


High collocation of sand lance and protected top predators: Implications for conservation and management

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Abstract

Spatial relationships between predators and prey provide critical information for understanding and predicting climate-induced shifts in ecosystem dynamics and mitigating human impacts. We used Stellwagen Bank National Marine Sanctuary as a case study to investigate spatial overlap among sand lance (*Ammodytes dubius*), a key forage fish species, and two protected predators: humpback whales (*Megaptera novaeangliae*) and great shearwaters (*Ardenna gravis*). We conducted 6 years (2013–2018) of standardized surveys and quantified spatial overlap using the global index of collocation. Results showed strong, consistent collocation among species across seasons and years, suggesting that humpback whales and great shearwater distributions are tightly linked to sand lance. We propose that identifying sand lance habitats may indicate areas where humpbacks and shearwaters aggregate and are particularly vulnerable to human activities. Understanding how sand lance influence predator distributions can inform species protection and sanctuary management under present and future scenarios.

KEYWORDS

forage fish, great shearwaters, Gulf of Maine, humpback whales, seabirds, spatial overlap, Stellwagen Bank

1 | INTRODUCTION

Spatial relationships between predators and prey provide important ecological insights. The degree and scale of spatial overlap between predators and prey can indicate the potential strength of their ecological interactions (Carroll et al., 2019). Understanding species' interactions is critical for predicting and mitigating climate-induced changes in trophic dynamics and ecosystem structure (Gilman, Urban, Tewksbury, Gilchrist, & Holt, 2010).

Predator–prey relationships are also important for conservation and management.

Inferring predator dependence on prey species through spatial overlap studies may better inform management of prey populations (Eero et al., 2012; Koehn et al., 2020). Further, understanding where and when predators aggregate in response to prey can help in assessing and managing negative interactions between predators and human activities (Santora et al., 2020).

Sand lances (*Ammodytes* spp.) are key marine forage fish across the northern hemisphere (Engelhard et al., 2014). In

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the Northwest Atlantic Ocean, sand lance are consumed by at least 72 species (Staudinger et al., 2020). Shifts in the abundance and distribution of several predators is linked to fluctuations in abundance and distribution of sand lance (Kenney, Payne, Heinemann, & Winn, 1996; Payne et al., 1990; Richardson, Palmer, & Smith, 2014). However, spatial overlap among sand lance and their predators has not been quantified in any location or over any spatial scale.

We used Stellwagen Bank National Marine Sanctuary (SBNMS), a 2,180 km² federal Marine Protected Area in the southwestern Gulf of Maine (GOM), as a case study to investigate seasonal spatial overlap between northern sand lance (*Ammodytes dubius*) and two protected top predators, the humpback whale (*Megaptera novaeangliae*) and great shearwater (*Ardenna gravis*; hereafter referred to as shearwaters). We focused on humpbacks and shearwaters due to their frequent occurrence and high abundance in SBNMS, their use of sand habitat and known consumption of sand lance, and their increased vulnerability to human activities in SBNMS compared with other species (Office of National Marine Sanctuaries (ONMS), 2020).

2 | METHODS

2.1 | Study location and data collection

SBNMS is an ideal location to study spatial relationships between sand lance and predators. The sanctuary often

hosts the highest density of sand lance across the northeast shelf (Richardson et al., 2014). SBNMS is accessible and relatively small, allowing sampling of the entire area at relatively high spatial and temporal resolutions. Further, protected species are impacted by substantial year-round human activities in the sanctuary, and management may be informed by their distribution.

Eleven total surveys for sand lance, humpbacks and shearwaters were conducted during fall (September to November; $n = 5$), spring (April to June; $n = 5$), and summer (July; $n = 1$) from 2013 to 2018. Poor weather conditions during fall 2018 resulted in an incomplete survey that was not included in our analysis. Our survey design included 44 sites across Stellwagen Bank (~1 km apart in most areas) to cover potential sand lance habitat (Figure 1) (Robards, Willson, Armstrong, & Piatt, 2000). The number of sites sampled during each cruise ranged from 13 to 43 depending on logistics and time constraints (Table 1).

We sampled sand lance using U.S. Geological Survey's Seabed Observation and Sampling System (SEABOSS) (Blackwood & Parolski, 2001), equipped with a modified Van Veen benthic grab (sediment and infauna) sampler (0.1 m²). At each site, the SEABOSS was deployed to the sea floor to sample sediment. Upon recovery, we recorded the number of sand lance in the sediment sample. We note that sand lance counts from SEABOSS grabs were used as a proxy for sand lance abundance at sites, assuming the number of sand lance

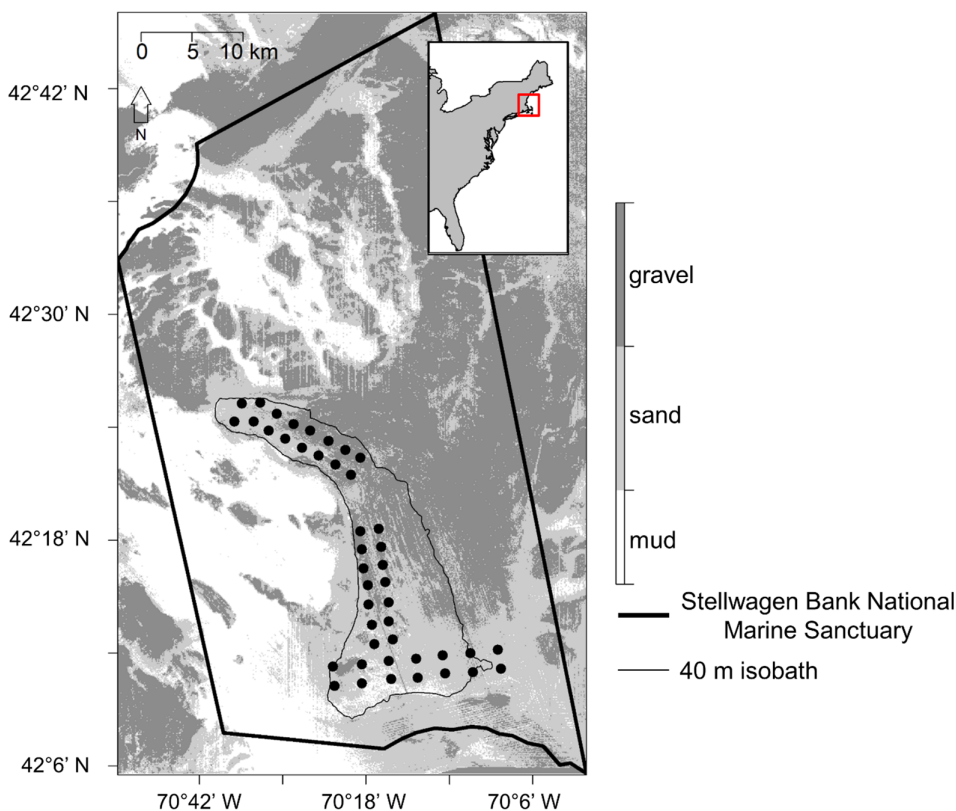


FIGURE 1 Map of the study area within Stellwagen Bank National Marine Sanctuary. The thin black line indicates the 40 m isobath (Stellwagen Bank proper). The thick black line marks the sanctuary boundaries. Black circles represent survey sites. Color indicates sediment type: dark gray-gravel, light gray-sand, and white-mud. Inset shows the location of the study site in relation to the U.S. East coast

TABLE 1 Summary of standardized surveys including number of sites and counts of sand lance, humpback whales and great shearwaters per cruise

Cruise	Sites surveyed	Sand lance	Humpback whale	Great shearwater
Fall 2013	20	0	1	0
Spring 2014	13	0	19	1
Fall 2014	22	85	16	410
Spring 2015	33	30	25	0
Fall 2015	40	19	41	396
Spring 2016	40	8	0	0
Fall 2016	30	124	23	31
Spring 2017	41	19	0	0
Fall 2017	42	4	0	18
Spring 2018	39	5	58	0
Summer 2018	41	9	12	39

Note: Cruises were conducted in spring and fall of each year starting in fall 2013. Summer cruises were added starting in 2018. The number of sites surveyed each cruise varied (see Figures S1–S3, Supporting Information for details).

in the sediment is representative of the total number of sand lance at a site (sediment and water column). During each SEABOSS deployment, trained observers documented abundances of marine mammals and seabirds from the vessel's flying bridge. All observed individuals were identified to species level when possible. Typically, three people performed surveys: one observer on each side of the vessel and one data recorder. We counted seabirds within 400 m of the vessel for 5 min and marine mammals within 800 m of the vessel for 10 min. 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). We chose these sampling distances and times based on our ability to reliably identify species and to avoid double counting of individuals. Bird observation periods were short and began immediately upon reaching a site to account for birds potentially being attracted to the boat over time. Whale observation

TABLE 2 Equations for spatial metrics

Center of gravity (CG)	$CG = \sum_{i=1}^N x_i s_i z_i / \sum_{i=1}^N s_i z_i$, where z_i are sample values at locations x_i , with areas of influence s_i (weighting factors in cases of irregular sampling)
Inertia (I)	$I = \sum_{i=1}^N (x_i - CG)^2 s_i z_i / \sum_{i=1}^N s_i z_i$
Global index of collocation (GIC)	$GIC = 1 - (\Delta CG^2 / \Delta CG^2 + I_1 + I_2)$, where ΔCG is the distance between the CGs of two populations with densities $z_1(x)$ and $z_2(x)$ at point x , and I_1 and I_2 are their respective inertias

Note: We refer the reader to Bez and Rivoirard (2000), Woillez, Poulard, Rivoirard, Petitgas, and Bez (2007), Woillez, Rivoirard, and Petitgas (2009), and Petitgas, Woillez, Rivoirard, Renard, and Bez (2017) for further description.

periods were chosen based on animal-borne tag data showing many humpback dives in Stellwagen Bank to be near 5 min in duration (Wiley unpublished data), increasing the chance whales were counted only once during sampling.

Humpback whales occur in SBNMS from March to December and could have been observed on all cruises. However, most great shearwaters arrive in late June and occupy sanctuary foraging grounds until late fall. Our spring cruises typically occurred in early May, when we did not expect to observe shearwaters and therefore, did not consider them in our spring calculations.

2.2 | Spatial statistics

We used spatial metrics to describe the distribution of each species and then quantify spatial overlap among species. For each cruise, we calculated the center of gravity and inertia for each species (Table 2) (Bez & Rivoirard, 2000; Woillez et al., 2007; Woillez et al., 2009). The center of gravity represents the mean spatial location of the sampled population. The inertia is the variance of the location of individuals in the sampled population and describes dispersion of the population around its center of gravity. Together, the center of gravity and the inertia describe the spatial distribution of the sampled population. These two metrics were used to calculate the global index of collocation (GIC) to quantify spatial overlap between pairs of species for each cruise (Table 2). The GIC is a spatial statistic that captures the extent to which two populations are geographically distinct by comparing the distance between their centers of gravity and the inertias (Bez & Rivoirard, 2000; Petitgas et al., 2017; Woillez et al., 2007; Woillez et al., 2009). GIC ranges from 0 to 1, where 0 indicates each population is concentrated on a

TABLE 3 Global index of collocation values calculated for all possible cruises and species comparisons

Cruise	Sand lance and humpbacks	Sand lance and shearwaters	Humpbacks and shearwaters
Fall 2013	No sand lance	No sand lance	No bird data ^a
Spring 2014	No sand lance	–	–
Fall 2014	0.7	0.99	0.64
Spring 2015	0.78	–	–
Fall 2015	Not enough data ^b	Not enough data ^b	0.95
Spring 2016	No whales	–	–
Fall 2016	0.96	0.98	0.97
Spring 2017	No whales	–	–
Fall 2017	No whales	Not enough data ^b	No whales
Spring 2018	0.98	–	–
Summer 2018	0.92	0.96	0.95

Note: Global index of collocation measures overlap at a regional scale and ranges from 0 to 1, where 0 indicates each population is concentrated on a single but different location (no individuals of either species co-occurred at any site) and 1, where the centers of gravity coincide. Spring cruises typically occurred before great shearwaters arrive in the sanctuary for summer foraging, and therefore, we did not consider any metrics including shearwaters during spring.

^aBird data was not collected in Fall 2013.

^bSand lance only recorded at two sites, cannot calculate inertia for calculation of Global Index of Collocation.

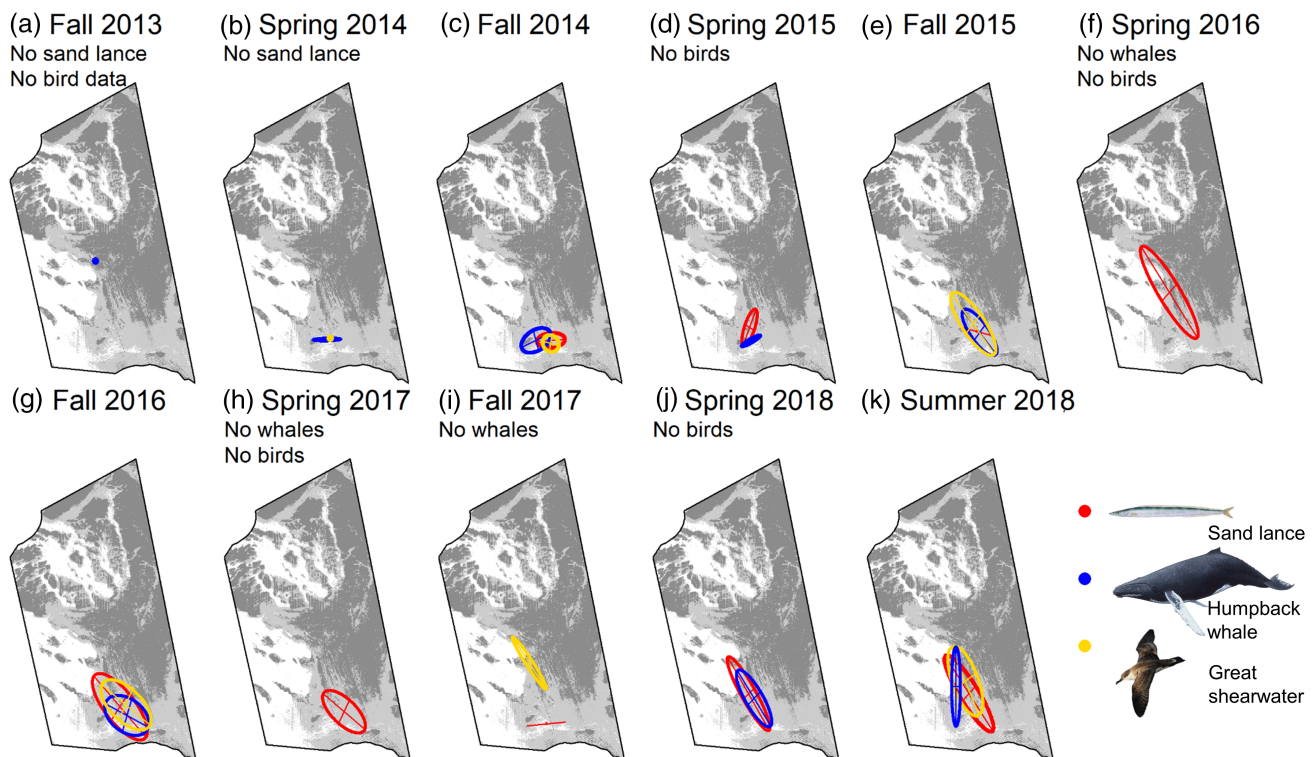


FIGURE 2 Spatial overlap of sand lance, humpback whales and great shearwaters in Stellwagen Bank National Marine Sanctuary by cruise. Cross-hairs represent the center of gravity or the mean location of the sampled population. Ellipses represent the inertia or the variance of the location of the sampled population and describes the dispersion of the population around its center of gravity variance. The center of gravity and inertia were only calculated when species were observed at >2 sites. Single dots indicate only one individual was observed at one site. Lines indicate that individuals were only observed at two sites. Dark gray = gravel substrate, light gray = sand substrate, white = mud substrate

single but different location (no individuals of either species co-occurred at any site) and 1, where the centers of gravity coincide. The GIC measures geographical similarity at a broad scale across the study area. There are many ways to quantify spatial overlap among species (Carroll et al., 2019). We chose the GIC because (a) it is a simple, easily interpretable statistic, (b) we were interested in predator–prey overlap at regional scales within SBNMS, and (c) we were able to incorporate abundance data. Though we refer to overlap on a sanctuary-scale, we note our sampling design focuses only on Stellwagen Bank proper and does not encompass the entire sanctuary. However, our survey does sample all potential sand lance benthic habitat (Robards et al., 2000), and we believe it represents most locations where overlap between sand lance and predators could occur. Therefore, we refer to any overlap between sand lance and predators as occurring at the sanctuary scale.

We could not assess spatial overlap among all species for all cruises. The center of gravity (mean location) required observations of individuals (predators or prey) at ≥ 2 sites, while the inertia (variance) required observations of individuals at ≥ 3 sites. If cruise data did not meet these criteria, we could not calculate these metrics and therefore, could not calculate the GIC. All spatial metrics were calculated using the “RGeostats” package (Renard et al., 2017) in R (R Core Team, 2018).

3 | RESULTS

We observed sand lance, humpbacks and shearwaters in the sanctuary on four of 11 cruises (Table 1). No sand lance were observed on two cruises and no whales were observed on three cruises (Table 1). We did not consider shearwaters in spring, though one shearwater was observed in spring 2014. Two cruises resulted in observations of sand lance at ≤ 2 sites (Table 1, Figure S1, Supporting Information). Lack of observations or observations at ≤ 2 sites prevented calculation of metrics and spatial overlap between pairs of species in 21 of 33 potential opportunities. We were able to calculate GIC in 12 instances over 6 cruises (Table 3).

GIC values ranged from 0.64 to 0.99, with 75% of values (9/12) greater than 0.9, suggesting strong collocation among species (Table 3). Collocation among all three species consistently occurred on or near the southwest corner of Stellwagen Bank (Figure 2).

We combined all cruises together to quantify overlap over the entire study period (2013–2018). For both sand lance and humpbacks and sand lance and shearwaters, combined GIC was 0.99. For humpbacks and shearwaters, combined GIC was 0.98. Combined

collocation among all three species occurred on the SW corner of Stellwagen Bank (Figure S4, Supporting Information).

4 | DISCUSSION

We found strong regional collocation among sand lance, humpbacks and shearwaters across seasons and years. While GIC does not quantify potential predator–prey encounters, we suggest that humpbacks and shearwaters consistently aggregate on the southwest corner of Stellwagen Bank targeting sand lance as prey. This area provides optimal sand lance burrowing habitat: coarse grain sand (0.5–1 mm) and shallow depths (20–25 m) (Robards et al., 2000). Our sampling method captured sand lance in or just above the sediment, indicating that observed fish were likely targeting this aspect of the environment and not a dynamic feature that may change over time. The consistent collocation of humpbacks and shearwaters in prime sand lance benthic habitat supports the idea that these predators are feeding on sand lance, though additional work is needed to exclude predators targeting other fishes (herring, mackerel) that may also prey on juvenile sand lance.

There are a few caveats to our results. Overall counts in our samples were low, with 0–2 individuals (predators or prey) recorded per site for many cruises (Figures S1–S3, Supporting Information). This prevented calculation of spatial metrics for many cruises. Low counts reflect challenges in sampling these species in time and space. Our data is a snapshot of predator and prey abundance and may not be representative of seasonal or annual trends. Further, the highly patchy distribution and behavior of sand lance can make sampling difficult. Video footage was usually recorded during SEABOSS deployments, and on occasion sand lance were observed in video footage (swimming or burrowing), but not in sediment grabs and vice versa. This suggests that SEABOSS grabs alone underestimate sand lance abundance at each site and that observation variability impacts metrics. The spatial scale of observations and sampling limitations are important considerations for future work.

This work has important implications for conservation and management in SBNMS. Our results suggest that distributions of humpbacks and shearwaters in the sanctuary are tightly linked to sand lance. SBNMS and surrounding waters are experiencing rapid marine climate changes (Pershing et al., 2015), and sand lance appear particularly vulnerable to increasing temperatures and ocean acidification (Hare et al., 2016; Murray, Wiley, & Baumann, 2019). Climate-induced shifts in the

abundance or distribution of sand lance may lead to substantial changes in trophic dynamics and ecosystem structure within SBNMS, impact the health and fitness of these predators, and disrupt the ecosystem services they provide (Office of National Marine Sanctuaries (ONMS), 2020).

Interactions with fishing gear are serious concerns for humpbacks (Hayes et al., 2018). Over 75% of GOM humpback whales show scarring consistent with entanglement in fishing gear (Robbins, 2012), and SBNMS is a hotspot for humpback whale entanglement reports (U.S. Department of Commerce, 2010). Using standardized surveys, Wiley, Moller, and Zilinskas (2003) mapped distributions of baleen whales and fishing gear in SBNMS. Whales had the highest risk of interaction with fixed fishing gear on the southwest corner of Stellwagen Bank, the same area where we demonstrated strong collocation between humpbacks and sand lance. The spatial and temporal persistence of collocation over a relatively small spatial scale suggests management actions such as mandating rope-less fishing, could minimize impacts to fishers while substantially reducing entanglement risk for whales.

We believe implications of this work extend beyond SBNMS. Humpbacks and shearwaters frequently use other sand habitats throughout the Northeast U.S. shelf (Payne et al., 1990; Pittman, Costa, Kot, Wiley, & Kenney, 2006; Powers, Wiley, Allyn, Welch, & Ronconi, 2017). Great shearwaters are the most frequently bycaught seabird in Northeast and mid-Atlantic U.S. waters (Hatch, 2018), and 50% of shearwater bycatch in the GOM occurs in a small area east of Cape Cod (Hatch, Wiley, Murray, & Welch, 2016) characterized by sandy sediment and high sand lance abundance (Clark, Manning, Costa, & Desch, 2006; Staudinger et al., 2020). GOM fisheries often target species that occur in sand habitats (e.g., trap-pot fishery for lobster or crab, Wiley et al., 2003) or feed on sand lance (e.g., currently, a gillnet fishery for spiny dogfish, and Atlantic cod, Richardson et al., 2014). As sand lance have well-defined habitat requirements, we propose that identifying sand lance habitat could indicate other areas in the Northeast U.S. shelf where entanglement and bycatch risk could be high for humpbacks and shearwaters, providing a mechanism for focusing management of these species as well as other baleen whale and seabird species.

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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.

CONFLICT OF INTEREST

The authors have no conflicts of interest.

AUTHORS' CONTRIBUTIONS

D.N.W. and M.A.T. designed the study, D.N.W., L.K., J.K.L., H.B. secured funding, T.L.S., D.N.W., M.A.T., P.H., L.K., J.J.S., J.K.L., and H.B. collected the data, T.L.S. conducted analyses and wrote the paper with critical input from all authors.

ETHICS STATEMENT

All research followed sanctuary guidelines.

DATA ACCESSIBILITY STATEMENT

All data and code are available on github (https://github.com/tammysilva/Collocation_sand_lance_predators).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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