la présente étude confirme qu'à l'automne 2012, la zone d'observation DBO3 constituait un endroit où les baleines grises pouvaient se nourrir à la fois d'amphipodes benthiques et d'euphausiacés.

**Mots-clés :** baleines grises; euphausiacés; distribution; amphipodes

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## INTRODUCTION

The Pacific Arctic region has undergone remarkable alterations in its biological and physical environment. The increased amount of incoming solar radiation absorbed by the oceans, due to reduced sea ice, has caused ocean temperatures to rise across the Arctic (Polyakov et al., 2020). Furthermore, warm water inflows from the Pacific Ocean through the Bering Strait have increased (Woodgate, 2018), contributing to higher sea temperatures in the Beaufort Gyre (Polyakov et al., 2020). These changes in the physical environment have caused significant changes in the biological environment. Chlorophyll *a* concentration and annual phytoplankton net primary production have increased in the Chukchi Sea because of reduced sea ice and increased nutrient supply from the Pacific Ocean (Lewis et al., 2020). Both local blooms and phytoplankton advection from the Pacific Ocean have supported benthic hotspots in the Pacific Arctic region; however, recent environmental changes have been predicted to affect benthic organisms by altering strong pelagic – benthic coupling processes (Grebmeier et al., 2015). In fact, as sea ice decreases and water temperatures increase, research shows northward shifts in high benthic-biomass areas and changes in the dominant macrofaunal composition (Grebmeier et al., 2018). Matsuno et al. (2011) have also suggested that increased inflow of seawater from the Pacific Ocean has increased Pacific mesozooplankton species in the Chukchi Sea. Given that average water transport in the Bering Strait is one of the factors affecting the number of euphausiids arriving off Barrow in the fall (Berline et al., 2008), researchers suggest that an increased inflow of seawater from the Pacific Ocean will increase the number of euphausiids in the Chukchi Sea (e.g. Moore, 2016; Brower et al., 2018). It is important to monitor these remarkable changes to predict future climate change and address ecosystem conservation. Upper trophic-level species are considered indicators of ecosystem change because they reflect ecosystem dynamics through changes in habitat use and body condition (Moore and Kuletz, 2019). Therefore, understanding their habitat use and body condition is essential.

Gray whales (*Eschrichtius robustus*) are a sentinel species in the Pacific Arctic region (Moore, 2008). Gray whales migrate south – north along the western coast of North America, moving south in winter to reproduce, and north in summer to feed (Swartz, 2018). Some gray whales remain to feed in the Chukchi Sea from May to November (Clarke et al., 2023), and in the Chirikov Basin from May to December (Brower et al., 2022). Although their diet is comprised of a wide variety of species, including benthic, planktonic, and nektonic organisms (Nerini, 1984; Feder et al., 1994), they are the only baleen whales that prey on benthos. In the Chukchi Sea, the distribution of gray whales is associated with that of benthic amphipods (Brower et al., 2017). In the Chirikov Basin, one of the main feeding grounds for gray whales in the 1980s, the sighting rate for this species decreased markedly from the 1980s to the

2000s, coincident with a decline in benthic amphipods (Moore et al., 2003). Based on these reports, benthic amphipods seem to be a driving factor in the distribution of gray whales in the Pacific Arctic region.

The relationship between gray whales and euphausiids has also received attention as a response to the expected increase in plankton influx from the Pacific Ocean. Bluhm et al. (2007) found that gray whales in the south-central Chukchi Sea occurred in high relative abundance in an area containing few benthic amphipods but with high densities of other benthic and pelagic fauna, including euphausiids. The area studied by Bluhm et al. (2007) is almost the same as that of the Distributed Biological Observatory 3 (DBO3) (Fig. S1), which is one of the stations in the Distributed Biological Observatory program that measures the biological response to physical changes in the northern Bering Sea and Beaufort Sea in the Pacific Arctic (Moore and Grebmeier, 2018). Moore et al. (2022) analyzed the monthly relationship between gray whale sighting rates from 2009 to 2019 and environmental factors that affect gray whale prey availability, such as currents and wind. They suggested that the availability of euphausiids was promoted by the current and wind near the head of Barrow Canyon. Although there is no direct dietary evidence, such as stomach contents, that gray whales feed on euphausiids in the Pacific Arctic region, they were reported to skim-feed on euphausiids off Utquigvik, Alaska (Moore et al., 2022). Bluhm et al. (2007) conducted a spatial analysis of gray whales and euphausiids using data in 2003 and found that gray whales were spatially related to pelagic fauna, including euphausiids or other benthic organisms, rather than benthic amphipods. Despite the increased research attention being paid to the relationship between gray whales and euphausiids, the only spatial analysis connecting these cetaceans and the prey species was based on the aforementioned 2003 data (Bluhm et al., 2007). And, compared to studies on gray whales and benthic amphipods (e.g., Schonberg et al., 2014; Brower et al., 2017), little research has directly analyzed the distributional relationship between gray whales and euphausiids.

To understand the relationships between gray whales, benthic amphipods, and euphausiids after 2003, we compared the distribution of prey species (euphausiids and benthic amphipods) with that of gray whales. We predicted that the distribution of gray whales would correlate with that of euphausiids. To verify this hypothesis, we conducted multiple ship-based surveys to collect data on the positions of cetaceans, and, using net sampling, compared them to euphausiid distribution. We also sampled benthic amphipods for comparison with whale distributions. Finally, we employed a statistical model to investigate the factors influencing gray whale density. The analysis was conducted for the entire study area (the northern Bering Sea, Chukchi Sea, and adjacent waters) (Fig. S1).

In addition to the above analysis, we performed an additional analysis to understand the distributional relationship between gray whales and their prey using

data collected only in the DBO3 area (Fig. S1), where the Bluhm et al. (2007) study described earlier found correlations between gray whales and euphausiids (Bluhm et al., 2007). It is important to keep in mind that our entire study area was more expansive (larger) than the DBO3 area. Only an analysis of this larger area could have yielded different results from those of Bluhm et al. (2007), who first suggested the distributional link between gray whales and euphausiids. Therefore, we conducted the additional analysis using only the data gathered in the DBO3 area in order to align the analytical area with Bluhm et al. (2007). We calculated the density of gray whales in the DBO3 area to understand the variation among the four surveys. For this, we compared, statistically, the distributional characteristics of euphausiids sampled in the DBO3 area. To understand the distributional characteristic of the euphausiids sampled in each survey, we then used cluster analysis to classify sampling stations in the DBO3 area. Benthic amphipods were not analyzed because they were only sampled in 2013.

## METHODS

### Field Study

Ship surveys were conducted in August 2007, July 2008, and July 2013 by the T/S *Oshoro Maru* of Hokkaido University, Japan, and in September and October 2012 by the R/V *Mirai* of the Japan Marine Science and Technology Center. Table S1 presents the survey period, time, and distance for each year. Following Clarke et al. (2016), we defined July and August as summer, and September and October as fall.

Cetacean sightings were recorded when each vessel moved between the oceanographic and biological sampling stations during daylight hours, starting one hour after sunrise and ending one hour before sunset. During the midnight sun, observations were made while the vessels were moving. Observations were conducted from the compass deck (*Oshoro Maru*: approximately 10 m above sea level; *Mirai*: 16.3 m above sea level) when the wind speed was less than 20 knots or visibility was better than approximately one nautical mile (nmi) (Fig. 1). Under other conditions, surveys were conducted on bridges (*Oshoro Maru*: 8.5 m above sea level; *Mirai*: 13.6 m above sea level). During the surveys, one to three observers scanned the survey area (90° on both sides of the bow). When gray whales were sighted, their position, the time, sighting angle, radial distance, and number were recorded. We were unable to approach any sightings for species identification because our surveys were not dedicated to sightings, but rather, involved various types of sampling and observations. Sight data from 2007 and 2008 were provided by Sekiguchi et al. (2011) and Sekiguchi (2015, 2021). Sight data from 2013 were provided by Sekiguchi et al. (2011) and Sekiguchi (2015). Details of the protocols from *Oshoro Maru* are described by Sekiguchi et al. (2014).

Zooplankton sampling was conducted at 43, 45, 51, and 12 stations in 2007, 2008, 2012, and 2013, respectively (Fig. 1). Zooplankton were collected either during the daytime or night by vertical tows using a NORPAC Net (mouth diameter of 45 cm, mesh size of 335 µm) in 2007, 2008 and 2012, and by oblique tows using a BONGO net (mouth diameter of 70 cm, 330 µm) in 2013. Sampling was performed at a depth of 5 m above the sea floor, or at a depth of 150 m where the water depth exceeded 150 m. The volume of water filtered through the net was calculated from the flow meter measurements at the mouth of the net. Net sampling is a common and effective method for understanding the distribution of various zooplankton (Matsuno et al. 2011; Ashjian et al., 2017). However, in the case of euphausiids, there is a possibility of underestimating their distribution, especially during daylight sampling using vertical tows, because of their high mobility and good vision (Berline et al., 2008; Ashjian et al., 2017). This sampling bias must be taken into account when interpreting net samples.

Benthic samples were collected from 17 stations during the *Oshoro Maru* cruise in 2013 (Fig. 1d). Three replicates of 0.1 m<sup>2</sup> Smith – McIntyre grabs were used for sampling at each station. These samples were washed on 1 mm sieve screens, preserved in 10% formalin solution, and stored in one-litre plastic containers for laboratory analysis.

### Data Analysis

**Analysis of the Entire Study Area:** We defined the entire study area as all the region where we conducted visual and prey sampling surveys in the northern Bering Sea, Chukchi Sea, and adjacent waters (Fig. 1). We used ArcGIS 10.0 (ESRI Inc., Redlands, California, USA) to spatially analyze the distribution of the gray whales. We created 25 km grids along the sighting survey line. The densities of gray whales (ind./km<sup>2</sup>) were calculated for each grid by dividing the search area by the number of gray whales detected in the grid (e.g., Ferguson et al., 2005). Bad weather data were excluded from the analysis. The search area was calculated by multiplying the search distance by the effective search width. The effective search width was calculated using R 4.4.0 (R Core Team, 2024) and Distance 2.0.0 package. Using either a half-normal or hazard rate detection function, the year effect was used as a covariate term to calculate the effective search width by year. The model with the minimum Akaike information criterion (AIC) was selected as the optimal model.

Euphausiids were collected from the zooplankton net samples, and biomass (mg wet weight/m<sup>3</sup>: mgWW/m<sup>3</sup>), abundance (ind./m<sup>3</sup>), and average weight of individual euphausiids (mg wet weight: mgWW) were calculated for each station. Biomass was calculated by dividing the total wet weight of the euphausiids picked up by the volume of filtered water. Abundance was calculated by dividing the total number of euphausiids picked up by the volume of filtered water. The average weight of individual euphausiids

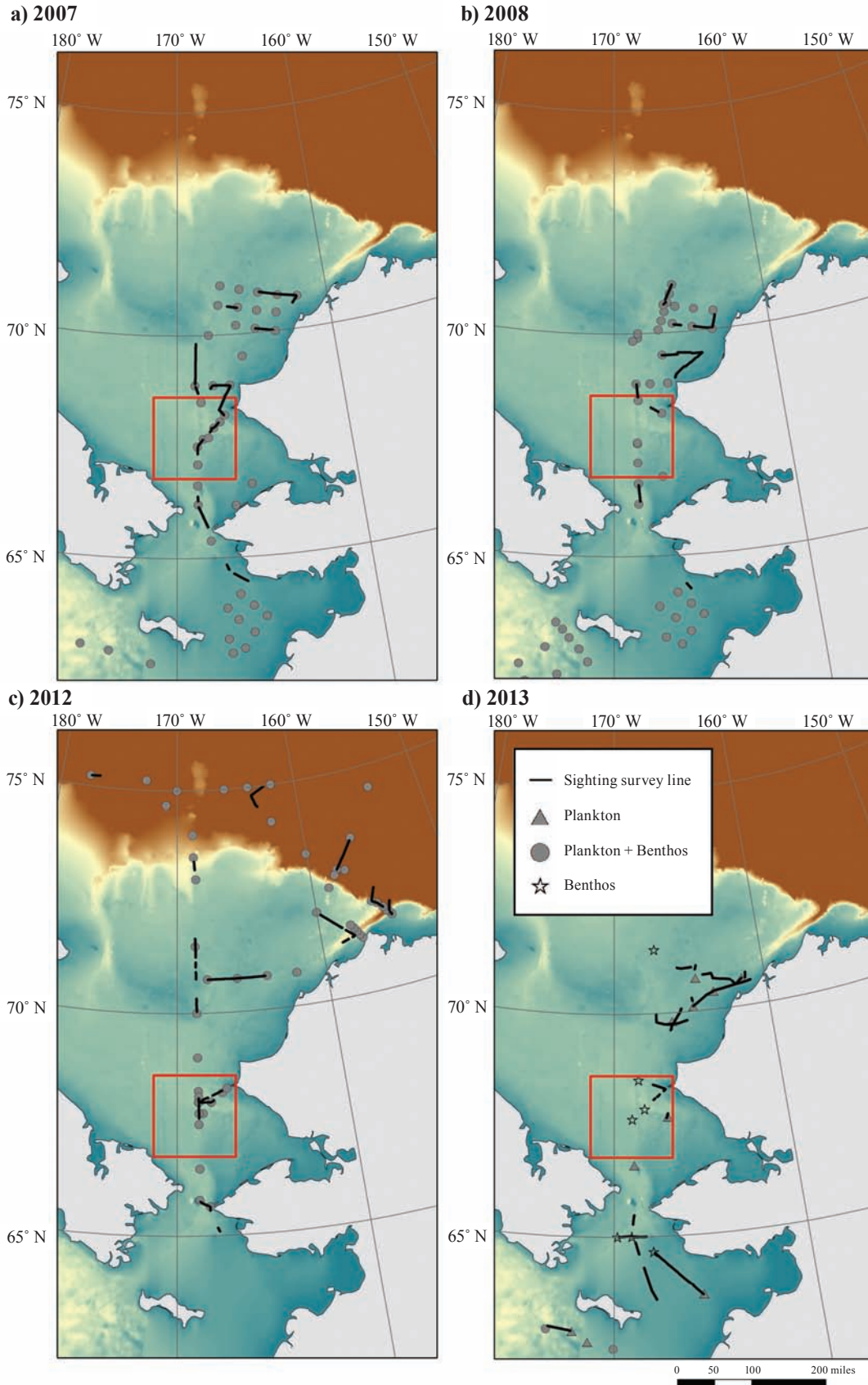


FIG. 1. Track lines and sampling stations for the (a) 2007, (b) 2008, (c) 2012, and (d) 2013 surveys. Black lines indicate sighting survey lines under good weather conditions. Gray circles indicate the stations of net sampling of plankton. Gray triangles indicate the stations where net sampling of plankton and Smith-McIntyre grab samples were taken. Stars indicate the Smith-McIntyre grab-only stations.

was calculated by dividing the total wet weight of the euphausiids picked up by the total number of euphausiids collected from the net sampling. Gray whales have coarser baleens than other baleen whales and their smallest prey size reported is 3 mm (Nerini, 1984; Guerrero, 1989). The mesh sizes of the plankton nets we chose were smaller than the reported smallest prey size; therefore, the size of euphausiids may have influenced gray whale distributions. However, it was difficult to measure the size of all euphausiids. Thus, we used the average weight of the individual euphausiids as a simple indicator of euphausiid size.

Amphipods were collected from Smith – McIntyre grab samples, and their wet weights were measured. The biomass (g wet weight/m<sup>2</sup>; gWW/m<sup>2</sup>) of the wet samples was calculated per unit area of the grab sample after excluding sand, pebbles, and seashells. The samples were fixed in buffered 10% formalin, then preserved in 70% ethanol for several months before being sorted.

To analyze the distributional relationship between gray whales and their prey, we used ArcGIS to undertake the following process: we created circles with a radius of 40 km in the GIS from benthic sampling stations in the 2013 survey (Fig. S2). We calculated the number of gray whales found annually within the circles and the survey distances. We also averaged the abundance, biomass, and average weight of a single euphausiid from the sampling stations within the circles. The stations where no euphausiids were sampled were excluded from the calculation of the average weight of a single euphausiid in the circles because there was no information on the average weight of a single euphausiid at the stations where no euphausiids were sampled. We used generalized linear mixed-effects models to investigate the distributional relationships between gray whales and their prey species. Statistical analyses were conducted using R 4.4.0 (R Core Team, 2024). The `glmer.nb` function in the `lme4` package (Bates et al., 2015) was used to fit the generalized linear mixed-effects models with a negative binomial distribution to account for overdispersion in the gray whale count data. The predictor variables included the biomass of amphipods, euphausiid abundance, euphausiid biomass, and average weight of a single euphausiid as fixed effects. The year was used as the random effect. The search area, calculated by multiplying the sighting survey distance and effective search width by year, was used as an offset term to account for differences in the total survey area among the areas. The explanatory variables were selected based on AIC using the exhaustive search to examine all combinations of variables. The model with the lowest AIC and models with  $\Delta\text{AIC} \leq 2$  from that model were chosen as better-fitting models (Burnham and Anderson, 2002). In general, models with  $\Delta\text{AIC} \leq 2$  are considered equally supported or not significantly different from the lowest AIC model (Burnham and Anderson, 2002; Leroux, 2019). The variance inflation factor was used to verify the absence of multicollinearity among the explanatory variables (Borcard et al., 2011).

Grids, rather than circles, are often used in analyses to understand the relationship between whales and their prey species (e.g., Murase et al., 2013; Brower et al., 2017). However, there were not many sighting survey lines or sampling stations in this study. The results of the preliminary analysis using grids were not robust because the starting position of the grids (e.g., whether it began from the left or right end of the survey line, or whether it was specified by latitude and longitude) could have affected the analysis of the relationship between gray whales and their prey. To avoid arbitrary adjustments to the analysis range, we used circles from the sampling stations. The scale size was set to a 40 km radius, in alignment with previous studies on distributional relationships with prey species, such as benthos and euphausiids, on a scale of tens of kilometers, such as 10, 40, and 50 km (e.g., Skern-Mauritzen et al., 2011; Murase et al., 2013; Brower et al., 2017). However, benthic sampling was conducted only in 2013. Benthos are considered indicators of long-term environmental conditions due to their immobility and long lifespan (Warwick, 1993; Grebmeier et al., 2015), although decadal-scale variability has been observed (e.g., Moore et al., 2003; Grebmeier et al., 2018). Furthermore, previous studies conducted in the Chirikov Basin and Point Hope between 1998 and 2015 suggested that areas abundant in amphipods tended to stabilize between 2007 and 2013 (Grebmeier et al., 2018). Therefore, the amphipod data during our survey period were considered relatively stable compared to those of euphausiids and were used in the analysis for all years.

**Analysis of the DBO3 Area:** We analyzed the distributional relationship between gray whales and prey species not only in the entire study area but also in the DBO3 area. In the DBO3 area, Bluhm et al. (2007) reported that gray whale distributions were associated with euphausiids. Therefore, we compared the density of gray whales and the distribution characteristics of euphausiids among surveys to understand the changes in the relationships between them. We calculated the number of gray whales and the distances surveyed per year in the DBO3 area. We also calculated the survey areas per year by multiplying the survey distances by the effective search width of each year. We calculated the gray whale densities in the DBO3 area by dividing the number of gray whales by the survey areas. We tested the differences in the abundance, biomass, and average weight of a single euphausiid sampled from the DBO3 area among the four surveys. To do this, we first tested for normality using the Shapiro test (Shapiro and Wilk, 1965), then used the Kruskal – Wallis test (Kruskal and Wallis, 1952), followed by the Steel-Dwass test (Steel, 1961). Only the stations where euphausiids were sampled were used for statistical tests to compare differences in the average weight of a single euphausiid. Hierarchical cluster analysis, using Ward's method (Ward, 1963), was used to characterize the euphausiids sampled from the DBO3 area. Sampling stations were classified based on the abundance, biomass, and average weight of a single euphausiid. Cluster

size was examined using the gap statistic (Tibshirani et al., 2001). The mean, minimum, and maximum values for each of the three variables, as well as the number of stations for each survey year, were then calculated to understand the characteristics of each cluster. Only stations where euphausiids were sampled were used for cluster analysis.

## RESULTS

### *Gray Whale Distribution*

Overall, 160 gray whales were observed in 55 groups in the entire study area (Fig. 2; Table 1). They were sighted from the Bering Strait up to Point Lay in August 2007 and July 2008 (Fig. 2a, b, 0.01 – 0.07 ind./km<sup>2</sup>). A high density of gray whales was found off Point Hope in September and October 2012 (0.15 ind./km<sup>2</sup>) and in the northern Chirikov Basin in July 2013 (0.29 ind./km<sup>2</sup>) (Fig. 2c, d). They were also observed off Point Franklin during the summer of 2013 (0.01 – 0.06 ind./km<sup>2</sup>) (Fig. 2d).

### *Euphausiid Distribution*

There were some variations in the euphausiid distribution throughout the study area. The abundance of euphausiids (ind./m<sup>3</sup>) was high from the Bering Strait to the area off Cape Lisburne in the summer. The abundance was 143 ind./m<sup>3</sup> off Cape Lisburne in August 2007 and 224 – 345 ind./m<sup>3</sup> in the northern Bering Strait in July 2008 (Fig. 3a). Higher biomass of euphausiids were observed off Cape Lisburne in August 2007 (174 mgWW/m<sup>3</sup>), off Point Hope in September and October 2012 (207 mgWW/m<sup>3</sup>), and off Point Barrow in September and October 2012 (99 – 128 mgWW/m<sup>3</sup>) (Fig. 3b). The average wet weight of a single euphausiid was high off Point Hope and Point Barrow in September and October 2012 (24 and 46 mgWW, respectively) (Fig. 3c).

### *Amphipod Distribution*

Across the 17 sampling stations, biomass of amphipods varied from 0.20 to 200.35 gWW/m<sup>2</sup> (Fig. 4). A greater biomass was found in the northern Chirikov Basin (63.85 – 200.35 gWW/m<sup>2</sup>), off Point Hope (25.78 – 48.64 gWW/m<sup>2</sup>), and off Icy Cape (17.20 gWW/m<sup>2</sup>; Fig. 4).

### *Distributional Relationships*

Gray whales were sighted in areas with either high amphipod or euphausiid abundance (Figs. 2 – 4). Areas with high densities of gray whales (Fig. 2) coincided with amphipod-abundant areas in the northern Chirikov Basin, off Point Hope, and off Point Franklin (> 17 gWW/m<sup>2</sup>). In fall of 2012, the biomass of euphausiids and the average weight of a single euphausiid were high off Point Hope, where gray whales were observed (Figs. 2 and 3).

TABLE 1. Results of sighting survey. Numbers indicate the total groups and number of gray whales observed in the 4-year survey.

	2007	2008	2012	2013	Total
Groups	5	3	23	24	55
Individuals	9	7	45	99	160

As a result of modelling the density of gray whales using generalized linear mixed-effects models (Table 2), the biomass of amphipods was selected as a significant explanatory variable in all models. The density of gray whales tended to increase as the biomass of the amphipods increased. Euphausiid abundance, biomass, and the average wet weight of a single euphausiid were also selected; however, these were not significant variables.

### *Changes in Distribution Characteristics in the DBO3*

The distribution characteristics of gray whales and euphausiids in the DBO3 area varied across the four surveys. The density of gray whales in the DBO3 area ranged from 0.00 to 0.035 ind./km<sup>2</sup> in four surveys. The 2012 survey had the highest density of gray whales at 0.035 ind./km<sup>2</sup>. In contrast, the 2008 and 2013 surveys had no observations at 0.00 ind./km<sup>2</sup> (Fig. 5). The maximum, median, and average euphausiid abundances were highest (224.10, 137.31, and 122.33 ind./m<sup>3</sup>, respectively) in 2008 compared with the rest of the surveys (16.96 – 43.52, 6.48 – 82.93, and 6.45 – 82.93 ind./m<sup>3</sup>, respectively) (Fig. 6). Biomass and average wet weight of a single euphausiid were highest in 2012 in terms of maximum and average (Biomass: 207.46, 63.07 mgWW/m<sup>3</sup>, average wet weight of a single euphausiid: 23.95, 8.31 mgWW) compared to the other surveys (Biomass: 26.33 – 46.97, 12.23 – 44.01 mgWW/m<sup>3</sup>, average wet weight of a single euphausiid: 0.16 – 1.85 mgWW, 0.11 – 0.60 mg WW) (Fig. 6). However, the Kruskal – Wallis test showed significant differences in abundance (chi-squared=13.386, df=3, p-value=0.0039) and average wet weight of a single euphausiid (chi-squared=15.579, df=3, p-value=0.0014) across the four surveys, but did not show significant differences in biomass (chi-squared=3.398, df=3, p-value=0.3343) across the four surveys. The Steel – Dwass test showed that there were no significant differences in the average wet weight of a single euphausiid between 2013 and the other years (2007 vs. 2013, 2008 vs. 2013, and 2012 vs. 2013); however, there were significant differences in the other combinations (2007 vs. 2008, 2007 vs. 2012, and 2008 vs. 2012). Additionally, there were significant differences in abundance only in the 2007 vs. 2008 and 2008 vs. 2012 combinations, and no significant differences were observed in the other combinations (2007 vs. 2012, 2007 vs. 2013, 2008 vs. 2013, and 2012 vs. 2013).

Cluster analysis of euphausiid samples classified the plankton sampling stations in the DBO3 area into three clusters. Cluster 3 had the largest biomass and average wet weight of a single euphausiid (biomass range: 66.32 – 207.45 mgWW/m<sup>3</sup>, average wet weight of a single

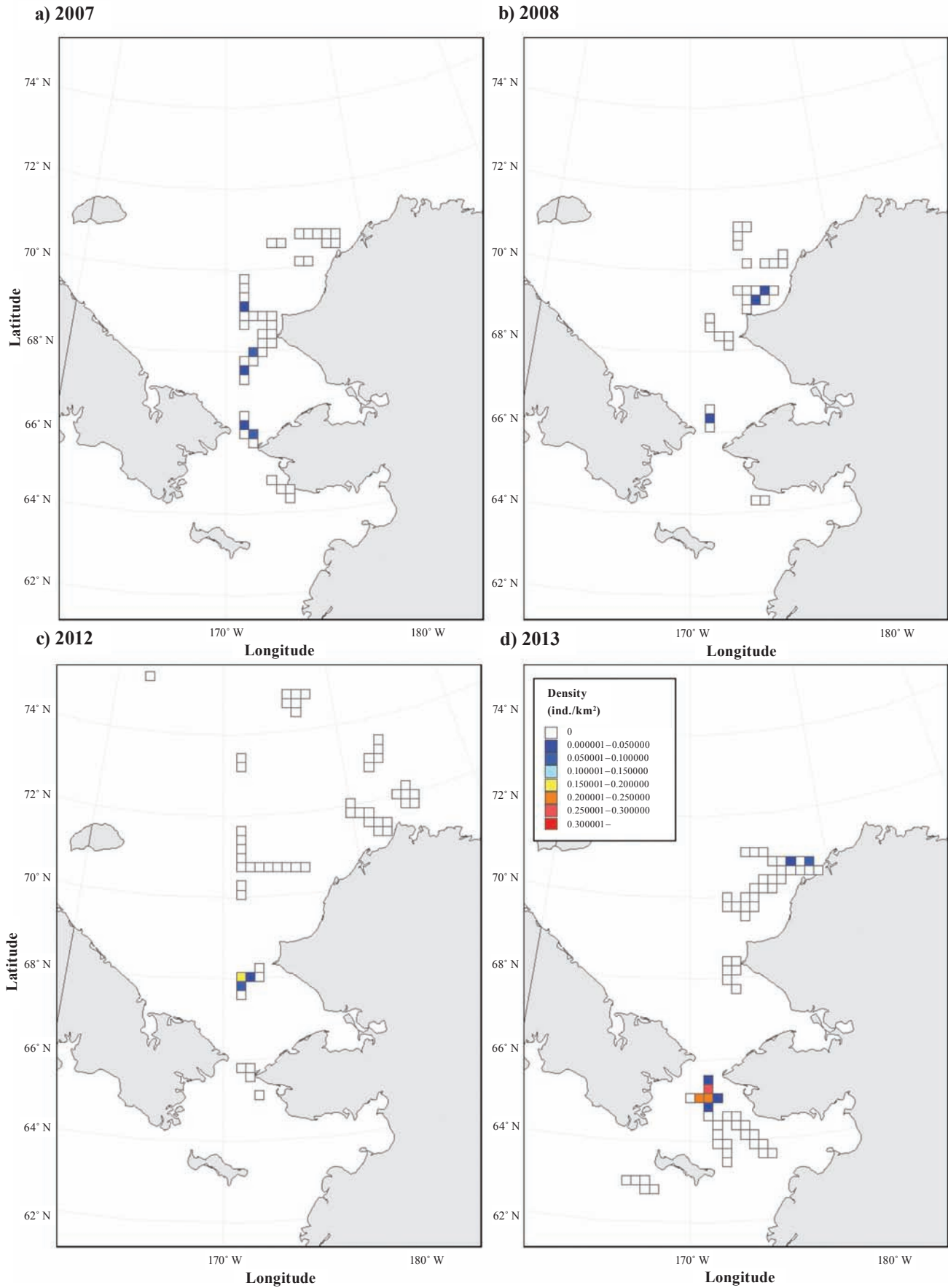


FIG. 2. Density (ind./km<sup>2</sup>) of gray whales in 2007 (a), 2008 (b), 2012 (c), and 2013 surveys (d).

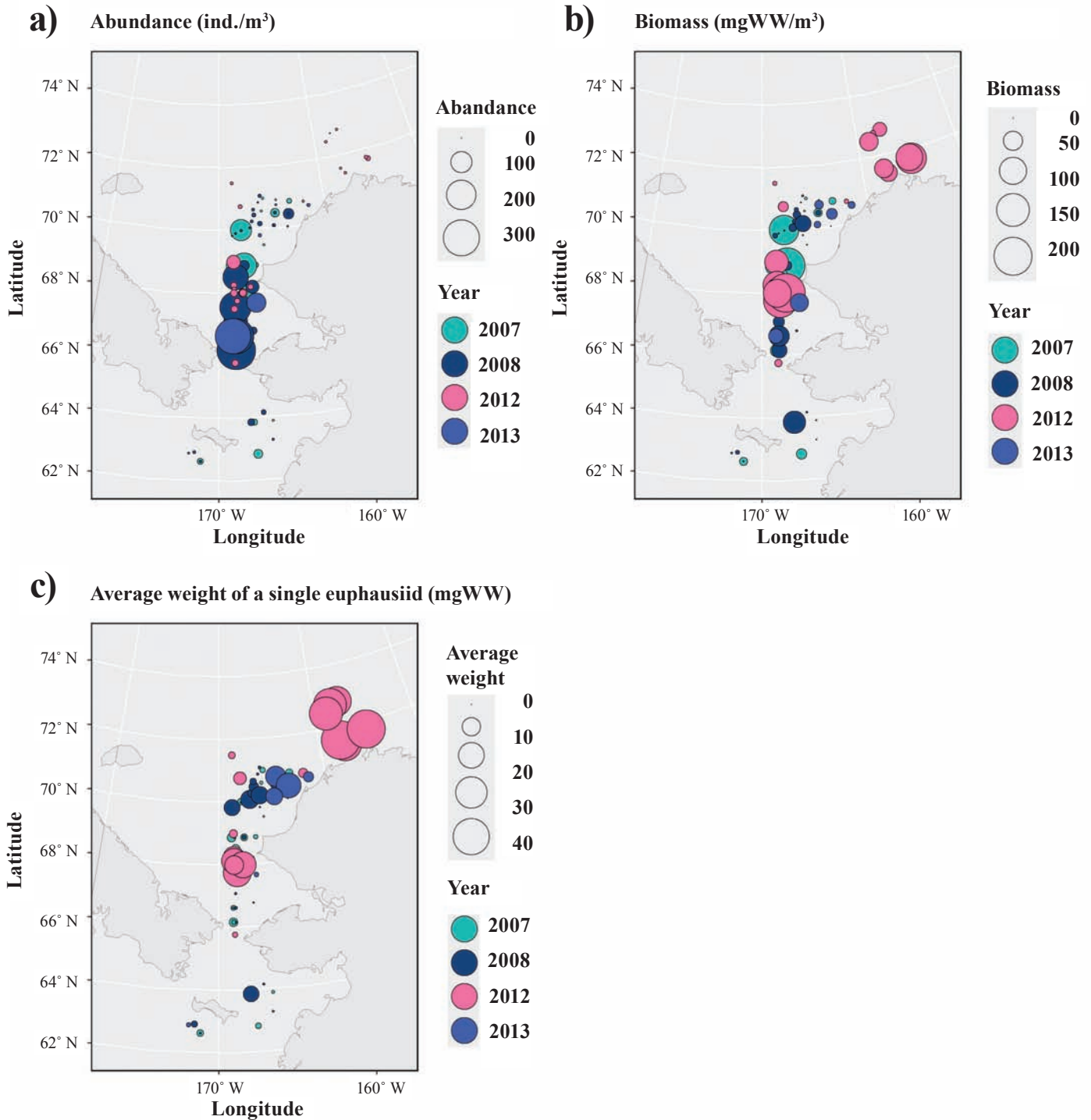


FIG. 3. Spatial distribution of euphausiids. Circle sizes indicate abundance (ind./m<sup>3</sup>) (a), biomass (mgWW/m<sup>3</sup>) (b), and average weight of a single euphausiid (mgWW) (c) in 2007 (light blue), 2008 (dark blue), 2012 (pink), and 2013 (blue).

euphausiid range: 10.56 – 23.95 mgWW) (Table 3). This cluster was found only in 2012 (Table 3).

## DISCUSSION

In our study area, gray whales were observed off Point Hope, in the Chirikov Basin, and off Point Franklin, where

amphipods were abundant. Statistical analysis of the entire study area showed that gray whale densities were related to amphipod biomass but unclearly related to euphausiids. In the DBO3 area, gray whale density was highest in 2012. The biomass and average weight of a single euphausiid were higher at five sampling stations in 2012 than at stations in the other years.

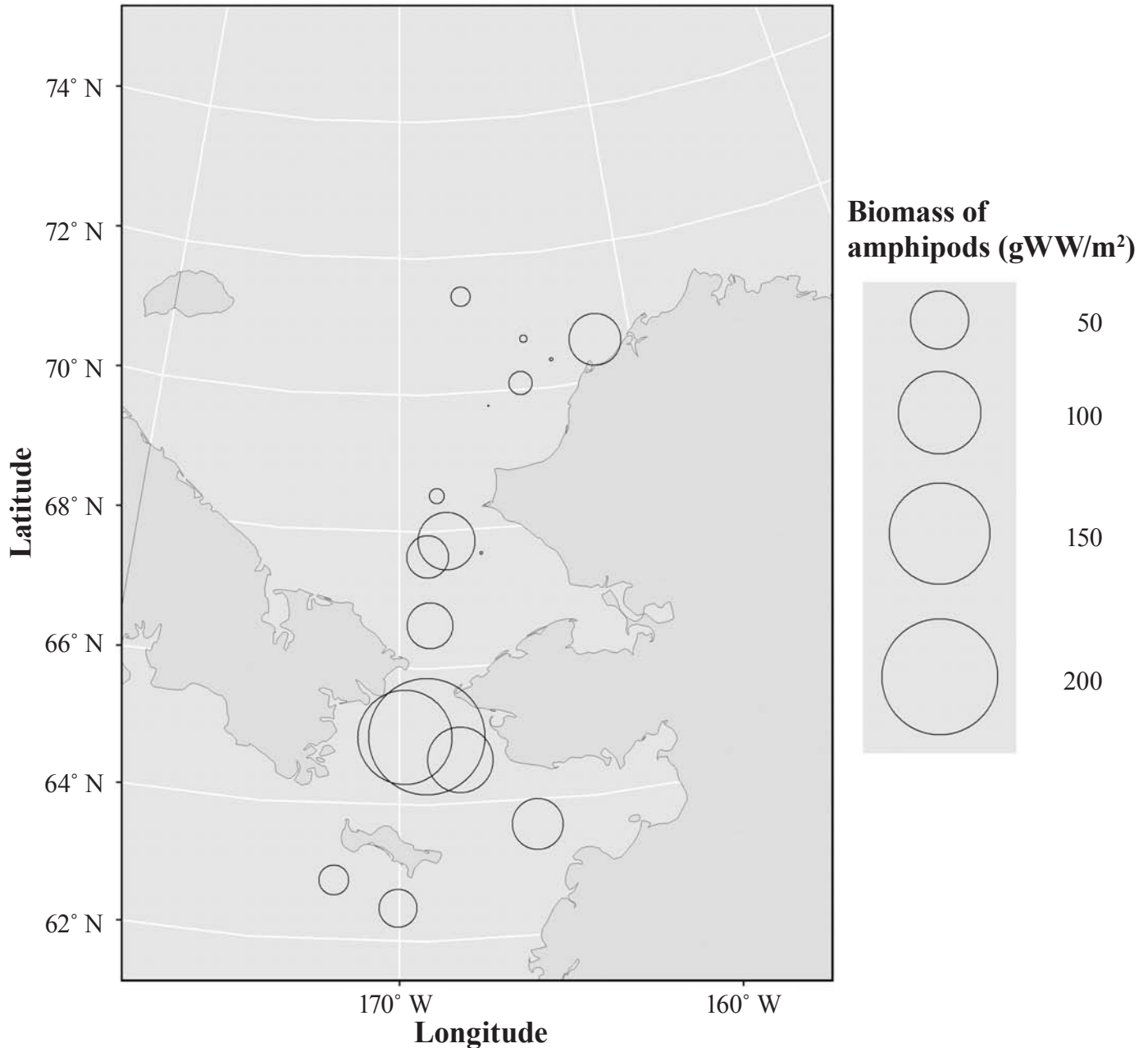


FIG. 4. Distribution of benthic amphipods in the 2013 survey. Circle size indicates the biomass of benthic amphipods (gWW/m<sup>2</sup>) in 2013.

#### *Euphausiid Distribution*

Our study analyzed euphausiid distribution in the Pacific Arctic region by considering the average weight of a single euphausiid. Euphausiids tended to be large and had high biomass during fall, particularly in the DBO3 area. The maximum and median values of euphausiid biomass, as well as the average wet weight of a single euphausiid, were highest in the fall of 2012 compared to the other survey years. However, there were no significant differences in biomass across the surveys. The discrepancy between the difference visible in the boxplot and the statistical difference may be attributed to the small number of stations with

higher biomass in 2012. The small number of sampling stations with higher biomass and larger euphausiids may be explained by the extremely high patchiness of euphausiids (Ashjian et al., 2017), or by their ability to escape from nets, especially during daylight in the case of vertical tows, owing to their high mobility and good vision (Berline et al., 2008; Ashjian et al., 2017). Acoustic surveys, combining echosounder and net sampling, where plankton echoes are observed, may be an effective way to bridge the gap between sampling stations and obtain a more precise euphausiid distribution (e.g., De Robertis et al., 2010; Murase et al., 2013). Statistical analysis also showed no significant differences in the average wet weight of a single euphausiid

TABLE 2. Details of selected better-fitting models. Only fixed effects were presented. BBA: biomass of benthic amphipods; AE: abundance of euphausiids; BE: biomass of euphausiids; AWE: average wet weight of a single euphausiid. \*p-value &lt; 0.05.

Intercept	BBA	AE	BE	AWE	offset (area)	AIC	ΔAIC
-13.580 *	0.152 *				+	61.6	0.00
-13.910 *	0.137 *			0.093	+	61.8	0.20
-13.650 *	0.123 *		0.024		+	62.2	0.60
-14.230 *	0.144 *	0.005		0.105	+	63.2	1.60
-13.730 *	0.157 *	0.003			+	63.4	1.80
-13.850 *	0.127 *		0.012	0.067	+	63.6	2.00

between 2012 and 2013. This was probably due to the small number of sampling stations in the DBO3 area in 2013.

Cluster analysis showed that higher biomass and larger euphausiids were observed only in the fall of the 2012 survey, but not in the other summer surveys, which was probably related to their growth. Euphausiids spawn in the northern Bering Sea in spring, and some are advected into the Chukchi Sea while growing (Berline et al., 2008). Our finding that euphausiids were larger in fall than in summer in the DBO3 area is consistent with a previous study that used moored acoustic equipment and net sampling off Point Hope (Kitamura et al., 2017). According to those previous findings, net sampling revealed that euphausiids were larger in the fall than in the spring, and differences in backscatter strength at multiple frequencies indicated that dominant zooplankton were larger in the fall than in the spring.

Higher biomass and larger euphausiids were also observed off Point Barrow in the fall of 2012, similar to those observed off Point Hope in the fall of 2012. The high biomass off Point Barrow in the fall is also consistent with previous studies (Ashjian, 2010, 2017). However, we did not survey off Point Barrow during the summers of 2007, 2008, and 2013; therefore, seasonal changes off Point Barrow could not be observed in this study.

#### *Gray Whales and Prey in the Northern Bering and Chukchi Seas*

During our surveys, aggregations of gray whales were observed off Point Hope (in the fall of 2012) and in the northern Chirikov Basin (summer 2013). Three hotspots for gray whales have been reported in the northern Bering and Chukchi seas during the summer feeding season: the Chirikov Basin, off Point Hope, and off Point Franklin (Grebmeier et al., 1989; Moore et al., 2003; Bluhm et al., 2007; Brower et al., 2017; Brower et al., 2022; Clarke et al., 2023). During aerial surveys, high numbers of gray whales were observed off Point Franklin in June to October 2009–12 (Brower et al., 2017) and during the summer of 2013 (Clarke et al., 2014). However, during our summer survey in 2013, only a few gray whales were observed off Point Franklin. This might be due to our limited survey effort in that area compared to these aerial survey studies (Clarke et al., 2014; Brower et al., 2017). In the Chirikov Basin, gray whale occurrence decreased in 2002 compared to the high levels of gray whale occurrence documented in the 1980s (Moore et al., 2003), and infaunal amphipod

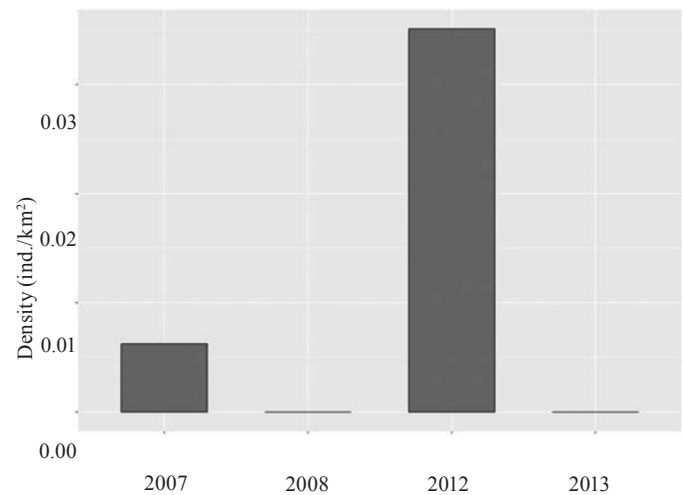


FIG. 5. Gray whale densities in the DBO3 area off Point Hope for each of the survey years 2007, 2008, 2012, and 2013.

beds have declined in recent years (2010–19; Moore et al., 2022). However, other research suggests that the Chirikov Basin is still an important feeding area for gray whales from May to December (Brower et al., 2022). Findings pointing to this ongoing presence include sightings from aerial surveys in the basin from 2010 to 2019 (Moore et al., 2022), acoustic detections in late May through December 2012–18 (Moore et al., 2022), and 41 days of stay from June to July 2017, the latter of which were revealed by satellite tracking and estimated to have included feeding behavior (based on behavior estimation using state – space model) (Urbán et al., 2021). The dense gray whale aggregations in the Chirikov Basin during our surveys may support the suggestion that the basin is still an important feeding area for gray whales.

Our results indicated that gray whale distribution was statistically related to areas where amphipods were abundant in the northern Bering Sea and Chukchi Sea. Amphipods were abundant off Point Franklin, off Point Hope, and in the northern Chirikov Basin, where gray whales were observed. Benthic amphipods have been reported as the dominant prey species and are essential factors influencing gray whale distribution in known feeding areas, such as the Chirikov Basin in the 1980s and the 2010s (Grebmeier et al., 1989; Moore et al., 2003; Grebmeier et al., 2018; Moore et al., 2022), and off Point Franklin from 2009 to 2017 (Schonberg et al., 2014; Brower et al., 2017; Moore et al., 2022). Our study supports these

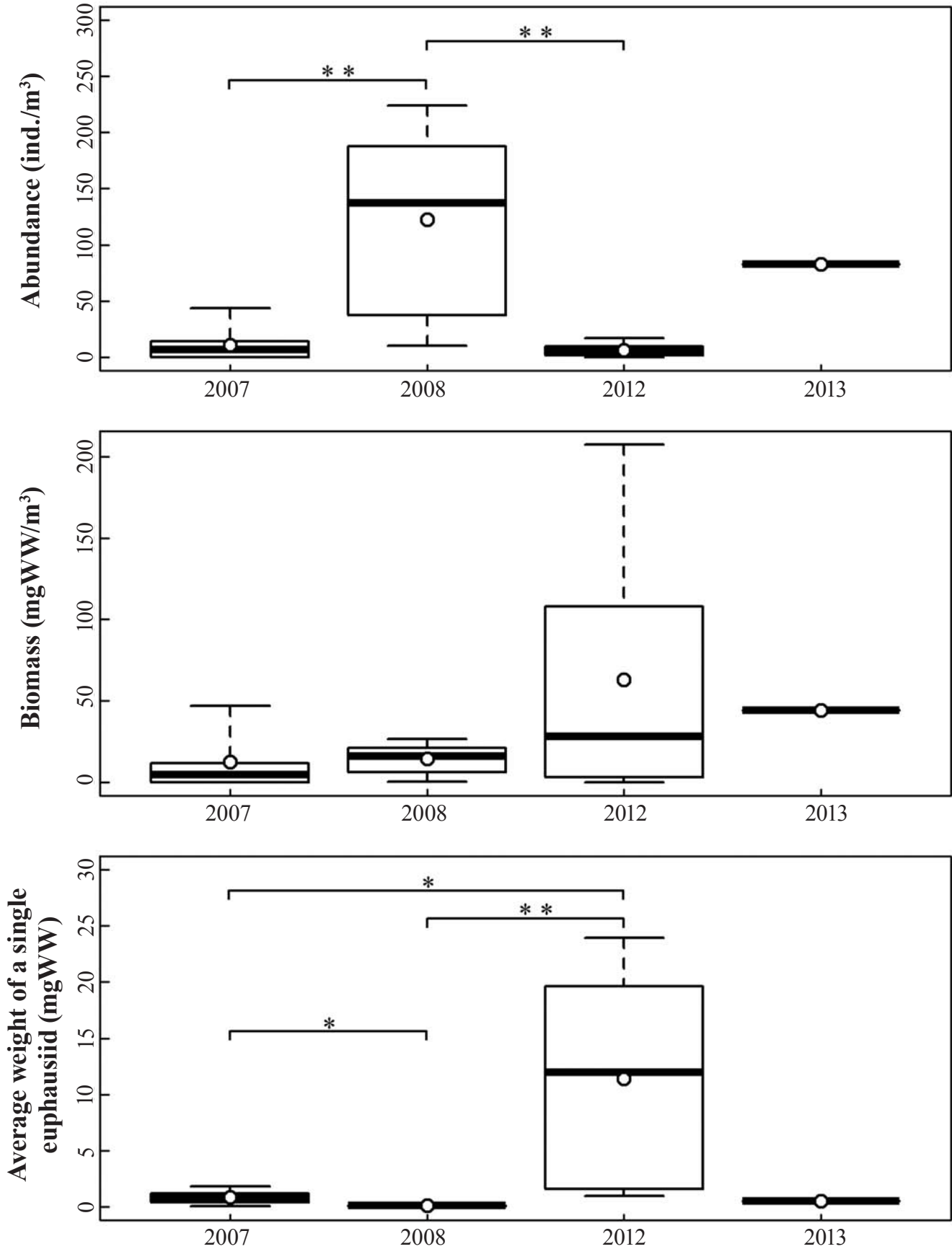


FIG. 6. Boxplot of euphausiids characteristics in the DBO3 area for each survey. Open circles indicate average values.

TABLE 3. Characteristics of euphausiids at the stations classified into three clusters by cluster analysis. Only stations in the DBO3 area were analyzed.

Cluster	Abundance (ind./m <sup>3</sup> )			Biomass (mgWW/m <sup>3</sup> )			Average weight of a single euphausiid (mgWW)			Stations (#)			
	Min	Average	Max	Min	Average	Max	Min	Average	Max	2007	2008	2012	2013
1	1.34	20.80	82.93	0.11	17.07	46.97	0.04	0.84	1.85	7	2	3	1
2	129.10	171.50	224.10	15.65	19.82	26.33	0.07	0.12	0.14	0	4	0	0
3	3.59	7.67	10.21	66.32	128.94	207.45	10.56	17.43	23.95	0	0	5	0

findings. Although there may have been variations between the four surveys we conducted, data on benthic amphipods from 2013 were used in all analyses. For example, it has been reported that the average biomass in the area between the Chirikov Basin and the waters off Point Hope was lower in 2007 and 2008 than in 2012 and 2013 (Stewart et al., 2023). However, given the results from a previous study (Grebmeier et al., 2018) and the low mobility and long lifespan of benthos (Warwick, 1993; Grebmeier et al., 2015), we consider the amphipods data collected during the survey period of the present study to be relatively stable compared to euphausiid data. As mentioned above, this does not mean there was no variation in the four survey years. It is important to note that the annual variation of the data in this period might overestimate the benthic amphipod distribution or the relationship between gray whales and benthic amphipods.

Statistical analysis of the entire study area did not reveal a clear distributional relationship between gray whales and euphausiids. In contrast, Bluhm et al. (2007) found that, in September 2003, the distribution of gray whales was more related to pelagic fauna, including euphausiids or other benthic, rather than to benthic amphipods. This discrepancy may arise from differences in the study areas. Bluhm et al. (2007) surveyed the area off Point Hope, which is almost identical to the DBO3 area, in September. In contrast, our survey area was more extensive, spanning from the Chirikov Basin to the Chukchi Sea and covering the period from June to October. In our study area, euphausiid biomass and size tended to be high in only two regions during fall: off Point Hope and off Point Barrow. The small number of areas with high euphausiid biomass and size might have resulted in a smaller effect on the entire study area. Furthermore, the absence of gray whales off Point Barrow might have resulted in an unclear relationship between gray whales and euphausiids. Although euphausiid biomass and size were high off Point Hope and Point Barrow in the 2012 fall survey, gray whales were only observed off Point Hope. We observed some whales off Point Barrow, but they could not be identified to the species level. These were recorded as unidentified baleen species (Fig. S3). Clarke et al. (2016) reported that gray whales were present off Barrow in the fall of 2009 – 15; therefore, some of the unidentified baleen whales sighted off Barrow during our surveys could have been gray whales. In this case, the relationship between gray whales and euphausiids may have been underestimated.

### *Gray Whales and Prey in the DBO3 Area*

Data from our 2012 fall survey indicated that an increase in large euphausiids might have influenced the increase in gray whales in the DBO3 area. Bluhm et al. (2007) previously reported that gray whale distribution was associated with euphausiids in the DBO3 area in September 2003, which is why we focused on this area. Our results from the DBO3 area show that gray whales had the highest density in the 2012 fall survey. Clarke et al. (2016) reported that, based on 2009 – 15 sighting surveys in the Chukchi Sea, gray whales were widely distributed in summer (June and August) and aggregated off Point Hope and Point Barrow in autumn (September and October). They also stated that density was highest in September. In our study, we found a high number of large euphausiids off Point Hope in the fall compared with the other surveys. This suggests that the presence of large euphausiids might have influenced the increase in gray whales in the fall of 2012 in the DBO3 area.

In contrast, Moore et al. (2022) analyzed the annual variability in the seasonality of encounter rates using visual survey data around the DBO3 area from 2014 – 19. They found that the encounter rate was highest in September only in 2016, but not in the other years. These results may indicate that seasonal changes in the number of gray whales in the DBO3 area vary annually. However, our findings are the first since 2003 (Bluhm et al., 2007) to use direct comparison between gray whales and their two types of prey to confirm both the presence of high biomass and large euphausiids at Point Hope, and that Point Hope is grounds for gray whales to feed on both benthic amphipods and euphausiids in the fall.

### CONCLUSION

This study examined the distributional relationship between gray whales and their prey, euphausiids and benthic amphipods, in the Pacific Arctic region using shipboard surveys conducted in 2007, 2008, 2012, and 2013. Our results showed that the distribution of gray whales was related to that of benthic amphipods throughout the entire survey area. However, the whales' relationship to euphausiids remains unclear. This may indicate that euphausiids have a smaller effect on gray whale distribution compared to benthic amphipods in the Pacific

Arctic region. Yet, net sampling of euphausiids may have introduced a sampling bias, making it difficult to conclude that gray whales and euphausiids bear no distributional relationship. In the DBO3 area, the increase in biomass and larger euphausiids during the fall may have influenced the increase in gray whale sightings. Even after the 2003 survey, the DBO3 area was confirmed to be an area for gray whales, especially in the fall, where they could feed on both benthic amphipods and euphausiids.

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