A hierarchical modelling approach to estimating humpback whale abundance from sand lance abundance

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Abstract

The primary prey of humpback whales in the southwestern Gulf of Maine is sand lance. Despite this established relationship, we lack models to further understand the influence of sand lance on humpback whales or to predict humpback abundance or distribution in response to climate-related changes in sand lance abundance or distribution. We used a subset of long-term standardized survey data (2013-2019) from Stellwagen Bank National Marine Sanctuary and a Bayesian hierarchical modelling approach to explore the influence of sand lance on humpback whales at multiple spatial and temporal scales while accounting for sampling variability and propagating uncertainty. We developed zero-inflated Poisson mixed effects models for both sand lance and humpbacks, using modelled sand lance abundance as a predictor in the whale model. Results showed a statistically clear positive correlation between sand lance and humpback whales. Regional mean abundances of both species increased from north to south, though site-level variation within regions showed more variability. Results suggest annual variation in abundance of both species, with potentially different influences. We demonstrate one management application of our method by examining entanglement risk for humpback whales. Whale aggregations were more likely to occur in a high density area of fixed fishing gear that overlaps with an area of higher sand lance abundance. Our work suggests that humpback whale distribution in the larger Gulf of Maine may be impacted by climate-related fluctuations in sand lance abundance. Predicting future distributions of humpback whales is important for ecosystem-based management, including mitigation of human impacts, and our work serves as a foundation for further model development.

Keywords (6 max): forage fish, predator-prey, Gulf of Maine, Bayesian, Stellwagen Bank, habitat use, spatial overlap,

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Introduction

In the southwestern Gulf of Maine (GOM), the preferred prey of humpback whales (*Megaptera novaeangliae*) is sand lance (*Ammodytes* spp.). Shifts in the abundance and distribution of humpbacks into and out of the southwestern GOM have been linked with fluctuations in the abundance of sand lance during several time periods since the late 1970s. Steady increases in humpback whale densities from 1978-1982 correlated with increased sand lance densities (Payne et al. 1986). Fluctuations in humpback whale abundance followed fluctuations in sand lance abundance from 1982-1988 (Payne et al. 1990) and a decline in humpback whale abundance on Stellwagen Bank from 1988-1994 was concurrent with a decline in presumed sand lance density and an increase in humpback abundance on nearby Jeffrey's Ledge, where humpbacks feed predominately on herring (Weinrich et al. 1998).

While the link between humpbacks and sand lance in the southwestern GOM is clear, current evidence is limited to linear correlations. We lack statistical models to further understand the strength of this relationship over time and space, or to predict changes in the abundance and distribution of either species in response to climate change.

Here, we aimed to advance our understanding of the sand lance-humpback relationship by using a Bayesian hierarchical modeling approach to account for: spatial and temporal variability, uncertainty in the association of humpback abundance with latent abundance of sand lance, and the observation process. We fit zero-inflated Poisson mixed effects models to a subset of a unique, long-term dataset of humpback whale and sand lance counts from seasonal standardized surveys in Stellwagen Bank National Marine Sanctuary, a federal MPA in the southwestern GOM. The sanctuary is a critical foraging area for humpbacks and in some years, hosts the highest sand lance densities in the GOM (Richardson et al. 2014), providing an ideal location to further explore the relationship between these species and to work toward building a predictive modeling framework.

Methods

Data collection

Field work was described in Silva et al. (2020). Briefly, 13 seasonal surveys for sand lance and humpback whales were conducted from 2013 - 2019 (Fall: September – November; n=5; Spring: April – June, n=6; Summer: July, n=2) in Stellwagen Bank National Marine Sanctuary. The survey included 44 sites (~1 km apart in most areas) in

3 blocks (north, central, south) across Stellwagen Bank designed to sample all potential sand lance habitat (Fig. 1A).

Sand lance are a benthopelagic species that spend time both in the water column and in the sediment (Robbards 2000). We sampled sand lance in the sediment using the U.S. Geological Survey Seabed Observation and Sampling System (SEABOSS) (Blackwood & Parolski, 2001), equipped with a modified Van Veen benthic grab sampler ($0.1 m^2$). At each site, the SEABOSS was deployed to the sea floor to sample sediment and the number of sand lance in each sample was recorded. We assumed the number of sand lance recorded in each grab sample was representative of the total number of sand lance at each site (water column + sediment).

During each SEABOSS deployment, trained observers (typically 1 on either side of the vessel) recorded the number of humpback whales in an 800 m radius around the vessel for 10 minutes. We chose the sampling distance and observation period based on our ability to reliably identify species and to limit the possibility of double counting individuals (based on typical humpback dive durations of ~5 minutes, Wiley unpublished data). Distances were estimated using a hand-held, fixed interval range finder calibrated using laser range finders and a buoy at known distance in relation to the horizon (Heinemann, 1981).

Some cruises resulted in no observations of sand lance or whales or very small total species counts (two individuals). We excluded these data from analysis. We also excluded summer data since there were only two cruises. Here we used data from five cruises (n=164), with sampling effort spread over four years and fairly equally across seasons and sites (Table 1, Table S1).

Modeling

Model structure

Count data for sand lance and humpback whales contained mostly zeroes (Fig. 1B, C) and preliminary models using Poisson and negative binomial distributions fit poorly. We implemented a zero-inflated Poisson mixed effects model using a Bayesian hierarchical framework. Several aspects of our study make it well suited for this approach. First, our study design includes simple categorical covariates that are nested within several spatial and temporal scales, inviting a hierarchical structure as well as random effects (Hobbs & Hooten 2015). Second, this framework allows us to incorporate sampling variability, which we believe is important given our data collection method (Pavanato et al. 2017). Third, we can propagate uncertainty throughout prey and predator models. Lastly, Bayesian methods allow for inference using true probability statements, which better represent ecological data and are more useful for managers making decisions (Wade 2000).

Sand lance sub-model

We modeled sand lance counts, sl_{ijk}, at site i in block j in year k, using a zero-inflated mixture model,

$$sl_{ijk} \sim \begin{cases} 0 & f\ z_{ijk}^{sl} = 0 \\ ss\ \left(\lambda_{ijk}^{sl}\right) & f\ z_{ijk}^{sl} = 1 \end{cases}$$

where λ_{ijk}^{sl} is the mean number of sand lance per sediment sample at site *i* in block *j* in year *k*,

z_{ijk}^{sl} is a random variable describing seasonal zero-inflation in sand lance availability:

$$z_{ijk}^{sl} \sim Ber\quad ull\ \left(\phi_{m(ijk)}^{sl}\right)$$

$$\phi_{m(ijk)}^{sl} \sim \quad (0,1)$$

where $\phi_{m(ijk)}^{sl}$ is the probability of success (sand lance captured) for season *m* and 1 - $\phi_{m(ijk)}^{sl}$ is the probability of zero inflation . Sand lance in Stellwagen Bank National Marine Sanctuary exhibit seasonal differences in behavior. In fall, sand lance spend more time on or in the sediment in estivation prior to spawning (Suca et al. 2021). We hypothesized that these seasonal differences in bottom time would influence the chance of sand lance capture in sediment grabs. If z = 0, the mean number of sand lance equaled zero. If z = 1, the number of sand lance in the count was distributed as a Poisson random variable with mean λ_{ijk}^{sl} (Fig. 2).

We described λ_{ijk}^{sl} as a log linear function of block, site, and year,

$$\ln\left(\lambda_{ijk}^{sl}\right) = \beta_j^b + \beta_i^s + \beta_k^y$$

$$\beta_j^b \sim N(0, 10)$$

$$\beta_i^s \sim N(0, \sigma_{sl}^2)$$

$$\beta_k^y \sim N(0, \tau_{sl}^2)$$

$$\frac{1}{\sigma_{sl}^2} \sim Gamma(0.01, 0.01)$$

$$\frac{1}{\tau_{sl}^2} \sim Gamma(0.01, 0.02)$$

Data exploration suggested that sand lance counts differed substantially by block (Fig. 1B, C). Our model structure assumed that each block had an overall mean number of sand lance, with site- and annual-specific effects. Site and year were treated as random effects to capture spatial and temporal variation in expected sand lance counts. We had no existing knowledge to inform choice of priors, therefore we used vague priors on all parameters. For site- and year- level variance, we used the conjugate gamma prior on the precision of normal distributions. After initial model runs, we chose to increase the precision (decrease variance) for $\frac{1}{\tau_{sl}^2}$ to 0.02 in order to decrease initial autocorrelation in MCMC chains.

Humpback whale sub-model

The humpback whale sub-model was similar to the sand lance model. We modeled humpback whale counts,w_{ijk} at site i in year k, using a zero- inflated mixture model,

$$w_{ijk} \sim \begin{cases} 0 & f\, z_{ijk}^{w} = 0 \\ ss \quad \left(\lambda_{ijk}^{w}\right) & f\, z_{ijk}^{w} = 1 \end{cases}$$

where z_{ijk}^{w} is a random variable describing if whales were observed (z=1) or not (z=0) and λ_{ijk}^{w} is the mean number of whales at site i in year k (Fig. 2). We used a Bernoulli distribution with a uniform prior for z,

$$z_{ijk}^{w} \sim Ber \quad ull\left(\phi_{m(ijk)}^{w}\right)$$

$$\phi_{m(ijk}^{w} \sim \quad (0{,}1)$$

where $\phi_{m(ijk)}^{w}$ in season *m* represents the probability of success (whales observed) and 1-$\phi_{m(ijk)}^{w}$ is the probability of zero inflation. The annual migratory cycle of humpback whales consists of arrival on higher latitude feeding grounds (including the sanctuary) in spring and departure from feeding grounds to lower latitude breeding grounds in fall (Clapham et al. 1993). We hypothesized that whale presence in SBNMS, and therefore, sampling variability, may be influenced by their migratory cycle. If z = 1, the number of whales was distributed as a Poisson random variable with a mean, λ_{ijk}^{w}. If z = 0, the number of whales equaled zero.

Based on the established correlations between sand lance and humpbacks (Payne et al. 1986, Payne et al. 1990), we hypothesized that humpback whale counts were correlated with sand lance abundance and included expected sand lance abundance as a covariate in the humpback model. We described λ_{ijk}^{w} for each data point as a log linear function of expected sand lance abundance, site, and year (Fig. 2),

$$\ln\left(\lambda_{ijk}^{w}\right) = \alpha_{sl}\ln(\lambda_{ijk}^{sl}) + \theta_i^{s} + \theta_k^{y}, \text{ where}$$

$$\alpha_{sl} \sim N(0, 10)$$

$$\theta_i^s \sim N(0, \sigma_w^2)$$

$$\theta_k^y \sim N(0, \tau_w^2)$$

$$\frac{1}{\sigma_w^2} \sim Gamma(0.01, 0.01)$$

$$\frac{1}{\tau_w^2} \sim Gamma(0.01, 0.02)$$

Since we assume humpback counts were correlated with sand lance counts, and the mean number of sand lance was assumed to vary by block, we did not include block as a covariate in the whale model. We included site and year as random effects to capture spatial and temporal variation in whale counts that may not be attributable to sand lance. We had no existing knowledge to inform choice of priors, therefore we used vague priors on all parameters as in the sand lance sub-model.

Model fitting and analysis

Models were implemented using Markov chain Monte Carlo (MCMC) algorithms in JAGS (Just Another Gibbs Sampler; Plummer 2003) called from R using the package *rjags* (Plummer 2011). We ran four chains with 1 million iterations, a burn-in of 50,000, adaptation period of 50,000 and a thinning parameter of 1/1000 to account for high autocorrelation in the chains. The total sample size consisted of 3800 draws (4 chains * ((1 million iterations – 50,000 burn-in) / 1000))).

We assessed convergence by inspecting trace plots to ensure well-mixed chains (Hobbs and Hooten 2015) and calculating Gelman-Rubin statistics (Rhat) (Gelman and Rubin 1992) for all parameters using the *MCMCvis* package (Youngflesh 2018). Rhat values close to 1 indicate convergence with values less than 1.2 acceptable (Gelman 1996, Zuur et al. 2012).

We assessed model fit using posterior predictive checks, which evaluate the ability of a model to generate new observations that resemble our observed data. We simulated new data for sand lance and whale counts based on the posterior predictive distributions for the mean number of sand lance and whales. We defined the mean, variance and proportion of zeroes in our simulated datasets as test statistics. Goodness of fit was evaluated using Bayesian p values (P_B), the probability that the test statistic calculated from our simulated data is more extreme than the test statistic calculated from observed data. Very large or very small P_B (<0.1 or >0.9) indicate poor model fit. We conducted posterior predictive checks for each species and also summarized results by block, season and year.

Applications

We used model results to examine two applications that could have potential management implications: locating sand lance 'hot-spots' and exploring entanglement risk to humpback whales. We used posterior probability distributions for the site parameter to find the probability that a site had a greater than block average number of sand lance. To explore entanglement risk, we estimated the probability of a whale aggregation at each site and examined overlap between sites and fixed fishing gear locations. To estimate site probabilities of whale aggregations, we used the new counts of whales generated for posterior predictive checks and found the proportion of those values that were greater than our arbitrarily chosen aggregation size (n=5). We explored potential overlap between whale aggregations and fixed fishing gear by creating a density map of trap-pot gear locations from 2014-2016 from Vessel Trip Report (VTR) data (NOAA Fisheries) using the *spatstat* package (Baddeley et al. 2015).

Results

Sand lance sub-model

Trace plots and Gelman-Rubin statistics confirmed convergence of most parameters. Twelve λ_{ijk}^{sl} values had Rhat values between 1.2 and 1.3. These values correspond to sites that never had sand lance observations, suggesting the model could not separate true vs. false zeroes for these data points. Two z_{ijk}^{sl} values also had Rhat > 1.2 & < 1.3. For all fixed effects and variance components, Rhat values were <1.1 and effective sample sizes (n.eff) were > 3200.

Overall posterior predictive checks for the mean, variance and proportion of zeroes for sand lance showed no evidence of lack of fit (Bayesian p-values: mean = 0.53, variance = 0.73, proportion of zeroes = 0.79; Fig. S2). Posterior predictive checks summarized by block (Bayesian p-value range: 0.52 – 0.84), year (Bayesian p-value range: 0.38 – 0.90), and season (Bayesian p-value range: 0.50 – 0.82) also showed no obvious lack of fit (Figs. S3 – S5).

Predicted sand lance abundance varied by block and increased from north to south, with median estimates of 0.07 sand lance / block (north), 0.73 sand lance / block (central), and 3.74 sand lance / block (south) (Fig. 3A, Table 2). Some annual differences in abundance were observed (credible intervals overlapped in most years), with the largest fluctuations in abundance occurring in the south. Median sand lance estimates for the south in most years (2014, 2015, 2016) was greater than average, while median estimates for the central block were at or below average in these years. Highest abundances in all blocks occurred in 2016. Abundance estimates for the north showed little to no difference by year with median annual estimates essentially the same as the near-zero block average (Fig. 3A). In the south and central blocks, median abundance estimates were below average in 2018 (Fig. 3A).

Parameter values suggested site-level variation in sand lance abundance (Fig. 4A, Table 2). Above average sand lance abundance was predicted for one northern site, two central sites, and one southern site (Fig. 4A). The 95% credible intervals of the marginal posterior for three additional sites (one northern, 2 southern) were almost entirely above zero. Southern and central blocks had mixtures of sites with median estimates above and below average expected abundance, while all but three northern median estimates were predicted to have below average abundance (Fig. 4A), which was not surprising given that sand lance were only observed at 2 sites in the northern block throughout the study period (Fig. S1).

The probability of sand lance availability was slightly greater in the fall (median = 0.42, 95% CI = 0.29 – 0.59) than the spring (median = 0.33, 95% CI = 0.17 – 0.56) (Table 2), though overlapping credible intervals suggest little difference between seasons.

Humpback whale sub-model

Trace plots and Gelman-Rubin statistics confirmed convergence of most parameters. One λ_{ijk}^{w}value and seven z_{ijk}^{w}values had Rhat values between 1.2 and 1.3. For all fixed effects and variance components, Rhat values were <1.1 and effective sample sizes (n.eff) were > 3200.

Overall posterior predictive checks for the mean, variance and proportion of zeroes for humpbacks showed no evidence of lack of fit (Bayesian p-values: mean = 0.51, variance = 0.78, proportion of zeroes = 0.71; Fig. S2). Posterior predictive checks summarized by block (Bayesian p-value range: 0.27 – 0.86), year (Bayesian p-value range: 0.31 – 0.90) and season (Bayesian p-value range: 0.48 – 0.91) also showed no obvious lack of fit (Figs. S3 – S5).

Humpback whales showed a statistically clear positive correlation with sand lance (median = 0.35, 95% credible interval = 0.05 – 0.70; Fig. 4C, Table 2). Using this relationship, estimated humpback abundance also increased from north to south, with highest expected abundances in every year occurring in the south (Fig. 4B). Some annual differences in humpback abundance were observed, but year-to-year variation differed from sand lance. Median values for predicted humpback abundance in all sites alternated from below average in 2014 and 2016, to at or above average in 2015 and 2018, respectively (Fig. 4B).

The posteriors for the parameter values suggested site-level variation in humpback abundance (Fig. 4B). Above average humpback abundance was predicted for two central sites and three southern site (Fig. 4B). The range of 95% credible intervals for three additional sites (one central, two southern) were almost entirely above zero. No northern sites showed clear differences in humpback abundance, though median and 50% Bayesian credible intervals were above average for two northern sites. Southern and central blocks had mixtures of sites with median estimates above and below average (Fig. 4B). Only one site (C6) showed clear, above average estimates for both humpbacks and sand lance (Fig. 4A, B).

The probability of humpback availability was slightly greater in the fall (median = 0.53, 95% credible interval = 0.36 – 0.71) than the spring (median = 0.47, 95% credible interval = 0.3 – 0.66) (Table 2), though overlapping credible intervals suggests little difference between seasons. The median probability of observing whales was greater than the probability of observing sand lance in both seasons (Table 2).

Applications

Sites that were likely to have greater than average sand lance abundance, or sand lance 'hot-spots', were identified in all blocks (Fig. 5). The probability that a site had greater than block-average sand lance abundance was >0.75 for two northern sites, four central sites, and five southern sites (Fig. 5).

Probabilities of at least 5 whales at a site ranged from 0 – 0.34, with whale aggregations being most likely in the southern block at site S11 (Fig. 6). The three (S10, S11, S14) sites with the highest probabilities of whale aggregations overlapped with a high density area of trap-pot gear on the SW corner of Stellwagen Bank. The probability of >3 whales at sites was greater with sites S11 and S14 having probabilities of whale aggregations ≥ 0.5.

Discussion

Ecology

We demonstrated a statistically clear, positive correlation between sand lance and humpback whales, supporting findings from previous work and confirming persistence of this relationship over time (Payne et al. 1986, Payne et al. 1990, Weinrich et al. 1998). While prior studies linked shifts in humpback distributions with fluctuations in sand lance abundance at broad scales across large feeding areas, we showed relationships at an intermediate (block) scale within a single feeding area. This result is consistent with Silva et al. (2020) that applied spatial metrics to the same dataset and found high spatial collocation between humpbacks and sand lance in southern Stellwagen Bank.

The clear relationship between humpbacks and sand lance suggests that relative effects of sites and year would vary similarly for both species, but this was not the case. Only one site (C6) had a positive effect on both sand lance and humpback abundance. Differences in site effects for sand lance and humpbacks are likely due to a combination of scale mismatch and habitat selection by sand lance. Correlations between predators and prey are often scale-dependent (Rose & Legget 1990, Fauchald et al 2000). Our site-level observations of sand lance and humpbacks are collected at very different spatial scales – 0.1 m^2 for sand lance and an 800 m radius for humpbacks. Further, sand lance benthic distributions are highly patchy, ranging from 0 to 44 fish in a single grab sample (Table S1). Humpback counts within 800 m are likely not reflective of sand lance counts in 0.1 m^2 which may be further complicated by the patchy benthic distribution of sand lance. While benthic habitat selection by sand lance is likely based on preferred sediment grain size (coarse grain sand) and sufficient oxygen flow (Meyer et al 1979, Robards 2000), the average patch size of sand lance on the bottom is unknown. Identifying correlations between predators and prey at the scale of prey patches would likely require observations at the scale of an individual humpback whale (Redfern et al. 2006). Hazen et al. (2009) and Kirchner et al. (2018) associated humpback foraging with individual pelagic sand lance schools using data from 3D motion sensor tags on individual whales and prey data from echosounders. Alternatively, conducting multiple sand lance grabs at a site, within an 800 m radius may show better agreement between site effects for sand lance and humpbacks.

The complex behavior of sand lance could also contribute to differences in site parameter estimates. We assumed that the number of sand lance in each grab sample reflects the relative total number of fish at a site (water column + sediment), which may not be true. Sand lance are generally thought to spend daytime periods feeding in the water column and to return to the bottom at night, during periods of low light, during estivation, and/or in response to predators (Robards 2000). While our findings of sand lance in the sediment during the day provide evidence that diel behavior of sand lance is actually more complex, it is likely that pelagic sand lance abundance is greater than benthic sand lance abundance during the day. This may lead to observations of whales at a site, but not of sand lance, even though sand lance may be present in the water column. Sampling pelagic sand lance abundance may improve correlations at the site level. Nevertheless, the site-level variation in abundance of humpbacks and sand lance shown here suggest that scale considerations in future modeling or management actions could be important.

Differences in year effects between species could reflect challenges with sampling, but may also suggest true differences driven by different environmental factors. Our sampling is conducted once per season in any year, capturing a small snapshot of animal abundance. Counts used here and resulting parameter estimates may not be representative of actual annual trends in abundance. For example, opportunistic sightings data collected from whale watching and research cruises in the sanctuary during this time period show that humpback whale abundance was relatively high in 2016 (Robbins, unpublished data), concurrent with the highest sand lance abundance in our study. It is possible that whales were not present at the time of our survey, or that they were present, but were outside our 800m observation radius. However, different year effects between species could also reflect true differences in animal abundance. Predicted sand lance abundance was lowest in 2018 when predicted humpback abundance was highest. It is possible that humpbacks were targeting other prey during this time. Humpbacks in the GOM also eat herring and mackerel (Hain et al. 1982, Geraci et al. 1989). Without direct observations of surface feeding, it is not possible to determine what whales were targeting as prey or if they were foraging at all during our surveys. More frequent surveys or sampling for additional forage fish species may better explain yearly differences.

We clarify here that because site and year were treated as random effects, it is a common approach to only interpret differences between sites and years using only the magnitude of their variance components and not the individual random effects. However, it is also common for the values for the random effects themselves to also be of interest, and our estimation approach also allows us to quantify the uncertainty associated with their estimates via their credibility intervals. However, because the block specific means vary, the relative effect of the same magnitude site effect on the sand lance and whale densities will vary by blocks. We also fit a model with block-specific variances for site effects. This had minimal influence on the results, but did lead to decreased precision in site parameter estimates particularly for N sites where few sand lance and whales were observed. We emphasize that the site comparisons we do make, particularly in the identification of sand lance hot-spots in the application below, are relative to block-specific mean abundances and are only relevant within their respective blocks (not across blocks). We also note that based on the current model and our approach to use random site effect values to identify hot-spots, there is little reason to believe that these same sites will persist as hot-spots in the future.

Modeling

Our model performed well in predicting the overall mean counts of whales and sand lance from our dataset, but tended to underestimate both the proportion of zeroes and the variance in counts for each species (posterior predictive checks, Figs S2 - S5). The underestimate of variance may be due to underestimation of zeroes. This may be partially driven by fewer observations in the north or some northern sites with no sand lance observations, leading to an overestimate of the mean in the northern block, while underestimating the variance and proportion of zeroes.

A preliminary zero-inflated negative binomial model performed slightly better in estimating the proportion of zeroes and variance for both sand lance and humpbacks (Bayesian p value range: 0.35 – 0.54), but performed slightly poorer in estimation of mean abundance (Bayesian p values: 0.43, 0.45). Results from the zero-inflated negative binomial were similar to those presented here and given a marginally better performance, we chose to present the simpler zero-inflated Poisson model.

We attempted to account for zero-inflation due to seasonal sampling variability by including season as a covariate in the zero-inflation portion of the model. Successful observation (whale presence) of whales and capture of sand lance was more likely in the fall, though overlapping credible intervals and the tendency of the model to underestimate zero-inflation suggests that additional factors may influence zero-inflation.

Further model developments and extensions

The current model structure is specific to Stellwagen Bank National Marine Sanctuary. Our survey design and sampling method is neither directly applicable to other geographic areas or methodologies, nor suited for future prediction or forecasting. However, the current model demonstrates value in using simple geographic covariates to gain understanding of species distributions and the utility of a Bayesian hierarchical framework for representing ecological relationships. Model results here provide insight into variation in abundance and distribution over several spatial and temporal scales that can inform selection of environmental covariates to further model development. We first discuss potential ways to extend the model for SBNMS based on our results, and then briefly mention additional factors known to influence sand lance and humpback abundance on broader scales that should be considered for model expansion to larger / new geographic areas.

While we demonstrate a clear relationship between humpbacks and sand lance in the sanctuary, data on the availability of alternative prey sources is necessary to fully understand variation in humpback abundance and distribution and the threshold abundance of various prey species that influence humpback movements into and out of areas. There may years where sand lance abundance is low (such as 2018 here), but alternative prey is able to support a small number of humpbacks.

The site-level variation in sand lance abundance seen here is likely partially driven by preferred sediment grain sizes. The USGS has produced extensive, fine-scale sediment data for SBNMS (Valentine 2019). Our survey sampled multiple sand types (very coarse to medium sand), but grain size data suggest that fewer northern sites are classified as coarse grain sand (0.5 – 1 mm), the preferred sediment size of sand lance, which may contribute to decreased benthic sand lance abundance in the northern block (Robards et al. 2000). Grain size should be incorporated into future models. Given the seasonal behavioral changes exhibited by sand lance, grain size may be more important for sand lance in the fall as they spend more time in the sediment, suggesting a need for an interaction between season and grain size. Further, the distribution of sand lance likely reflects a balance between suitable benthic habitat and prey availability (Van der Kooij et al. 2008). Copepods, primarily of the genus *Calanus*, primarily compose sand lance diets where they have been studied (Meyers et al. 1979, Danielsen et al.2016, Staudinger et al. 2020, Suca et al. 2021). On Stellwagen Bank, *Calanus finmarchichus* was primary prey of sand lance during most months when feeding occurs (Suca et al. 2021). Sand lance abundance across the northeast Shelf was also correlated with lagged *Calanus finmarchicus* abundance (Suca et al. 2021) Including *Calanus* abundance in future models may help explain both site-level and block-level variation in sand lance abundance.

Year to year and block-level variation in sand lance abundance suggests that additional dynamic environmental covariates should be included in future models. One potential factor is the strength of the Western Maine Coastal Current, a current driven by fresh water runoff and local wind forcing that flows southwestward around the Gulf of Maine with peak inputs during the spring (Bigelow 1927, Geyer et al. 1992). The Western Maine Coastal Current is an important source of *Calanus* to Massachusetts Bay and inter-annual variability in transport, combined with local wind forcing, can impact both primary productivity and zooplankton abundance (Jiang et al. 2007, McManus et al. 2014, Suca et al. 2021). Metrics related to the strength of the Western Maine Coastal Current may help explain changes in sand lance abundance.

In addition to prey abundance, hydrology and predation influence sand lance abundance on broad scales (Suca et al. 2021). In the northwest Atlantic, sand lance abundance oscillates out of phase with the abundance of herring and mackerel, which are known to prey on larval sand lance (Staudinger et al. 2020, Suca et al 2021). Lagged herring abundance and the proportion of warm slope water were linked in declines in sand lance abundance (Suca et al. 2021). Other studies have found correlations between sand lance and oceanographic variables such as bottom temperature and salinity (Van der Kooij et al. 2008). Model adaptation for areas larger should consider these variables.

One limitation to further study of sand lance abundance in general is lack of data. Sand lance data collected in the Gulf of Maine are sparse (Richardson et al. 2014) and to our knowledge, no data exists at a scale as fine as our survey. Given the importance of sand lance to humpbacks, as well as commercial fishes and seabirds (Staudinger et al. 2020), collecting additional sand lance data throughout the Gulf of Maine should be a priority, particularly given the push towards ecosystem based management (Koehn et al. 2020).

Application

We applied our results to examine overlap between humpback whale aggregations and fixed gear to demonstrate one potential management application. Over 75% of GOM humpbacks show scarring consistent with entanglement (Robbins 2012) and entanglement remains a serious threat, including within the sanctuary (U.S. Department of Commerce 2010). We show that sites more likely to have whale aggregations overlap with an area of high density trap-pot gear on southern Stellwagen Bank. Wiley et al. (2003) used standardized survey data to show that whales had the highest risk of interaction with fixed fishing gear in the same location (southern Stellwagen Bank). Our results show that the location of highest entanglement risk for humpbacks has remained consistent for almost two decades, but also provides tangible probabilities that whale aggregations are present in areas of high risk. Further, our hierarchical model structure shows two potential spatial scales for management options, regional (block) and small scale (~1km), based on a clear relationship between humpbacks and sand lance and identification of both sand lance hotspots (where whales could be) and whale aggregation sites.

Conclusion

We fit a Bayesian hierarchical model to a unique dataset to advance our understanding of the sand lance - humpback whale relationship in the southwestern Gulf of Maine. Our work explored this predator-prey relationship with a novel approach, extending our knowledge past simple correlations and providing new insight into the abundance and distribution of sand lance and humpbacks over multiple spatial and temporal scales that can inform further model developments. Models to predict both sand lance and humpback abundance in SBNMS and beyond will become crucial for understanding potential changes to predator-prey dynamics and ecosystem structure due to climate change. Sand lance appear especially vulnerable to increasing temperatures and ocean acidification (Hare et al. 2016, Murray et al. 2019, Suca et al. 2021). Declines in sand lance abundance and serious changes to the NE US forage fish complex are predicted under current carbon emissions (Suca et al. 2021). Climate-induced shifts in the abundance and distribution of sand lance will likely lead to shifts in the abundance and distribution of humpbacks. Understanding how humpback whales will respond to fluctuations in forage fish abundance is critical for predicting and mitigating human impacts, like those from entanglement.

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The scientific results and conclusions, as well as any views or opinions expressed herein, are those of the authors and do not necessarily reflect the views of the Office of National Marine Sanctuaries, NOAA or the Department of Commerce.

Data Accessibility Statement

All data and code are available on github (https://github.com/tammylsilva/sand_lance_humpback_bayesian_model).

Conflict of Interest

The authors have no conflicts of interest.

Authors' Contributions

Field research design & funding acquisition: DW, Data collection: DW, TS, Model conceptualization & analysis: TS, GF, Writing – original draft: TS, Writing – review & editing: TS, DW, GF.

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Table 1. Summary of data used in the model (n=164). The number of sites sampled and the total number of sand lance and humpback whales observed is given for each cruise. The number of sites with and without observations of sand lance and whales is shown to provide an idea of zero inflation.

			Total Sites sampled			Sites with observations / sites without observations					
						Sand lance			Whales		
Cruise	**Sand lance**	**Whales**	**N**	**C**	**S**	**N**	**C**	**S**	**N**	**C**	**S**
Fall 2014	85	16	4	5	13	0 / 4	3 / 2	11 / 2	0 / 4	2 / 3	4 / 9
Spring 2015	30	11	12	14	7	0 / 12	5 / 9	2 / 5	0 / 12	1/13	2 / 5
Fall 2015	19	41	14	12	14	0 / 14	1 / 11	1 / 13	2 / 12	4 / 8	6 / 8
Fall 2016	124	23	9	9	12	2 / 7	0 / 9	7 / 5	1 / 8	1 / 8	7 / 5
Spring 2018	5	58	12	13	14	1 / 11	1 / 12	1 / 13	3 / 9	6 / 7	8 / 6

Table 2. Posterior medians, means, standard deviation and 95% credible intervals for selected model parameters. Posterior summaries for site effects were omitted here (shown in Fig. 4). Summaries for posterior distributions for other model parameters are included in the supplementary material.

Sand lance sub-model					
				Bayesian Credible Interval	
Parameter	**Median**	**Mean**	**SD**	**2.50%**	**97.50%**
$\beta^{b}_{central}$	-0.31	-0.36	1.12	-2.74	1.73
β^{b}_{north}	-2.6	-2.7	1.37	-5.69	-0.27
β^{b}_{south}	1.32	1.28	0.96	-0.73	3.15
β^{y}_{2014}	0.15	0.18	0.84	-1.44	1.98
β^{y}_{2015}	0.4	0.42	0.84	-1.21	2.2
β^{y}_{2016}	0.96	1	0.84	-0.6	2.81
β^{y}_{2018}	-1.43	-1.49	0.91	-3.46	0.12
σ^{2}_{sl}	2.49	2.89	1.77	0.82	7.33
τ^{2}_{sl}	1.47	3.38	8.91	0.25	16.87
$\phi^{sl}_{fall(ijk)}$	0.42	0.43	0.08	0.29	0.59
$\phi^{sl}_{spring(ijk)}$	0.33	0.34	0.1	0.17	0.56

Humpback whale sub-model					
				Bayesian Credible Interval	
Parameter	**Median**	**Mean**	**SD**	**2.50%**	**97.50%**
α_{sl}	0.35	0.36	0.16	0.05	0.70
Θ^{y}_{2014}	-0.5	-0.55	0.39	-1.4	0.12
Θ^{y}_{2015}	0.07	0.05	0.32	-0.64	0.62
Θ^{y}_{2016}	-0.56	-0.62	0.42	-1.58	0.06
Θ^{y}_{2018}	0.66	0.68	0.39	-0.02	1.51
σ^{2}_{w}	1	1.14	0.66	0.25	2.73
τ^{2}_{w}	0.42	0.86	2.46	0.05	3.91
$\phi^{w}_{fall(ijk)}$	0.53	0.53	0.09	0.36	0.71
$\phi^{w}_{spring(ijk)}$	0.47	0.47	0.09	0.3	0.66

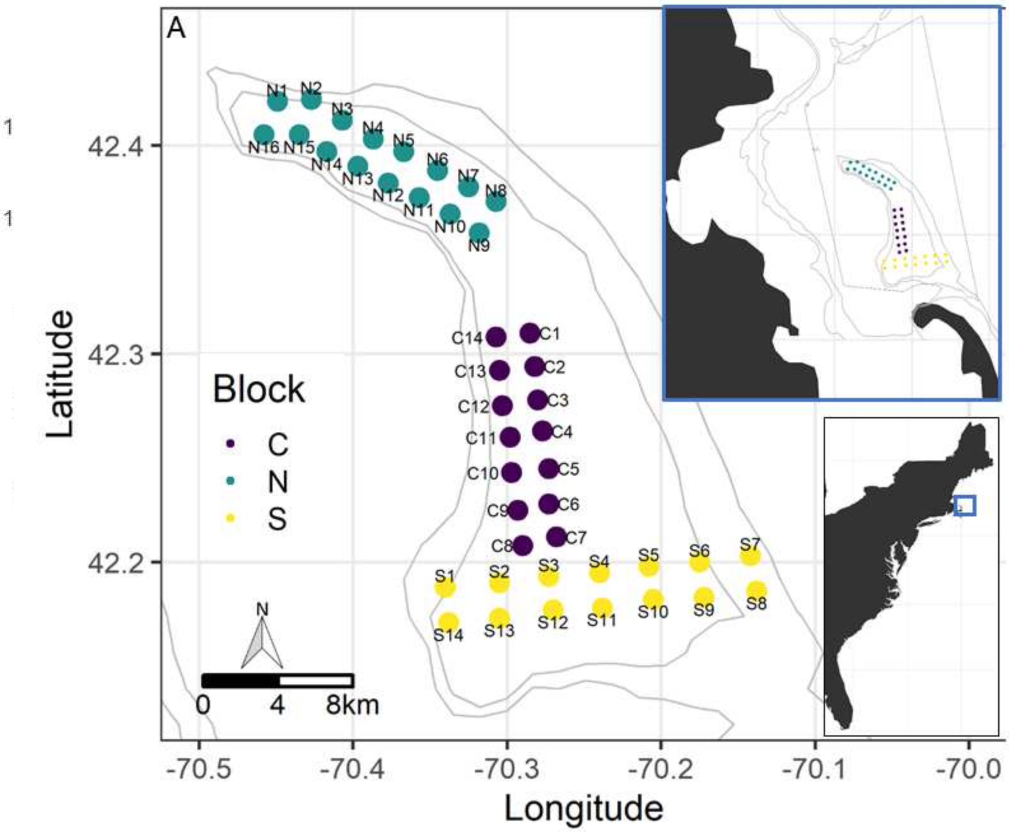
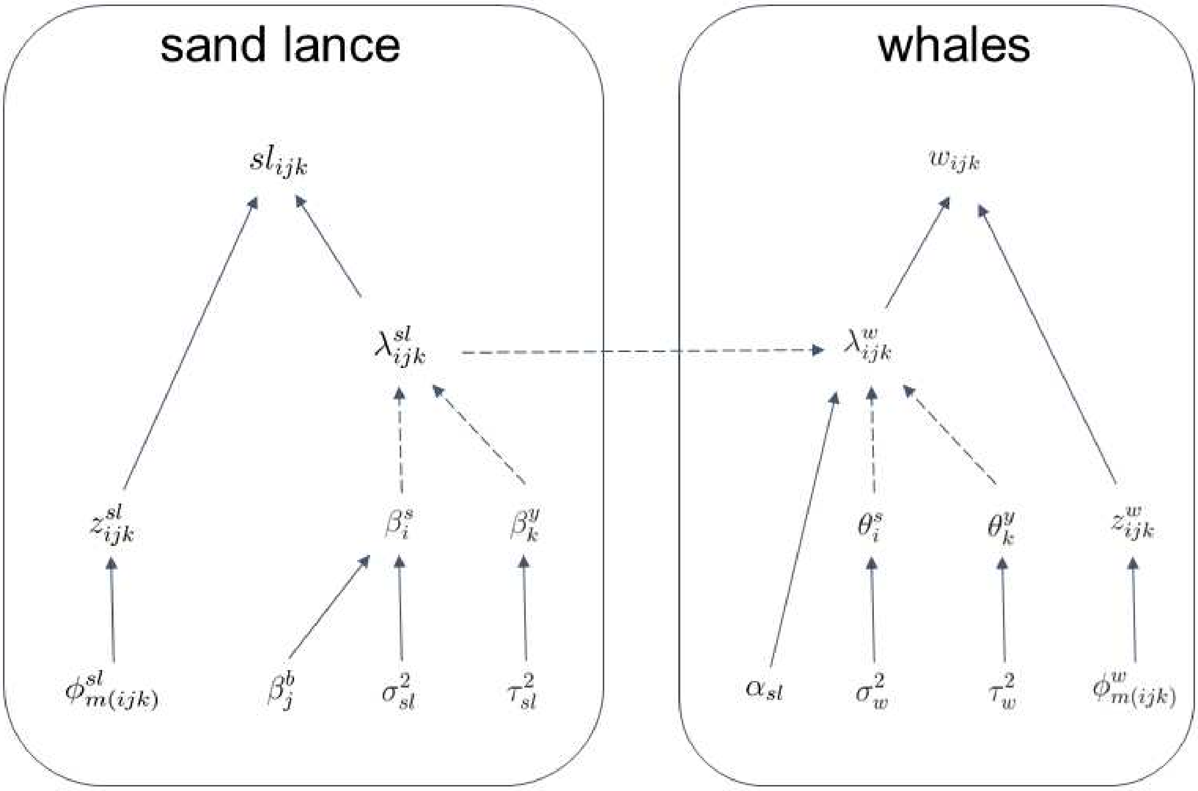


Figure 1. Map of the survey design and summary of data used in the model. A) Map shows Stellwagen Bank proper and the 44 sites included in the survey. Sites are organized into 3 blocks: North (N-green), Central (C-purple), and South (S-yellow). Sites within blocks were ~ 1km apart and were designed to sample all potential sand lance benthic habitat. Thin gray lines represent the 50m (outer) and 40m (inner) isobaths. Inset maps show the survey location within Stellwagen Bank National Marine Sanctuary (rectangular boundaries) off the coast of Massachusetts (top) and the location of the study site off the northeast U.S. B) Histogram of sand lance counts used in the model (n=164) colored by block. The inset shows counts equal to one between 17 and 44 that may be difficult to see. C) Histogram of humpback whale counts used in the model (n=164) colored by block.



$$[z^{sl}_{ijk}, \beta^{s}_{i}, \beta^{b}_{j}, \beta^{y}_{k}, \sigma^{2}_{sl}, \tau^{2}_{sl}, \phi^{sl}_{m(ijk)}, z^{w}_{ijk}, \Theta^{s}_{i}, \Theta^{y}_{k}, \sigma^{2}_{w}, \tau^{2}_{w}, \phi^{w}_{m(ijk)}, \alpha_{sl} \mid sl_{ijk}, w_{ijk}] \propto \prod_{n=1}^{164} [sl_{ijk} \mid z^{sl}_{ijk}]\,[z^{sl}_{ijk} \mid \phi^{sl}_{m(ijk)}]\,[\beta^{s}_{i} \mid \beta^{b}_{j}, \sigma^{2}_{sl}]\,[\beta^{y}_{k} \mid \tau^{2}_{sl}]\,[\phi^{sl}_{m(ijk)}]\,[\beta^{b}_{j}]\,[\sigma^{2}_{sl}]\,[\tau^{2}_{sl}]\,[w_{ijk} \mid z^{w}_{ijk}]\,[z^{w}_{ijk} \mid \phi^{w}_{m(ijk)}]\,[\Theta^{s}_{i} \mid \sigma^{2}_{w}]\,[\Theta^{y}_{k} \mid \tau^{2}_{w}]\,[\phi^{w}_{m(ijk)}]\,[\sigma^{2}_{w}]\,[\tau^{2}_{w}]\,[\alpha_{sl}]$$

Figure 2. Bayesian network and full expression for the posterior and joint distributions for hierarchical zero-inflated Poisson mixed effects model of sand lance and humpback whale abundance. Sand lance counts at site *i* in block *j* in year *k*, sl_{ijk} was modelled as a Poisson random variable with mean λ^{sl}_{ijk}. The mean number of sand lance, λ^{sl}_{ijk} was modeled as a log linear function of block β^{b}_{j}, site β^{s}_{i}, and year β^{y}_{k}. Site and year were treated as random effects with variance σ^{2}_{sl} and τ^{2}_{sl}, respectively. Seasonal zero inflation in sand lance availability was described by z^{sl}_{ijk}, where $\phi^{sl}_{m(ijk)}$ is the probability of zero inflation for season *m*. Humpback whale counts at site *i* in block *j* in year *k*, w_{ijk}, was modeled as a Poisson random variable with mean λ^{w}_{ijk}. The mean number of whales λ^{w}_{ijk}, was described as a log linear function of expected sand lance abundance λ^{sl}_{ijk} and its regression coefficient, α_{sl}, site θ^{s}_{i} and year θ^{y}_{k}. Site and year were treated

as random effects with variance σ_w^2 and τ_w^2, respectively. Seasonal zero inflation in the observation of whales was described by z_{ijk}^w, where $\phi_{m(ijk)}^w$ was the probability of zero inflation for season *m*. Solid lines indicate stochastic relationships and dashed lines indicate deterministic relationships.

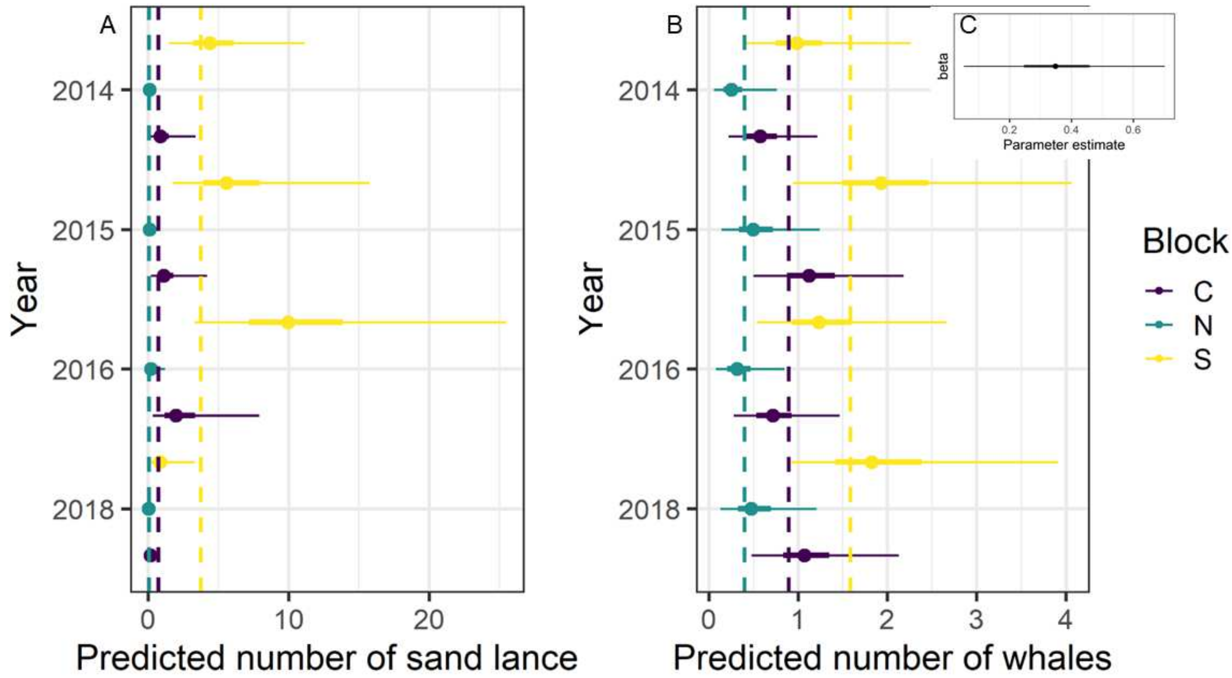


Figure 3. Predicted numbers of sand lance and humpback whales by block and year. Dashed vertical lines represent median abundance estimates for each block (N = green, C = purple, S = yellow). Points represent median abundance estimates for each block in each year. Thicker lines represent 50% Bayesian credible intervals and thinner lines represent 95% Bayesian credible intervals. A) Predicted numbers of sand lance. B) Predicted number of humpback whales. C) Parameter estimate for the influence of sand lance abundance on humpback abundance. This relationship was used to estimate block median abundance for humpbacks (dashed vertical lines) in (B).

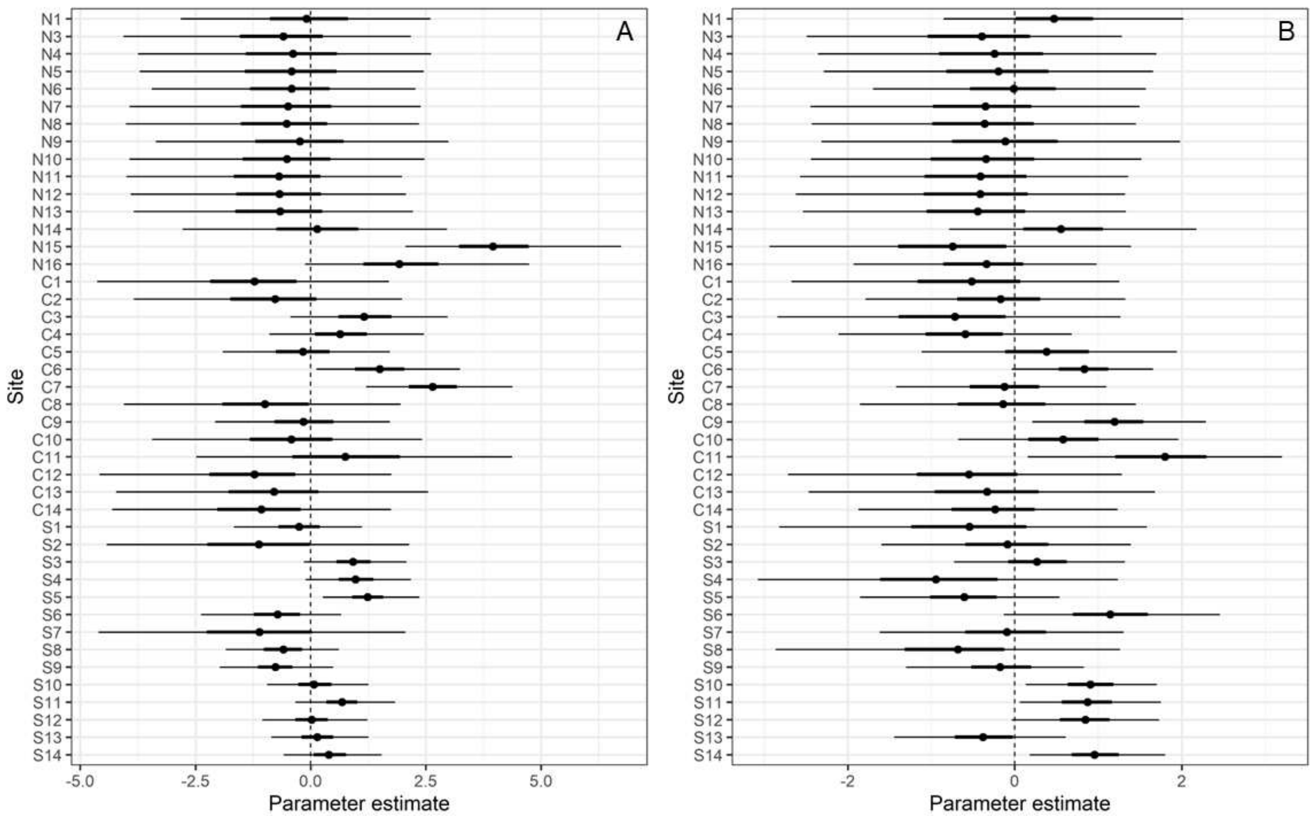


Figure 4. Summaries of posterior distributions for site effects for A) sand lance and B) humpback whales. Sites are ordered from north to south. Dashed vertical lines at 0 represent no deviation from the average abundance. Estimates greater than zero represent sites with greater than block average abundance while parameters below zero represent sites with less than block average abundance. Points represent posterior medians, thicker lines represent 50% credible intervals and thinner lines 95% credible intervals.

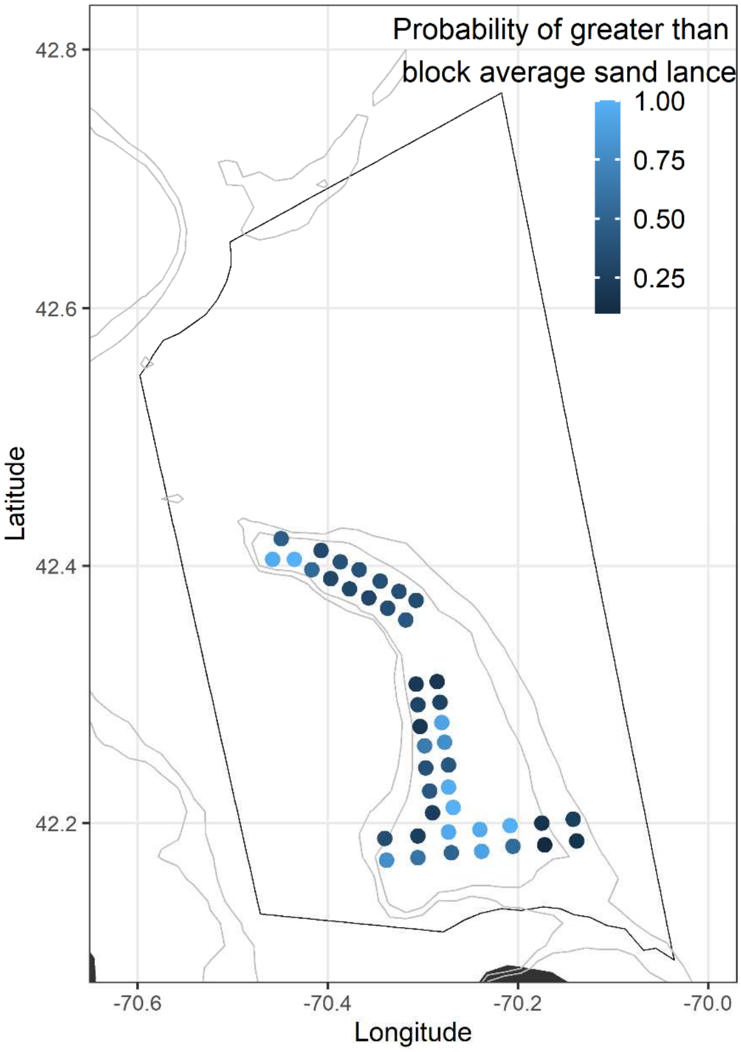


Figure 5. Probabilities that sites have greater than block average sand lance abundance. Predictions were based on an average year. Site N2 was never sampled in this subset of data and therefore, has no probability estimate and is missing in the map. Dark line represents Stellwagen Bank National Marine Sanctuary boundaries. Gray lines represent the 50 m (outer) and 40 m (inner) isobaths indicating Stellwagen Bank proper.

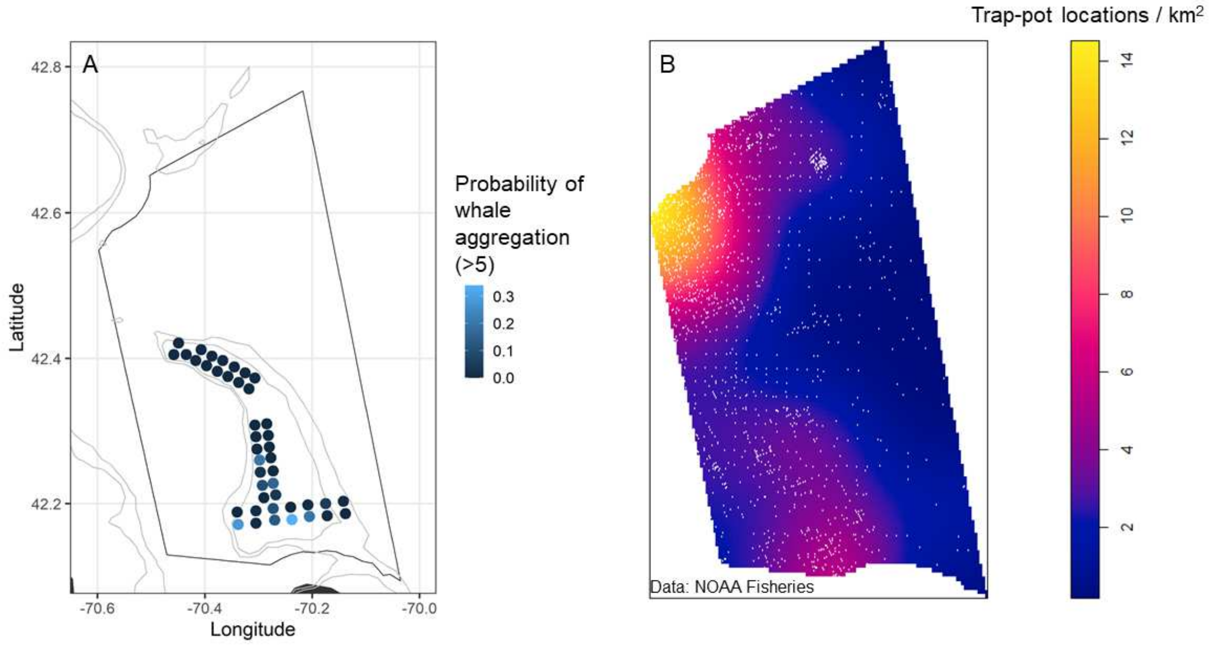


Figure 6. Assessment of humpback whale entanglement risk. A) Probability that whale aggregations (>5 whales) occur at sites. Predictions were based on an average year. Site N2 was never sampled in this subset of data and therefore, has no probability estimate and is missing in the map. Dark line represents Stellwagen Bank National Marine Sanctuary boundaries. Gray lines represent the 50 m (outer) and 40 m (inner) isobaths indicating Stellwagen Bank proper. B) Density of trap-pot fishing locations in Stellwagen Bank National Marine Sanctuary from 2014 – 2016. Data - NOAA Fisheries.