Differing prey associations and habitat use suggest niche partitioning by fin and humpback whales off Kodiak Island

Abigail McCarthy[1,], Alex De Robertis[1], Stan Kotwicki[1], Kathy Hough[2], Paul Wade[1], Christopher Wilson[1]

[1]Alaska Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 7600 Sand Point Way NE, Seattle, WA 98115, USA

[2]National Marine Sanctuary Foundation for Olympic Coast National Marine Sanctuary, National Ocean Service, National Oceanic and Atmospheric Administration, 115 East Railroad Avenue, Port Angeles, WA 98362, USA

ABSTRACT: Fin *Balaenoptera physalus* and humpback *Megaptera novaeangliae* whales share foraging areas and may compete for the same prey, but little is known about the extent to which they partition prey resources. Visual cetacean surveys and simultaneous acoustic-trawl surveys of prey were conducted around 2 submarine canyons off Kodiak Island, Alaska, in 2004 and 2006. Statistical models were used to examine the associations between sightings of fin and humpback whales and measures of their potential prey and environment. Observations and models indicate that fin whales were disproportionately abundant in areas with the highest observed euphausiid concentrations, while humpback whales were abundant at lower euphausiid concentrations and in areas where juvenile walleye pollock were abundant. Fin whales were abundant in the areas where euphausiid biomass was deepest and in the deepest areas surveyed (>150 m depth). In contrast, humpback whales primarily occurred in shallower areas and near more shallowly distributed euphausiids. The different depth and prey affinities of fin and humpback whales suggest niche and habitat partitioning between these 2 co-occurring species. Abundance models built using acoustic estimates of prey density are a useful tool to further understanding of the abundance, distribution, and behavior of these animals.

KEY WORDS: Fisheries acoustics · Cetacean habitat · Niche partitioning · Fin whales · Humpback whales · Euphausiids

1. INTRODUCTION

Worldwide, both fin *Balaenoptera physalus* and humpback *Megaptera novaeangliae* whale populations aggregate in highly productive coastal environments such as those in the North Pacific off northern California (Fleming et al. 2016), British Columbia (Darlings et al. 1996, Dalla Rosa et al. 2012), and Kodiak Island (Waite et al. 1999); and in the Atlantic, including the Bay of Fundy (Hazen et al. 2009), the Gulf of Maine (Clapham & Seipt 1991, Clapham et al. 2003), the Gulf of St. Lawrence (Simard & Lavoie 1999), Newfoundland (Whitehead & Carscadden 1985), and the Barents Sea (Mizroch et al. 2009, Skern-Mauritzen et al. 2011, Ressler et al. 2015). High productivity in these regions during summer months creates foraging hotspots for multiple species, including fin and humpback whales (Mizroch et al. 2009, Block et al. 2011). The energy-rich prey they consume in high latitude feeding grounds fuels their long distance migrations to breed, and increases survival rates of calves (Baker et al. 1985, Calambokidis et al. 2001, Goldbogen et al. 2007, 2008, Sigler et al. 2012, Williams et al. 2013). Because both species

often forage simultaneously in the same productive coastal habitats, there is potential for competitive interactions.

A persistent question in ecology is how 2 organisms with overlapping diets partition resources so they can coexist in the same niche or ecological space (Werner & Gilliam 1984, Warren et al. 2008). Physiological and behavioral adaptations to facilitate this partitioning result from competitive pressure and demonstrably occur in plants (Kelly et al. 2008, Leibold 2008) and terrestrial and aquatic animals (Dumas 1956, Siemers & Schnitzler 2004). Species with similar environmental requirements can minimize direct competition through spatial, temporal, and trophic partitioning (Hutchinson 1957, Porter 1976, Fox & Bellwood 2013). For example, terrestrial animals may spatially partition a niche and modulate sun exposure through movement up or down a tree trunk (Dumas 1956), whereas aquatic organisms may spatially partition by inhabiting different depths (Porter 1976, Cullen & MacIntyre 1998). Temporal partitioning can be mechanistic and direct, as with terrestrial animals shifting their niches diurnally or nocturnally and thus avoiding direct competition (Kronfeld-Schor & Dayan 1999, Albrecht & Gotelli 2001), or it can be more dynamic and occur through sensitivity to seasonal fluctuations and long-term climate conditions (Engelbrecht et al. 2007, Kelly et al. 2008). Trophic partitioning occurs when organisms consume different prey assemblages (Ross 1986), and often occurs in tandem with some form of fine-scale spatial partitioning, especially in the marine environment (Fox & Bellwood 2013, Hinke et al. 2015).

Large cetaceans exhibit multiple forms of niche partitioning. Both trophic and spatial partitioning occur between minke *B. acutorostrata* and humpback whales (Friedlaender et al. 2006, 2009b) and between fin and humpback whales in highly productive cold water feeding areas (Witteveen et al. 2015, Herr et al. 2016, Witteveen & Wynne 2016). Trophic partitioning occurs between blue *B. musculus*, fin, humpback, and minke whales in the Gulf of St. Lawrence (Gavrilchuk et al. 2014), as does a combination of spatial and temporal partitioning in relation to dynamic oceanographic features (Doniol-Valcroze et al. 2007). In the Bering Sea, fin and humpback whale distributions were associated with higher euphausiid (krill) biomass, and minke whale distributions were associated with higher juvenile walleye pollock *Gadus chalcogrammus* (hereafter pollock) biomass (Zerbini et al. 2016). In the same study, fin whales aggregated near the shelf edge and humpbacks aggregated on the mid-shelf, suggesting both trophic niche partitioning and spatial partitioning (Zerbini et al. 2016). Blue whales and humpback whales exhibit resource partitioning in the California Current through spatial, temporal, and trophic partitioning, with blue whales foraging exclusively on euphausiids during the seasonal peak on the shelf break, and humpbacks foraging on a wider variety of prey both on the shelf break and inshore waters in both summer and fall (Fossette et al. 2017). In some cases, niche partitioning is less clear, with 2 or more species appearing to target the same prey simultaneously. In the Barents Sea, both fin and humpback whale occurrences were correlated with euphausiid aggregations, suggesting possible direct competition for prey (Skern-Mauritzen et al. 2011, Ressler et al. 2015). Understanding the mechanisms by which sympatric fin and humpback whales niche-partition helps us to better understand the potential impacts they may have on prey populations and on prey availability for other top predators.

The region near Kodiak Island, Alaska, is a foraging area for both fin and humpback whales during summer months (Waite et al. 1999, Baraff 2006, Zerbini et al. 2006, Witteveen & Quinn 2007, Mizroch et al. 2009, Witteveen et al. 2015, Zerbini et al. 2016). The potential for competition exists as both species have been recorded foraging on the same prey items (e.g. euphausiids, copepods, capelin *Mallotus catervarius*, mackerel *Scomber japonicus*, pollock) in this region and in other foraging hotspots (Nemoto 1959, Dolphin 1988, Clapham & Meade 1999, Flinn et al. 2002). While population levels of both fin and humpback whales are increasing in the Gulf of Alaska (GOA), including in the Kodiak Island region, they have not yet risen to pre-whaling levels (Zerbini et al. 2006, Witteveen & Quinn 2007, Mizroch et al. 2009, Allen & Angliss 2015). With low (but increasing) population sizes, we would not expect to see direct competition driven by large-scale prey depletion in this area (Clapham & Brownell 1996, Friedlaender et al. 2006). But, given the high energy costs for foraging dives (Croll et al. 2001, Acevedo-Gutiérrez et al. 2002, Hazen et al. 2015) and the need to target the highest density patches of prey to maximize foraging efficiency and energy gain (Hazen et al. 2009, Burrows et al. 2016, Fossette et al. 2017), there is potential for localized depletion of prey in this region (Witteveen et al. 2006, Straley et al. 2018), which could be a factor in influencing behavior of these 2 species (Clapham & Brownell 1996).

Recent tagging and stable isotope studies in coastal bays around Kodiak Island have considered

how fin and humpback whales partition their foraging environment (Witteveen et al. 2008, 2015, Witteveen & Wynne 2016). The tagging study (Witteveen et al. 2015) focused on the nearshore and inner bays around Kodiak and measured individual fin and humpback dive behavior for brief periods of time, concurrent with acoustically quantified prey abundance generalized to trophic level. The isotope study (Witteveen & Wynne 2016) examined the relative contributions of zooplankton and forage fishes to fin and humpback whale diets in coastal bays in the Kodiak and Shumagins regions. These studies suggest that in the Kodiak region in nearshore waters, fin whales are functionally planktivores, while humpback whales switch from consuming zooplankton to forage fishes, depending on the relative abundance of these prey (Anderson & Piatt 1999, Witteveen & Wynne 2016). Additional research suggests that spatial segregation of fin and humpback whales may occur by depth (Wynne et al. 2005). Evidence from other ecosystems also suggests that humpback and fin whales may undergo prey switching between zooplankton and forage fishes (Skern-Mauritzen et al. 2011, Ressler et al. 2015, Fleming et al. 2016), and that fin whales may forage in areas with lower prey densities than humpbacks (Baraff 2006, Witteveen et al. 2015, Witteveen & Wynne 2016). Alternately, it has been suggested that it may be critical for larger rorquals, such as fin whales, to exploit the densest prey patches (Acevedo-Gutiérrez et al. 2002, Goldbogen et al. 2007, 2012). The 2 species' foraging behaviors and prey preferences remain a research need in the GOA and particularly in the offshore areas around Kodiak Island (Witteveen et al. 2015, Witteveen & Wynne 2016, Wright et al. 2016).

In 2004 and 2006, the Alaska Fisheries Science Center conducted acoustic-trawl surveys northeast of Kodiak Island, focused on capelin and pollock (Wilson et al. 2003, Hollowed et al. 2007, Logerwell et al. 2007, Walline et al. 2012), that also included opportunistic visual observations of marine mammals. Together, these data allowed for concurrent measurements of the distribution of large cetaceans, the oceanographic features of their habitat, characterization of the available prey fields using acoustic and midwater trawl sampling, and an evaluation of prey partitioning in the fin and humpback foraging grounds. This single-platform, concurrent sampling approach complements short-term focal follows and stable isotope work in previous studies in the area by providing detailed data on prey availability and cetacean behavior simultaneously over several months in more offshore environments. A better understanding of the environmental and prey conditions that influence niche partitioning of these whales can potentially inform management by ensuring that marine protected areas are designed to include suitable habitat and by incorporating prey requirements into fisheries management processes (Trites et al. 1997, Gregr & Trites 2001, Bailey & Thompson 2009).

2. MATERIALS AND METHODS

2.1. Study site

Barnabas and Chiniak are 2 adjacent troughs on the east side of Kodiak Island in the GOA, USA, which support high primary production from April–November (Hollowed et al. 2007). This region is a summer feeding ground for humpback and fin whales (Waite et al. 1999, Zerbini et al. 2006, Witteveen & Quinn 2007). The 2 troughs have similar bathymetric features, with depths in the surveyed area ranging from 50–250 m, and an average depth of approximately 135 m.

The Alaska Fisheries Science Center conducted acoustic-trawl surveys of Barnabas and Chiniak Troughs with the NOAA ship 'Miller Freeman' in 2004 and 2006 with the goal of understanding the drivers of distribution of capelin and pollock and their relationship to commercial fishing in these regions (see Fig. 1; Logerwell et al. 2007, Walline et al. 2012). Opportunistic visual observations of marine mammals were collected during the acoustic-trawl survey. Three replicate survey passes were completed in Barnabas and 4 in Chiniak from 13 August through 6 September 2004. Five survey passes were completed in each trough from 11 August through 5 September 2006. Chiniak and Barnabas troughs (see Figs. 1 & 2) were surveyed using parallel transects spaced 5.5 km apart, with transect start and end points located at depths of 75–100 m past the trough edges. Vessel speed averaged 6.0 m s^{-1} (11.7 knots) during acoustic data collection. The acoustic-trawl surveys took place during daylight hours (approximately 14–15 h d^{-1}).

2.2. Cetacean survey

A single observer made visual cetacean observations during daylight hours of the acoustic-trawl survey. Line-transect data were collected using standard cetacean survey protocols (e.g. Zerbini et al.

2006). As there was only a single observer, most scanning for whales was done by eye, but a set of pedestal-mounted 20× power 'big-eye' binoculars were used to estimate the angle from the trackline to the sighting, radial distance to the sighting (from ret-icles in the ocular), and to confirm species identifica-tion. All sighting and environmental data were entered into the program WINCRUZ (available for download at the SWFSC PRD software portal; Friday et al. 2013), a computer database interfaced to a GPS unit to gather positional and navigational informa-tion. Only sightings of whales obtained while the observer was 'on-effort', when the Beaufort sea state was 5 or lower, and when visibility was >3 km were used. Radial distance to each sighting was calculated using 'approximation 2' of Lerczak & Hobbs (1998) from the binocular reticle measurements and plat-form height. Perpendicular distance was calculated by multiplying the radial distance by the sine of the angle to the sighting. The latitude and longitude of each whale sighting was calculated from the GPS posi-tion of the ship and the angle and radial distance to the sighting. The observer recorded species, group size, and location of sightings. As tracklines were 5.5 km apart, only sightings within 2.75 km of the trackline were compiled and used in the final analysis. As there was only a single observer, the cetacean observa-tions were not continuous: observations were made along 45% of the survey transects in 2004 and 65% in 2006.

2.3. Acoustic-trawl survey

Acoustic-trawl methods (Simmonds & MacLennan 2005) were used in the collection and analysis of acoustic and trawl data to determine the abundance of potential prey. Acoustic backscatter was measured continuously during day-light hours along the cruise track with centerboard-mounted Simrad EK500 (38 kHz) and EK60 (18, 120, 200 kHz) echosounders, which were synchro-nized to transmit simultaneously. In 2006, a Simrad EK60 echosounder was used at the 4 frequencies described above. The echosounders were calibrat-ed using the standard sphere method (Foote et al. 1987) at the beginning and end of each cruise. Acoustic data were processed with Sonardata echoview software (version 4.9).

Trawl hauls were conducted to identify the size and species composition of the primary sound-scat-tering organisms detected with the echosounder. Trawl hauls were targeted in areas of high backscat-ter, and the catch was sampled to determine the spe-cies and size compositions of the sound-scattering organisms (Wilson et al. 2003). An Aleutian Wing 30/26 pelagic trawl fitted with a 13 mm codend liner (Honkalehto et al. 2009) was used to sample midwa-ter fish aggregations. A poly Nor'eastern bottom trawl with roller gear was used to sample demersal fishes (Wilson et al. 2003). A Methot trawl with a mouth opening of 5.2 m^2, constructed with 2 × 3 mm oval mesh with a 1 mm mesh codend was used to sample suspected euphausiid aggregations (Hol-lowed et al. 2007). A total of 59 midwater trawls were conducted (28 in Chiniak and 31 in Barnabas) in 2004. Five bottom trawl hauls and 6 Methot hauls were also conducted in each trough during the study period. A total of 47 midwater trawl hauls were con-ducted in 2006 (23 in Chiniak and 24 in Barnabas). Fourteen bottom trawl hauls (11 in Barnabas, 3 in Chiniak) and 4 Methot tows (2 trough^{-1}) were con-ducted during the study period (Fig. 1). Each midwa-ter and bottom haul catch was weighed and enumer-ated, a subsample of ~300 pollock >10 cm standard lengths (SL) were measured, and ~50 were weighed.
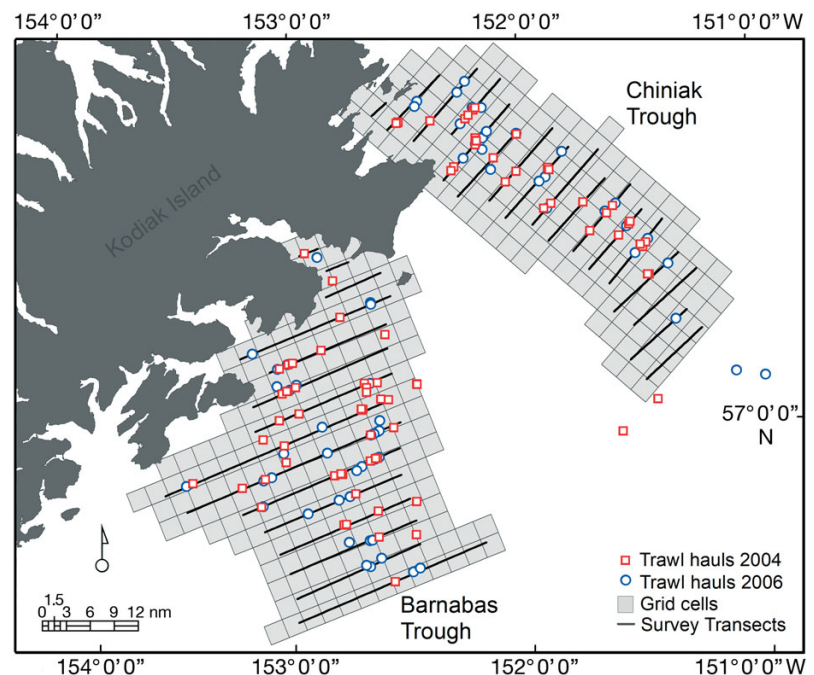

Fig. 1. Survey regions (Barnabas and Chiniak Troughs) for summer 2004 and 2006 cruises aboard the NOAA Ship 'Miller Freeman'. Red boxes: trawl hauls performed in 2004; blue circles: hauls in 2006. Survey transects were similar for all passes and both years

When age-0 pollock (≤10 cm) or capelin (10–17 cm) were captured, approximately 50 length and 10 length–weight measurements were collected. Methot catches were processed by first removing large medusae and then preserving a subsample of the remaining catch in 3.7% buffered formaldehyde solution. The organisms in the Methot samples were later sorted and identified in the laboratory using a binocular microscope.

2.4. Acoustic data analysis

Acoustic backscatter was attributed to several species groups (Table 1), based on interpretation of the depth distribution and aggregation patterns observed in the echosounder data and the results of targeted trawl sampling (Walline et al. 2012). The primary sound scatterers were large pollock (95% were >35 cm in both troughs), euphausiids, and a mixture of capelin and age-0 walleye pollock. Backscatter from euphausiids in the 18–200 kHz range is strongly frequency-dependent (Demer & Conti 2005, McKelvey & Wilson 2006). An index of euphausiid abundance was generated using a multifrequency technique based on observations from trawl ground-truthed euphausiid aggregations in Alaska (De Robertis et al. 2010) and applied to these data. Volume backscatter was averaged into 5 ping × 5 m cells, and volume backscattering 12–32 dB higher at 120 kHz relative to 18 kHz (i.e. 15.8–158.5 fold higher at 120 kHz) was classified as euphausiids. The nautical area scattering coefficient (s_A; m^2 nmi^{-2}) at 38 kHz for fishes and near-surface backscatter, and at 120 kHz for euphausiids, was calculated in 10 m vertical layers (14 m below surface to 0.5 m off bottom) in 0.5 nmi horizontal intervals along the survey track. The mean-weighted depth (MWD) was calculated for each of the species groups.

The echo integral from the age-0 pollock and capelin mixture was partitioned into backscatter from each species based on the proportion of the species in the trawl catches, the size distribution, and the target strength (TS) of each species (De Robertis et al. 2017, their Eq. 4). We used the TS to fork length (FL, cm) relationship for pollock (TS = 20log[FL] − 66.0; Traynor 1996) and a TS to total length (TL, cm) relationship to capelin, derived from *in situ* measurements in the GOA (TS = 20log[TL] − 70.3; Guttormsen & Wilson 2009). Given that conversion of euphausiid backscatter to abundance remains uncertain (Hunt et al. 2016), we did not calculate euphausiid biomass and abundance from the backscatter measurements. Euphausiid backscatter is a reasonable crude index of abundance and an effective proxy for biomass in this region (Ressler et al. 2012, Simonsen et al. 2016). Acoustic backscatter can be used as proxy for animal abundance as it is proportional to abundance if scattering strength is constant (Foote 1983) and was used as a proxy for biomass for all potential prey species for consistency. Acoustic analyses were performed using Echoview software version 8.0.

Table 1. Predictor variables for surveys off Kodiak Island in summer 2004 and 2006

Predictor variable	Description
Krill	Euphausiid backscatter, mean nautical area scattering coefficient in (m^2 nmi^{-2}) per grid cell
Adult pollock	*Gadus chalcogrammus* backscatter, mean nautical area scattering coefficient in (m^2 nmi^{-2}) per grid cell
Age-0 pollock	*Gadus chalcogrammus* young-of-year backscatter, mean nautical area scattering coefficient in (m^2 nmi^{-2}) per grid cell
Capelin	*Mallotus villosus* backscatter, mean nautical area scattering coefficient in (m^2 nmi^{-2}) per grid cell
Chlorophyll	Chlorophyll (μg m^{-2})
SST	Sea surface temperature (°C) from shipboard sensors
Depth	Water column depth (m)
Trough	Chiniak or Barnabas troughs east of Kodiak Island
Effort	Distance (nmi) per grid cell during which observers were manning 'big eyes' and whale search effort was 'on'
Mean-weighted depth (MWD)	Water-column depth (m) at which the majority of prey backscatter occurs

2.5. Oceanographic data

Underway sea surface temperature (SST), salinity from a Sea-Bird Electronics SBE-21 probe, and raw voltage from a Turner Designs 10AU flourometer were measured through the survey from water obtained from a ship intake on the hull that was located 5 m below the surface of the water. Temperature and salinity profiles were collected at trawl sites from the downcast of a Sea-Bird CTD system, and discrete chlorophyll samples were collected at 10 m intervals from 50 m depth to the surface (Hollowed et al. 2007, Logerwell et al. 2007). Surface chlorophyll samples were used to calibrate the underway fluorometry data and calculate chlorophyll values in µg m^{-2} for the survey area. Oceanographic data were processed using Matlab version R2015b.

2.6. Statistical analyses

Acoustic data, cetacean sighting data, and oceanographic data were collected at different spatial and temporal resolutions (Table 1, Fig. 2). Thus, it was necessary to summarize them on a common spatial scale. We computed semi-variograms of the acoustic backscatter and cetacean count data to estimate the appropriate grid cell size to minimize spatial autocorrelation. These analyses (not shown) revealed that scaling the data to a 4.0 km grid cell would eliminate most of the spatial autocorrelation in both the measurements of acoustic backscatter and the whale sighting data. A 4.0 km grid-cell was used to minimize spatial autocorrelation for both data types and include all of the data points from the parallel transects (Fig. 1). Effort was defined as the distance along a transect within a given grid cell where whale observations were taken. Cells with missing acoustic or environmental data or where

<2.3 km (1.25 nmi, half of the distance between transects) of whale observations were taken were eliminated from further analysis. After this process, 72% of the originally surveyed cells remained. The whale sighting effort coverage in the cells retained in the analysis was 90%.
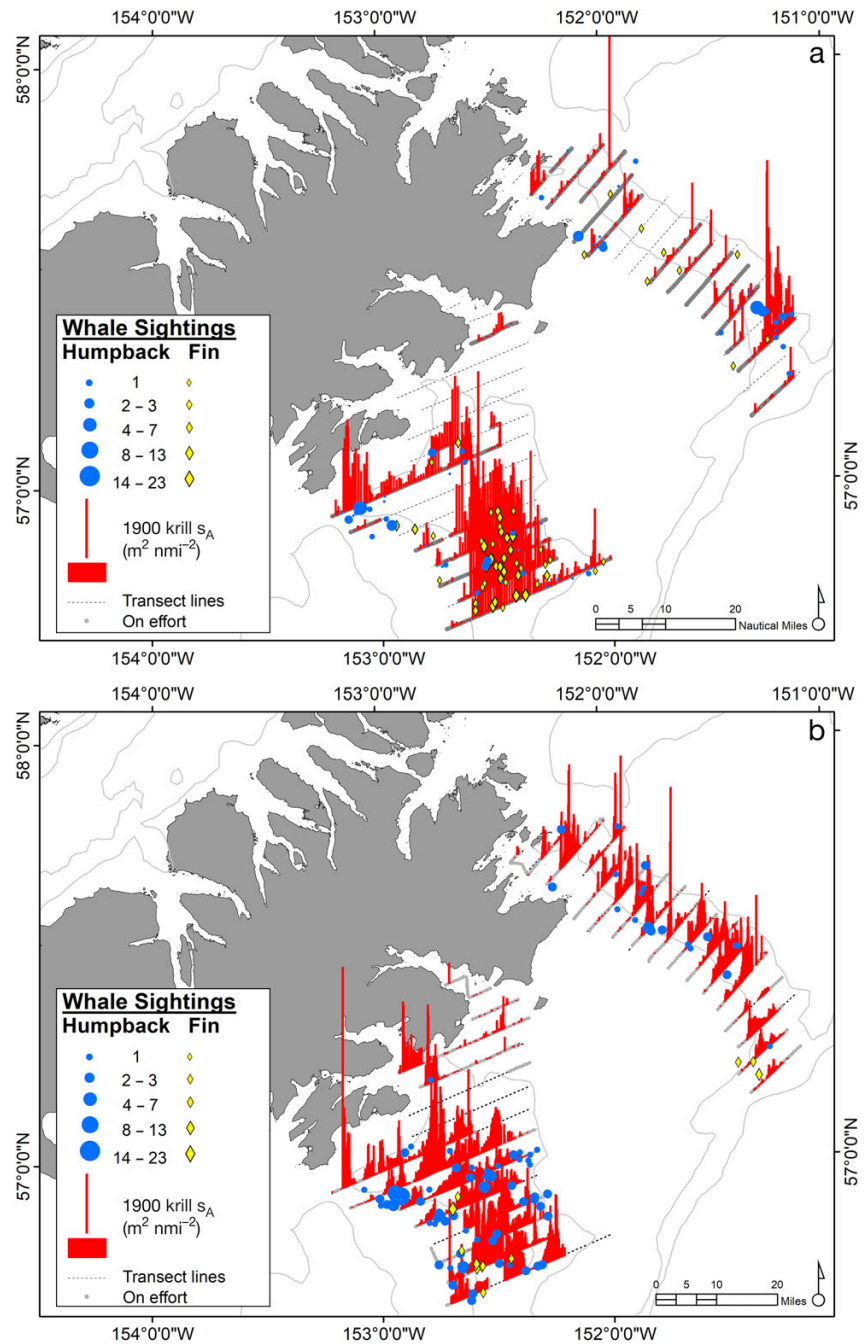

Fig. 2. Euphausiid (krill) acoustic backscatter at 120 kHz (s_A; m^2 nmi^{-2}) and fin and humpback whale sightings by group size during summer (a) 2004 survey passes 7 and 8 and (b) 2006 survey passes 9 and 10 aboard the NOAA Ship 'Miller Freeman'. Pale grey dots: whale observer 'on effort'; dashed lines: transects; light gray lines: 100 and 200 m depth contours

2.6.1. Data exploration

We conducted a univariate data exploration to visualize the environmental conditions and prey density under which fin and humpback whales were likely to be found. This visualization allowed us to compare the prey conditions with which whales were associated to those available to the whales within the survey area. Mean environmental conditions, prey density, and presence/absence of fin and humpback whales by grid cell were used in this analysis. To evaluate whether whales were disproportionately present in grid cells with high concentrations of fishes or zooplankton or specific environmental conditions, we compared the cumulative distribution of each of the measured environmental metrics weighted by whale presence to the distribution of these metrics in the entire surveyed area. This produced an index of the minimum level of environmental conditions (e.g. temperature or prey density) in the grid cells at which a given proportion of fin and humpback whale sightings occurred for each of the acoustically measured potential prey fields and each of the environmental variables.

We computed the value of the minimum prey backscatter (or oceanographic variable) that occurred at a given percentile of cells with positive sightings for both fin and humpback whales (De Robertis & Cokelet 2012). To do this, we sorted the whale sightings (W), which were paired with prey backscatter or oceanographic measurements (E), in ascending order of E, and computed the minimum values of E with a given percentile, P (i.e. 5th, 25th, 50th, 75th, 95th) of the cells where whales were observed. This can be expressed as the lowest value of the environmental or prey variable in a cell, E_j that fulfills the following expression:

$$\sum_{i=1}^{j} W \geq \frac{P}{100} \left(\sum_{i=1}^{n} W, i \right) \tag{1}$$

where i and j are indices into the sorted vector of E, and n is the total number of grid cells. We performed an equivalent analysis for each of the prey variables, where E = prey backscatter (i.e. s_A), and for each of the oceanographic measurements, where E = temperature (°C), chlorophyll (µg m^{-2}), or depth (m), and we paired these variables with both fin and humpback whale counts. This allowed a comparison of the prey and ocean conditions in the survey region with the conditions at the locations where whales were observed. Box plots were used to summarize the cumulative distribution of cetaceans in relation to prey backscatter (krill, capelin, and juvenile and adult pollock), prey depth in the subset of cells where the prey was found, and habitat (oceanographic variables; see Fig. 3). Comparing the 10th, 25th, 50th, 75th, and 90th percentiles of the environmental measurements in the study area with the conditions under which whales were sighted allows one to visualize whether the whales are disproportionately abundant under a given range of environmental conditions (e.g. are whales associated with high prey abundances?). This portion of the statistical analysis was done using Matlab version R2015b.

2.6.2. Multivariable analysis

We developed a multivariable predictive model of whale abundance that simultaneously considered the different environmental and potential prey variables in relation to cetacean sightings. Preliminary analysis indicated that whale count data were overdispersed with respect to the binomial distribution (i.e. additional variance in the response data; see Fig. 3 in Hinde & Demétrio 1998) and were zero-inflated (ZI; Zuur et al. 2009). Initial investigation of the grid-cell-aggregated count data indicated that both fin and humpback whales exhibited distributions that were better characterized by a negative binomial (NB) distribution than a Poisson distribution as the variance was 5 or more times the mean (see Table 2, Fig. 3; Zuur et al. 2009, Preisser et al. 2012). Within the negative binomial family, we considered 2 generalized linear models: NB and zero-inflated negative binomial (ZINB). We performed Vuong's non-nested hypothesis test (Vuong 1989), which indicated that due to the zero-inflation, the ZINB was a better fit for the data.

The ZINB regression model consists of a NB generalized linear model (GLM) used to describe the expected cetacean count and a logit regression used to model the zero observations (Ver Hoef & Boveng 2007, Zuur et al. 2009, 2012). The probability that we measure a certain number of cetaceans in a given grid cell is $\Pr(Y_i)$, $\Pr(Y_i) \sim \text{ZINB}(\mu_i, \pi_i, k)$. The variance structure for the ZINB model is var $(Y_i) = (1 - \pi_i) \times \mu_i \times (1 + \pi_i \times \mu_i + \mu_i / k)$, where k is the dispersion parameter of the negative binomial distribution; and the equation for the mean is $E(Y_i) = \mu_i \times (1 - \pi_i)$. The count portion (NB distributed) of the model represented by μ_i (Eq. 2) predicts the expected cetacean observed count, and the zero portion of the model with probability π_i (Eq. 3) predicts only the excess zeros (Zeileis et al. 2008, Zuur et al. 2009, 2012). The predictor variables are included in both portions of the model as shown:

$$\mu_i = e^{\alpha + \beta_1 \times X_{i1} + \ldots + \beta_q \times X_{iq}} \qquad (2)$$

where X represents a matrix of the prey and environmental variables (i:q) included in Table 1, α is the population intercept, and β is vector of slopes. In the zero portion of the model, υ is the intercept and γ is a vector of slopes:

$$\pi_i = \frac{e^{\upsilon + \gamma_1 \times X_{i1} + \ldots + \gamma_q \times X_{iq}}}{1 + e^{\upsilon + \gamma_1 \times X_{i1} + \ldots + \gamma_q \times X_{iq}}} \qquad (3)$$

The combined model prediction, the mean of the ZI and NB components presented together, represents the expected whale count observed in a given cell (Lambert 1992, Martin et al. 2005, Zuur et al. 2009, Otero et al. 2016). The predictor variables in the full model include potential prey and environmental predictors (Table 1), with MWD and acoustic proxies for abundance included for each of the prey variables. Basin (i.e. Chiniak or Barnabas) was included as a factor variable to account for differences in whale abundance between basins (see Table 2). The relationships for other covariates and whale abundance were similar when models were fit to each basin separately, which indicates a lack of strong interactions with basin, although confidence intervals were broader. MWD for the potential prey species can only be included in the model where the prey are present, and cells where a given prey category was not present (11% of cells) were excluded. We used stepwise backward selection based on Akaike's information criterion (AIC; Akaike 1987) to obtain a final model. AIC was calculated for the full model with the 2 whale species as response variables. Second, reduced models were run by removing one predictor variable at a time. If the AIC of the reduced model was lower than the AIC of all other reduced models and the full model, that variable was removed. This

process continued until no further reduction in the AIC was achieved.

The predictor effects from final models are presented as partial dependence plots highlighting individual variables (i.e. plots where all other predictors are kept constant at their means, Minami et al. 2007; Hastie et al. 2009). These partial dependence plots represent the dependence of predicted whale count on individual variables which were significant in the final model. The predicted effects are shown over the observed range of values of the predictors during the surveys. Analyses, treatment, and visualization of data for this portion of the analysis were performed in R v.3.4.9 using packages 'pscl' (v.1.4.9; Zeileis et al. 2008), 'MASS' (v.7.3-49; Venables & Ripley 2013), 'AER' (v.1.2-7; Kleiber et al. 2020), and 'ggplot2' (v.3.2.0; Wickham et al. 2016).

3. RESULTS

3.1. Biological summary

Overall, sightings of whales were high for the entire survey, and there were more than 4 times as many humpback whales (n = 1055) as fin whales (n = 247) in the area around Kodiak Island. In 2004, humpback whales were sighted at a rate of 0.66 animals nmi^{-1} of search effort, and fin whales at a rate of 0.20 animals nmi^{-1}. In 2006, humpback whales were sighted at a rate of 0.38 animals nmi^{-1} of search effort, and fin whales at a rate of 0.05 animals nmi^{-1} (Table 2). Humpback and fin whales were more abundant in Chiniak, where over both years of the study, humpback whales were sighted at a rate of 0.61 nmi^{-1},

Table 2. Basic statistics (mean [SD]) for humpback and fin whale counts, krill and fish acoustic backscatter (s_A; m^2 nmi^{-2}), and oceanographic variables for surveys off Kodiak Island in Barnabas and Chiniak Troughs in summer 2004 and 2006. Backscatter cannot be summed over the survey area by year

	Barnabas 2004	Chiniak 2004	Total	Barnabas 2006	Chiniak 2006	Total
Humpback whales (sightings per grid cell)	1.170 (3.33)	1.780 (4.45)	566	0.410 (1.38)	1.180 (5.3)	489
Fin whales (sightings per grid cell)	0.050 (0.22)	0.710 (1.91)	171	0.020 (0.17)	0.210 (1.39)	76
Effort (km)	2.200 (0.42)	2.320 (0.32)	1530	2.320 (0.45)	2.340 (0.37)	2454
Krill	102.680 (137.1)	284.230 (328.9)	–	85.180 (175.8)	168.220 (210.1)	–
Adult pollock	110.420 (212.9)	179.000 (401.7)	–	63.610 (124.7)	52.490 (152.1)	–
Age-0 pollock	215.800 (439.4)	237.560 (553)	–	603.920 (902.8)	310.600 (787.1)	–
Capelin	98.280 (290.9)	21.100 (81.08)	–	315.250 (596.7)	63.280 (295.4)	–
Chlorophyll (µg m^{-2})	12.550 (7.29)	8.980 (3.45)	–	9.490 (5.64)	8.050 (3.08)	–
SST (°C)	10.310 (0.43)	10.750 (0.4)	–	10.460 (0.5)	10.820 (0.41)	–

and fin whales were sighted at a rate of 0.17 nmi^{-1}. In Barnabas, humpback whales were sighted at a rate of 0.30 nmi^{-1} and fin whales were sighted at a rate of 0.02 nmi^{-1}.

In the context of population assessments of humpback and fin whale populations in the North Pacific (Muto et al. 2018), our sighting rates are relatively high, suggesting high overall population numbers in the study area during our study period. In a survey of the southeastern Bering Sea in 2000, humpback whales were sighted at a rate of 0.0033 nmi^{-1}, and fin whales were sighted at a rate of 0.024 nmi^{-1} (Moore et al. 2002). Between 2001 and 2003, a survey of the Aleutian Islands and GOA found 0.035 fin whales km^{-2} (0.12 nmi^{-2}) and 0.054 humpback whales km^{-2} (0.18 nmi^{-2}) in the Kodiak Island region (Zerbini et al. 2006).

The composition of potential prey items differed between survey years. Higher backscatter from adult pollock and euphausiids was observed in 2004 than in 2006 (Table 2), but higher backscatter from capelin and age-0 pollock was observed in 2006 (Table 2). During the 2004 survey, adult pollock was the predominant species caught by weight in midwater trawls (95.3%) and age-0 pollock were the most abundant by numbers (32.0%), followed by adult pollock (23.9%), euphausiids (20.7%), and capelin (14.0%). Euphausiids were the predominant catch in Methot trawl hauls, both by weight (68.4%) and numbers (99.2%). The remainder of the Methot catch by weight consisted of large jellyfish (Scyphozoa; 31%) unlikely to contribute to the acoustic observations (De Robertis & Taylor 2014). During the 2006 survey, adult pollock made up more than half of the catch in midwater trawls by weight (51.0%), while age-0 pollock were the most abundant by numbers (31.0%), followed by age-1 pollock (22.0%), capelin (20.2%), euphausiids (10.5%), and adult pollock (4.6%). Euphausiids again were the predominant catch in Methot trawl hauls, both by weight (72.1%) and numbers (99.9%). Jellyfish (Scyphozoa) composed the majority of the remaining Methot catch (27%).

A subset of Methot hauls were assessed for species composition, 6 of 15 methot tows in 2004 and 2 of 4 methot tows in 2006. *Thysanoessa inermis* and *T. spinifera* dominated these euphausiid catches in both 2004 and 2006. In 2004, *T. inermis* (mean length 21 mm) accounted for 67% of the catch and *T. spinifera* (mean length 16 mm) accounted for 31% of the catch. In 2006, *T. inermis* (mean length 17 mm) accounted for 95% of the catch and *T. spinifera* (mean length 26 mm) accounted for 4%, which was similar to

Methot samples from the same region in 2011 and 2013 (Simonsen et al. 2016).

In both years, most adult pollock were detected as dense near-bottom aggregations. Age-0 pollock (5–10 cm SL) were often spatially co-located with capelin. These mixed aggregations of age-0 pollock and capelin typically occurred higher in the water column than adult pollock and were broadly distributed throughout Chiniak Trough and predominantly in the northern portion of Barnabas Trough.

3.2. Exploratory analysis

Fin whale sightings were restricted largely to the areas with the highest euphausiid backscatter in the survey area, while humpback whales were found over a wider range of available prey concentrations (Fig. 3). Fin whales were consistently observed in areas with the deepest euphausiid aggregations (Fig. 3c,d). Humpback whales tended to occur in areas with higher euphausiid concentrations, though to a lesser degree than fin whales, and humpbacks were also more frequently sighted in areas with higher age-0 pollock concentrations than those in the surveyed area (Fig. 3a,b).

Fin whale sightings were almost entirely restricted to the top 50% of euphausiid backscatter available in grid cells in both 2004 (Fig. 3a) and in 2006 (Fig. 3b). Fin whale sightings occurred more often in the deepest 65% of the euphausiid depth distribution by cell in 2004 and in the deepest 60% of the euphausiid depth distributions in 2006 (Fig. 3c,d). Fin whales were primarily distributed in deep water. In 2004, 90% of the fin whale sightings occurred in water >150 m depth, which accounts for 35% of the survey area (Fig. 3g); in 2006 the same trend continued, with 50% of fin whale sightings occurring in water deeper than 150 m (Fig. 3j). Although the total environmental variation in SST was only about 1.5°C, fin whales were more likely to occur in warmer water in both years (Figs. 3e,h). Fin whales were also seen more often in the deepest part of the adult pollock depth distribution in 2006 (Fig. 3b), although this is likely due to fin whales targeting deep euphausiid aggregations, which co-occur with adult pollock.

Humpback whale sightings in both 2004 and 2006 occurred more often in the highest 50% of the euphausiid backscatter in the survey area; however, this pattern in distribution was less pronounced than it was for fin whales (Fig. 3a,b). Humpback whales were observed more often in the upper 50% of the age-0 pollock backscatter in the surveyed area in
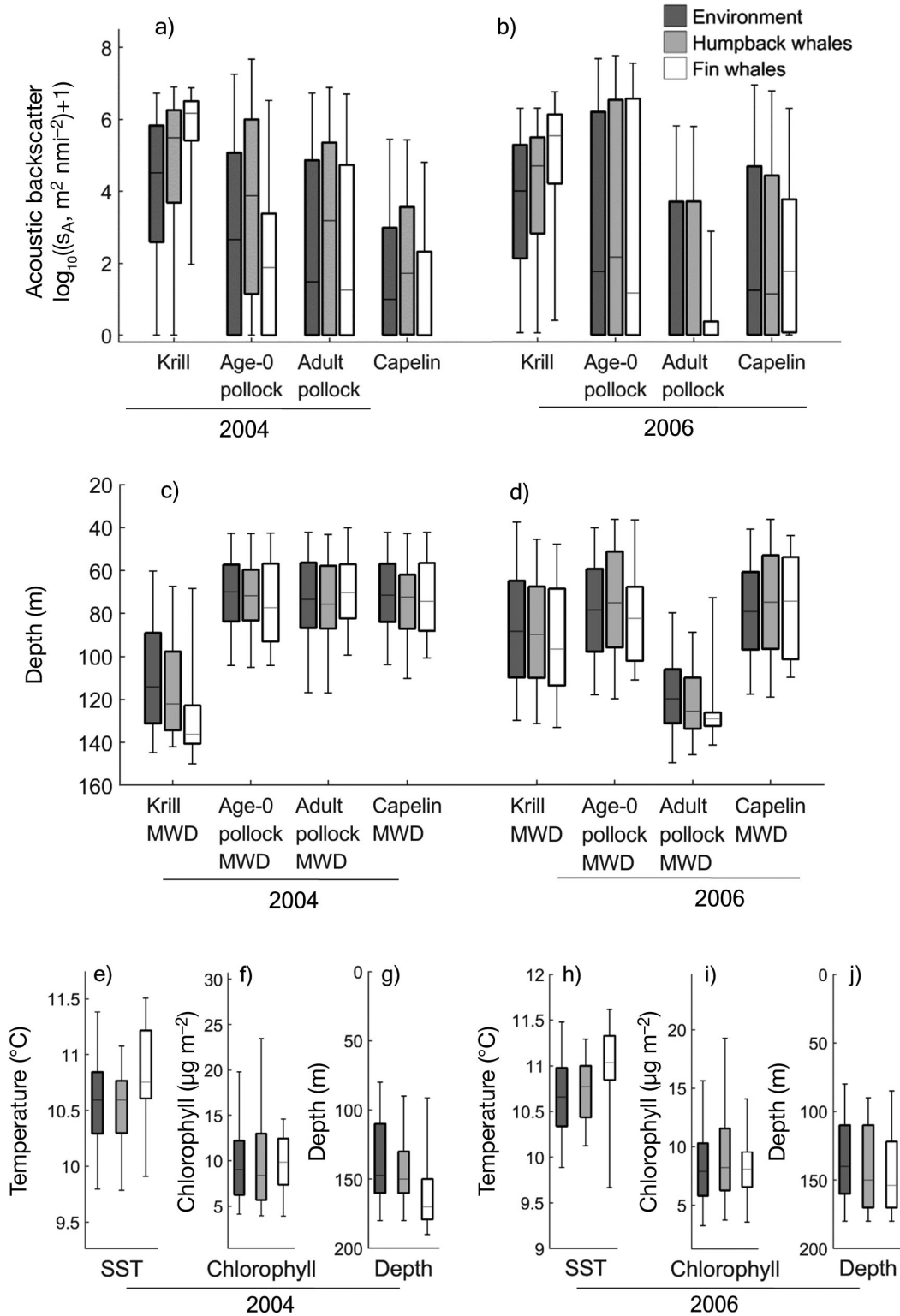
Fig. 3. Conditions in the environment sampled and in areas where fin and humpback whales were observed. Box plots show the environmental features at which the 5th, 25th, 50th, 75th, and 95th percentiles of total whale sightings occurred for prey backscatter in (a) 2004 and (b) 2006; prey depth in (c) 2004 and (d) 2006; and sea surface temperature (SST), chlorophyll concentration, and depth in (e−g) 2004 and (h−j) 2006, respectively. 'Environment' box plots represent the same percentiles for the entire survey area. Cases where the distributions in the sampled environment differ from those where whales were detected indicate that the whales are disproportionately present under a subset of environmental characteristics

2004 (Fig. 3a) and tended to be observed more in areas with higher age-0 pollock concentrations in 2006 (Fig. 3b). Humpback whales were observed in a wider range of depths than fin whales in both years of the survey (Fig. 3g,j), and did not show noticeable trends in distribution relative to SST. Neither species of whale was associated with increased chlorophyll concentration (Fig. 3f,g).

3.3. Multivariable analysis

The final model for prediction of whale sightings for both fin and humpback whales included the following predictors: krill density, krill depth, age-0 pollock density, water column depth, trough (i.e. Barnabas vs. Chiniak), search effort, and year in multivariable predictive models with cetacean count as the response. Final model results are presented in Table 3. The structure of the 2 final models predicting humpback (Eq. 4) and fin (Eq. 5) whale distributions are below. The terms pertaining to the count portion of the model are given in black, and those in the zero-inflated portion in grey. In both cases, search effort had little impact on AIC but was retained in the model:

$$Hcount \sim krill + krill\_mwd + pk0 + factor(trough) + factor(year) \mid krill + pk0 + effort \quad (4)$$

$$Fcount \sim krill\_mwd + factor(trough) \mid krill + factor(year) + Beaufort + effort \quad (5)$$

For fin and humpback whales, trough was significant in predicting the whale count per grid cell, with fewer whales of either species in Barnabas and a lower total count in 2006 than in 2004 (Tables 2 & 3, see Figs. 4–8). Models for both fin and humpback whales included year as a factor, and residuals plotted relative to predictor values for each of the 2 years were similar, suggesting that the magnitude and trend of predictors of whale presence were similar in both years. Predicted sightings of both fin (Fig. 4) and humpback (Fig. 5) whales increased with euphausiid backscatter, although the relationships differed. In the case of fin whales in Chiniak, for example, a steep increase in predicted sightings occurred between euphausiid s_A of 500 and 1000 m^2 nmi^{-2} (Fig. 4), whereas predicted sightings for humpbacks increased gradually and steadily with greater euphausiid concentrations in both troughs (Fig. 5). While bootstrapped 95% CIs are wide for these models, trends persist throughout those CIs. Model

Table 3. Model components and model fit for zero-inflated negative binomial models of humpback and fin whale counts. MWD: mean-weighted depth; $^{***}p < 0.0001$; $^{**}p < 0.001$; $^{*}p < 0.05$; $^{\cdot}p < 0.1$

| Parameter	Estimate	95% CI		z-value	Pr(>|z|)
Humpback whale model					
Count model coefficients (negative binomial with log link)					
(Intercept)	1.646	0.485	2.808	2.778	0.005**
Krill	0.001	0.000	0.001	2.171	0.030*
Krill MWD	−0.013	−0.022	−0.003	−2.681	0.007**
Age-0 pollock	0.000	0.000	0.000	1.799	0.072˙
Trough (factor)	0.632	0.190	1.074	2.800	0.005**
Year (factor)	−0.562	−1.018	−0.107	−2.421	0.015*
Zero-inflation model coefficients (binomial with logit link)					
(Intercept)	2.573	0.516	4.630	2.452	0.014*
Krill	−0.007	−0.013	0.000	−1.930	0.054˙
Age-0 pollock	−0.001	−0.001	0.000	−2.505	0.012*
Effort	−0.845	−1.753	0.062	−1.825	0.068˙
Fin whale model					
Count model coefficients (negative binomial with log link)					
(Intercept)	−4.311	−6.016	−2.585	−4.899	0.000***
Krill MWD	0.023	0.011	0.035	3.839	0.000***
Trough (factor)	1.866	1.007	2.725	4.259	0.000***
Zero-inflation model coefficients (binomial with logit link)					
(Intercept)	4.072	0.929	7.215	2.539	0.011*
Krill	−0.004	−0.006	−0.002	−3.771	0.000***
Year (factor)	1.283	0.507	2.058	3.242	0.001**
Beaufort	−0.314	−0.597	−0.032	−2.184	0.029*
Effort	−0.675	−1.909	0.559	−1.072	0.284
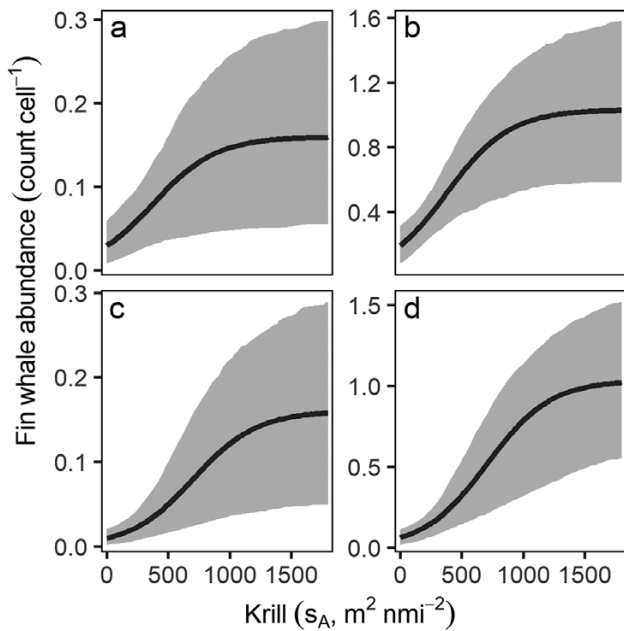
Fig. 4. Predicted fin whale sightings with krill backscatter (s_A) varied and other model components held constant. Shading represents bootstrapped 95% CIs. (a) Barnabas and (b) Chiniak basins in 2004; (c) Barnabas and (d) Chiniak basins in 2006

Fig. 5. Predicted humpback whale sightings with krill backscatter (s_A) varied and other model components held constant. Shading represents bootstrapped 95% CIs. (a) Barnabas and (b) Chiniak basins in 2004; (c) Barnabas and (d) Chiniak basins in 2006

Fig. 6. Predicted fin whale sightings with krill mean-weighted depth (MWD) varied and other model components held constant. Shading represents bootstrapped 95% CIs. (a) Barnabas and (b) Chiniak basins in 2004; (c) Barnabas and (d) Chiniak basins in 2006
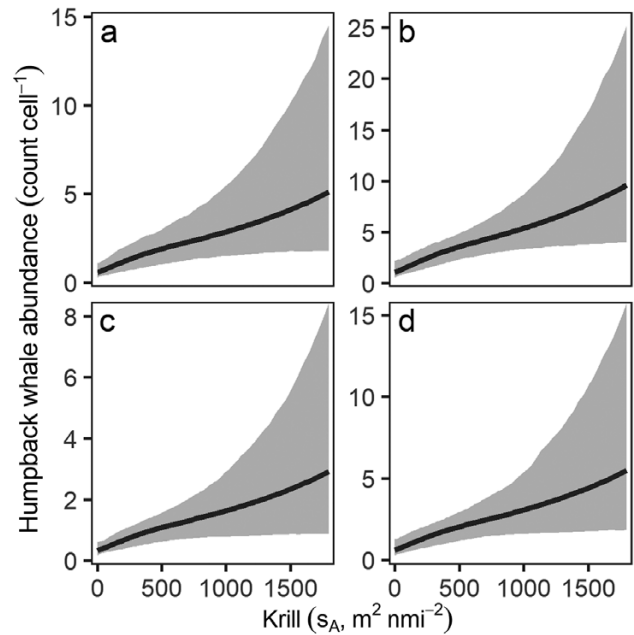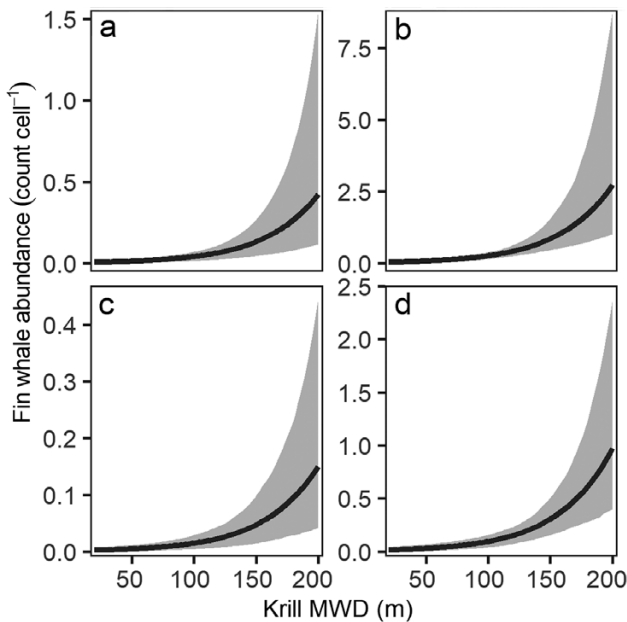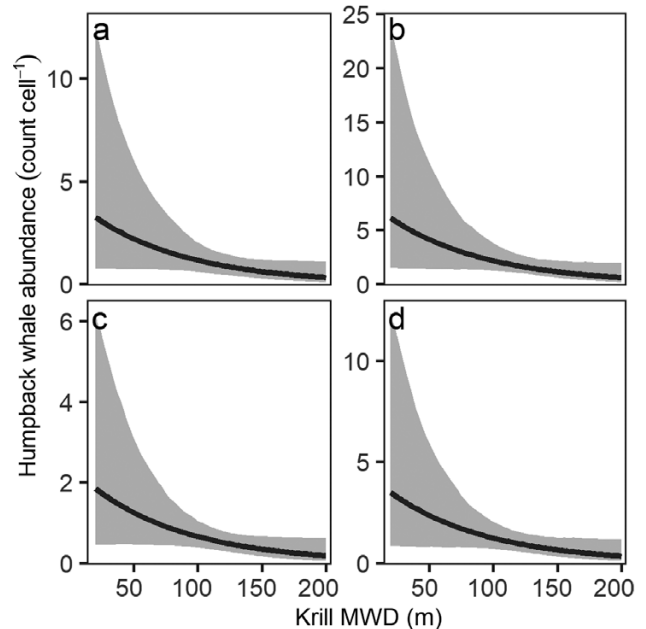

Fig. 7. Predicted humpback whale sightings with krill mean-weighted depth (MWD) varied and other model components held constant. Shading represents bootstrapped 95% CIs. (a) Barnabas and (b) Chiniak basins in 2004; (c) Barnabas and (d) Chiniak basins in 2006

effects for the predicted whale sightings differed with respect to euphausiid depth (Figs. 6 & 7). That is, increased euphausiid MWD was associated

with increased fin whale sightings, but decreased humpback sightings. Finally, humpback whales were associated with higher age-0 pollock densities
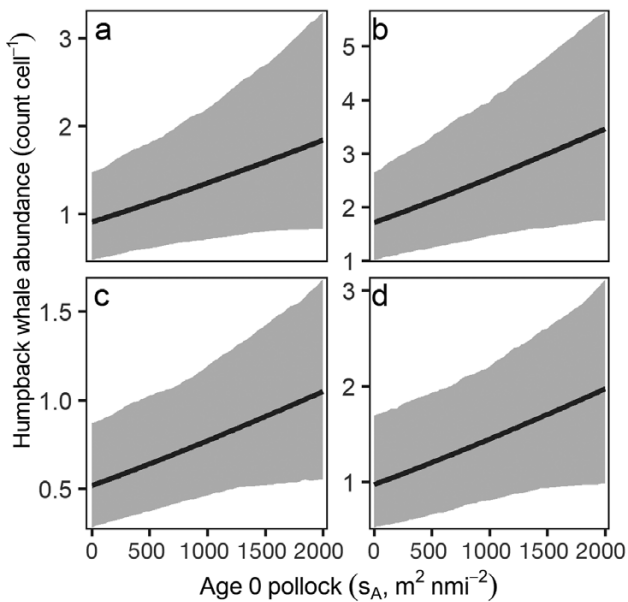
Fig. 8. Predicted humpback whale sightings with age-0 pollock s_A varied and other model components held constant. Shading represents bootstrapped 95% CIs. (a) Barnabas and (b) Chiniak basins in 2004; (c) Barnabas and (d) Chiniak basins in 2006

(Fig. 8), whereas age-0 pollock was dropped from the fin whale model (Table 3).

4. DISCUSSION

Concurrent observations of the distribution of whales and their prey suggest that fin and humpback whales engage in spatial and trophic niche partitioning at their feeding grounds near Kodiak, Alaska. The most notable contrast in how fin and humpback whales shared available habitat in the study area was seen in exploratory analyses suggesting that fin whales targeted the deepest, densest patches of euphausiids available, while humpback whales were associated with shallower and lower-density aggregations of euphausiids. Building on the exploratory analyses, multivariable predictive models suggested that euphausiid depth was an important predictor of fin whale sightings. Combined, the exploratory and multivariable approaches provide evidence that fin whale habitat use in this region differs from that of humpbacks. This may be due to the ability of fin whales to more efficiently target deeper prey patches due to their larger body size compared to humpback whales. Recent work examining diving behavior relative to prey patch depth suggests that whale foraging behavior is driven in part by species-specific

morphological differences (Friedlaender et al. 2015, Keen & Qualls 2018).

Sightings of both fin and humpback whales were related to euphausiid abundance near Kodiak, but analyses suggested that the whales may have different foraging thresholds. Fin whales were associated with the highest euphausiid abundances in the area, and predicted fin whale sightings increased steeply at intermediate levels of euphausiid backscatter ($500–1000 \ m^2 \ nmi^{-2}$), which suggests that they exhibited threshold foraging on euphausiid patches. The relationship between euphausiid backscatter and predicted humpback whale sightings was linear and more gradual than it was for fin whales, suggesting a lower foraging threshold. This contrast could be related to species-specific differences in energetic requirements and ability to efficiently forage at lower prey concentrations. Larger body size means that fin whales require more energy than humpback whales, so they must target the densest available prey patches to be efficient (Croll et al. 2001, Goldbogen et al. 2007, 2012). Comparatively, humpbacks generally exploit lower density prey aggregations with lower search costs rather than seeking out deeper, higher density prey aggregations (Friedlaender et al. 2009b, Tyson et al. 2016, Fossette et al. 2017, Keen & Qualls 2018). Recent work also suggests that fin whales and other large cetaceans are optimized for deeper diving to target dense prey (Hazen et al. 2015, Keen 2017, Keen & Qualls 2018). The combined factors of higher energetic requirements and more efficient foraging at depth may account for differences in associations seen in the present study.

The concentration of forage fishes near Kodiak had little effect on the presence of fin whales, but humpback whales were more likely to be found in areas where age-0 pollock were abundant. Although fin whales consume fishes in other areas (Nemoto 1959, Pauly et al. 1998, Sigler et al. 2012), we detected no relationship between fin whales and forage fishes in our study area. Given that fin whales were strongly associated with dense euphausiid patches, but not with forage fish, suggests prey partitioning by fin whales. In contrast, we observed that humpback whales were spatially associated with both euphausiids and small fishes. Differences in the prey partitioning strategies of fin and humpback whales are supported by prior work in the Kodiak region (Witteveen et al. 2015, Witteveen & Wynne 2016, Wright et al. 2016). Humpback whales also demonstrate an ability to switch target prey with changing prey availability (Friedlaender et al. 2009a, Hazen et al. 2009, Fleming et al. 2016), and this may account for findings in this

study. Historically, there have been reports of humpback whale predation on juvenile pollock (15–30 cm SL; Nemoto 1959, Kawamura 1980), but we are aware of no published work that addressed patterns in their distribution in relation to age-0 pollock (SL ≤ 10 cm). While other studies have suggested that humpback and fin whales may also exploit oily fish like capelin (Krieger & Wing 1984, Piatt & Methven 1992, Witteveen et al. 2015, Fleming et al. 2016, Wright et al. 2016), this was not observed in our study despite some seasonal overlap. There may be several explanations for why euphausiids, and not capelin, appear to be a driver of whale distributions near Kodiak. First, euphausiids are relatively abundant near Kodiak (Simonsen et al. 2016), and this may attract whales to the area. Second, while capelin consistently occur on the Kodiak shelf, they exhibit high spatial, temporal, and interannual variability (Jones et al. 2014, McGowan et al. 2019, 2020), and therefore they may be more costly to exploit, in spite of their high caloric content. Finally, it is possible that the capelin densities, even those in patches within the study area, were insufficient to make foraging for them energetically viable. Future studies of the predator–prey interactions of these species could be helpful in elucidating these patterns.

While prey abundance was an important predictor of fin and humpback whale presence, environmental variables were not. In this study, SST and chlorophyll were not related to whale distribution, but have been useful predictors in larger scale, basin-wide studies (Gregr & Trites 2001, Moore et al. 2002, Zerbini et al. 2016). Within our survey area, Chiniak Trough consistently had higher numbers of whales of both species, possibly due to higher fishing pressure in Barnabas. Despite the difference in magnitude, the predictive trends in the models persist between the 2 troughs. Given that prey availability changes within this survey area over both seasonal (Hollowed et al. 2007, Logerwell et al. 2007) and longer time scales (Anderson & Piatt 1999), and that environmental conditions change over short and long time scales, there is potential that the relationships shown by this work have shifted over time.

This study provides evidence that sympatric fin and humpback whales near Kodiak Island, Alaska, exhibit spatial and trophic prey partitioning through different foraging strategies and efficiencies. This work demonstrated the importance of simultaneously collecting acoustic-based estimates of prey and visual estimates of cetaceans, and future applications of this approach will likely lead to improvements of the predictive models needed for conservation and management. Evidence for niche partitioning observed here, together with previous observations (Friedlaender et al. 2006, Witteveen et al. 2015), suggests a mechanism that reduces or eliminates interspecific competition between these frequently co-occurring Balaenopteridae. More work is needed to determine whether foraging strategies that reduced competition in this study are used by fin and humpback whales elsewhere and also to determine short- and long-term temporal trends in niche partitioning by these 2 species in the Kodiak Island region.

LITERATURE CITED

Acevedo-Gutiérrez A, Croll D, Tershy B (2002) High feeding costs limit dive time in the largest whales. J Exp Biol 205: 1747–1753

Akaike H (1987) Factor analysis and AIC. Psychometrika 52: 317–332

Albrecht M, Gotelli N (2001) Spatial and temporal niche partitioning in grassland ants. Oecologia 126:134–141

Allen BM, Angliss RP (2015) Alaska marine mammal stock assessments, 2014. NOAA Tech Memo NMFS-AFSC-301

Anderson PJ, Piatt JF (1999) Community reorganization in the Gulf of Alaska following ocean climate regime shift. Mar Ecol Prog Ser 189:117–123

Bailey H, Thompson PM (2009) Using marine mammal habitat modelling to identify priority conservation zones within a marine protected area. Mar Ecol Prog Ser 378: 279–287

Baker CS, Herman LM, Perry A, Lawton WS, Straley JM, Straley JH (1985) Population characteristics and migration of summer and late-season humpback whales (*Megaptera novaeangliae*) in southeastern Alaska. Mar Mamm Sci 1:304–323

Baraff LS (2006) Summer distribution and habitat characteristics of fin whales (*Balaenoptera physalus*) and humpback whales (*Megaptera novaeangliae*) off northeast Kodiak Island, Alaska. MSc thesis, University of Alaska Fairbanks, Fairbanks, AK

Block BA, Jonsen ID, Jorgensen SJ, Winship AJ and others (2011) Tracking apex marine predator movements in a dynamic ocean. Nature 475:86–90

Burrows JA, Johnston DW, Straley JM, Chenoweth EM and others (2016) Prey density and depth affect the fine-scale foraging behavior of humpback whales *Megaptera novaeangliae* in Sitka Sound, Alaska, USA. Mar Ecol Progr Ser 561:245–260

Calambokidis J, Steiger GH, Straley JM, Herman LM and others (2001) Movements and population structure of humpback whales in the North Pacific. Mar Mamm Sci 17:769–794

Clapham PJ, Brownell RL Jr (1996) Potential for interspecific competition in baleen whales. Rep Int Whaling Comm 46:361–367

Clapham PJ, Meade JG (1999) *Megaptera novaeangliae.* Mamm Species 604:1–9

Clapham PJ, Seipt IE (1991) Resightings of independent fin whales, *Balaenoptera physalus*, on maternal summer ranges. J Mammal 72:788–790

Clapham PJ, Barlow J, Bessinger M, Cole T and others (2003) Abundance and demographic parameters of humpback whales from the Gulf of Maine, and stock definition relative to the Scotian Shelf. J Cetacean Res Manag 5:13–22

Croll DA, Acevedo-Gutiérrez A, Tershy BR, Urbán-Ramírez J (2001) The diving behavior of blue and fin whales: Is dive duration shorter than expected based on oxygen stores? Comp Biochem Physiol A Mol Integr Physiol 129:797–809

Cullen JJ, MacIntyre JG (1998) Behavior, physiology and the niche of depth-regulating phytoplankton. In: Anderson DM, Cembella AD, Hallegraeff GM (eds) Physiological ecology of harmful algal blooms. NATO ASI Series, Vol 41. Springer, Berlin, p 559–580

Dalla Rosa L, Ford JK, Trites AW (2012) Distribution and relative abundance of humpback whales in relation to environmental variables in coastal British Columbia and adjacent waters. Cont Shelf Res 36:89–104

Darlings J, Calambokidis J, Balcomb K, Bloedel P and others (1996) Movement of a humpback whale (*Megaptera novaeangliae*) from Japan to British Columbia and return. Mar Mamm Sci 12:281–287

De Robertis A, Cokelet ED (2012) Distribution of fish and macrozooplankton in ice-covered and open-water areas of the eastern Bering Sea. Deep Sea Res II 65-70:217–229

De Robertis A, Taylor K (2014) *In situ* target strength measurements of the scyphomedusa *Chrysaora melanaster*. Fish Res 153:18–23

De Robertis A, McKelvey DR, Ressler PH (2010) Development and application of an empirical multifrequency method for backscatter classification. Can J Fish Aquat Sci 67:1459–1474

De Robertis A, Taylor K, Wilson CD, Farley EV (2017) Abundance and distribution of Arctic cod (*Boreogadus saida*) and other pelagic fishes over the US Continental Shelf of the Northern Bering and Chukchi Seas. Deep Sea Res II 135:51–65

Demer DA, Conti SG (2005) New target-strength model indicates more krill in the Southern Ocean. ICES J Ma Sci 62:25–32

Dolphin WF (1988) Foraging dive patterns of humpback whales, *Megaptera novaeangliae*, in southeast Alaska: a cost–benefit analysis. Can J Zool 66:2432–2441

Doniol-Valcroze T, Berteaux D, Larouche P, Sears R (2007) Influence of thermal fronts on habitat selection by four rorqual whale species in the Gulf of St. Lawrence. Mar Ecol Prog Ser 335:207–216

Dumas PC (1956) The ecological relations of sympatry in *Plethodon dunni* and *Plethodon vehiculum*. Ecology 37:484–495

Engelbrecht BM, Comita LS, Condit R, Kursar TA, Tyree MT, Turner BL, Hubbell SP (2007) Drought sensitivity shapes species distribution patterns in tropical forests. Nature 447:80–82

Fleming AH, Clark CT, Calambokidis J, Barlow J (2016) Humpback whale diets respond to variance in ocean climate and ecosystem conditions in the California Current. Glob Change Biol 22:1214–1224

Flinn RD, Trites AW, Gregr EJ, Perry RI (2002) Diets of fin, sei, and sperm whales in British Columbia: an analysis of commercial whaling records, 1963–1967. Mar Mamm Sci 18:663–679

Foote KG (1983) Linearity of fisheries acoustics, with addition theorems. J Acoust Soc Am 73:1932–1940

Foote KG, Knudsen HP, Vestnes G, MacLennan DN, Simmonds EJ (1987) Calibration of acoustic instruments for fish density estimation: a practical guide. ICES Coop Res Rep 144:1–63

Fossette S, Abrahms B, Hazen EL, Bograd SJ and others (2017) Resource partitioning facilitates coexistence in sympatric cetaceans in the California Current. Ecol Evol 7:9085–9097

Fox R, Bellwood D (2013) Niche partitioning of feeding microhabitats produces a unique function for herbivorous rabbitfishes (Perciformes, Siganidae) on coral reefs. Coral Reefs 32:13–23

Friday NA, Zerbini AN, Waite JM, Moore SE, Clapham PJ (2013) Cetacean distribution and abundance in relation to oceanographic domains on the eastern Bering Sea shelf, June and July of 2002, 2008, and 2010. Deep Sea Res II 94:244–256

Friedlaender AS, Halpin PN, Qian SS, Lawson GL, Wiebe PH, Thiele D, Read AJ (2006) Whale distribution in relation to prey abundance and oceanographic processes in shelf waters of the Western Antarctic Peninsula. Mar Ecol Prog Ser 317:297–310

Friedlaender AS, Hazen EL, Nowacek DP, Halpin PN and others (2009a) Diel changes in humpback whale *Megaptera novaeangliae* feeding behavior in response to sand lance *Ammodytes* spp. behavior and distribution. Mar Ecol Prog Ser 395:91–100

Friedlaender AS, Lawson GL, Halpin PN (2009b) Evidence of resource partitioning between humpback and minke whales around the western Antarctic Peninsula. Mar Mamm Sci 25:402–415

Friedlaender AS, Goldbogen JA, Hazen EL, Calambokidis J, Southall BL (2015) Feeding performance by sympatric blue and fin whales exploiting a common prey resource. Mar Mamm Sci 31:345–354

Gavrilchuk K, Lesage V, Ramp C, Sears R, Bérubé M, Bearhop S, Beauplet G (2014) Trophic niche partitioning among sympatric baleen whale species following the collapse of groundfish stocks in the Northwest Atlantic. Mar Ecol Prog Ser 497:285–301

Goldbogen JA, Pyenson ND, Shadwick RE (2007) Big gulps require high drag for fin whale lunge feeding. Mar Ecol Prog Ser 349:289–301

Goldbogen JA, Calambokidis J, Croll DA, Harvey JT and others (2008) Foraging behavior of humpback whales: kinematic and respiratory patterns suggest a high cost for a lunge. J Exp Biol 211:3712–3719

Goldbogen JA, Calambokidis J, Croll DA, McKenna MF and others (2012) Scaling of lunge-feeding performance in rorqual whales: mass-specific energy expenditure increases with body size and progressively limits diving capacity. Funct Ecol 26:216–226

Gregr EJ, Trites AW (2001) Predictions of critical habitat for five whale species in the waters of coastal British Columbia. Can J Fish Aquat Sci 58:1265–1285

Guttormsen MA, Wilson CD (2009) *In situ* measurements of capelin (*Mallotus villosus*) target strength in the North Pacific Ocean. ICES J Mar Sci 66:258–263

Hastie T, Tibshirani R, Friedman J (2009) Model assessment and selection. The elements of statistical learning. Springer, New York, NY

Hazen EL, Friedlaender AS, Thompson MA, Ware CR, Weinrich MT, Halpin PN, Wiley DN (2009) Fine-scale prey aggregations and foraging ecology of humpback whales *Megaptera novaeangliae.* Mar Ecol Prog Ser 395:75–89

Hazen EL, Friedlaender AS, Goldbogen JA (2015) Blue whales (*Balaenoptera musculus*) optimize foraging efficiency by balancing oxygen use and energy gain as a function of prey density. Sci Adv 1:e1500469

Herr H, Viquerat S, Siegel V, Kock KH and others (2016) Horizontal niche partitioning of humpback and fin whales around the West Antarctic Peninsula: evidence from a concurrent whale and krill survey. Polar Biol 39: 799–818

Hinde J, Demétrio CG (1998) Overdispersion: models and estimation. Comp Stat Data Anal 27:151–170

Hinke JT, Polito MJ, Goebel ME, Jarvis S and others (2015) Spatial and isotopic niche partitioning during winter in chinstrap and Adélie penguins from the South Shetland Islands. Ecosphere 6:125

Hollowed AB, Wilson CD, Stabeno PJ, Salo SA (2007) Effect of ocean conditions on the cross-shelf distribution of walleye pollock (*Theragra chalcogramma*) and capelin (*Mallotus villosus*). Fish Oceanogr 16:142–154

Honkalehto T, Jones D, McCarthy A, McKelvey D, Guttormsen M, Williams K, Williamson N (2009) Results of the echo integration-trawl survey of walleye pollock (*Theragra chalcogramma*) on the US and Russian Bering Sea shelf in June and July 2008. NOAA Tech Memo NMFS-AFSC-194

Hunt GL, Ressler PH, Gibson GA, De Robertis A and others (2016) Euphausiids in the eastern Bering Sea: a synthesis of recent studies of euphausiid production, consumption and population control. Deep Sea Res II 134:204–222

Hutchinson GE (1957) Concluding remarks. Cold Spring Harb Symp Quant Biol 22:415–427

Jones D, Ressler PH, Stienessen S, McCarthy AL, Simonsen KA (2014) Results of the acoustic-trawl survey of walleye pollock (*Gadus Chalcogrammus*) in the Gulf of Alaska, June–August 2013 (DY2013-07). AFSC Processed Rep 2014-06. Alaska Fisheries Science Center, Seattle, WA

Kawamura A (1980) A review of food of balaenopterid whales. Sci Rep Whales Res Inst 32:155–197

Keen EM (2017) Aggregative and feeding thresholds of sympatric rorqual whales within a fjord system. Ecosphere 8:e01702

Keen EM, Qualls KM (2018) Respiratory behaviors in sympatric rorqual whales: the influence of prey depth and implications for temporal access to prey. J Mammal 99:27–40

Kelly CK, Bowler MG, Pybus O, Harvey PH (2008) Phylogeny, niches, and relative abundance in natural communities. Ecology 89:962–970

Kleiber C, Zeileis A (2020) AER: applied econometrics with R. R package version 1.2-7. https://cran.r-project.org/package=AER

Krieger KJ, Wing BL (1984) Hydroacoustic surveys and identification of humpback whale forage in Glacier Bay, Stephens Passage, and Frederick Sound, southeastern Alaska, summer 1983. NOAA Tech Memo NMFS F/NWC-66

Kronfeld-Schor N, Dayan TJO (1999) The dietary basis for temporal partitioning: food habits of coexisting *Acomys* species. Oecologia 121:123–128

Lambert D (1992) Zero-inflated Poisson regression, with an application to defects in manufacturing. Technometrics 34:1–14

Leibold MA (2008) Return of the niche. Nature 454:39–41

Lerczak JA, Hobbs RC (1998) Calculating sighting distances from angular readings during shipboard, aerial, and shore-based marine mammal surveys. Mar Mamm Sci 14:590–98 (see also errata Mar Mamm Sci 14:903)

Logerwell EA, Stabeno PJ, Wilson CD, Hollowed AB (2007) The effect of oceanographic variability and interspecific competition on juvenile pollock (*Theragra chalcogramma*) and capelin (*Mallotus villosus*) distributions on the Gulf of Alaska shelf. Deep Sea Res II 54:2849–2868

Martin TG, Wintle BA, Rhodes JR, Kuhnert PM and others (2005) Zero tolerance ecology: improving ecological inference by modelling the source of zero observations. Ecol Lett 8:1235–1246

McGowan DW, Horne JK, Thorson JT, Zimmermann M (2019) Influence of environmental factors on capelin distributions in the Gulf of Alaska. Deep Sea Res II 165:238–254

McGowan DW, Goldstein ED, Arimitsu ML, Deary AL and others (2020) Spatial and temporal dynamics of Pacific capelin *Mallotus catervarius* in the Gulf of Alaska: implications for ecosystem-based fisheries management. Mar Ecol Prog Ser 637:117–140

McKelvey DR, Wilson CD (2006) Discriminant classification of fish and zooplankton backscattering at 38 and 120 kHz. Trans Am Fish Soc 135:488–499

Minami M, Lennert-Cody CE, Gao W, Román-Verdesoto M (2007) Modeling shark bycatch: the zero-inflated negative binomial regression model with smoothing. Fish Res 84:210–221

Mizroch SA, Rice DW, Zwiefelhofer D, Waite J, Perryman WL (2009) Distribution and movements of fin whales in the North Pacific Ocean. Mammal Rev 39:193–227

Moore S, Waite J, Friday N, Honkalehto T (2002) Cetacean distribution and relative abundance on the central-eastern and the southeastern Bering Sea shelf with reference to oceanographic domains. Prog Oceanogr 55:249–261

Muto M, Helker V, Angliss RP, Allen BA and others (2018) Alaska marine mammal stock assessments, 2017. NOAA Tech Memo NMFS-AFSC-378

Nemoto T (1959) Food of baleen whales with reference to whale movements. Sci Rep Whales Res Inst 14:149–290

Otero J, Álvarez-Salgado XA, González ÁF, Souto C, Gilcoto M, Guerra Á (2016) Wind-driven upwelling effects on cephalopod paralarvae: *Octopus vulgaris* and *Loliginidae* off the Galician coast (NE Atlantic). Prog Oceanogr 141:130–143

Pauly D, Trites A, Capuli E, Christensen V (1998) Diet composition and trophic levels of marine mammals. ICES J Mar Sci 55:467–481

Piatt JF, Methven DA (1992) Threshold foraging behavior of baleen whales. Mar Ecol Prog Ser 84:205–210

Porter JW (1976) Autotrophy, heterotrophy, and resource partitioning in Caribbean reef-building corals. Am Nat 110:731–742

Preisser JS, Stamm JW, Long DL, Kincade ME (2012) Review and recommendations for zero-inflated count regression modeling of dental caries indices in epidemiological studies. Caries Res 46:413–423

Ressler PH, De Robertis A, Warren JD, Smith JN, Kotwicki S (2012) Developing an acoustic survey of euphausiids to understand trophic interactions in the Bering Sea ecosystem. Deep Sea Res II 65–70:184–195

Ressler PH, Dalpadado P, Macaulay GJ, Handegard N, Skern-Mauritzen M (2015) Acoustic surveys of euphausiids and models of baleen whale distribution in the Barents Sea. Mar Ecol Prog Ser 527:13–29

Ross ST (1986) Resource partitioning in fish assemblages: a review of field studies. Copeia 1986:352–388

Siemers BM, Schnitzler HU (2004) Echolocation signals reflect niche differentiation in five sympatric congeneric bat species. Nature 429:657–661

Sigler MF, Kuletz KJ, Ressler PH, Friday NA, Wilson CD, Zerbini AN (2012) Marine predators and persistent prey in the southeast Bering Sea. Deep Sea Res II 65–70: 292–303

Simard Y, Lavoie D (1999) The rich krill aggregation of the Saguenay-St. Lawrence Marine Park: hydroacoustic and geostatistical biomass estimates, structure, variability, and significance for whales. Can J Fish Aquat Sci 56: 1182–1197

Simmonds E, MacLennan D (2005) Fisheries acoustics, 2nd edn. Fish and aquatic resources series, Vol 10. Blackwell Science, Oxford

Simonsen KA, Ressler PH, Rooper CN, Zador SG (2016) Spatio-temporal distribution of euphausiids: an important component to understanding ecosystem processes in the Gulf of Alaska and eastern Bering Sea. ICES JMar Sci 73: 2020–2036

Skern-Mauritzen M, Johannesen E, Bjørge A, Øien N (2011) Baleen whale distributions and prey associations in the Barents Sea. Mar Ecol Prog Ser 426:289–301

Straley JM, Moran JR, Boswell KM, Vollenweider JJ and others (2018) Seasonal presence and potential influence of humpback whales on wintering Pacific herring populations in the Gulf of Alaska. Deep Sea Res II 147: 173–186

Traynor JJ (1996) Target-strength measurements of walleye pollock (*Theragra chalcogramma*) and Pacific whiting (*Merluccius productus*). ICES J Mar Sci 53:253–258

Trites AW, Christensen V, Pauly D (1997) Competition between fisheries and marine mammals for prey and primary production in the Pacific Ocean. J Northwest Atl Fish Sci 22:173–187

Tyson R, Friedlaender A, Nowacek D (2016) Does optimal foraging theory predict the foraging performance of a large air-breathing marine predator? Anim Behav 116: 223–235

Venables WN, Ripley BD (2013) Modern applied statistics with S-PLUS. Springer Science+Business Media, New York, NY

Ver Hoef JM, Boveng PL (2007) Quasi-Poisson vs. negative binomial regression: How should we model overdispersed count data? Ecology 88:2766–2772

Vuong QH (1989) Likelihood ratio tests for model selection and non-nested hypotheses. Econometrica 57:307–333

Waite JM, Dahlheim ME, Hobbs RC, Mizroch SA and others (1999) Evidence of a feeding aggregation of humpback whales (*Megaptera novaeangliae*) around Kodiak Island, Alaska. Mar Mamm Sci 15:210–220

Walline PD, Wilson CD, Hollowed AB, Stienessen SC (2012) Short-term effects of commercial fishing on the distribution and abundance of walleye pollock (*Theragra chalcogramma*). Can J Fish Aquat Sci 69:354–368

Warren DL, Glor RE, Turelli M (2008) Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution 62: 2868–2883

Werner EE, Gilliam JF (1984) The ontogenetic niche and species interactions in size-structured populations. Annu Rev Ecol Syst 15:393–425

Whitehead H, Carscadden J (1985) Predicting inshore whale abundance—whales and capelin off the Newfoundland coast. Can J Fish Aquat Sci 42:976–981

Wickham H, Chang W, Wickham MH (2016) Package 'ggplot2': create elegant data visualisations using the grammar of graphics. v.3.2.0. https://github.com/tidyverse/ggplot2/releases/tag/v3.2.0

Williams R, Vikingsson GA, Gislason A, Lockyer C, New L, Thomas L, Hammond PS (2013) Evidence for density-dependent changes in body condition and pregnancy rate of North Atlantic fin whales over four decades of varying environmental conditions. ICES J Mar Sci 70: 1273–1280

Wilson CD, Hollowed AB, Shima M, Walline P, Stienessen S (2003) Interactions between commercial fishing and walleye pollock. Alsk Fish Res Bull 10:61–77

Witteveen BH, Quinn TJ II (2007) A feeding aggregation of humpback whales *Megaptera novaeangliae* near Kodiak Island, Alaska: historical and current abundance estimation. Alsk Fish Res Bull 12:187–196

Witteveen BH, Wynne KM (2016) Trophic niche partitioning and diet composition of sympatric fin (*Balaenoptera physalus*) and humpback whales (*Megaptera novaeangliae*) in the Gulf of Alaska revealed through stable isotope analysis. Mar Mamm Sci 32:1319–1339

Witteveen BH, Foy RJ, Wynne KM (2006) The effect of predation (current and historical) by humpback whales (*Megaptera novaeangliae*) on fish abundance near Kodiak Island, Alaska. Fish Bull 104:10–20

Witteveen BH, Foy RJ, Wynne KM, Tremblay Y (2008) Investigation of foraging habits and prey selection by humpback whales (*Megaptera novaeangliae*) using acoustic tags and concurrent fish surveys. Mar Mamm Sci 24:516–534

Witteveen BH, De Robertis A, Guo L, Wynne KM (2015) Using dive behavior and active acoustics to assess prey use and partitioning by fin and humpback whales near Kodiak Island, Alaska. Mar Mamm Sci 31:255–278

Wright DL, Witteveen B, Wynne K, Horstmann-Dehn L (2016) Fine-scale spatial differences in humpback whale diet composition near Kodiak, Alaska. Mar Mamm Sci 32:1099–1114

Wynne K, Foy R, Buck LJK (2005) Gulf apex predator–prey study (GAP): final report FY2001–2003. University of Alaska, Kodiak, AK

Zeileis A, Kleiber C, Jackman S (2008) Regression models for count data in R. J Stat Softw 27:1–25

Zerbini AN, Waite JM, Laake JL, Wade PR (2006) Abundance, trends and distribution of baleen whales off western Alaska and the central Aleutian Islands. Deep Sea Res I 53:1772–1790

Zerbini AN, Friday NA, Palacios DM, Waite JM and others (2016) Baleen whale abundance and distribution in relation to environmental variables and prey density in the Eastern Bering Sea. Deep Sea Res II 134:312–330

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Zero-truncated and zero-inflated models for count data. Mixed effects models and extensions in ecology with R. Springer, New York, NY

Zuur AF, Savaliev AA, Ieno EN (2012) Zero-inflated models and generalized linear mixed models with R. Highland Statistics, Newburgh