Gray whale distribution relative to benthic invertebrate biomass and abundance: northeastern Chukchi Sea 2009-2012

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Abstract

The shallow continental shelf waters of the Bering and Chukchi seas are the northernmost foraging grounds of North Pacific gray whales (*Eschrichtius robustus*). Benthic amphipods are considered the primary prey of gray whales in these waters, although no comprehensive quantitative analysis has been performed to support this assumption. Gray whale relative abundance, distribution, and behavior in the northeastern Chukchi Sea (69°-72°N, 155-169°W) were documented during aerial surveys in June-October 2009-2012. Concurrently, vessel-based benthic infaunal sampling was conducted in the area in July-August 2009-10, September 2011, and August 2012. Gray whales were seen in the study area each month that surveys were conducted, with the majority of whales feeding. Statistical analyses confirm that the highest densities of feeding gray whales were associated with high benthic amphipod abundance, primarily within 70 km of shore from Point Barrow to Icy Cape, in water <50 m deep. Conversely, gray whales were not seen in 40-km x 40-km cells containing benthic sampling stations with 85 m^{-2} or fewer amphipods. Continuing broad-scale aerial surveys in the Chukchi Sea and prey sampling near feeding gray whales will be an important means to monitor and document ongoing and predicted ecosystem changes.

Keywords: Eschrichtius robustus, Amphipods, Climate change, Alaska, Aerial survey, Benthic-dominated ecosystem, Pelagic-dominated ecosystem, Benthic foraging, Sentinel

1. Introduction

The gray whale (*Eschrichtius robustus*) is a large baleen whale that occurs in the North Pacific and Arctic oceans. The majority of gray whales belong to the eastern North Pacific (ENP) stock, which migrates seasonally along the western coast of North America between summer foraging grounds in the northern Bering and Chukchi seas and calving and wintering grounds in the lagoons of Baja California, Mexico. Records of gray whales in the northeastern Chukchi Sea date back to 1925 (Marquette and Braham 1982) and can be used to document shifts in their distribution, relative abundance, and foraging, likely in response to changing ecological conditions and the density and distribution of prey. Comparing these changes over time, while taking into account gray whale population size, may provide insight into predator-prey relationships and spatio-temporal patterns in oceanic production (Moore 2008).

The shallow continental shelves of the northern Bering and Chukchi seas are considered the primary northern foraging grounds of gray whales. High concentrations of gray whales have been documented in the northeastern Chukchi Sea (Clarke et al. 1989, 2013; Miller et al. 1986), along the Chukotka coast (Berzin 1984; Heide-Jørgensen et al. 2012), in the south-central Chukchi Sea (Bakhmutov et al. 2009; Berzin 1984; Bluhm et al. 2007; Clarke and Moore 2002; Moore et al. 2003; Wilke and Fiscus 1961), in the Chirikov Basin in the northern Bering Sea (Berzin 1984; Clarke and Moore 2002; Moore et al. 2000), and near St. Lawrence Island in the Bering Sea (Braham 1984; Moore et al. 2003; Wilke and Fiscus 1961). These areas are benthic-dominated ecosystems with high primary and secondary production resulting in high benthic prey densities (Coyle 1981; Feder et al. 1994; Grebmeier et al. 1989, 2006a; Highsmith and Coyle 1990; Stoker 1978). When gray whales feed on benthic organisms, they suction the organisms out of the sediment and strain the mud through their baleen, resulting in mud plumes that are visible at the surface of the water and detectable during aerial and shipboard surveys. Pelagic feeding by gray whales is much harder to detect during aerial and vessel surveys than benthic feeding; thus, pelagic prey may be underrepresented in diet data, particularly if samples are collected only from areas where gray whales are observed near visible mud plumes.

Range-wide, gray whales have been documented feeding on a variety of benthic epifaunal and infaunal invertebrates, including amphipods (Blanchard and Feder 2014; Coyle 1981; Darling et al. 1998; Dunham and Duffus 2001, 2002; Feder et al. 1994; Heide-Jørgensen et al. 2012; Nerini 1984; Oliver et al. 1984; Stoker 1978; Yablokov and Bogoslovskaya 1984), cumaceans (Coyle 1981; Moore et al. 2007), mysids (Darling et al. 1998; Dunham and Duffus 2001, 2002; Newell and Cowles 2006), and ghost shrimp (Darling et al. 1998; Dunham and Duffus 2001, 2002), and pelagic organisms, including euphausiids (Benson et al. 2002; Bluhm et al. 2007), porcelain crab larvae (Darling et al. 1998; Dunham and Duffus 2001, 2002; Newell and Cowles 2006), and herring eggs and larvae (Darling et al. 1998). Nerini (1984) lists 90 different genera of prey found in the stomachs of hunted or stranded gray whales.

In the Bering and Chukchi seas, few studies of gray whale foraging, particularly sampling near feeding gray whales or collection of stomach samples, have been conducted due to the regions' remote location and harsh weather conditions. Foraging gray whales in the Bering and Chukchi seas are distributed in areas of dense benthic amphipod communities, particularly ampeliscid amphipods, and it has been assumed gray whales associated with mud plumes in these areas are feeding on benthic prey (Blanchard and Feder 2014; Coyle 1981; Feder et al. 1994; Heide-Jørgensen et al. 2012; Nerini 1984; Stoker 1978). Stomach samples from >300 animals taken by Soviet whalers in the Bering Sea (Nerini 1984; Yablokov and Bogoslovskaya 1984) and sampling of gray whale mud plumes in the Bering Sea (Grebmeier and Harrison 1992) have confirmed ampeliscid amphipods are the dominant prey of gray whales there. It is suspected that gray whales in the south-central Chukchi Sea may have a more varied diet (Bluhm et al. 2007). In the northeastern Chukchi Sea, qualitative analyses have been performed linking gray whales and their benthic amphipod prey from data collected via broad-scale aerial surveys for marine mammals (Clarke et al. 1989, 2011a, b, c, 2012, 2013; Moore and Clarke 1992; Moore et al. 1986), side-scan sonar of gray whale feeding pits in the seafloor (Nelson et al. 1994), and benthic infaunal sampling (Feder et al. 1994; Grebmeier et al. 2006a; Blanchard et al. 2013; Schonberg et al. 2014). Previous benthic analyses have been constrained either temporally (data that are decades old: Feder et al. 1994) or spatially (sampling that did not overlap well with feeding gray whale distribution: Blanchard et al. 2013; Schonberg et al. 2014). In this paper, we build on previous studies and perform a quantitative analysis of contemporary gray whale and benthic infaunal data that overlap temporally and spatially to statistically determine the relationship between gray whale relative abundance and distribution and amphipod abundance and biomass. To do this, we used broad-scale marine mammal aerial survey data (Clarke et al. 2011a, b, c, 2012, 2013) and infaunal sampling conducted offshore (predominantly >70 km from shore) (Schonberg et al. 2014, Schonberg et al., Hanna Shoal Ecosystem Study, http://arcticstudies.org/hannashoal/index.html) and near the coast (predominantly <70 km from shore) (Lovvorn et al. 2015; Dasher et al. 2015a,b; Alaska Monitoring and Assessment Program) on the northeastern Chukchi Sea shelf, 2009-2012.

2. Methods

2.1 Aerial survey study area and survey design

Aerial line transect surveys were conducted by the Marine Mammal Laboratory (formerly the National Marine Mammal Laboratory) of the Alaska Fisheries Science Center and the Bureau of Ocean Energy Management (BOEM) in the northeastern Chukchi Sea as part of the Aerial Surveys of Arctic Marine Mammals (ASAMM) project. The gray whale analysis area addressed herein, extending 69°-72°N and 156°-169°W, comprised 48% (~110,000 km^2) of the entire ASAMM study area. This area was chosen because it is where gray whales were most consistently observed (Fig. 1). The analysis area included

Barrow Canyon and continental shelf waters <200 m deep. Survey effort was designated as on effort (transect lines and circling from transect) or off effort (search effort and associated circling, which were not on transect lines). Survey protocols were identical during on- and off-effort periods. Circling was designated when the aircraft occasionally made brief (<10 minutes) diversions from transect or search effort to circle sightings to verify species, group size, or presence or absence of calves. Surveys were flown every day, weather permitting. When cloud ceilings were <305 m or Beaufort wind force was >5, survey flights were redirected to transect lines with better conditions. The survey was aborted when conditions consistently did not meet these minimum altitude or wind force requirements.

Surveys were flown in high-wing, twin-engine turbo aircraft (DeHavilland Twin Otter or Turbo Commander) at altitudes of 305-460 m and speeds of 210-220 km/h. Visual surveys were conducted by two primary observers, one on each side of the plane, looking out of bubble windows and reporting environmental conditions and all marine mammal sighting data to a data recorder. The majority of ASAMM observers returned from previous survey seasons; observers new to ASAMM were paired with experienced observers. All observers received the same training, and observer performance was evaluated with observer sighting histograms and by confirming species ID and sighting location during circling effort. The data recorder used a laptop computer, connected to a global positioning system (GPS), to log species, group size and composition (number of calves), plane position, altitude, declination angle to sighting (via clinometer), behavior, percent ice cover (estimated as a percentage of the visible sea surface), and visibility. Custom software used the declination angle, altitude, aircraft heading, and side of plane to automatically calculate each sighting's geographic position. When a declination angle was not available for a sighting, the aircraft's position at the time of sighting was the geographic position used for analysis. While circling, due to the pitch and roll of the aircraft, declination angles to sightings were not recorded. A continuously updated map display enabled the data recorder to track all sightings and assist in the identification of duplicate sightings within any one survey. Additional survey design methods can be found in Clarke et al. (2013).

2.2 Gray Whale Relative Abundance, Distribution, and Behavior

Analyses were limited to 2009-2012 when aerial survey data were consistently collected from mid-June or early July through October to facilitate comparisons of gray whale sighting rates across months and years, and to complement the benthic data. The analysis area was divided into a 40-km x 40-km grid to compare sighting rates across the resulting 94 cells in the study area. The total area of any cell at least partially overlapping the analysis area was incorporated into the analysis (Fig. 1); all further reference to the analysis area includes the total area of all cells. Distance on effort (km) per cell was calculated usingR version 3.3.0 (R Core Team 2016) using packages sp (Pebesma and Bivand 2005; Bivand et al. 2013), maptools (Bivand and Lewin-Koh 2015), rgeos (Bivand and Rundel 2015), and rgdal (Bivand et al. 2015). Analyses were limited to cells with ≥100 km of on-effort flightlines, pooled across all months and years, to minimize potential bias due to low survey effort unrepresentative of the entire cell.

All on-effort gray whale sightings were included in the analysis regardless of the Beaufort wind force or visibility conditions at the sighting time. Beaufort wind force was not found to affect gray whale sightability on ASAMM surveys during conditions of Beaufort wind force 0-5 (Ferguson and Clarke 2013). To compute gray whale relative abundance, sighting rates (number of individuals per km of effort) were calculated as the total number of individual gray whales divided by the total kilometers on-effort (denoted as tr-km) that were surveyed within each cell. Sightings made on-effort were pooled in this analysis to be inclusive of animals sighted while circling in the vicinity of the original transect sighting. Behaviors were entered as swim, dive, feed, mill, mate, rest, and several types of displays (Clarke et al. 2013). Feeding was recorded when whales were observed surfacing with mud plumes streaming from their mouths or were closely associated with fresh mud plumes at the surface. Percentages of feeding gray whales relative to total gray whales sighted on effort were also computed. Sighting rates were not corrected for availability or perception bias because Ferguson and Clarke (2013) found no evidence of spatial variability in gray whale detectability in the area corresponding to the current gray whale analysis.

2.3 Benthic Chukchi Sea Offshore Monitoring in Drilling Area (COMIDA)

As part of BOEM's Chukchi Sea Offshore Monitoring in Drilling Area (COMIDA) Chemical and Benthos (CAB) and Hanna Shoal programs, the University of Texas Marine Science Institute conducted a quantitative assessment of the biomass, abundance, and community structure of infaunal populations using benthic data collected in summers 2009, 2010 (Schonberg et al. 2014), and 2012. Benthic grabs were collected at 70 stations over the 3-year period in the northeastern Chukchi Sea. Most (89%) of the stations were located in the gray whale analysis area; the remaining 8 stations were located north of the analysis area between 72° and 73°N, near Hanna Shoal (Fig. 1). Station water depths ranged from 25 m near Hanna Shoal to 130 m in Barrow Canyon, but most stations were located on the broad Chukchi shelf at depths primarily 40 to 60 m.

In summers 2009 and 2010, COMIDA benthic sampling station locations were randomly selected using probability-based computations in ArcGIS 9.3 (Environmental Systems Resource Institute [Esri, 2009]) within thirty 1260 km^2 hexagonal tessellated cells (White et al. 1992) spanning the Bureau of Ocean Energy Management Lease Sale 193 area (Fig. 2). In 2012, the survey shifted focus to the Hanna Shoal region, where station locations were randomly generated within 20 hexagonal grid cells. Multiple (n = 3-4) double van Veen grabs (0.1 m^{-2}) were collected at each station. Additional sampling and processing details can be found in Schonberg et al. (2014).

2.4 Benthic Alaska Monitoring and Assessment Program

Coastal benthic sampling was conducted under the Alaska Monitoring and Assessment Program (AKMAP) by the Alaska Department of Environmental Conservation and University of Alaska Fairbanks, Institute of Marine Science. Research cruises were conducted in the southern portion of the gray whale analysis area from 23 August to 3 September 2010, in the northern part of the area in September 2011, and in various parts of the area in August 2012. Three double van Veen grabs were collected at each of 66 stations over the 3-year period in the northeastern Chukchi Sea and epibenthic beam trawls were collected at 58 stations in 2010-2011. Most AKMAP stations (93%) were located within the gray whale analysis area; the remaining 5 stations were located south of the analysis area between 68° and 69°N (Fig. 1). Station water depths ranged from 13 m in a shallow area 6 km from shore to 112 m in Barrow Canyon, but most stations were located within the Chukchi coastal-shelf ecosystem at depths primarily 20 to 50 m. Additional AKMAP survey design details can be found in Dasher et al. (2015a, b).

2.5 Benthic sample processing

AKMAP and COMIDA used similar protocols to process infaunal samples. The area of each grab sample was ~0.1 m^{-2} and the depth of sediments sampled was ~10 cm. Grab samples were rinsed over a 1 mm sieve. Samples were processed for taxonomic identification, counted, and measured for wet weight biomass (gww). Grab-caught amphipod abundance and biomass were converted to individual m^{-2} and g m^{-2}, respectively. Epibenthic invertebrates were sampled (one trawl per station) with a 3.05-m plumbstaff beam trawl with 7-mm mesh in the body, 4-mm codend liner, double tickler chain, and 16-cm chains attached to the footrope at 16 cm intervals. Time at the bottom for each trawl was 2–5 min at a speed relative to water of 1–1.5 kt. Trawl samples were sorted by taxa and counted on deck. Trawl-caught amphipod abundance and biomass were converted to individuals km^{-2} and kg km^{-2}, respectively.

2.6 Gray whale and amphipod association

To compare gray whale distribution and relative abundance with prey distribution and relative abundance, on-effort sighting rates from July-August 2009-2010, September 2011, and August 2012 were assessed using both qualitative and quantitative methods. Sample size limitations in both the benthic and gray whale datasets precluded a detailed quantitative spatio-temporal analysis at monthly or annual resolution. Therefore, qualitative methods were used to compare spatial and temporal patterns in gray whale sighting rates and infauna data. Gray whale data and summary statistics were plotted with pooled COMIDA and AKMAP infaunal amphipod abundance (m^{-2}) and amphipod biomass (gww m^{-2}) in ArcMap 10.3.1 (Environmental Systems Resource Institute [Esri, 2015]) to provide a visual reference for comparing the spatio-temporal association between the taxa.

To statistically investigate the relationship between gray whale relative abundance and infaunal abundance and biomass, non-parametric generalized additive models (GAMs) were constructed. For each cell, the GAMs predicted the number of individual gray whales sighted on transect, normalized by survey effort, as a function of infaunal amphipod abundance or biomass, or “other” infaunal abundance or biomass. The “other” infauna category included all taxa except amphipods. Amphipod abundance and biomass were highly correlated with other infaunal abundance and biomass, so amphipod and other infauna were not used as explanatory variables in a single model. Gray whale relative abundance was modeled as a Tweedie distribution (Tweedie 1984; Dunn and Smith 2005) with a natural logarithmic link function. Quasi-Poisson, Poisson, and negative binomial models were also considered, but examination of model residuals (Ver Hoef and Boveng 2007) suggested that the Tweedie distribution provided a better fit to the data. The model formulae can be represented as

$$ln(E(W_i)) = ln(\mu_i) = \alpha + s(Amp_i) + offset(ln(L_i))$$

and

$$ln(E(W_i)) = ln(\mu_i) = \alpha + s(Other_{i)} + offset(ln(L_i))$$

where

W_i: random variable for the number of individual gray whales in cell *i*, with W_i referring to the associated observations and $E(W_i)$ the expected value (mean) of W_i;

μ_i: number of individual gray whales expected to be observed in cell *i*;

α: intercept;

Amp_i: mean infaunal amphipod biomass or abundance in cell *i*;

$Other_i$: mean other infaunal biomass or abundance in cell *i*;

s( ): smooth function (Wood 2006) of infaunal covariate used to describe gray whale relative abundance; this function is parameterized in the model-fitting process;

L_i: length (km) of transect effort in cell *i*, which was incorporated into the model as a constant (an "offset") to account for spatially heterogeneous survey effort throughout the study area.

The GAMs incorporated only the 58 cells for which both infaunal benthic samples and at least 100 km of aerial survey effort existed. Data were pooled across time. Like the sighting rate analysis described above, it was not necessary to adjust the sighting data for availability or perception bias because they were assumed to be constant in the gray whale analysis area (Ferguson and Clarke 2013). For cells with multiple benthic samples, mean values of infaunal covariates were used in the model.

To assess the modeled association between gray whale relative abundance and infaunal abundance or biomass, three quantitative criteria and one qualitative criterion were used. The quantitative criteria used for model selection included ∆AIC (Burnham and Anderson 1998), percent explained deviance (percentage of the deviance of the null model that was explained by a model with an infaunal predictor variable), and RMSPE (root mean square prediction error). AIC is Akaike's Information Criterion, and ∆AIC ("delta AIC") is the difference between the minimum AIC and the candidate model's AIC. RMSPE is defined as

$$RMSPE = \sqrt{\frac{\sum\left(W_i - \widehat{W_i}\right)^2}{n}}$$

where W_i is the observed number of gray whales in cell *i*, $\widehat{W_i}$ is the predicted number of gray whales in cell *i*, and the summation is over all n=58 cells in the analysis. Qualitatively, model predictions and the observed relative abundances were compared by plotting both in ArcMap 10.3.1 (Environmental Systems Resource Institute [Esri, 2015]) and comparing the geographic distribution of the highest predicted sighting rates and highest observed sighting rates.

The GAM analysis was conducted in R version 3.3.0 (R Core Team 2016) using packages sp (Pebesma and Bivand 2005; Bivand et al. 2013), maptools (Bivand and Lewin-Koh 2015), rgeos (Bivand and Rundel 2015), rgdal (Bivand et al. 2015), and mgcv (Wood 2006).

3. Results

3.1 Aerial survey effort

Aerial surveys were flown in 2009-2012 from mid-June or early July through late October, but monthly survey effort varied geographically among years. A total of 104,464 on-effort kilometers were flown in the analysis area during all four years combined, primarily (32%) in 2012, followed by 2011, 2009, then 2010 (Fig. 2, Table 1). Survey effort in 2012 was highest because summer (July-August) surveys were added for the first time between 155°W-157°W and additional surveys were flown in July focusing on eastern Chukchi Sea beluga whales (*Delphinapterus leucas*) (Clarke et al. 2013). Also in 2012 the survey aircraft circled more frequently over cetacean sightings to more accurately estimate group size and determine calf presence. About 12% of all on- and off-effort survey time in 2012 was spent circling compared with 5% in 2009 and 3% in 2010 and 2011. Survey effort by month was greatest (28%) in September (29,632 km), followed by July, August, and October; June survey effort (5,786 km) was limited to 2009, 2011, and 2012, spanning only part of the month (Table 1). October survey effort was relatively low due to inclement survey conditions. Survey effort from 155°W to 157°W was limited to October 2009, September-October 2010, August-October 2011, and July-October 2012.

3.2 Gray whale relative abundance and distribution

A total of 515 sightings of 853 gray whales were seen on effort in all years (Fig. 3). Gray whales were seen in every month of every year that ASAMM surveys occurred, although sighting numbers and sighting rates varied temporally and spatially. The highest sighting rate in all months and years combined occurred between Point Barrow and Icy Cape in cell 77 (0.0642 whales/tr-km) and cell 54 (0.0574 whales/tr-km) (Fig. 3).

The highest on-effort number of whales and sighting rate per year (all cells combined) occurred in 2012 (207 sightings of 390 whales, 0.0114 whales/tr-km) followed by 2009, 2011, and 2010 (Fig. 3, 4, and 5,

Table 1). The increased numbers of gray whales and higher sighting rates in 2012 versus 2009-2011 suggest an increase in gray whale use of this area rather than the result of increased survey effort. Additional analysis by the authors of transect-only sighting rates showed increased circling in 2012 was not the reason for higher sighting rates. In all four survey years combined, the majority (97%) of the 853 gray whales were seen on the continental shelf from Point Lay to east of Point Barrow (Fig. 3). From Point Barrow south to Point Franklin, gray whales were seen predominantly <38 km from shore on the continental shelf shoreward of Barrow Canyon. Sighting rates were particularly high in cell 77 in this area in 2009, 2010, and 2011 (Fig. 4A-C). From Point Franklin to just south of Icy Cape, gray whales were predominantly seen on the continental shelf, up to 80 km offshore. Sighting rates in this area were highest in cell 54 in 2009, 2010, and 2012 (Fig. 4A, B, D) and cells 53 and 64 in 2012 (Fig. 4D). From Icy Cape to Point Lay, most gray whales were seen on the shelf <5 km from shore in 2009, 2011, and 2012 (Fig. 4A, C, D). In 2012, gray whales were also sighted northeast of Point Barrow on the continental shelf, shoreward of Barrow Canyon (10-26 km from shore), and north of Dease Inlet (9-16 km from shore) (Fig. 4D). Sighting rates and sightings were lowest elsewhere in the study area, including Barrow Canyon and offshore of the Canyon, >80 km offshore from Point Franklin to Icy Cape, >5 km offshore from Icy Cape to Point Lay, and south of Point Lay.

In each month, gray whales predominantly occurred on the continental shelf from Point Barrow to Icy Cape (Fig. 6A-E). In June, distribution was predominantly on the continental shelf from Point Franklin to Icy Cape in cells 54 and 55 (Fig. 6A). July had the highest number of gray whale sightings and highest sighting rates (Fig. 6B). July distribution was more widespread on the shelf shoreward of Barrow Canyon from Point Barrow to Icy Cape (with sighting rates highest in cells 54 and 77) and within 5 km of shore from Icy Cape to Point Lay (Fig. 6B). In August, gray whale sightings and sighting rates remained high (with sighting rates highest in cells 53, 64, and 77), although gray whales were no longer sighted south of Icy Cape (Fig. 6C). In August-October, gray whales were sighted farther offshore between Point Franklin and Icy Cape, where the shelf empties into Barrow Canyon, with a few individuals sighted near Hanna Shoal (Fig. 6C-E). In September-October, numbers decreased by over 50%, with relatively low sighting rates (Fig. 6D, E).

3.3 Gray whale behavior

Behavior was recorded for 814 gray whales. The most frequently (67%) observed gray whale behavior in all months and years was feeding (544 whales), followed by swimming (213 whales), resting (38 whales), milling (11 whales), diving (7 whales), and displaying (1 whale). Interannual variability in the sighting rates of feeding gray whales (all cells combined) was similar to that of sighting rates of all gray whales: the highest feeding sighting rate was in 2012 (0.0070 whales/tr-km), followed by 2009 (0.0057 whales/tr-km), 2011 (0.0040 whales/tr-km), and 2010 (0.0032 whales/tr-km). The highest monthly feeding sighting rates (all years and cells combined) were in August (0.0090 whales/tr-km), July (0.0079 whales/tr-km), and June (0.0038 whales/tr-km). Proportionally, August had the highest percentage of feeding gray whales (72%), followed closely by September (68%) then October (65%).

3.4 Benthic communities and relative abundance

Polychaetes, bivalves, and crustaceans were the dominant groups collected in the COMIDA infaunal grabs. Seventy-six different species of amphipods in 50 genera and 34 families were identified in benthic grab samples (Dunton et al. 2014; Schonberg et al. 2014; Whiteaker 2012). Two of these amphipods, *Pontoporeia femorata* (Pontoporeiidae) and *Paraphoxus* sp. (Haustoriidae), were in the top 10 most abundant organisms in the combined 2009 and 2010 infauna data set (Schonberg et al. 2014). *Byblis* spp. (Ampelicidae), *Protomedeia* spp. (Isaeidae), and *Pontoporeia* spp. (Pontoporeiidae) dominated the amphipod abundance values from the 2012 sampling area, which focused on the vicinity of Hanna Shoal.

High abundance and biomass of amphipods were also found in the AKMAP infaunal grabs (Table 2). Fifty-eight different species of amphipods, from 44 genera and 20 families, were identified in benthic grab samples (Table 3). Amphipod abundance and biomass were particularly high in the northern half of the gray whale analysis area, sampled in 2011 and 2012. The most abundant families in this area were Isaeidae (particularly *Protomedeia spp.* and *Photis vinogradovi*) and Ampeliscidae (particularly *Ampelisca spp.*). In the southern half of the analysis area, sampled in 2010 and 2012, the most abundant amphipods were Isaeidae (particularly *Protomedeia spp.*). In the epibenthic beam trawls, scavenging amphipods, Uristidae (*Anonyx nugax*) and Stegocephalidae (*Stegocephalus* sp.) were collected, although they were not the dominant taxa in abundance or biomass (Table 4). *Anonyx nugax* were fairly abundant in the AKMAP 2011 sampling region where gray whale occurrence was high; more than 2 million *Anonyx nugax*/km^{-2} were estimated at AKMAP station 53 off Pt Franklin (Table 5).

Amphipod distribution, abundance, and biomass from the combined benthic data set varied throughout the analysis area. Amphipods comprised a higher proportion of total infaunal abundance than total infaunal biomass (Fig 7A, B). Many stations with higher amphipod abundance and biomass were associated with gray whale sightings (Figs. 8, 9). Amphipod abundance was highest at AKMAP station 35 (11,207 m^{-2}), located marginally at the entrance to Barrow Canyon in cell 77, and stations 36, 43, 48, and DF5 (6383-7330 m^{-2}), located on the shelf between Point Franklin and Icy Cape in cells 53, 54, and 64 (Fig. 8). Amphipod abundance values were generally lowest on the western portion of the analysis area, an area devoid of gray whale sightings based on aerial survey coverage. From Point Lay to Cape Lisburne up to 83 km from shore, amphipod abundance values were moderate, yet few gray whales were sighted.

Amphipod biomass was highest on the shelf between Wainwright and Icy Cape at AKMAP station 48 (125 gww m^{-2}) in cell 54, and AKMAP stations 35, 39, 47, and COMIDA station 48 (64-93 gww m^{-2}) on the western side of Barrow Canyon where the submarine canyon rises to meet the shelf in cells 76 and 77 (Fig. 9). As with the amphipod abundance, amphipod biomass was lowest in the western portion of the analysis area. Amphipod biomass was moderate 35 km northeast of Cape Lisburne and near Hanna Shoal; however, few gray whales were sighted in those areas.

3.5 Infauna as predictors of gray whale relative abundance

Predictions from the infaunal amphipod abundance (Fig. 10) and amphipod biomass (Fig. 11) GAMs reflected observed patterns in gray whale relative abundance (Fig. 8 and 9, respectively). The GAMs included a total of 672 gray whales that were sighted during 75,048 km of transect effort in 58 cells overlapping benthic sampling stations. The GAMs that included an infaunal covariate and survey effort fit the observed gray whale data better than the null model that included only survey effort, as measured by model selection methods ΔAIC, percent explained deviance, and RMSPE (Table 6). Furthermore, amphipod and other infauna abundance was a better predictor of gray whale relative abundance than biomass, based on all three quantitative criteria (Table 6). Finally, the best model overall was a function of infaunal amphipod abundance (Table 6). The GAMs predict the expected (mean) gray whale relative abundance for each cell, so it is anticipated that the observed values for each cell will be both higher and lower compared to the predictions. Predictions for gray whale relative abundance based on infaunal amphipod abundance were highest for cells 54 and 64 located on the shelf between Point Franklin and Icy Cape. These cells had the second and third highest gray whale sighting rates during the study period. Predictions for gray whale relative abundance based on infaunal amphipod biomass were highest for cells 45, 53, 54, 63, 64, 65, 76, and 77 located on the shelf between Point Franklin and Icy Cape and marginally at the entrance to Barrow Canyon, and cell 5 located near Cape Lisburne. Except for cell 5, these cells had some of the highest gray whale sighting rates. Predictions based on infaunal amphipod abundance and biomass were lowest for the western portion of the analysis area where there were few gray whale sightings.

4. Discussion

4.1 Distribution of feeding gray whales and amphipod availability

Study results provide quantitative empirical evidence that gray whale distribution, foraging, and habitat use are closely associated with the distribution, abundance, and biomass of infaunal amphipods in the northeastern Chukchi Sea. Infaunal amphipods, and possibly epibenthic amphipods, are likely the primary prey of gray whales in this area. Higher gray whale sighting rates during ASAMM 2009-2012 occurred near the benthic sampling stations with the highest amphipod densities; in contrast, stations with few amphipods had no gray whale sightings or the lowest sighting rates (Figs. 6, 7). Infaunal amphipod abundance and biomass were strong predictors of gray whale abundance (Figs. 8, 9). The model evaluation statistics suggest that infaunal abundance was a better predictor of contemporary gray whale relative abundance than infaunal biomass. These results were undoubtedly influenced by samples in cell 76, which had the highest amphipod biomass and the 4th highest other infaunal biomass, but a very low relative abundance of gray whales. Cell 76 included over 2300 km of aerial survey effort but only one benthic sample (3 August 2010). Amphipod abundance to the west and southwest of Point Lay and amphipod biomass near Hanna Shoal and to the northeast of Cape Lisburne were moderate; however, few gray whales were sighted in those areas. The area from Icy Cape to Point Barrow may provide a better foraging habitat because it is energetically more efficient for gray whales to feed on higher densities of amphipods.

Due to sample size limitations across time, model results were not extrapolated to predict gray whale relative abundance in the past or future. A variety of studies between 1986 and 2010 found high densities of amphipods between Icy Cape and Point Barrow (Feder et al. 1994; Grebmeier et al. 2006a; Blanchard and Feder 2014). In 2008-2010, amphipods dominated samples collected near feeding gray whales seen near Wainwright and along the Chukchi Sea coastline (Blanchard and Feder 2014). Blanchard and Feder (2014) reported the amphipod families of particular importance were Ampeliscidae (including *Byblis pearcyi*, *Byblis* spp.), Ischyroderidae (including *Ischyrocerus* spp.), and Isaeidae (including *Protomedeia* spp.). Few gray whales were seen and no amphipods were found in benthic samples collected from the northeastern Chukchi Sea Lease Sale 193 area (Fig. 2) (Blanchard and Feder 2014). Aerial surveys conducted in the northeastern Chukchi Sea in July-October 1982-1991 documented gray whale distribution and foraging behavior (Moore et al. 2000), with distributions and predominance of feeding behavior similar to the observations reported here (Clarke et al. 1989; Moore and Clarke 1992); due to differences in data collection methodology and survey platform, gray whale sighting rates from 2009-2012 cannot be directly compared to 1982-1991. In 1986, Feder et al. (1994) sampled benthic fauna at stations throughout the northeastern Chukchi Sea and collected high concentrations of amphipods (ranging 1562-6644 m^{-2}) at four coastal sampling stations near Point Franklin and one station offshore of Point Franklin in an area of high gray whale feeding occurrence from 1982 to 1991 (Clarke et al. 1989; Moore and Clarke 1992). The amphipod families Ampeliscidae (*Ampelisca eschrichti, Ampelisca macrocephala*, and *Byblis* spp.), Isaeidae (*Protomedeia* spp., *Photis* spp.), and Atylidae (now Dexaminidae) (*Atylus bruggeni*) dominated Feder et al.'s coastal stations.

The northeastern Chukchi Sea has been an important feeding ground for gray whales in summer and fall for decades. Gray whales were common from Icy Cape to Barrow in summer, and there are records of 22 gray whales taken by villagers off Point Barrow and Wainwright from 1925 to 1957 (Maher 1960; Marquette and Braham 1982). Feeding gray whales were documented in the Hanna Shoal region (located near 72°N and 162°W) in 1982-1991 (Moore and Clarke 1992), although the majority of the sightings occurred in 1986 (Ljungblad et al. 1987) and, therefore, may have been anomalous. Gray whales were rarely sighted on Hanna Shoal from 2009-2012. Minimal benthic sampling was conducted around Hanna Shoal from 1982-1991 because of the continued presence of sea ice in summer and fall; however, abundant tube-dwelling amphipods were collected in a sample taken there in 1988 (Nelson et al. 1994), and amphipods were found in two stations in 1986 (Feder et al. 1994), although not in the abundance that was found in the coastal sampling stations (Feder et al. 1994). In 2009-2012, amphipod abundance and biomass were not high at most COMIDA stations located on Hanna Shoal.

Gray whales forage where prey abundance and densities are high. They have been documented to shift their prey base to species that are abundant and energetically rich when biomass or prey density has decreased from gray whale predation or changing hydrographic conditions. Gray whales in Clayoquot Sound, Vancouver Island, Canada, fed on ampeliscid amphipods, but shifted to epibenthic mysids when amphipod biomass and density decreased from 1992 to 1996 (Feyrer and Duffus 2011). Conversely, in the 2001 feeding season in Clayoquot Sound, gray whales shifted from feeding on hyperbenthic mysids and pelagic porcelain crab larvae to benthic amphipods when large amphipods increased in body size (Dunham and Duffus 2001), likely increasing their caloric content (Highsmith and Coyle 1990, 1992); this shift may have coincided with the decline of planktonic prey abundance (Dunham and Duffus 2001). It also has been theorized that gray whale foraging on euphausiids in Monterey Bay, CA, in May 1999 was due to changes in prey availability during El Niño 1997-98 and La Niña 1999 (Benson et al. 2002). Gray whale distribution between Point Franklin and Icy Cape provides evidence for an intra-seasonal cycle in offshore distribution, shifting farther from shore in August. It is possible that intense feeding or changing hydrographic conditions reduced the density of available prey nearshore and gray whales moved farther offshore to available prey, either switching prey species or moving to denser amphipod patches. Arctic amphipods tend to produce dense patches rather than disperse widely (Coyle et al. 2007), which would make them susceptible to intense feeding by gray whales. Arctic amphipods also have slow growth rates and long generation times of up to six years (Coyle and Highsmith 1994), which means they are slow to recover from population declines.

5. Conclusions and Outlook

With the predicted effects of global climate change, the northeastern Chukchi Sea gray whale foraging area may undergo several changes. Global climate change has already resulted in warmer temperatures of the air and ocean, especially in the high northern latitudes; faster than anticipated rates of sea ice melting, the pace of which has increased since 2000; and sea level rise due to melting snow and sea ice (e.g., Frey et al. 2015; Jeffries et al. 2013; Wood et al. 2015). Longer periods of open water in the Arctic may lead to an increase in oil and gas development, shipping traffic, and tourism, and changes in marine biodiversity may lead to the commencement of commercial fishing in the Arctic (Huntington 2009; Huntington et al. 2015). The anthropogenic effects of increased human activity in the Arctic on marine mammals include increased risk of ship strikes, disrupted behavior (e.g., migrating, feeding, breeding, resting), environmental and noise pollution, habitat degradation, and the introduction of non-native species (Huntington 2009; Huntington et al. 2015; Moore et al. 2012; Reeves et al. 2014).

With climate change, the Bering and Chukchi seas are expected to experience an ecosystem shift from a benthic-dominated ecosystem to a pelagic-dominated ecosystem (Bluhm and Gradinger 2008; Grebmeier et al. 2006a). In addition, sea ice declines in both the southern and northern Bering Sea appear to be causing a northward shift in the cold water temperature barrier that limits crab and fish species (Grebmeier et al. 2010). This northward expansion of competitors for food could affect the size and type of prey available in the current benthic-dominated system (Coyle and Highsmith 1994). Furthermore, with the continued loss of sea ice, euphausiids, a predominantly herbivorous zooplankton, may increasingly be advected from the highly productive Bering Sea, in greater abundances, into the Arctic Ocean as the ecosystem changes from a benthic-dominated to a pelagic-dominated system. These Arctic ecosystem shifts are anticipated to change gray whale prey preferences accordingly, given the species' adaptive foraging strategy.

In addition to changing prey preferences, gray whales may also expand their range as arctic sea ice melts, to take advantage of new available areas. Gray whale distribution in the Arctic typically extends east to 155°W at the western extent of the Alaskan Beaufort Sea (Clarke et al. 2013) and west to 174°E near the northeastern Chukchi Sea/East Siberian Sea border (Shpak et al. 2013). Gray whales have occasionally been sighted as far east as the Canadian Beaufort Sea (Iwahara et al. 2016; Quakenbush et al. 2013; Rugh and Fraker 1981) and as far west as the Laptev Sea (Shpak et al. 2013), but their occurrence in those areas is considered extralimital or rare. Sea routes from the Pacific to Atlantic oceans (the Northwest Passage north of Alaska and through the Canadian Arctic Archipelago and the Northeast Passage across the northern coast of Eurasia) will remain open longer as arctic polar pack ice recedes. During the last 100,000 years when sea level and climatic conditions permitted, gray whales moved between the Pacific and Atlantic oceans at least several times (Alter et al. 2015). Recently, a gray whale was seen in the Mediterranean Sea (Scheinin et al. 2011) and another off the coast of Namibia (Elwen and Gridley 2013). These remarkable sightings can likely be attributed to longer and more extensive ice-free periods and may be more frequent with increasing sea ice melt.

Our study indicates the distribution and abundance of amphipods are a strong factor in determining gray whale distribution, behavior, and habitat use in the northeastern Chukchi Sea. Gray whale foraging locations are areas of high prey concentrations. The distribution of such locations may vary in space and time and, therefore, reflect changing environmental states in the North Pacific and Arctic oceans (Moore 2008). As such, the gray whale may be a sentinel of ecosystem changes and shifts to come resulting from predicted continued climate change effects (Moore 2008). To monitor and document ongoing and predicted trend changes, we recommend the following:

- Multi-decadal broad-scale aerial surveys;
- Pelagic and benthic prey sampling in areas of high gray whale occurrence, whether obviously feeding or not. Gray whale pelagic feeding behavior does not produce mud plumes and will be much harder to detect from aerial surveys.
- Broad-scale aerial surveys in June-July, which will be imperative to monitor the importance of this area to gray whales during annual sea ice retreat.

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Figures

Fig. 1 Gray whale analysis area boundary in the northeastern Chukchi Sea, 40-km x 40-km grid labeled by cell number, and 2009-2012 benthic sampling stations labeled by station ID.

Fig. 2 Aerial survey on-effort flightlines per year, 2009-2012, and total kilometers flown, 2009-2012 pooled, in the gray whale analysis area.

Fig. 3 Gray whale on-effort sightings per year, 2009-2012, and sighting rates per cell, all months (June-October) and all years (2009-2012) pooled. Cells labeled by cell ID number.

Fig. 4 Gray whale on-effort sightings and sighting rates per cell by year, all months pooled (June-October). 2009 (A), 2010 (B), 2011 (C), and 2012 (D). Cells labeled by cell ID number.

Fig. 5 Gray whale on-effort sighting rates by month and year.

Fig. 6 Gray whale on-effort sightings and sighting rates per cell by month, all years pooled (2009-2012). June (A), July (B), August (C), September (D), and October (E). Cells labeled by cell ID number.

Fig. 7 Infaunal amphipod abundance (individuals m^{-2}) (A) and biomass (gww m^{-2}; gww = grams wet weight) (B) relative to other infaunal abundance and biomass at benthic sampling stations.

Fig. 8 Gray whale sighting rates per cell, July-August 2009-2010, September 2011, and August 2012 pooled (cells with gray whale sightings labeled by cell number). Infaunal amphipod abundance (individuals m^{-2}) at benthic sampling stations, COMIDA and AKMAP data, July-August 2009-2010, September 2011, and August 2012 pooled.

Fig. 9 Gray whale sighting rates per cell, July-August 2009-2010, September 2011, and August 2012 pooled (cells with gray whale sightings labeled by cell number). Infaunal amphipod biomass (gww m^{-2}; gww = grams wet weight) at benthic sampling stations, COMIDA and AKMAP data, July-August 2009-2010, September 2011, and August 2012 pooled.

Fig. 10 Gray whale sighting rates per cell (labeled by cell number), predicted by infaunal amphipod abundance model. Sighting rates were predicted for cells that fell within the gray whale analysis area and contained both benthic samples and aerial survey effort. Data were pooled across time.

Fig. 11 Gray whale sighting rates per cell (labeled by cell number), predicted by infaunal amphipod biomass model. Sighting rates were predicted for cells that fell within the gray whale analysis area and contained both benthic samples and aerial survey effort. Data were pooled across time.

Table 2 Summary of kilometers on-effort (tr-km), number of gray whale sightings and individuals on-effort, and sighting rates (whales per on-effort kilometer)

	Jun				Jul				Aug			
Year	on-effort-km	sightings	whales	whales/ on-effort-km	on-effort-km	sightings	whales	whales/ on-effort-km	on-effort-km	sightings	whales	whales/ on-effort-km
2009	1313	9	15	0.0114	5273	38	73	0.0138	3984	48	75	0.0188
2010	0	0	0	0.0000	7183	30	43	0.0060	3977	18	30	0.0075
2011	3982	16	25	0.0063	4911	41	61	0.0124	6847	33	40	0.0058
2012	491	0	0	0.0000	10831	109	210	0.0194	6825	59	125	0.0183
Total	5786	25	40	0.0069	28198	218	387	0.0137	21633	158	270	0.0125

	Sep				Oct				Total			
Year	on-effort-km	sightings	whales	whales/ on-effort-km	on-effort-km	sightings	whales	whales/ on-effort-km	on-effort-km	sightings	whales	whales/ on-effort-km
2009	7218	19	21	0.0029	4722	11	16	0.0034	22511	125	200	0.0089
2010	5213	4	4	0.0008	3542	2	2	0.0006	19915	54	79	0.0040
2011	8998	32	49	0.0054	3012	7	9	0.0030	27750	129	184	0.0066
2012	8203	14	20	0.0024	7939	25	35	0.0044	34289	207	390	0.0114
Total	29632	69	94	0.0032	19216	45	62	0.0032	104464	515	853	0.0082

Table 2 Infaunal amphipod abundance (N m^{-2}) and biomass (gww m^{-2}; gww = grams wet weight) at AKMAP benthic grab sampling stations, August-September 2010, September 2011, August 2012. All months and years pooled.

Infaunal Grab Sampling Station	Amphipod Abundance (N m^{-2})	Amphipod Biomass (gww m^{-2})
AKCH10-001	126.7	0.213
AKCH10-002	180.0	1.137
AKCH10-003	570.0	2.265
AKCH10-004	23.3	0.052
AKCH10-005	816.7	1.492
AKCH10-006	653.3	48.933
AKCH10-007	1446.7	3.317
AKCH10-008	680.0	4.05
AKCH10-009	1196.7	1.957
AKCH10-010	46.7	0.34
AKCH10-011	1303.3	1.675
AKCH10-012	133.3	0.172
AKCH10-013	16.7	0.057
AKCH10-014	483.3	1.54
AKCH10-015	516.7	2.92
AKCH10-016	36.7	0.062
AKCH10-017	123.3	0.098
AKCH10-018	263.3	1.17
AKCH10-019	26.7	0.213
AKCH10-020	23.3	3.113
AKCH10-021	120.0	1.722
AKCH10-022	36.7	0.287
AKCH10-023	200.0	0.357
AKCH10-024	20.0	0.033
AKCH10-026	36.7	0.263
AKCH10-027	1193.3	2.473
AKCH10-029	213.3	2.393
AKCH10-030	143.3	0.245
AKCH10-105	273.3	0.347
AKCH11-032	261.7	1.375
AKCH11-034	90.0	0.233
AKCH11-035	11206.7	64.443

AKCH11-036	7111.7	39.269
AKCH11-037	1680.0	14.350
AKCH11-038	223.3	0.482
AKCH11-039	2120.0	93.030
AKCH11-040	120.0	3.210
AKCH11-041	83.3	0.197
AKCH11-042	153.3	0.252
AKCH11-043	6546.7	36.217
AKCH11-044	1860.0	18.005
AKCH11-045	326.7	0.835
AKCH11-046	313.3	6.192
AKCH11-047	2410.0	71.433
AKCH11-048	6383.3	125.077
AKCH11-049	4420.0	52.890
AKCH11-050	60.0	0.175
AKCH11-052	1050.0	2.618
AKCH11-053	993.3	14.497
AKCH11-054	236.7	0.517
AKCH11-055	4493.3	23.557
AKCH11-056	356.7	1.297
AKCH11-057	1836.7	9.187
AKCH11-058	70.0	0.457
AKCH11-060	983.3	45.192
AKCH11-062	2490.0	28.375
AKCH11-064	780.0	2.073
AKCH11-069	193.3	1.013
AKCH12-01	190.0	1.480
AKCH12-05	2080.0	5.485
AKCH12-06	3580.0	18.515
AKCH12-09	2830.0	9.060
AKCH12-DF001	1300.0	33.770
AKCH12-DF003	3230.0	32.370
AKCH12-DF005	7330.0	37.470

Table 3 Infaunal amphipod abundance (N m^{-2}) and biomass (gww m^{-2}; gww = grams wet weight) by taxa from AKMAP benthic grab sampling stations, August-September 2010, September 2011, August 2012. All stations, months, and years pooled.

Infaunal Grab Amphipod Taxa	Amphipod Abundance (N m^{-2})	Amphipod Biomass (gww m^{-2})
Acanthonotozoma monodenatum	8.3	0.235
Aceroides latipes	33.3	0.082
Ampelisca birulai	2,135.0	28.785
Ampelisca eschrichti	3,168.3	206.908
Ampelisca macrocephala	3,381.7	212.550
Ampelisca sp.	5,173.3	18.967
Amphipoda	9,015.0	43.507
Anonyx nugax	263.3	30.163
Anonyx sp.	10.0	0.023
Arctolembos arcticus	370.0	45.585
Argissa hamatipes	3.3	0.010
Arrhis luthkei	3.3	0.013
Atylus bruggeni	20.0	0.485
Bathymedon sp.	175.0	0.242
Byblis frigidis	1,086.7	51.337
Byblis gaimardi	10.0	0.513
Byblis pearcyi	16.7	0.653
Byblis robustus	21.7	0.788
Byblis sp.	3,181.7	11.588
Cheirimedeia macrodactyla	183.3	0.273
Cheirimedeia similicarpa	460.0	0.560
Cheirimedeia sp.	448.3	0.697
Crassicorophium crassicorne	576.7	0.913
Crassicorophium salmonis	223.3	0.363
Crassicorophium sp.	1,903.3	2.815
Deflexilodes sp.	6.7	0.015
Desdimelita desdichada	3,620.0	37.983
Dulichia sp.	3.3	0.007
Dyopedos arcticus	138.3	0.605
Eohaustorius eous	620.0	1.404
Ericthonius difformis	633.3	2.745
Ericthonius sp.	383.3	0.423
Grandifoxus sp.	1,378.3	2.048
Grandifoxus vulpinus	2,926.7	7.258
Guernea sp.	195.0	0.144
Haploops laevis	295.0	3.405

Harpinia serrata	36.7	0.067
Harpinia sp.	50.0	0.030
Harpiniopsis gurjanovae	3.3	0.007
Harpiniopsis kobjakovae	1,648.3	2.013
Hippomedon denticulatus	76.7	6.017
Hippomedon sp.	230.0	8.605
Isaeidae	590.0	0.880
Ischyrocerus latipes	1,326.7	12.410
Ischyrocerus megalops	86.7	0.205
Ischyrocerus sp.	4,246.7	4.859
Kroyera sp.	8.3	0.017
Lysianassidae	16.7	0.030
Machaironyx muelleri	678.3	0.972
Maera danae	1,355.0	13.272
Megamoera denata	690.0	5.360
Melita sp.	3.3	0.040
Melitidae	13.3	0.060
Monoculodes sp.	210.0	0.820
Monoculopsis longicornis	206.7	0.258
Odius cassigerus	11.7	0.030
Oedicerotidae	1,030.0	1.172
Onisimus krassini	10.0	0.100
Orchomene sp.	2,248.3	6.322
Photis sp.	680.0	0.739
Photis vinogradovi	9,598.3	24.640
Phoxocephalidae	63.3	0.102
Pleustes cataphractus	3.3	0.023
Pleustes panoplus	75.0	0.320
Pleustes sp.	6.7	0.023
Pleustidae	670.0	1.360
Podoceridae	160.0	0.157
Pontoporeia femorata	3,133.3	31.673
Priscillina armata	66.7	0.813
Protomedeia fasciata	1,671.7	4.395
Protomedeia sp.	18,370.0	38.019
Protomedeia stephenseni	153.3	0.440
Rhachotrophis sp.	5.0	0.088
Stenothoidae	535.0	0.783
Syrrhoe crenulata	26.7	0.102
Tiron biocellata	111.7	0.283
Unicola sp.	86.7	1.517
Westwoodia caecula	10.0	0.050
Westwoodilla caecula	105.0	0.277

Westwoodia sp.	40.0	0.082

Table 4 Epibenthic amphipod abundance (N/km^{-2}) and biomass (kg/km^{-2}) by taxa from AKMAP benthic beam trawl sampling stations, August-September 2010, September 2011. All stations, months, and years pooled.

Epibenthic Beam Trawl Amphipod Taxa	Amphipod Abundance (N/km^{-2})	Amphipod Biomass (kg/km^{-2})
Stegocephalidae	5,552,582	4,236
Uristidae	8,081,258	8,922

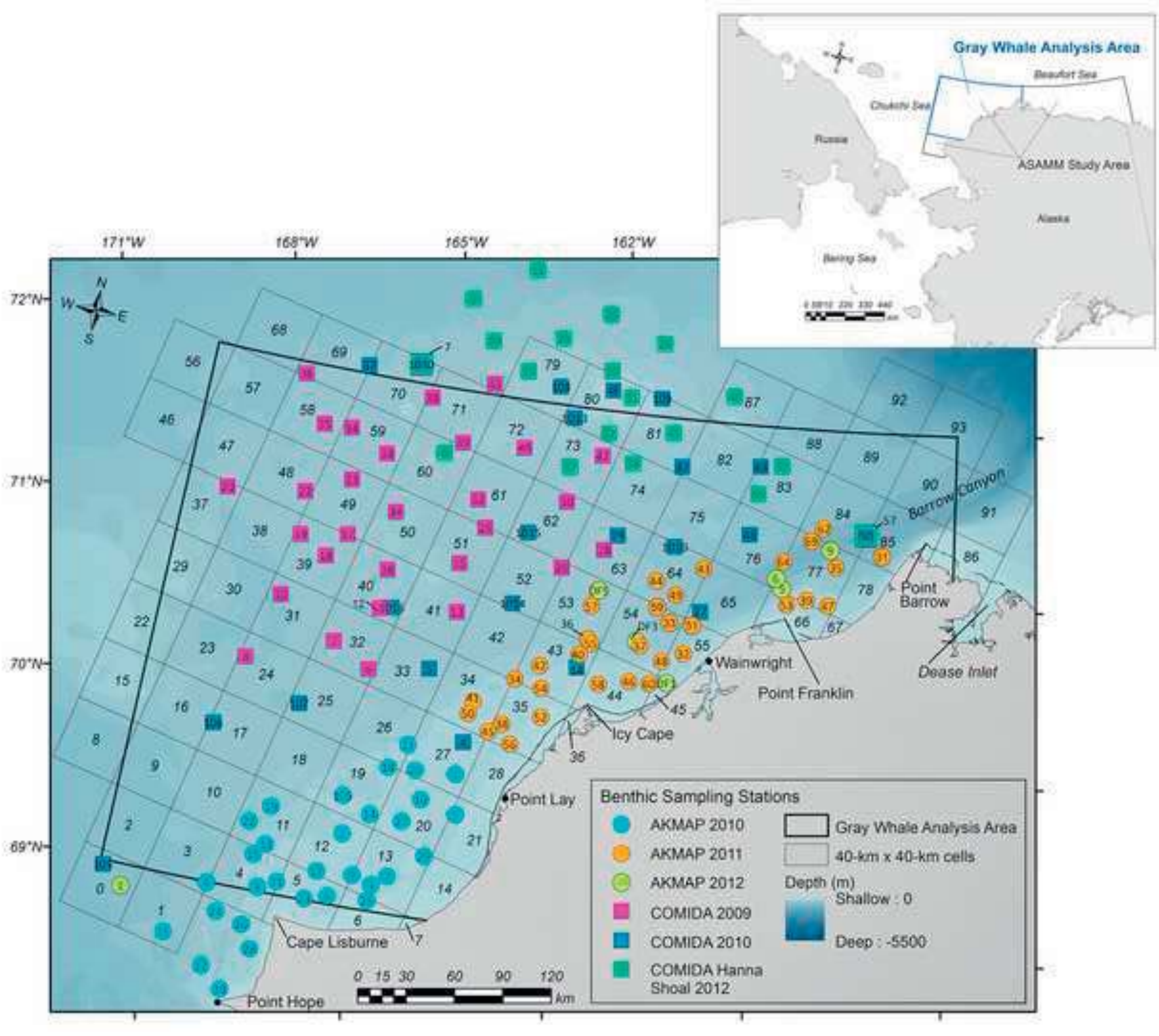
Table 5 Epibenthic amphipod abundance (N km^{-2}) and biomass (kg km^{-2}) at benthic beam trawl sampling stations, August-September 2010, September 2011. All months and years pooled.

Epibenthic Beam Trawl Sampling Station	Amphipod Abundance (N km^{-2})	Amphipod Biomass (kg km^{-2})
AKCH10-005	39,024	59
AKCH10-011	57,416	96
AKCH10-027	3,731	7
AKCH11-031	1,502,252	1,502
AKCH11-032	620,512	554
AKCH11-033	1,538,831	1,223
AKCH11-036	411,279	381
AKCH11-037	41,022	62
AKCH11-040	11,995	12
AKCH11-043	1,772,673	1,462
AKCH11-044	140,393	421
AKCH11-046	211,221	288
AKCH11-047	689,788	796
AKCH11-048	1,326,216	1,194
AKCH11-049	1,873,922	1,153
AKCH11-051	158,800	204
AKCH11-053	2,074,492	1,852
AKCH11-055	26,389	53
AKCH11-056	33,995	34
AKCH11-057	315,821	416
AKCH11-058	61,024	163
AKCH11-059	440,322	660
AKCH11-060	282,721	565

Table 6 Model evaluation statistics to compare the null model to the generalized additive models predicting gray whale sighting rates based on infaunal amphipod abundance or biomass

	∆AIC	% Explained Deviance	RMSPE
null model	25.1	NA	27.7
Infaunal amphipod abundance	0.0	69.4	13.5
Infaunal amphipod biomass	7.0	61.7	19.0
Other infaunal abundance	18.2	43.0	25.5
Other infaunal biomass	24.8	32.4	28.8

Figure


Gray Whale Analysis Area
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Barrow Canyon
Point Barrow
Dease Inlet
Point Franklin
Wainwright
Icy Cape
Point Lay
Cape Lisburne
Point Hope
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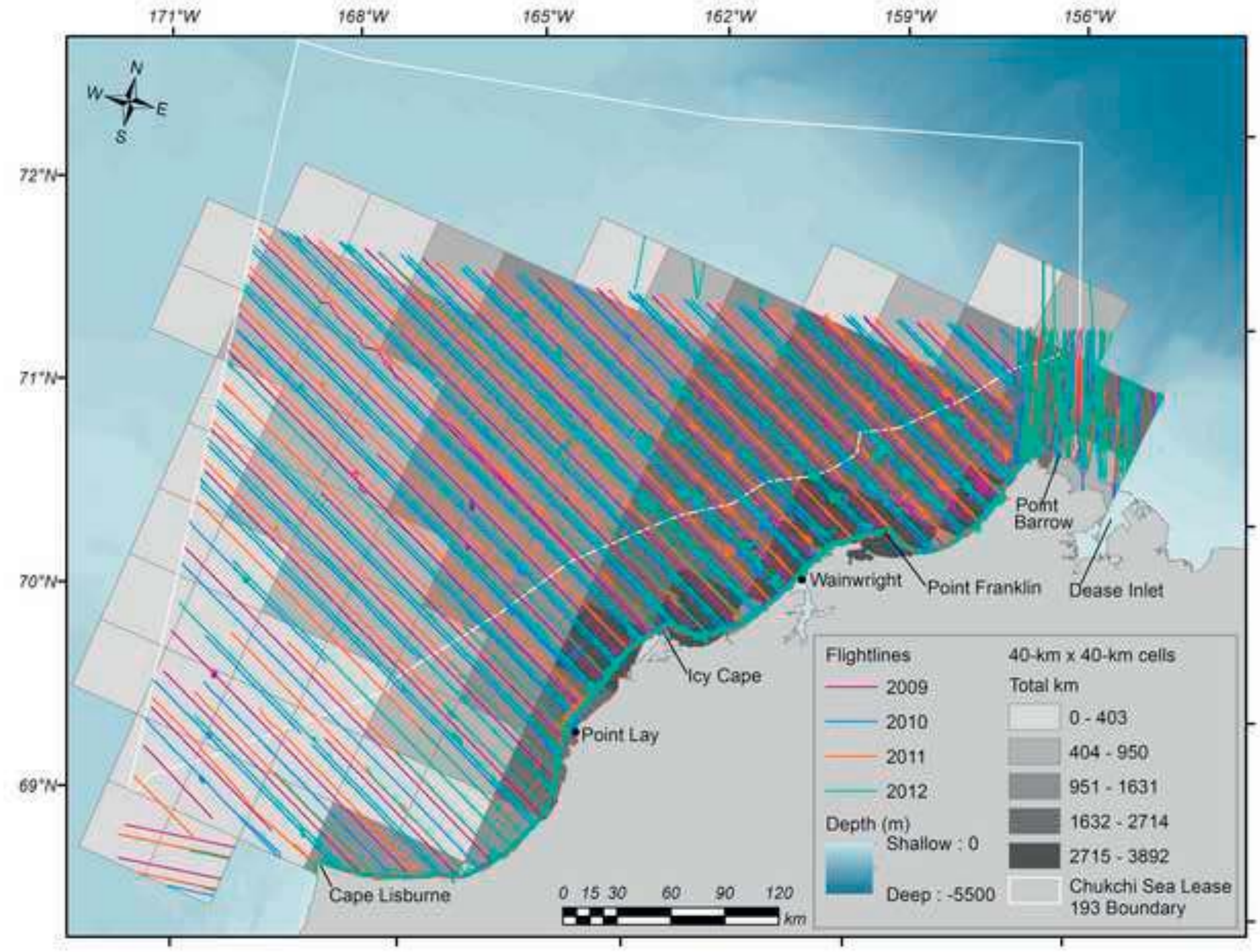
km
Benthic Sampling Stations
AKMAP 2010
AKMAP 2011
AKMAP 2012
COMIDA 2009
COMIDA 2010
COMIDA Hanna Shoal 2012
Gray Whale Analysis Area
40-km x 40-km cells
Depth (m)
Shallow : 0
Deep : -5500

Figure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72°N
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70°N
69°N
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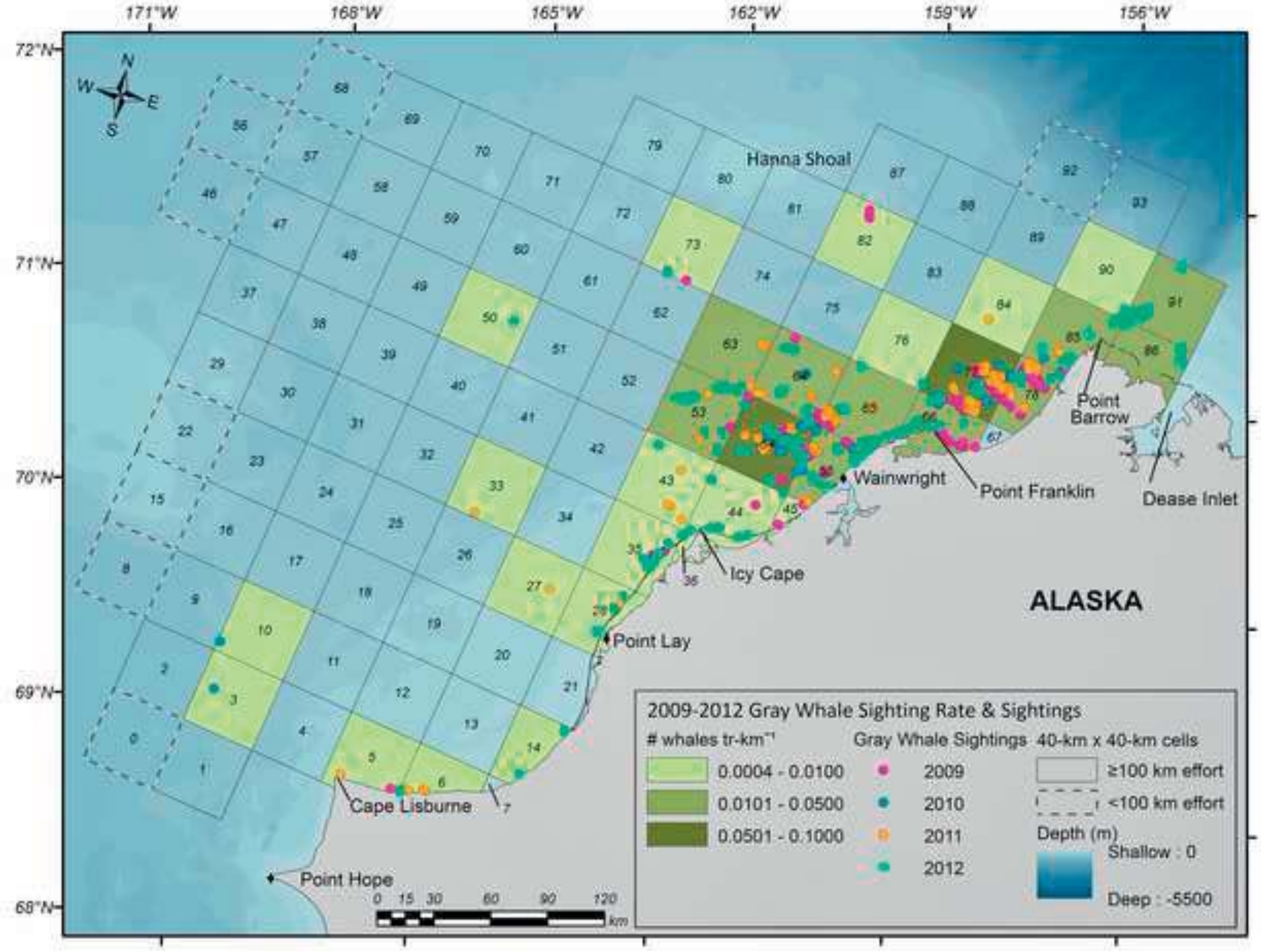
Point Barrow
Wainwright
Point Franklin
Dease Inlet
Icy Cape
Point Lay
Cape Lisburne
0 15 30 60 90 120 km
Flightlines
2009
2010
2011
2012
Depth (m)
Shallow : 0
Deep : -5500
40-km x 40-km cells
Total km
0 - 403
404 - 950
951 - 1631
1632 - 2714
2715 - 3892
Chukchi Sea Lease 193 Boundary

Figure



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km
2009-2012 Gray Whale Sighting Rate & Sightings
whales tr-km⁻¹
0.0004 - 0.0100
0.0101 - 0.0500
0.0501 - 0.1000
Gray Whale Sightings
2009
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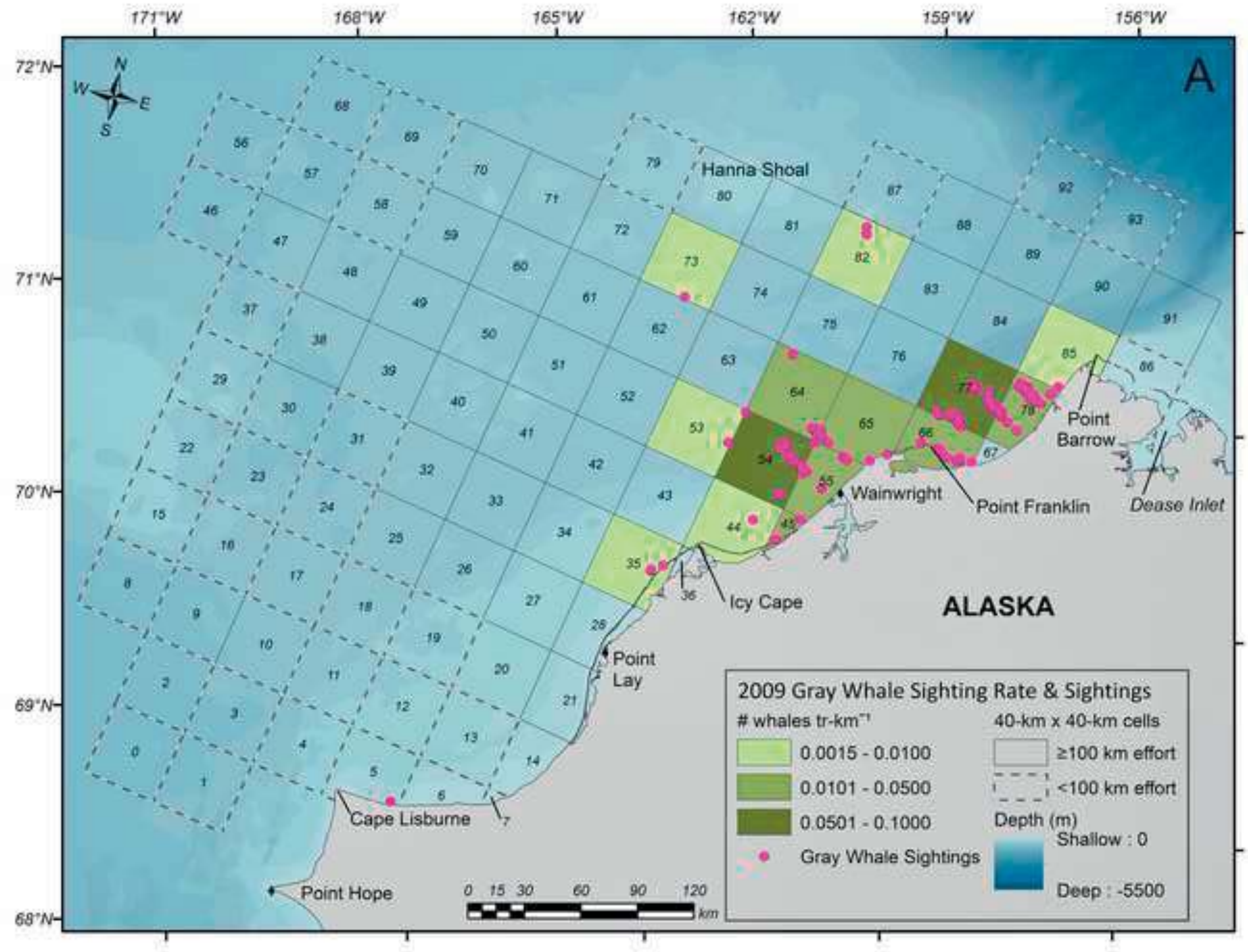
2011
2012
40-km x 40-km cells
≥100 km effort
<100 km effort
Depth (m)
Shallow : 0
Deep : -5500

Figure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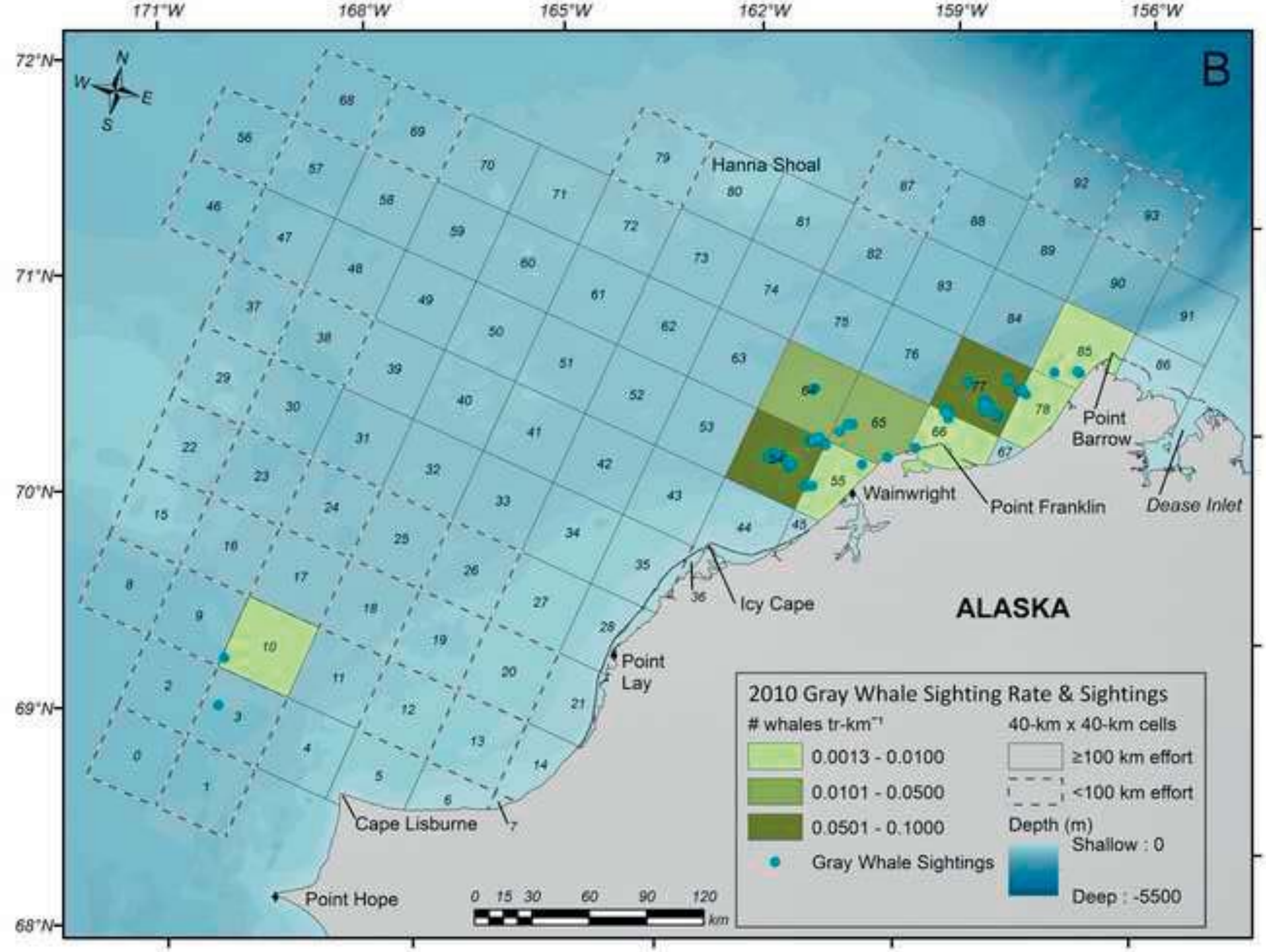
2009 Gray Whale Sighting Rate & Sightings
whales tr-km⁻¹
0.0015 - 0.0100
0.0101 - 0.0500
0.0501 - 0.1000
Gray Whale Sightings
40-km x 40-km cells
≥100 km effort
<100 km effort
Depth (m)
Shallow : 0
Deep : -5500
0 15 30 60 90 120 km

Figure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Cape Lisburne
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2010 Gray Whale Sighting Rate & Sightings
whales tr-km⁻¹
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0.0101 - 0.0500
0.0501 - 0.1000
Gray Whale Sightings
40-km x 40-km cells
≥100 km effort
<100 km effort
Depth (m)
Shallow : 0
Deep : -5500
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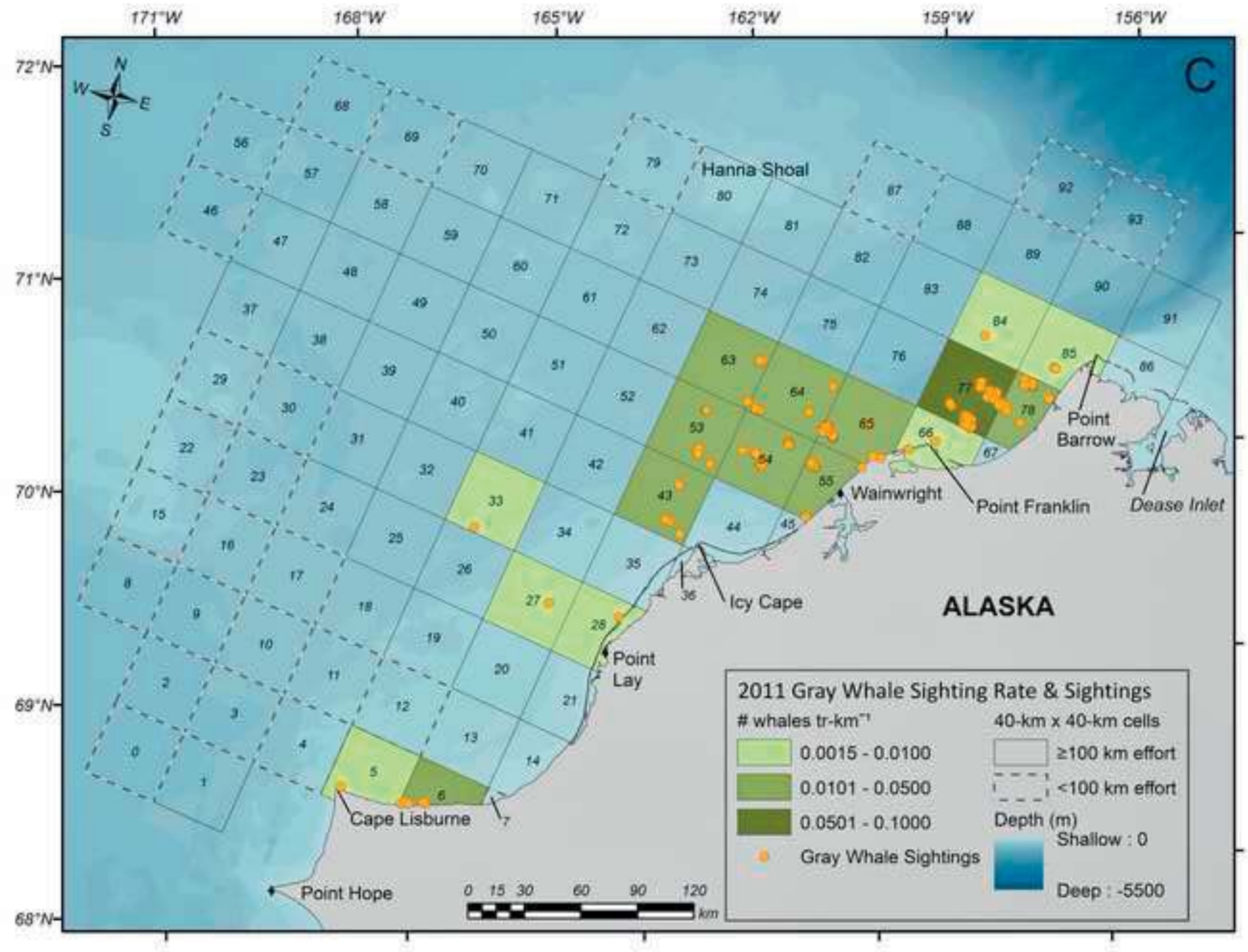
Figure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ALASKA
2011 Gray Whale Sighting Rate & Sightings
whales tr-km⁻¹
0.0015 - 0.0100
0.0101 - 0.0500
0.0501 - 0.1000
Gray Whale Sightings
40-km x 40-km cells
≥100 km effort
<100 km effort
Depth (m)
Shallow : 0
Deep : -5500
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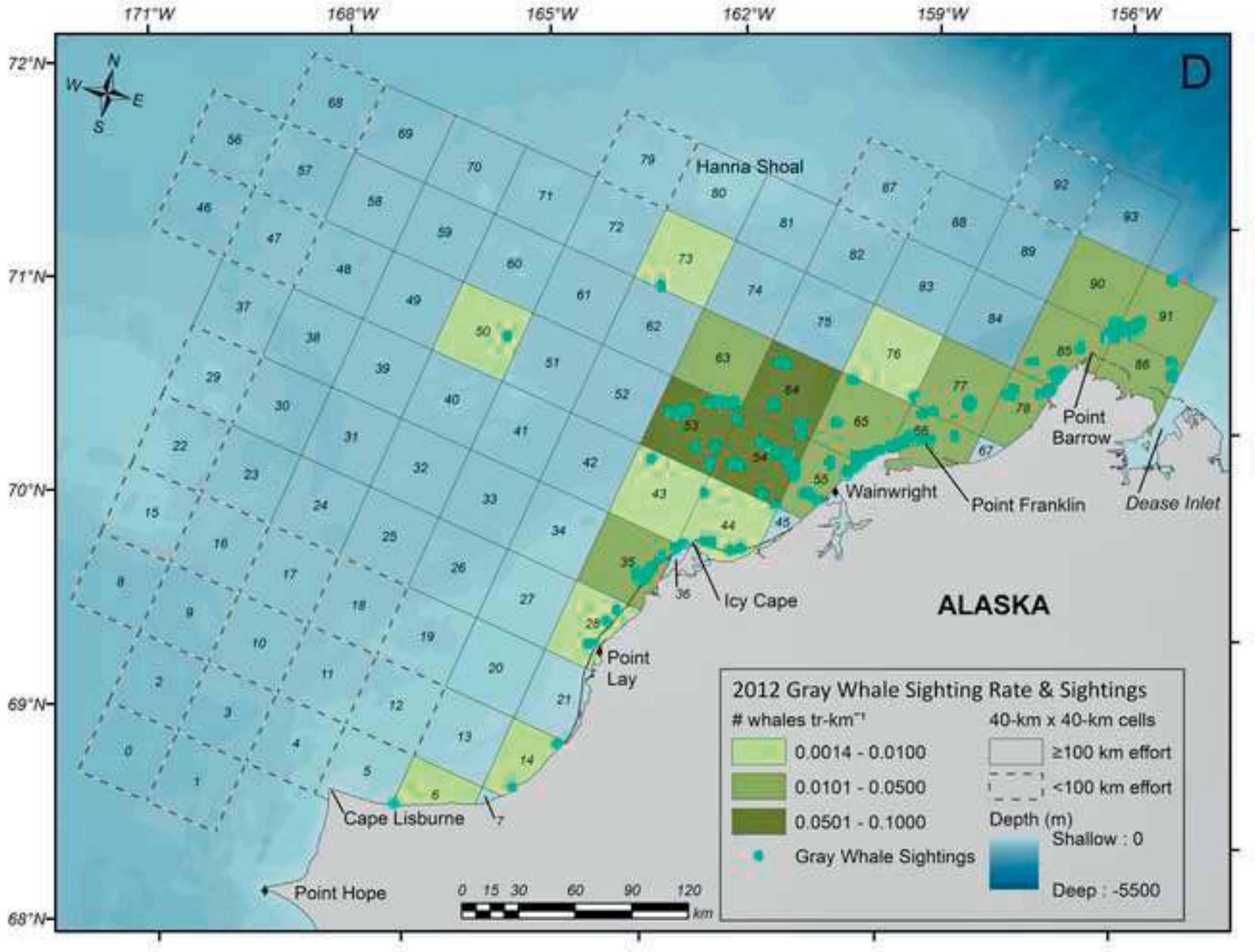
Figure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Icy Cape
Point Lay
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ALASKA
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2012 Gray Whale Sighting Rate & Sightings
whales tr-km⁻¹
0.0014 - 0.0100
0.0101 - 0.0500
0.0501 - 0.1000
Gray Whale Sightings
40-km x 40-km cells
≥100 km effort
<100 km effort
Depth (m)
Shallow : 0
Deep : -5500
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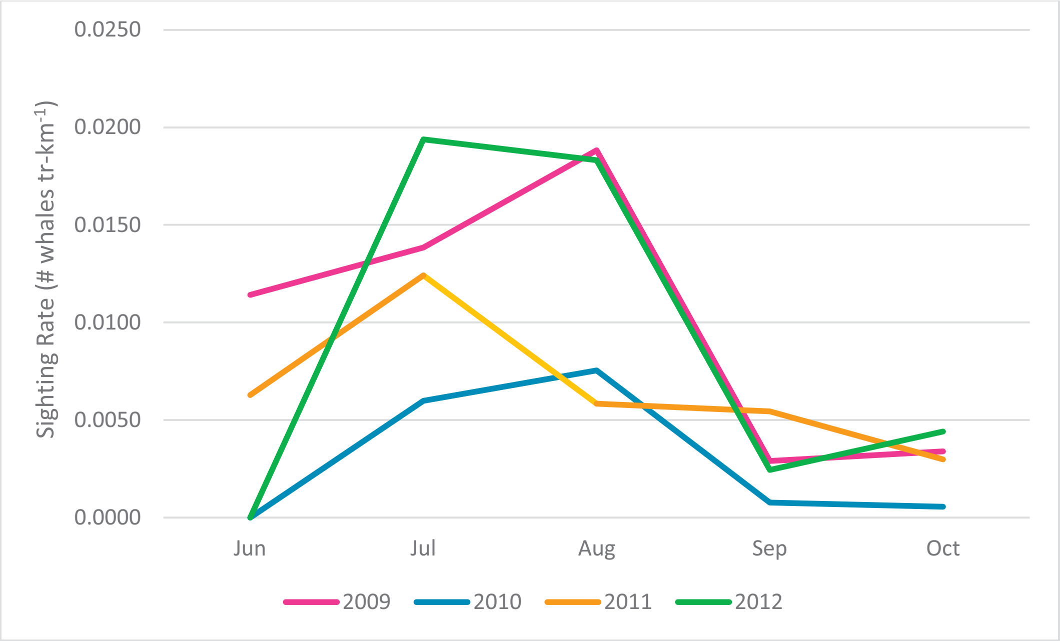
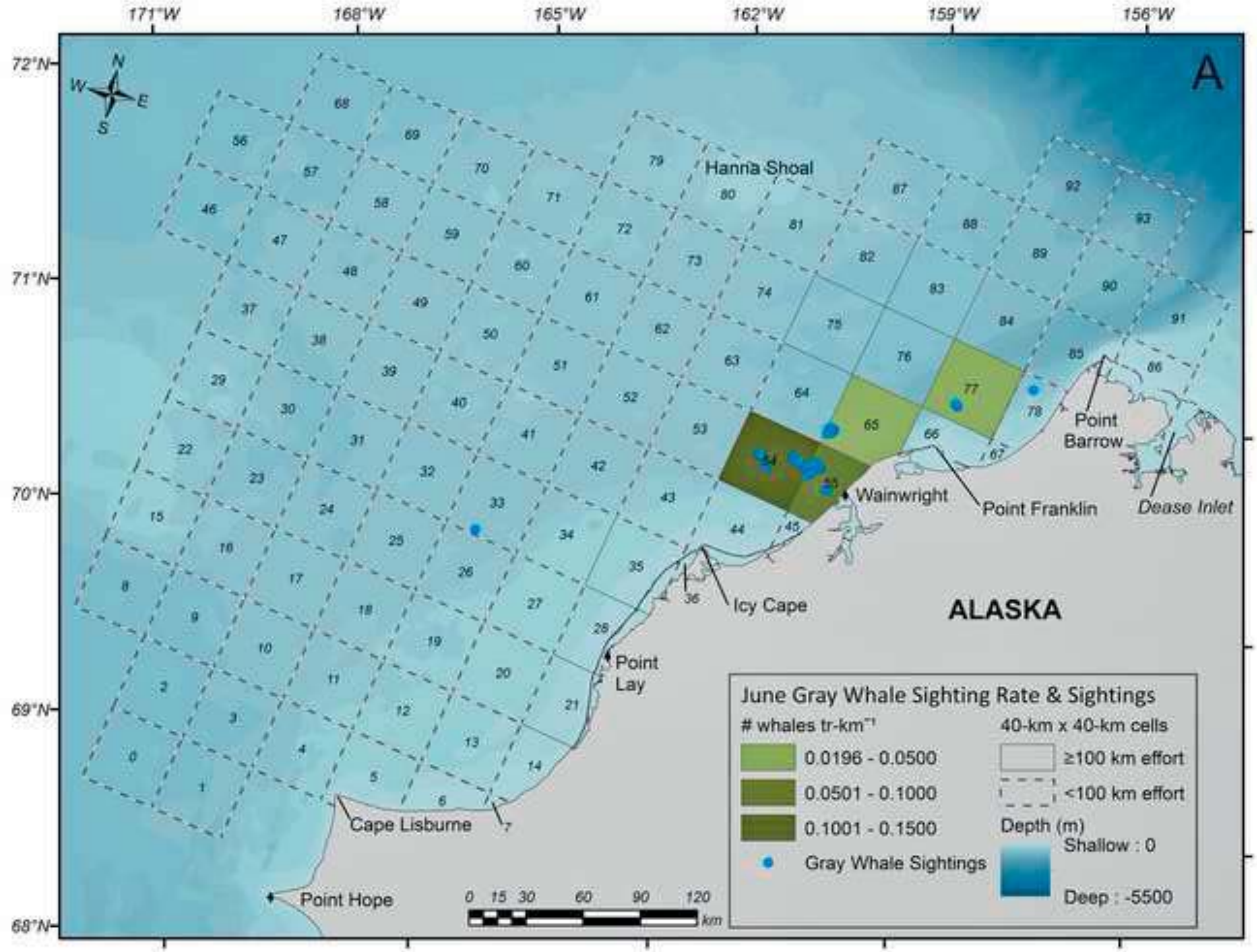
Figure



0.0250
0.0200
0.0150
0.0100
0.0050
0.0000
Sighting Rate (# whales tr-km-1)
Jun
Jul
Aug
Sep
Oct
2009
2010
2011
2012

Figure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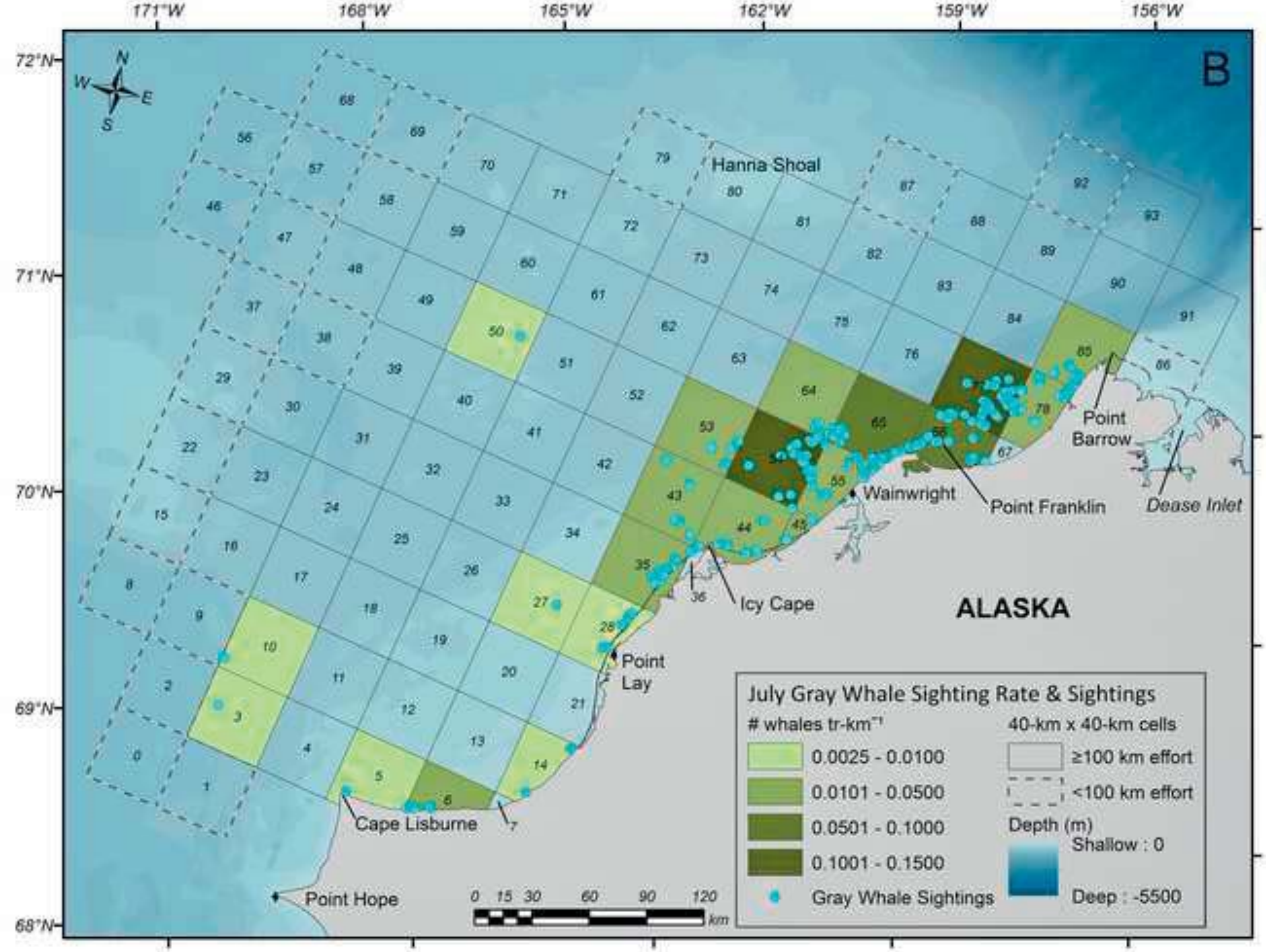
165°W
162°W
159°W
156°W
72°N
71°N
70°N
69°N
68°N
N
W
E
S
Hanna Shoal
Point Barrow
Dease Inlet
Point Franklin
Wainwright
Icy Cape
Point Lay
Cape Lisburne
Point Hope
ALASKA
0 15 30 60 90 120 km
June Gray Whale Sighting Rate & Sightings
whales tr-km⁻¹
0.0196 - 0.0500
0.0501 - 0.1000
0.1001 - 0.1500
Gray Whale Sightings
40-km x 40-km cells
≥100 km effort
<100 km effort
Depth (m)
Shallow : 0
Deep : -5500

Figure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165°W
162°W
159°W
156°W
72°N
71°N
70°N
69°N
68°N
Hanna Shoal
Point Barrow
Dease Inlet
Point Franklin
Wainwright
Icy Cape
36
ALASKA
Point Lay
Cape Lisburne
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Point Hope
0 15 30 60 90 120
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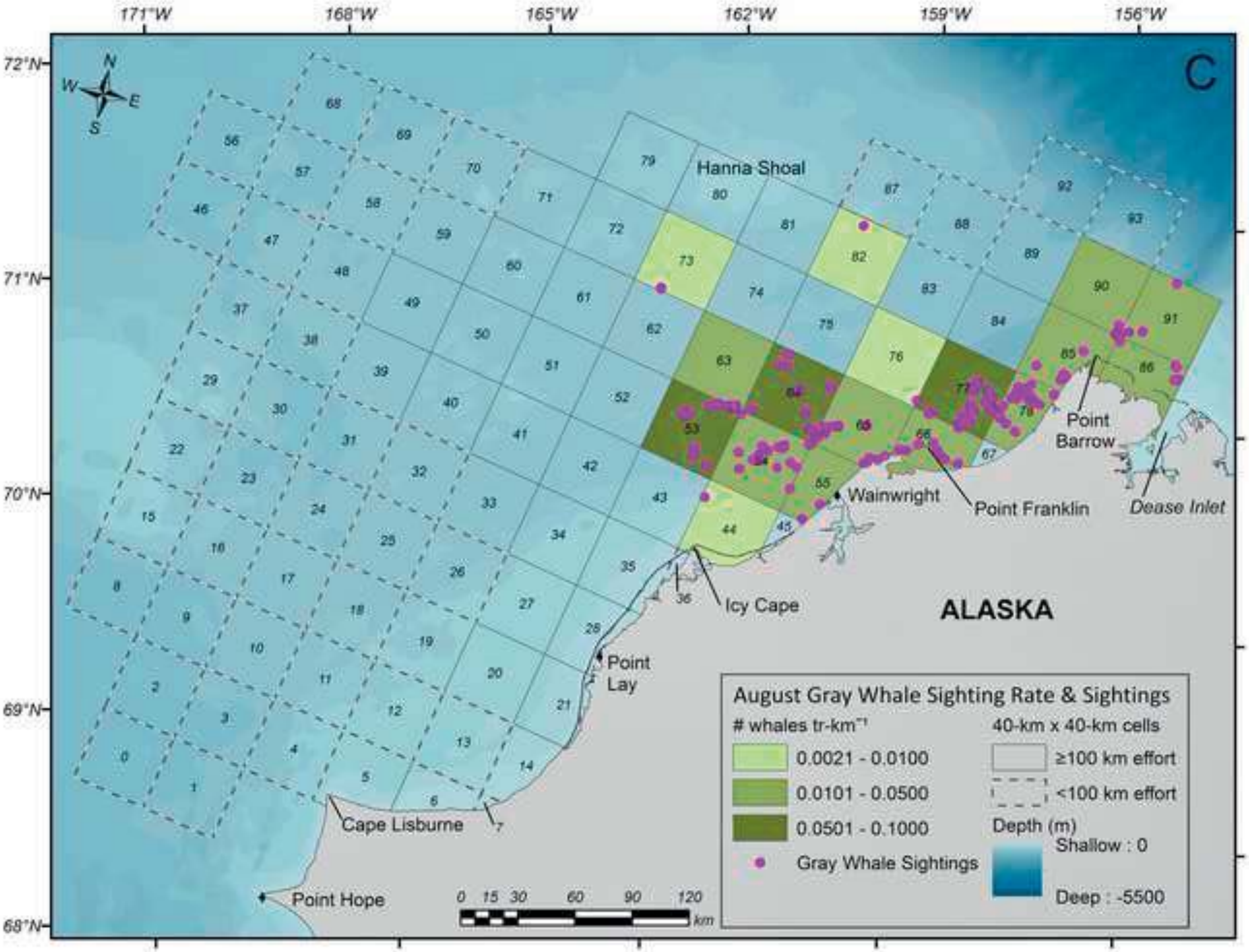
July Gray Whale Sighting Rate & Sightings
whales tr-km⁻¹
0.0025 - 0.0100
0.0101 - 0.0500
0.0501 - 0.1000
0.1001 - 0.1500
Gray Whale Sightings
40-km x 40-km cells
≥100 km effort
<100 km effort
Depth (m)
Shallow : 0
Deep : -5500

Figure



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162°W
159°W
156°W
72°N
71°N
70°N
69°N
68°N
Hanna Shoal
Point Barrow
Dease Inlet
Point Franklin
Wainwright
Icy Cape
Point Lay
Cape Lisburne
Point Hope
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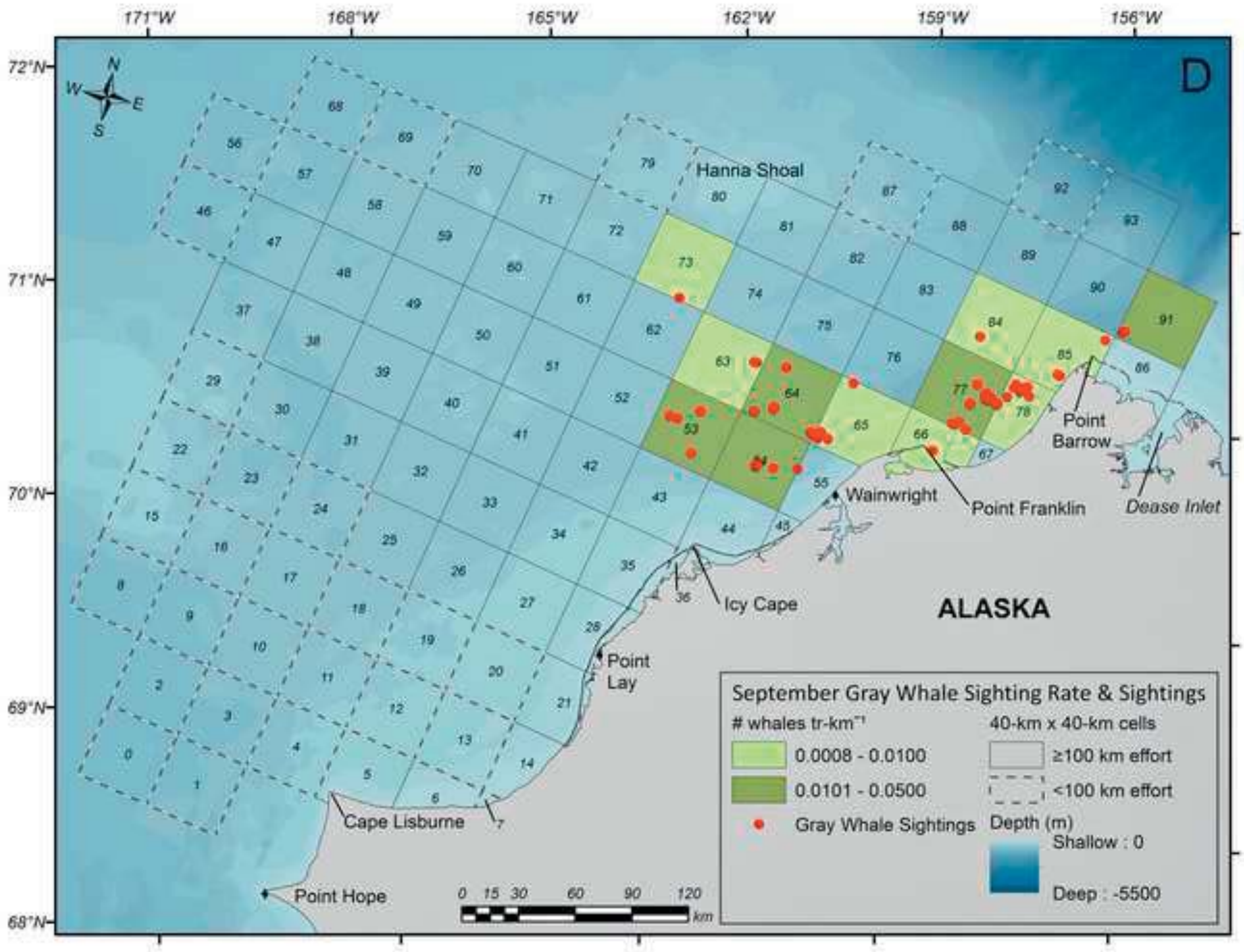
0 15 30 60 90 120
km
August Gray Whale Sighting Rate & Sightings
whales tr-km⁻¹
0.0021 - 0.0100
0.0101 - 0.0500
0.0501 - 0.1000
Gray Whale Sightings
40-km x 40-km cells
≥100 km effort
<100 km effort
Depth (m)
Shallow : 0
Deep : -5500

Figure


D
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171°W
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165°W
162°W
159°W
156°W
72°N
71°N
70°N
69°N
68°N
Hanna Shoal
Point Barrow
Dease Inlet
Point Franklin
Wainwright
Icy Cape
Point Lay
Cape Lisburne
Point Hope
ALASKA
0 15 30 60 90 120
km
September Gray Whale Sighting Rate & Sightings
whales tr-km⁻¹
0.0008 - 0.0100
0.0101 - 0.0500
Gray Whale Sightings
40-km x 40-km cells
≥100 km effort
<100 km effort
Depth (m)
Shallow : 0
Deep : -5500
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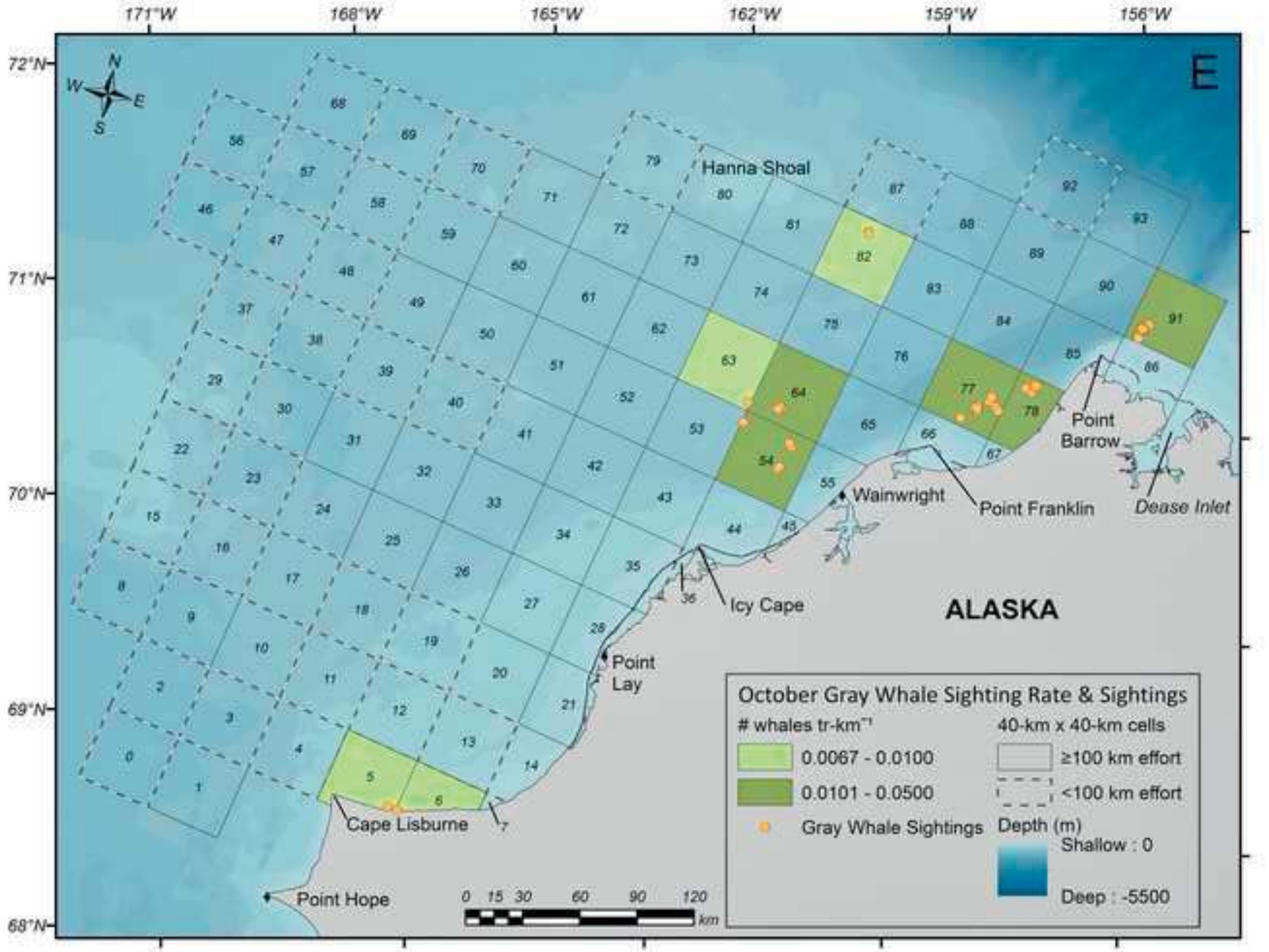
Figure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165°W
162°W
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156°W
72°N
71°N
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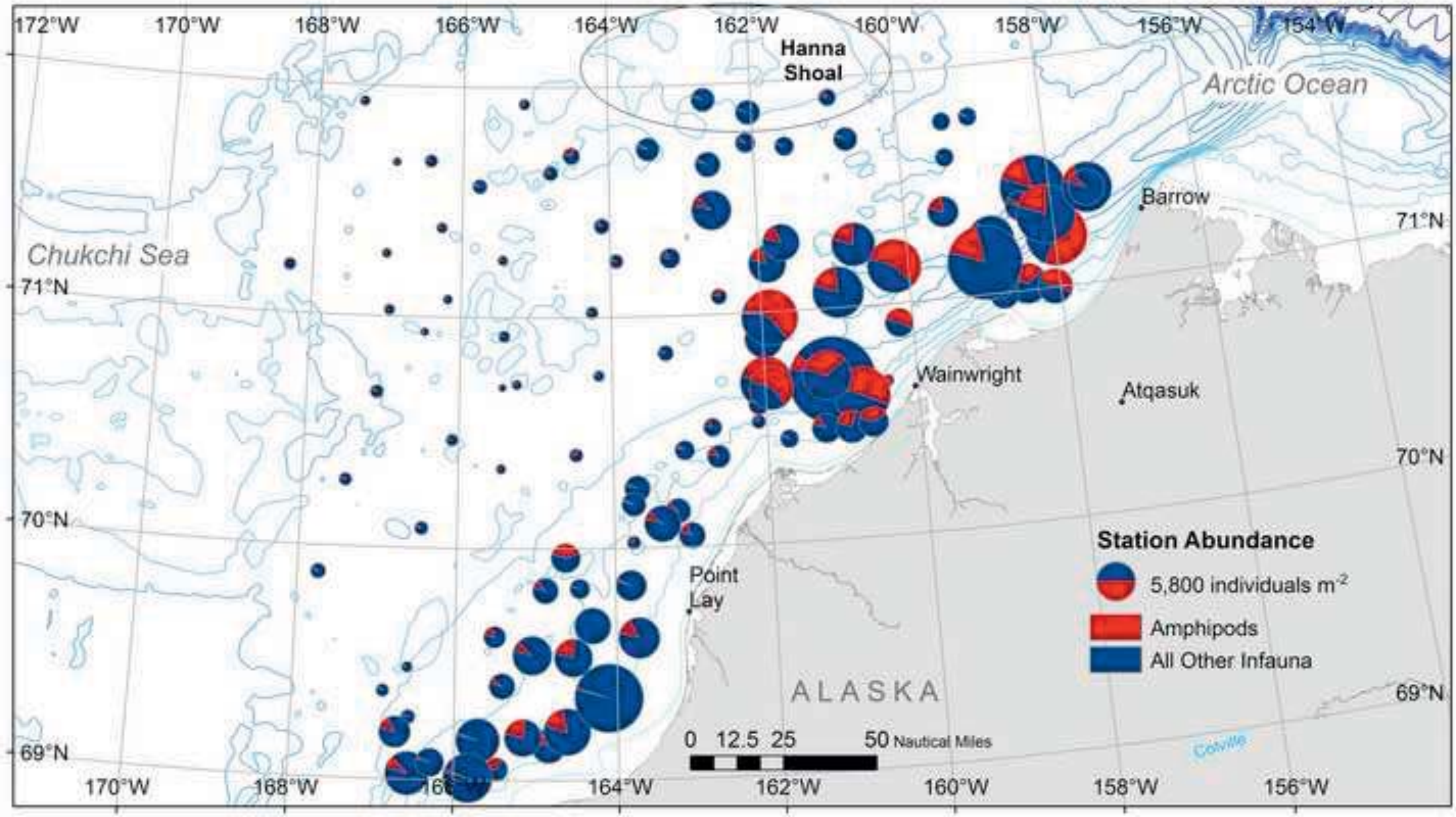
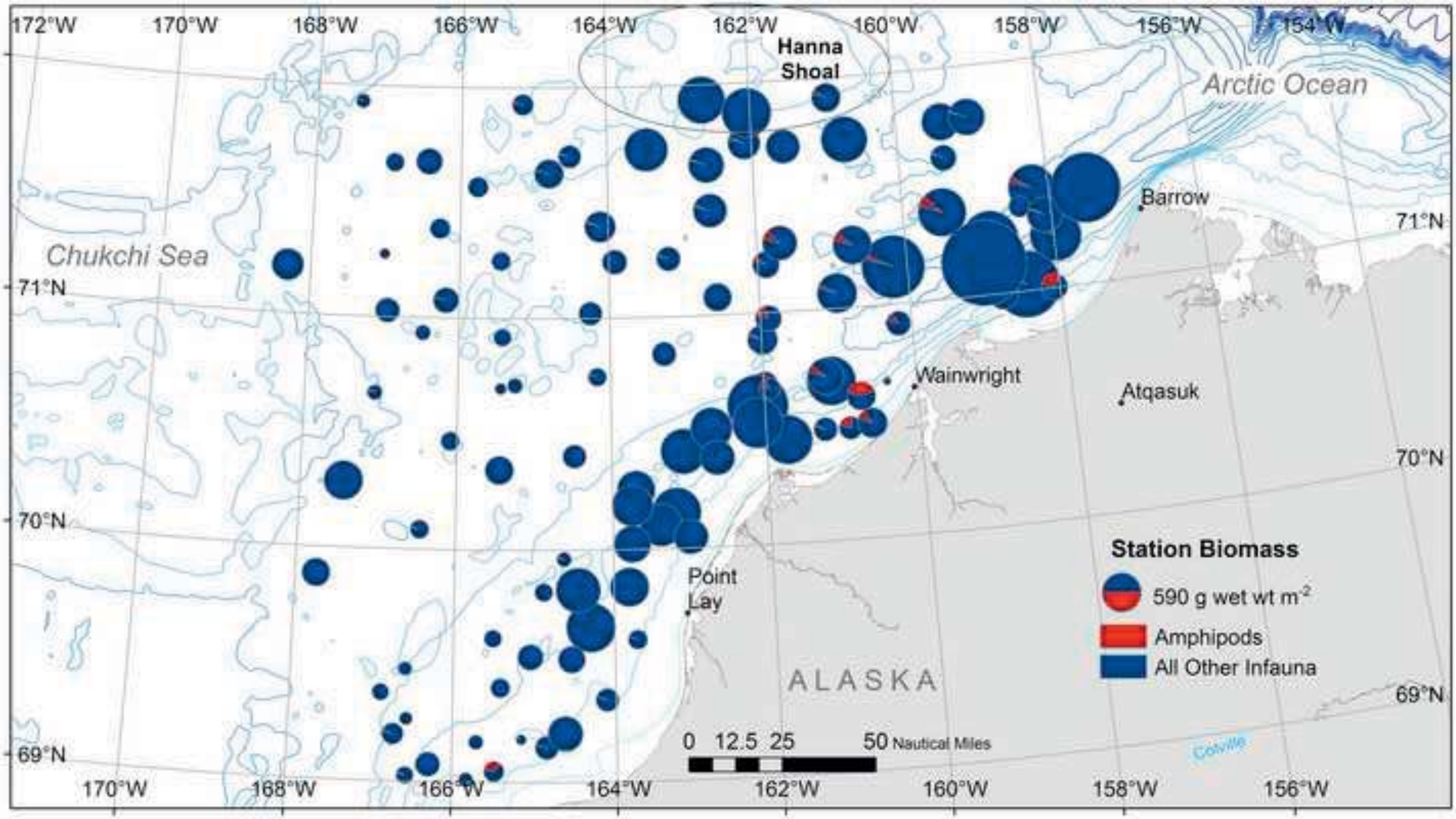
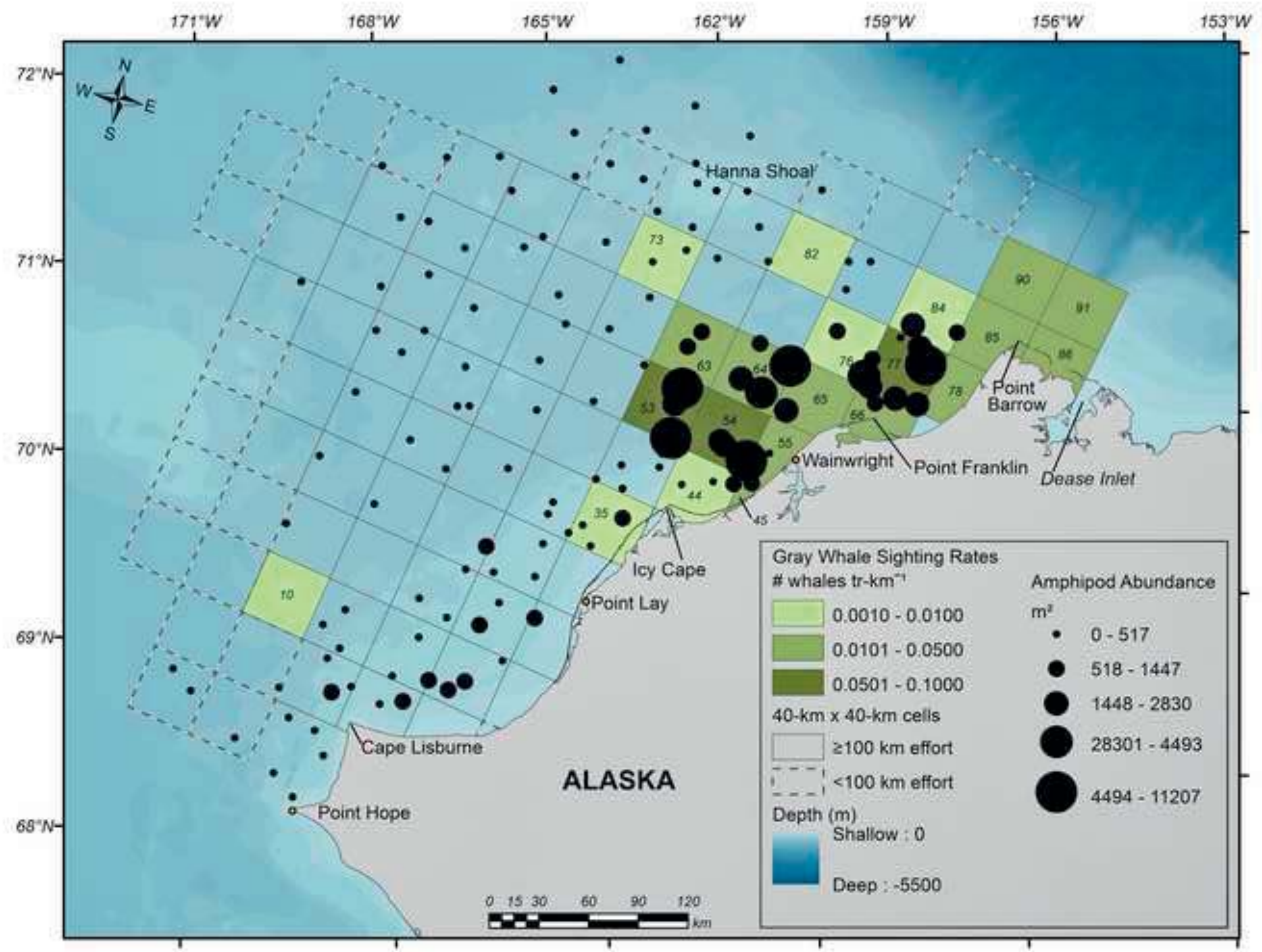
69°N
68°N
Hanna Shoal
Point Barrow
Dease Inlet
Point Franklin
Wainwright
Icy Cape
Point Lay
Cape Lisburne
Point Hope
ALASKA
0 15 30 60 90 120 km
October Gray Whale Sighting Rate & Sightings
whales tr-km⁻¹
0.0067 - 0.0100
0.0101 - 0.0500
Gray Whale Sightings
40-km x 40-km cells
≥100 km effort
<100 km effort
Depth (m)
Shallow : 0
Deep : -5500
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 61 62 63 64 65 66 67 68 69 70 71 72 73 74 75 76 77 78 79 80 81 82 83 84 85 86 87 88 89 90 91 92 93

Figure


172°W
170°W
168°W
166°W
164°W
162°W
160°W
158°W
156°W
154°W
Hanna
Shoal
Arctic Ocean
Chukchi Sea
Barrow
Wainwright
Atqasuk
Point
Lay
ALASKA
71°N
70°N
69°N
Station Abundance
5,800 individuals m-2
Amphipods
All Other Infauna
0 12.5 25 50 Nautical Miles
Colville


172°W
170°W
168°W
166°W
164°W
162°W
160°W
158°W
156°W
154°W
Hanna
Shoal
Arctic Ocean
Chukchi Sea
Barrow
71°N
71°N
Wainwright
Atqasuk
70°N
70°N
Point
Lay
Station Biomass
590 g wet wt m-2
Amphipods
All Other Infauna
ALASKA
69°N
69°N
0 12.5 25 50 Nautical Miles
Colville
170°W
168°W
166°W
164°W
162°W
160°W
158°W
156°W

Figure


171°W
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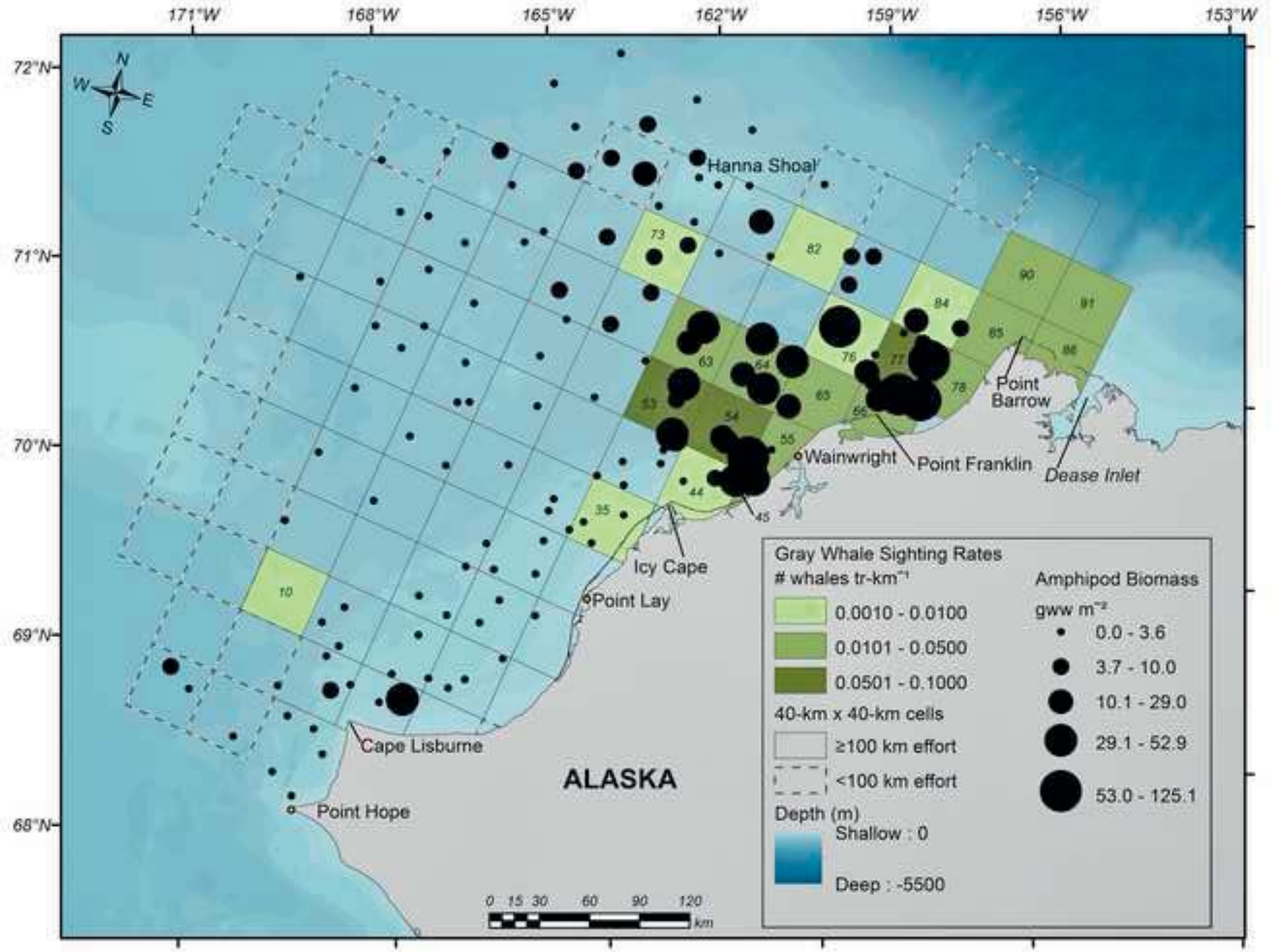
Point Barrow
Wainwright
Point Franklin
Dease Inlet
Icy Cape
Point Lay
Cape Lisburne
Point Hope
ALASKA
0 15 30 60 90 120
km
Gray Whale Sighting Rates
whales tr-km⁻¹
0.0010 - 0.0100
0.0101 - 0.0500
0.0501 - 0.1000
40-km x 40-km cells
≥100 km effort
<100 km effort
Depth (m)
Shallow : 0
Deep : -5500
Amphipod Abundance
m²
0 - 517
518 - 1447
1448 - 2830
28301 - 4493
4494 - 11207

Figure


171°W
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Point Barrow
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Wainwright
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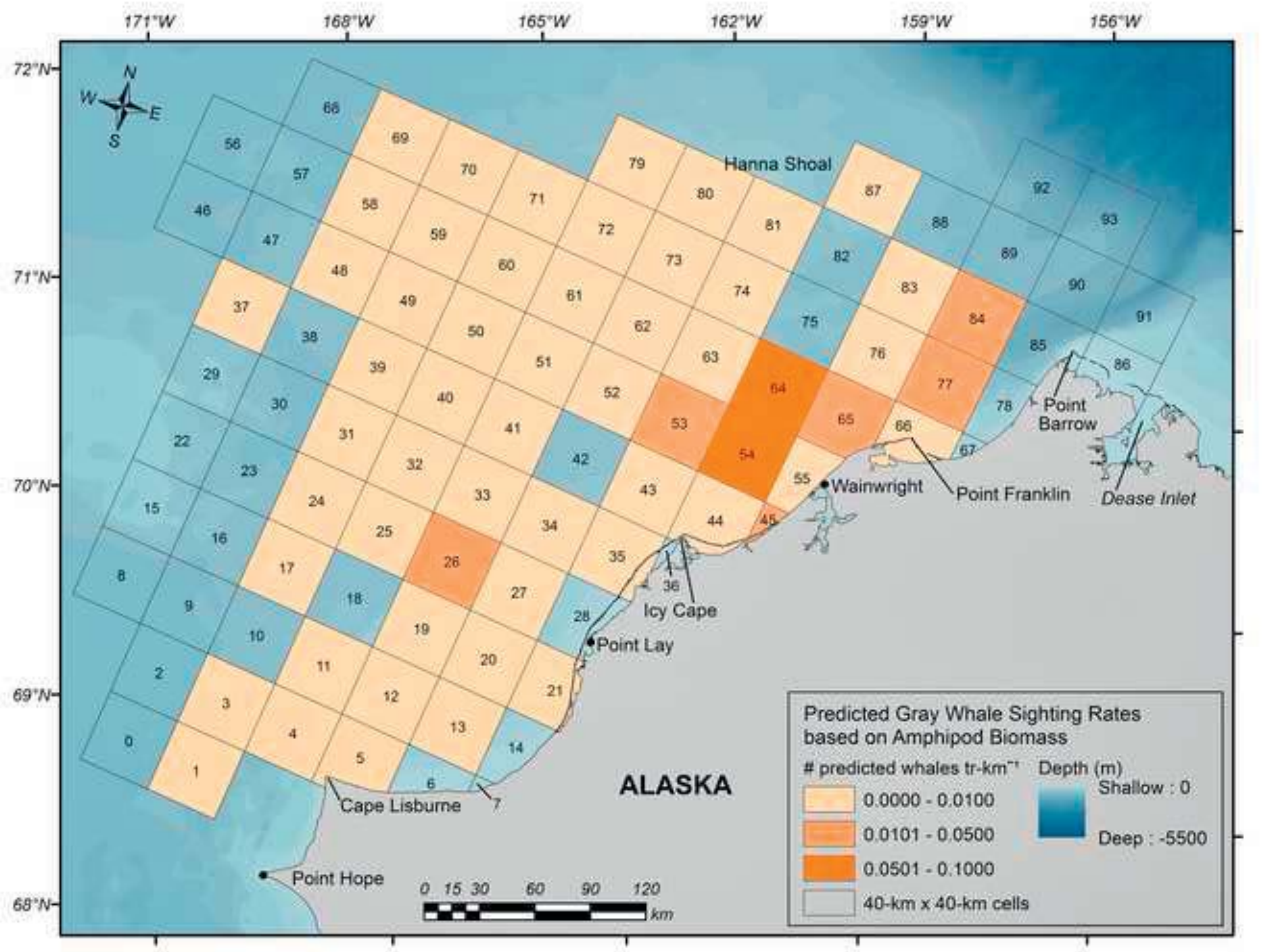
Point Lay
Cape Lisburne
Point Hope
ALASKA
0 15 30 60 90 120
km
Gray Whale Sighting Rates
whales tr-km⁻¹
0.0010 - 0.0100
0.0101 - 0.0500
0.0501 - 0.1000
40-km x 40-km cells
≥100 km effort
<100 km effort
Depth (m)
Shallow : 0
Deep : -5500
Amphipod Biomass
gww m⁻²
0.0 - 3.6
3.7 - 10.0
10.1 - 29.0
29.1 - 52.9
53.0 - 125.1

Figure


Predicted Gray Whale Sighting Rates
based on Amphipod Biomass
predicted whales tr-km⁻¹
0.0000 - 0.0100
0.0101 - 0.0500
0.0501 - 0.1000
40-km x 40-km cells
Depth (m)
Shallow : 0
Deep : -5500
171°W
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Point Barrow
Dease Inlet
Point Franklin
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Icy Cape
Point Lay
Cape Lisburne
Point Hope
ALASKA
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km
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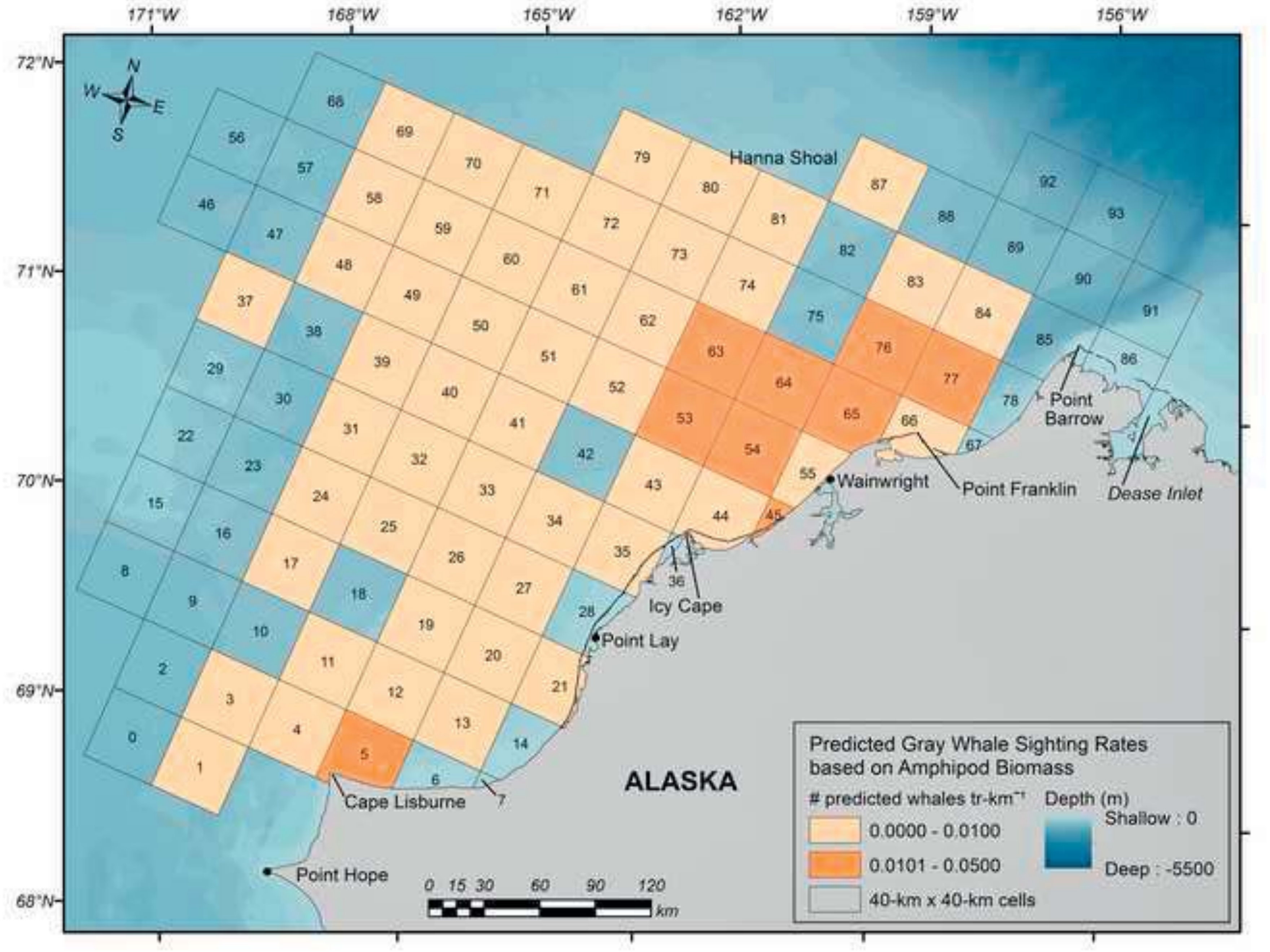
Figure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162°W
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156°W
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68°N
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Hanna Shoal
Point Barrow
Point Franklin
Dease Inlet
Wainwright
Icy Cape
Point Lay
Cape Lisburne
Point Hope
ALASKA
0 15 30 60 90 120 km
Predicted Gray Whale Sighting Rates based on Amphipod Biomass
predicted whales tr-km⁻¹
0.0000 - 0.0100
0.0101 - 0.0500
40-km x 40-km cells
Depth (m)
Shallow : 0
Deep : -5500
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