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Spatiotemporal patterns of overlap between short-finned pilot whales and the U.S. pelagic longline fishery in the Mid-Atlantic Bight: An assessment to inform the management of fisheries bycatch

Julia E.F. Stepanuk[a,*], Andrew J. Read[b], Robin W. Baird[c], Daniel L. Webster[c], Lesley H. Thorne[a]

[a] School of Marine and Atmospheric Sciences, Stony Brook University, Stony Brook, NY, 11794-5000, USA
[b] Nicholas School of the Environment, Duke University Marine Laboratory, Duke University, 135 Duke Marine Lab Road, Beaufort, NC, 28516, USA
[c] Cascadia Research Collective, 218½ W. 4th Avenue, Olympia, WA, 98501, USA

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ABSTRACT

Short-finned pilot whales (*Globicephala macrorhynchus*) depredate pelagic longlines along the shelf break of the Mid-Atlantic Bight. The mortality and serious injury of short-finned pilot whales in the U.S. pelagic longline fishery recently exceeded Potential Biological Removal levels defined under the U.S. Marine Mammal Protection Act, and bycatch mitigation techniques developed to date have been unsuccessful. We examine the spatial and temporal characteristics of pilot whale habitat use and longline fishing effort, quantify spatiotemporal patterns of pilot whale bycatch based on environmental factors, and assess the potential for a spatial management approach to mitigate pilot whale bycatch. We assess patterns of overlap and bycatch of pilot whales and longlines by applying Area Under the Curve and Williamson's Spatial Overlap Index analyses to telemetry data from short-finned pilot whales, along with longline fishing effort and Pelagic Observer Program (POP) fisheries observer data from 2014 and 2015. We found that proximity to the 1000 m isobath, season, and sea surface temperature (SST) were important variables influencing pilot whale-longline overlap and POP bycatch rates. Pilot whale density was consistently highest immediately inshore of the 1000 m isobath, but longline effort varied seasonally relative to the 1000 m isobath. Resultant seasonal patterns in pilot whale-longline overlap relative to the 1000 m isobath were strongly and significantly correlated with POP bycatch rates; the highest bycatch rates primarily occurred in fall and winter months, when longline effort shifted inshore near the 1000 m isobath. We observed differences in the distribution of logbook and POP longline sets relative to the 1000 m isobath; POP sets were more dispersed relative to this feature while the overall distribution of longline effort was typically focused at the 1000 m isobath. Since bycatch primarily occurred close to the 1000 m isobath, more bycatch might be observed if the observer effort better reflected the overall distribution of longline effort. In winter months, POP bycatch occurred in cooler waters than most observations of tagged pilot whales, and therefore the relationship between bycatch and SST during winter months requires further exploration. Together, our results suggest that a spatial management approach could be effective in reducing pilot whale bycatch in the pelagic longline fishery, and an improved understanding of the relationships between pilot whale bycatch and dynamic variables might allow high-risk regions for pilot whale bycatch to be further delineated.

1. Background

The incidental bycatch of marine mammals in fishing gear is a major conservation issue that affects marine mammal populations around the world (Gilman et al., 2006; Hamer et al., 2012; Moore et al., 2009; Read et al., 2006; Werner et al., 2015). Globally, reported bycatch rates in longline fisheries have increased in recent years, likely due to both increased monitoring of bycatch and increased fishing effort (Hamer et al., 2012). In some longline fisheries, cetacean bycatch occurs as a result of depredation, the damage or removal of bait or captured fish from fishing gear by marine predators (Rabearisoa et al., 2015). Depredation can provide a meal for foraging cetaceans at relatively low energetic cost, which may encourage individuals to alter their natural foraging patterns (Ashford et al., 1996; Gilman et al., 2006; Hall, 1998; Hamer et al., 2012). Depredation has been observed in many odontocete species (Ashford et al., 1996; Gilman et al., 2006; Hamer et al.,

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* Corresponding author.
E-mail address: Julia.stepanuk@stonybrook.edu (J.E.F. Stepanuk).

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2012; Werner et al., 2015), and can increase the risk of entanglement and hook ingestion (Hamer et al., 2012). Marine mammals are long-lived and have low reproductive rates, so increases in mortality rates due to bycatch can adversely affect their demography (Gilman et al., 2006; Read, 2008; Read et al., 2006; Werner et al., 2015).

The overlap between fishing effort and bycaught species can be used to inform the spatial management of bycatch in marine systems, particularly for highly migratory marine megafauna (Forney et al., 2011; McClellan et al., 2009; Wallace et al., 2013). Spatiotemporal patterns of fishing effort and/or the habitat use of bycaught species can be integrated into effective management plans (Becker et al., 2016; Hazen et al., 2016; Howell et al., 2008). Several sources of information can inform this approach, including broad distributional patterns, individual movements, and environmental drivers of the distributions of bycatch species (Forney et al., 2011; Garrison, 2007; Gredzens et al., 2014; Moore et al., 2009). Recent advances in satellite telemetry have significantly advanced our understanding of the habitat use and ecology of marine megafauna (Hart and Hyrenbach, 2009; Joyce et al., 2016; Vaudo et al., 2017). Satellite telemetry is particularly advantageous in the study of highly mobile marine animals (Ropert-Coudert and Wilson, 2005), and has been used to identify spatial components of habitat use (Baird et al., 2012; Baumgartner and Mate, 2005; Block et al., 2011; Eckert, 2006; Hart and Hyrenbach, 2009; Lowry et al., 1998) and to develop effective management strategies for cetacean species (Hart and Hyrenbach, 2009; Hazen et al., 2016; Kindt-Larsen et al., 2016).

Short-finned pilot whales (*Globicephala macrorhynchus*) are deep-diving odontocetes found in tropical and sub-tropical regions that exhibit diverse diets and diving behaviors, but primarily forage on deep-water fish and squid (Mintzer et al., 2008; Perrin et al., 2009; Quick et al., 2017). Although they do not typically feed on the swordfish and tunas targeted by the U.S. pelagic longline fishery in the Mid-Atlantic Bight (MAB), short-finned pilot whales depredate both bait and catch from this fishery (Gilman et al., 2006; McCreary and Poncelet, 2006; Garrison, 2007; Waring et al., 2016). Short-finned pilot whales are managed as a single stock in the Northwest Atlantic from Florida to Massachusetts (Hayes et al., 2017), and bycatch in the pelagic longline fishery is the leading cause of anthropogenic mortality for this stock (Hayes et al., 2017). The U.S. Marine Mammal Protection Act (MMPA) mandates that such mortality for each stock not exceed the Potential Biological Removal (PBR), a biological reference point, to ensure that marine mammal stocks are maintained in a good conservation status. When mortality levels exceed PBR, a Take Reduction Team is formed to identify mitigation strategies. The Pelagic Longline Take Reduction Team (PLTRT) was formed in 2005 when annual bycatch mortality of short-finned pilot whales was approaching PBR (McCreary and Poncelet, 2006; Moore et al., 2009; Waring et al., 2006). Mitigation measures investigated by the PLTRT have included: a shortened mainline length; the use of acoustic deterrents; and the delineation of the Cape Hatteras Special Research Area (CHSRA), which designates a region of increased observer requirements and compliance by fishermen in an area of high by-catch (Waring et al., 2016). Fishing restrictions in place when the current study was conducted included shortened mainline lengths (less than 20 nautical miles), additional observer coverage within the CHSRA, and the display of informational placards on active pelagic longline vessels (US OFR, 2009). However, these mitigation measures have not been successful in decreasing pilot whale bycatch, and bycatch levels for short-finned pilot whales recently exceeded PBR by 21% (Hayes et al., 2017). Thus, there is a critical need to develop new strategies to decrease the mortality of pilot whales in the pelagic longline fishery in the Northwest Atlantic.

Despite relatively high levels of bycatch of short-finned pilot whales, little was known about their seasonal movement patterns in the Northwest Atlantic until recently. At-sea surveys often combine sightings of short-finned and long-finned pilot whales (*G. melas*), because it is difficult to distinguish the two species at sea (Hain et al., 1985; Kenney et al., 1997; Kenney and Winn, 1987; Overholtz and Waring, 1991; Rone and Pace, 2012; Waring, 1993). In the Northwest Atlantic, the northern extent of the range of the short-finned pilot whale range overlaps with the southern extent of long-finned pilot whale habitat between New Jersey and George's Bank (Hayes et al., 2017). Bycatch in the pelagic longline fishery appears to be restricted largely to short-finned pilot whales (Hayes et al., 2017; McCreary and Poncelet, 2006). Recent deployments of satellite-linked transmitters on short-finned pilot whales have provided the first detailed information on their habitat use and movement patterns (Thorne et al., 2017).

To understand whether spatial management approaches could be used to reduce bycatch of pilot whales in the longline fishery, it is first necessary to examine the overlap between whales and the fishery and the influence of environmental variables on this pattern. Thus, our objectives were to: 1) assess spatial overlap between pilot whales and longlines along the northeastern coast of the United States; and 2) examine temporal patterns and environmental drivers of both overlap and observations of pilot whale bycatch.

2. Methods

2.1. Study area and pelagic longline fishery

Most bycatch of pilot whales in the U.S. Atlantic pelagic longline fishery occurs in the MAB and the Northeast Coastal (NEC) regions of the east coast of the United States (Garrison, 2007). The continental shelf in this region is broad (approximately 50–200 km from the shoreline to the edge of the continental shelf), but narrows as one progresses south, and is demarcated by a steep slope at the shelf break. Several submarine canyons occur in the MAB, the largest of which is Hudson Canyon in the New York Bight. We describe the shelf region east of the Hudson Canyon as the Southern New England Shelf (SNE shelf) for the purposes of this study and refer to canyons situated between Norfolk and Washington Canyons as the Mid-Atlantic canyons region (Brooke et al., 2017; Fig. 1). The steep slope at the edge of the continental shelf provides habitat for many marine mammal species, particularly sperm whales (*Physeter macrocephalus*), fin whales (*Balaenoptera physalus*), and short-finned pilot whales (Hain et al., 1985; Kenney et al., 1997; Thorne et al., 2017). Within the MAB, the Cape Hatteras region serves as foraging habitat for several species of marine mammal including short-finned pilot whales, bottlenose dolphins (*Tursiops truncatus*), and Cuvier's beaked whales (*Ziphius cavirostris*) and is also used by many pelagic longline vessels (Garrison, 2007; Hamazaki, 2002; Roberts et al., 2016; Schick et al., 2011; Thorne et al., 2017). In the MAB and NEC, the pelagic longline fishery targets swordfish (*Xiphias gladius*), yellowfin tuna (*Thunnus albacares)*, and bigeye tuna (*Thunnus obesus*), and primarily uses squid and mackerel as bait (Sakagawa et al., 1987; Witzell, 1999). Longline fishermen set gear where target fish species are expected to occur, and longline locations vary spatially and temporally based on factors such as sea surface temperature and the location of eddies (Hsu et al., 2015). Swordfish are typically fished at night with the use of light sticks near hooks, while fishermen targeting tuna usually fish during daylight hours (Sakagawa et al., 1987; Witzell, 1999; Beerkircher et al., 2002). Most bycatch occurs along the shelf break, defined as the region between the 200 m and 2000 m isobaths, between North Carolina and the Gulf of Maine (Garrison, 2007).

2.2. Longline fishing effort and Pelagic Observer Program fisheries bycatch

We used two data sources to examine longline fishing effort: self-reported longline logbook data from fishermen that includes the location and date of every longline set during the study period, as well as details of mainline, gangion, and floatline lengths, and target catch for all longline sets; and longline sets observed by the Pelagic Observer Program (POP), representing a subset of all longlines, that includes detailed information on gear, catch and bycatch in addition to the

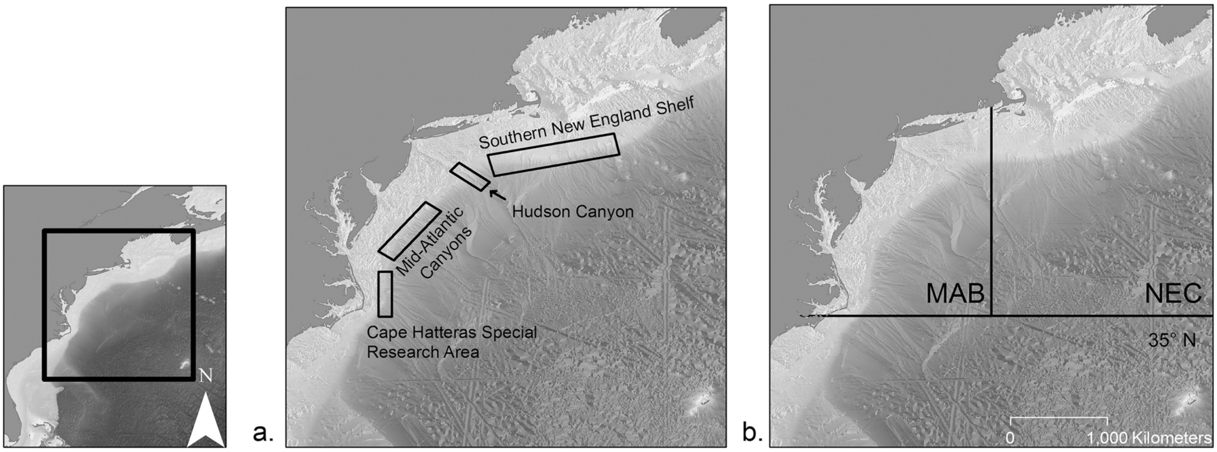

Fig. 1. a. Location of the Cape Hatteras Special Research Area, the Mid-Atlantic Canyons region, Hudson Canyon and the Southern New England Shelf. b. The delineation of the study site, comprised of the Mid-Atlantic Bight (MAB) and Northeast Coastal (NEC) zones, as delineated by The National Marine Fisheries Service (National Marine Fisheries Service 2002).

location and date of POP longline sets. To examine spatiotemporal patterns of longline fishing effort, we obtained logbook data from pelagic longline vessels fishing in the MAB and NEC regions during 2014 and 2015 from the Southeast Fisheries Science Center (SEFSC). The spatial information from the logbook data set only includes spatial coordinates of the start of the longline set in contrast to POP data, which includes more detailed spatial information (described below). Logbook data were filtered for erroneous points and incomplete data using several methods: data were removed when the reported values for the floatline, gangion, or mainline lengths were 0, and when the sum of the floatline length and mainline length plus 10 m exceeded the water depth at that point (bathymetry data detailed in Section 2.4). All sets with integer values of latitude or longitude, with erroneous or incomplete dates, with less than 100 hooks per set, or with a reported total catch that exceeded the number of hooks on the line were removed from the analysis (Hsu et al., 2015; Kot et al., 2010). In total there were 10,232 longline sets in 2014 and 13,455 in 2015 in the logbook sets included in the analysis. In both years combined, 10.3% of sets targeted swordfish, 42.4% targeted tuna, < 1% listed no species target, and 45.3% targeted mixed species.

We used POP data from the NEC and MAB regions in 2014 and 2015 to examine patterns of observed pilot whale bycatch in the longline fishery, as bycatch data are not recorded in the logbook data. The POP is run by the SEFSC and trains observers to record detailed information on fishing gear metrics, catch metrics, and to record the incidental bycatch of protected species including pilot whales. However, observers are only present on a small proportion of the overall fishing fleet (approximately 4.8%; Keene et al., 2006). We calculated the amount of Bycatch per Unit Effort (BPUE) in a given month or grid cell (grids described below) as number of pilot whales caught in each POP longline set divided by the number of POP longline sets in that month or spatial location. Longline sets in the POP database include four sets of spatial coordinates (the start and end location of the set, and start and end location of the haulback). Due to confidentiality requirements, our figures display time periods when POP data could be aggregated to include three or more vessels, regardless of the number of observed sets for each vessel. However, all analyses were conducted using the set-level data at a monthly or annual basis.

Logbook data were available for all longline sets, so we used these data to evaluate broad spatial patterns of longline effort. However, we used the more detailed spatial data available for longline sets in the POP database to establish the resolution for analyses of logbook data. We first established the potential area fished, calculated using the minimum convex hull (MCH) of the four points (start and end of set, and start and end of haul) from the POP data (Dunn et al., 2008). The mean MCH of the POP longline sets in the present study was 185 km^2, which would be represented by grid cells of 13.6×13.6 km; we therefore selected a resolution of 15 km for our analyses.

2.3. Pilot whale telemetry data

Our analyses used satellite-tag data of short-finned pilot whales to examine pilot whale foraging behavior (the same data as used in Thorne et al., 2017 to examine pilot whale distribution and foraging behavior). 39 individual short-finned pilot whales were tagged with Wildlife Computer SPOT5 tags (29 individuals) and Mk10-A satellite-linked depth-recording tags (10 individuals) in the Low Impact Minimally Percutaneous External-electronics Transmitter (LIMPET) configuration. Four tags transmitted for < 1 day and were excluded from analyses. Tags were deployed on pilot whales off Cape Hatteras in May, June and September 2014 and May, June and October 2015, and we included data collection obtained through December 2015. Species identification of pilot whales at the study site was confirmed by genetic analysis of biopsy samples. The minimum/maximum/median transmission durations of pilot whale tracks used in analyses were 6.5 days, 198.5 days, and 57.1 days, respectively. Spatial maps of pilot whale distribution are presented in Thorne et al. (2017).

SPOT5 tags were programmed to transmit location data daily for the first 60 days. After 60 days, tags were duty-cycled to transmit for 24 h every 3 days for 21 days and then every 5 days until the tag stopped recording to conserve battery and increase overall tag duration. Mk10-A tags were programmed to transmit daily for the first 20 days, then every third day for the next 30 days, and then every ninth day until the tag stopped recording. Position estimates were filtered to remove erroneous location estimates (Douglas et al., 2012; user defined settings: maximum rate of movements = 15 km/h, maximum redundant distance = 3 km, default rate coefficient for marine mammals = 25, location classes 2 and 3 retained). Individual tracks were resampled to a 12-hour time period to correct for temporal variability in signal transmissions due to non-uniform satellite transmissions. If four or more transmissions occurred within the 12-hour period, the Minimum Covariance Determinant (MCD) was used to calculate latitude and longitude. The MCD estimates multivariate location and scatter and is an effective determinant of outliers but can only be calculated for four or more points (Flemming et al., 2010). The MCD could not be calculated and the latitude and longitude coordinates, respectively, were averaged if fewer than four transmissions occurred within the 12-hour period. Preliminary data analyses showed that individual whales travelled slowly with a high turning rate within an average radius of 40 km (range +/− 5.9 km) from the initial tagging location. We therefore removed initial tag transmissions that occurred within 50 km of the tagging location from further analyses. All transmissions were retained once the individual traveled more than 50 km from the tagging location.

2.4. Environmental data

We examined distributions of pilot whales, longline fishing effort, and pilot whale bycatch relative to the 1000 m isobath and SST, which were identified as important variables in previous studies of pilot whale habitat use and bycatch (Garrison, 2007; Thorne et al., 2017). We assessed SST using daily images from the GHRSST Level 4 global blended SST dataset at a resolution of 0.01 decimal degrees (https://podaac.jpl.nasa.gov/dataset/JPL_OUROCEAN-L4UHfnd-GLOB-G1SST). We assessed bathymetry using the 30 arc-second resolution GEBCO grid (GEBCO_2014 Grid, version 20150318, www.gebco.net). In other marine mammal studies, the shelf break is often defined as the region between the 200 m and 2000 m isobaths (Garrison, 2007; Mullin and Fulling, 2003), and we used the 1000 m isobath as an indicator of proximity to deep water because longline sets were predominantly distributed around the outer edge of the continental shelf which was best represented by the 1000 m isobath. Pilot whales primarily occur between the 200 m and 1000 m isobaths (Garrison, 2007), which are separated by less than 15 km in the MAB except for regions northeast of the Hudson Canyon, where the slope is less steep. Thus, analyses of pilot whale, longline, and POP effort distributions were conducted relative to the 1000 m isobath.

2.5. Spatial patterns in pilot whale occurrence and longline effort

Density grids, which include all longline logbook sets and pilot whale transmissions in the study period, were used as inputs for the spatial overlap analysis (Section 2.6). Density grids were calculated at a 15 km resolution using logbook data, representing the number of POP longlines observed per 15 km × 15 km cell that contained at least 1 longline set. Density grids were similarly compiled for cells that contained at least 1 pilot whale observation from satellite tags (number of pilot whales per 15 km × 15 km grid cell). We did not correct pilot whale density grids for biases in months with few tags because pilot whales were found to consistently occupy regions in close proximity to the continental shelf break, even when individual effects were considered (Thorne et al., 2017), and occupied similar SST ranges between 2014 and 2015. To visualize seasonal spatial patterns in the distribution of longline effort, we also compiled separate spatial Kernel density grids for longline logbook sets at a 15 km scale for each month of 2014 and 2015, and calculated the 0.75, 0.90, 0.95, and 1.00 isopleths (bandwidth = 1) in the Geospatial Modelling Environment (Beyer, 2015).

2.6. Spatial overlap of pilot whales and longline effort

To examine the extent to which pilot whales and longlines generally use similar spatial regions, we assessed the overall spatial overlap of pilot whales and longline fishing effort by normalizing the density grids described above to values between 0 and 1 using Eq. (1):

$$\frac{(x - x_{min})}{(x_{max} - x_{min})} \tag{1}$$

where x is the individual grid cell, $x_{\min}$ is the minimum raster value, and $x_{\max}$ is the maximum raster value. Density grids were calculated for the entire study period (May 2014 – December 2015), as well as for each month of 2014 and 2015, respectively.

We quantified overall spatial overlap between the distribution of pilot whales and that of longline effort and assessed whether overlap was greater than expected by random chance. Density grids of pilot whale effort and longline effort were used as inputs to calculate Williamson's spatial overlap index (SOI, Eq. (2), Williamson, 1993):

$$SOI = \frac{\sum_{z=1}^{m} (N_z n_z)^{*} m}{\sum_{z=1}^{m} (N_z) \times \sum_{z=1}^{m} (n_z)} \tag{2}$$

where m is the total number of cells occupied by either a pilot whale or longline, N is pilot whale density, n is the density of longline effort (calculated using logbook data), and z is the sampling location (grid cell). Williamson's SOI provides a single value that represents overlap of the pilot whale and longline density grids for all sampling locations. SOI values of ~ 1 indicate that pilot whale occurrence is uniformly distributed in space relative to longline effort. SOI values > 1 represent overlap between pilot whales and longline sets that is greater than expected from a uniform distribution, and SOI values < 1 indicate that overlap is less than expected from a uniform distribution (Harden and Williard, 2012; McClellan et al., 2009; Williamson, 1993).

We first calculated SOI for the entire study region for both years together. Next, we calculated SOI relative to proximity to the 1000 m isobath, in three regions: one value for the region 15 km inshore of the 1000 m isobath, one for the region 15 km offshore of the 1000 m isobath, and one for any region more than 15 km from the 1000 m isobath. The 15 km distance was chosen to match the spatial resolution of the density grids as described in Section 2.5. To assess statistical significance, we calculated SOI and compared the observed value to a test distribution of 4999 SOI values obtained by iterating randomized pilot whale and longline density grids (Garrison et al., 2000; Harden and Williard, 2012).

2.7. Monthly patterns of pilot whale-longline overlap relative to environmental variables

In addition to assessing the broad spatial patterns of pilot whale-longline overlap described above, we sought to examine overlap at a finer temporal scale, and to investigate how overlap varies with environmental variables. Before examining monthly patterns in pilot whale-longline overlap, we first assessed whether POP longline sets were representative of the broader dataset of longline effort (logbook data), and thus whether the logbooks could be used to represent longline effort when examining trends in POP observed bycatch. We extracted values of SST and proximity to the 1000 m isobath at the start of set location (the only spatial coordinates available for both data sets) and assessed differences in the distribution of POP and logbook sets relative to these variables using Kolmogorov-Smirnov tests. We calculated the mean Kolmogorov-Smirnov significance value based on both the 1000 m isobath and SST for 10,000 replicated samples of 545 longline logbook sets to match the sample size of the POP dataset. We also created monthly plots of the kernel density of the longline logbook data and the POP dataset based on SST to assess seasonal differences between the logbook and POP distributions. These analyses showed differences between the two datasets (described in Results), so we used the POP data to examine trends in pilot whale-longline overlap and bycatch to account for biases in observer coverage that might influence the distribution of POP bycatch.

To assess pilot whale-longline overlap and bycatch relative to environmental variables, we extracted mean values of environmental variables (proximity to 1000 m isobath and SST) within the potential area fished (MCH) of each POP longline set. We then used kernel density smoothing estimators to analyze the distribution of pilot whales, POP longlines, and POP bycatch, respectively, relative to environmental variables for each month. The kernel density estimator provides a smoothing function where the integral of the curve equals 1, allowing density smoothing estimators to be compared between datasets. By integrating the region of overlap between the pilot whale kernel density function and the longline kernel density function (the area under the curve, AUC), we obtained a metric quantifying pilot whale-longline overlap relative to environmental variables for each month (Fig. 2). AUC was not calculated between January and April of 2014 or 2015 because no pilot whale tags were transmitting during those

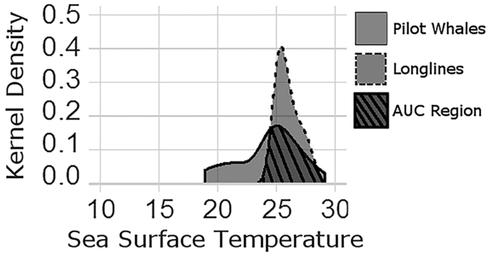

Fig. 2. Example of Area Under the Curve (AUC) analysis conducted for environmental variables on a monthly basis, shown here for sea surface temperature. The AUC region was used as a metrics of overlap between pilot whales and longlines.

months. We then compared the monthly overlap values calculated based on each environmental variable, respectively, with monthly values of BPUE from the POP data using Pearson's rank correlation coefficients, using months in which both pilot whale tag transmission data and POP observer data were available.

We conducted all analyses using the R statistical package (version 3.3.1) and the MASS, stats, rgdal, rgeos, reshape, raster, maptools, lubridate, and ggplot2 libraries.

3. Results

3.1. Spatial and temporal trends in the distribution of pilot whales, longlines, and pilot whale bycatch

Pilot whale bycatch was recorded in 50 sets, and involved 59 individual pilot whales. In most (42) sets in which bycatch was observed, a single pilot whale was involved, but two whales were observed in seven sets, and three whales were taken as bycatch in a single set. Longline sets were observed in 20 months during 2014 and 2015, with an average of 22 sets observed each month. Bycatch was recorded in 10 of the 20 months in which longline sets were observed and the overall rate of BPUE was 0.087 pilot whales per set in 2014 and 0.095 pilot whales per set in 2015. Rates of BPUE varied seasonally (Table 1), and data were limited in some months by observer effort. In 2014, the highest BPUE values occurred in January and February (combined BPUE = 0.25). However, these months had very low observer effort (a total of eight POP sets in the two months combined) and there were no pilot whale tags deployed during this time period, and as a result these months could not be used to examine BPUE relative to overlap. Of the remaining months in 2014, the highest BPUE values occurred from September through November (average BPUE value of 0.14), while in 2015, bycatch was observed in only July, October and December, and the highest BPUE occurred in December of 2015. Importantly, there was substantially more observer effort in December 2015 (81 POP sets; BPUE value of 0.32) than in December 2014 (fewer than three vessels observed by the POP).

Logbook and POP data both showed that the highest densities of longline sets occurred close to the 1000 m isobath, with a small number of sets extending into distant offshore waters (Figs. 3–5). Most longline sets occurred from July through October (1661 sets per month on average in 2014 and 2318 sets per month on average in 2015) compared to November through June of 2014 and 2015 (405 sets per month on average in 2014 and 531 sets per month on average in 2015). 69.3% of longline sets used squid alone or in combination as bait, 27.3% used both squid and mackerel, 2.0% used mackerel alone or in combination, and 1.3% used other bait aside from squid and mackerel. 66.0% of longline sets with squid alone or in combination, 52.5% of sets using both squid and mackerel, 29.1% of sets using mackerel alone or in combination, and 24.9% of sets using bait other than squid or mackerel were offshore of the 1000 m isobath. 68.7% of sets that targeted tuna, 44.8% of sets that targeted swordfish, and 58.1% of mixed target sets occurred offshore of the 1000 m isobath. Most of the pilot whale distribution was focused close to and slightly inshore of the 1000 m isobath (Fig. 6). POP longline sets were primarily concentrated around the 1000 m isobath, but POP bycatch occurred just inshore of the 1000 m isobath, matching the distribution of the pilot whales (Fig. 6). BPUE was highest 15 km inshore of the 1000 m isobath (Table 2). POP longline sets were roughly evenly distributed in regions 15 km inshore, 15 km offshore, and more than 15 km from the 1000 m isobath, while the majority of logbook longline sets (81%) occurred within 15 km of the 1000 m isobath. Pilot whale observations were approximately four times as prevalent 15 km inshore of the 1000 m isobath than 15 km offshore of the 1000 m isobath, or than regions more than 15 km from the 1000 m isobath (Table 2).

3.2. Overall spatial overlap between pilot whales and longlines

Overall, the SOI value was 4.06 (p = 1.70 E -13), representing significantly greater overlap between pilot whales and longline sets than expected from a uniform distribution. The SOI 15 km inshore of the 1000 m isobath also showed significant overlap (SOI = 1.791, p = 0.043), while the area 15 km offshore of the 1000 m isobath was greater than expected from a uniform distribution, with weak

Table 1

Pelagic Observer Program (POP), logbook longline data, and pilot whale telemetry data available by month for 2014 and 2015. January and February, March through May, and November and December are combined here to maintain data confidentiality due to the small number of POP vessels (less than 3) observed in these months. In addition, POP data (the number of pilot whales caught and the number of observed sets) from June 2015 are not included to maintain data confidentiality. Bycatch Per Unit Effort (BPUE) was calculated as the number of pilot whales caught divided by the number of observed sets. NA values indicate months in which no longline sets were observed. The number of pilot whale observations represents the total number of pilot whale satellite tag transmissions that were received in each month and the number of tags represents the number of tagged individual pilot whales in each month, after resampling to a 12-hour time step. LL represents the total number of longlines in each time period, as represented by the logbook data.

Month	2014						2015					
	No. Pilot Whales Caught	No. Obs. Sets	BPUE	No. Pilot Whale Transmissions	No. Tags	No. LL	No. Pilot Whales Caught	No. Obs. Sets	BPUE	No. Pilot Whale Transmissions	No. Tags	No. LL
January/ February	2	8	0.25	0	0	408	0	0	NA	0	0	45
March - May	0	5	0	49	3	405	0	5	0	44	3	535
June	0	30	0	303	9	1159	*	*	*	304	8	1179
July	1	30	0.03	372	7	1717	1	24	0.04	251	7	2431
August	2	30	0.07	94	6	1950	0	73	0	99	3	2991
September	9	56	0.16	173	11	1820	0	13	0	37	3	1622
October	6	57	0.11	203	7	1670	8	94	0.1	162	10	2231
November/ December	3	25	0.12	84	4	1103	19	87	0.22	594	16	2421

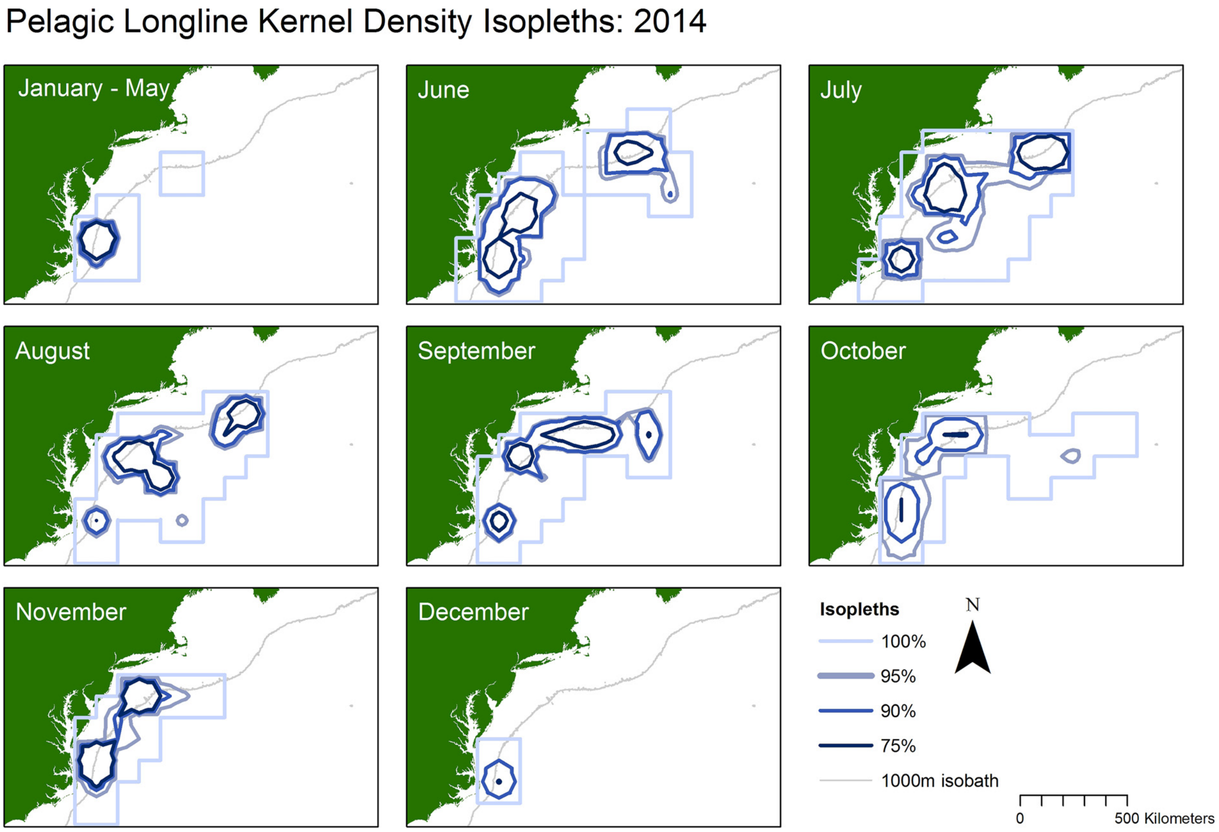

Fig. 3. Isopleths for the 75%, 90%, 95% and 100% Kernel density estimations (KDEs) of longline effort in the logbook database by month for 2014. To adhere to confidentiality requirements,longline sets were aggregated to a 100 km × 100 km grid for display purposes so that each grid cell contained at least three fishing vessels. For January-May and December, the 90% and 95% isopleths were identical due to the resolution of the aggregated longline grid.

significance (SOI = 1.256, p = 0.099). At distances further than 15 km from the 1000 m isobath, the SOI was 0.879 (p = 0.750), indicating that pilot whales were uniformly distributed in space relative to longline effort in this region.

3.3. Comparison of logbook vs. observer (POP) data for longline effort

The distributions of POP effort and longline logbook sets were significantly different based on SST and proximity to the 1000 m isobath (Kolmogorov-Smirnov tests, p-values: p = 0.022 and p = 0.004, respectively; Fig. 5, Supplementary Figs. 1 and 2). There were important differences in the spatial distribution of sets from the observer program and logbooks relative to these variables. In general, POP sets were more dispersed relative to the 1000 m isobath than the broader dataset of longline sets in the logbook dataset, which was densely aggregated around the 1000 m isobath (Fig. 5). This was also true when comparing logbook and POP sets on a monthly basis (Supplementary Fig. 1). POP sets occurred in lower SSTs than logbook sets (Fig. 5). Observer effort and longline logbook sets were similarly distributed based on SST in months with high BPUE in 2015 (October and December), but logbook sets occurred in warmer temperatures than POP sets in the months with high BPUE in 2014 (September and November; Supplementary Fig. 2). Due to the differences in observer effort and logbook effort, we used POP longline sets from the POP dataset for the AUC analysis rather than using the larger logbook effort dataset to generate AUC values.

3.4. POP pilot whale bycatch relative to pilot whale-longline overlap

3.4.1. Bycatch relative to the 1000 m isobath

There was a strong and significant relationship between monthly pilot whale-longline overlap (represented by AUC) and the monthly values of BPUE relative to proximity to the 1000 m isobath in both 2014 and 2015 (Pearson's rank correlation of 0.948 for 2014, p = 0.0003, and 0.816 for 2015, p = 0.0252; Fig. 7). The distribution of pilot whales was consistently focused inshore of the 1000 m isobath (81.0% of all pilot whale transmissions occurred within 15 km of the 1000 m isobath; Table 2), possibly due to the proximity to deep-water foraging regions in canyons and along the continental shelf edge, except for December 2014 when tagged pilot whales were located in offshore waters (Fig. 7). Longline sets exhibited greater variability around the 1000 m isobaths (Figs. 3,4,7). The distribution of longline sets relative to the 1000 m isobath was more variable during summer months but POP longline sets were more densely congregated around the 1000 m isobath between September and December in 2014 (Fig. 7a) and in November and December in 2015 (Fig. 7b), possibly due to restrictions of fishing in cold, winter months. The highest AUC values relative to the 1000 m isobath, representing the highest overlap with pilot whales, and the highest values of BPUE also occurred during these months.

3.4.2. Bycatch relative to sea surface temperature

The AUC analysis of pilot whale-longline overlap relative to SST varied seasonally; the highest percentage of overlap occurred from July to October in 2014 (Fig. 8a) and June to October in 2015 (Fig. 8b). There were no consistent trends when monthly overlap relative to SST was compared to rates of BPUE (Pearson's rank correlation of 0.202 for 2014, p = 0.631, Fig. 8a; and -0.078 for 2015, p = 0.868, Fig. 8b). Bycatch typically occurred within SST ranges of high longline effort rather than at the highest pilot whale density. This pattern was particularly evident in October and November of 2014, and in December of 2015, but could not be evaluated in January through April of both 2014 and 2015 as there were few longline logbook sets (and thus few POP longline sets) and no pilot whale tag transmissions in these months. There were subtle seasonal variations in the thermal ranges of pilot whales and POP longline sets, with both pilot whales and longlines

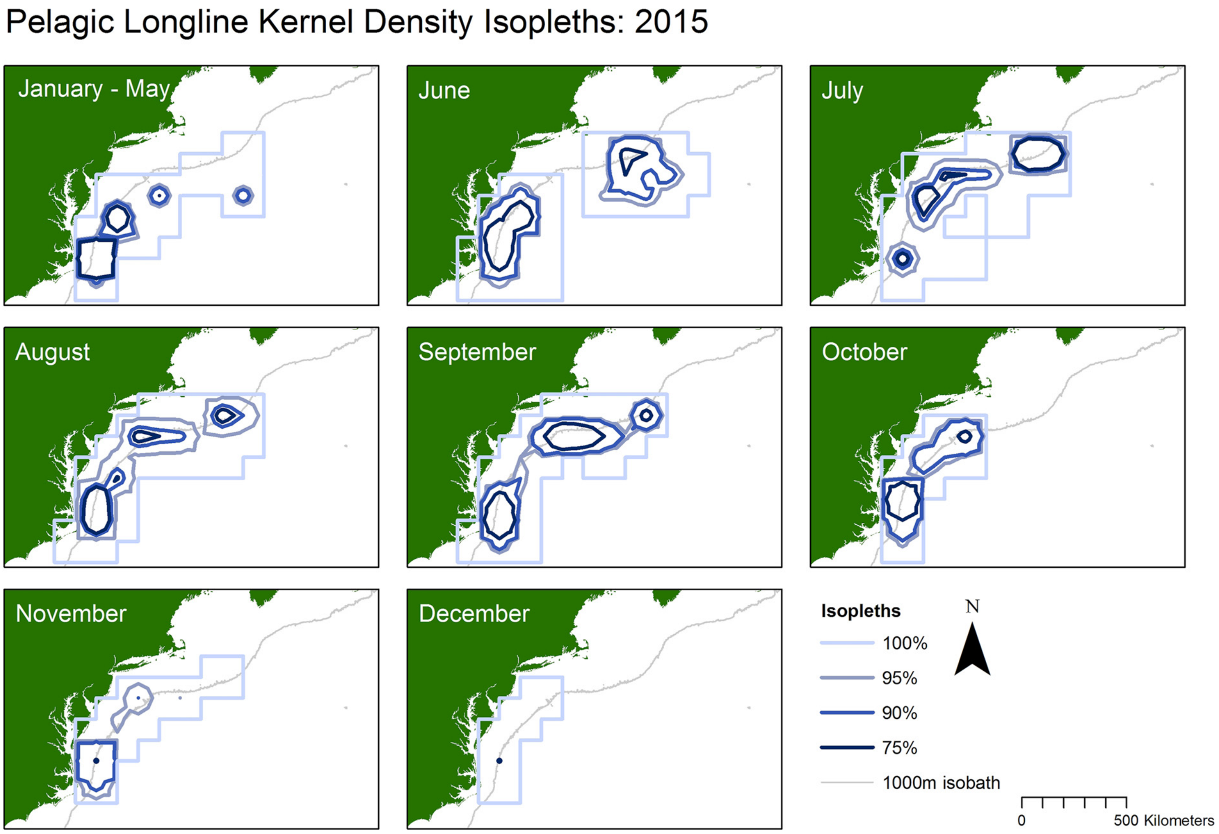

Fig. 4. Isopleths for the 75%, 90%, 95% and 100% Kernel density estimations (KDEs) of longline effort in the logbook database by month for 2014. To adhere to confidentiality requirements,longline sets were aggregated to a 100 km × 100 km grid for display purposes so that each grid cell contained at least three fishing vessels. For December, 75%, 90%, and 95% isopleths were identical due to the resolution of the aggregated longline grid.

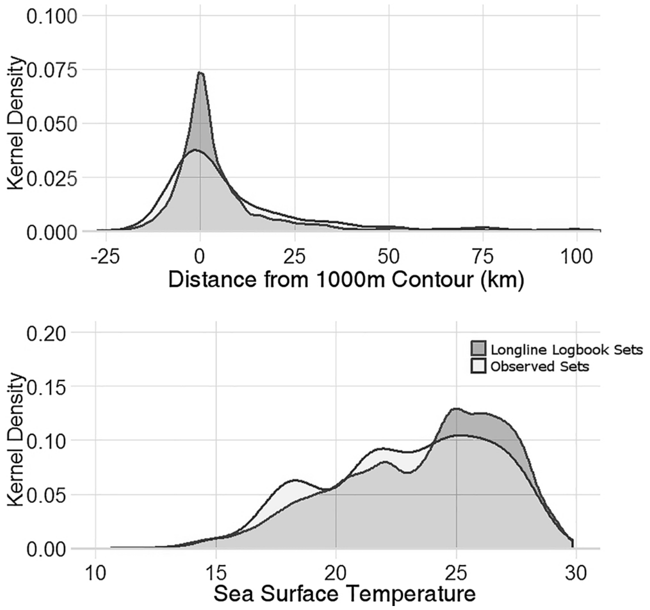

Fig. 5. Distribution of observed longline sets and logbook longline sets relative to proximity to the 1000 m isobath and sea surface temperature for all months of 2014 and 2015 combined.

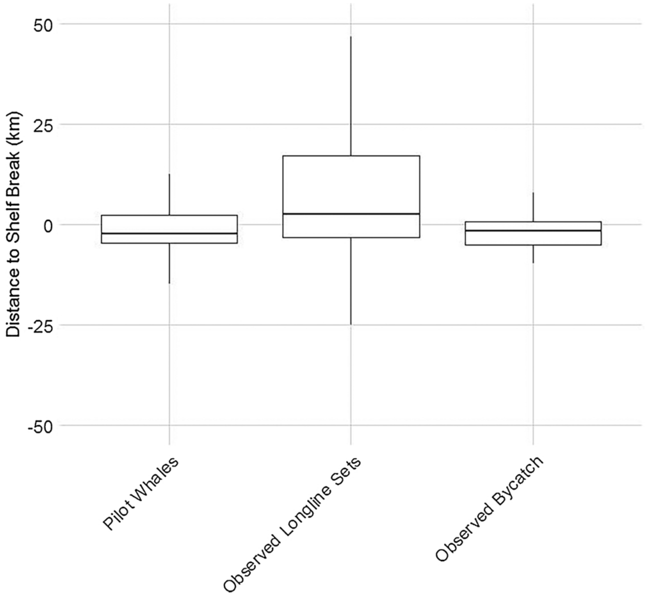

Fig. 6. Boxplot of proximity to the 1000 m isobaths for pilot whale satellite tag transmissions, POP longline sets, and POP pilot whale bycatch, respectively. Negative values represent regions inshore of the 1000 m isobath while positive values represent regions offshore of the 1000 m isobath.

occurring at higher temperatures from July-September in 2014 and 2015 than in other months. In colder months (October through December), pilot whales primarily occupied warmer SSTs than POP longline sets. Higher rates of bycatch also occurred in the fall and early winter months and were typically observed in colder SSTs than most observations of tagged pilot whales (Supplementary Fig. 3). In December 2015, when there was substantially higher observer effort than in other winter months and a large amount of bycatch was observed, the average temperature at which bycatch occurred was 18.3 °C, while the average temperature of pilot whale satellite tag observations was

Table 2
Number of observed longline sets and pilot whale transmissions, overall BPUE, and longline logbook sets for three regions: 15 km inshore of the 1000 m isobath, 15 km offshore of the 1000 m isobath, and > 15 km from the 1000 m isobath.

	< 15 km Inshore of the 1000 m Isobath	< 15 km Offshore of the 1000 m Isobath	> 15 km from the 1000 m Isobath
Number of POP Longline Sets	210	180	153
Number of Pilot Whale Observations	1913	464	556
BPUE	0.15	0.072	0.026
Number of Longline Logbook Sets	8877	10192	4618

22.5 °C and the average temperature at POP longline sets was 18.2 °C. Of the 26 POP bycatch events in December 2015, 24 occurred in the bottom quartile of SSTs observed at pilot whale satellite tag observations, indicating most bycatch occurred disproportionately in the coldest portions of pilot whale distribution during that month.

4. Discussion

We quantified spatial overlap between short-finned pilot whales and pelagic longline fishing effort to assess the potential use of a spatial management approach to mitigate pilot whale-longline bycatch. We found that there was significant spatial overlap between pilot whales and longlines, and that the distributions of pilot whales, longline effort, and BPUE were closely associated with the 1000 m isobath. Pilot whale-longline overlap relative to the 1000 m isobath was strongly and significantly correlated with POP observed rates of pilot whale-longline bycatch.

Both pilot whales and target species in the longline fishery may feed in regions of high productivity, which could lead to high overlap between longline effort and pilot whales on a broad scale. However, there are important differences in the foraging ecology of pilot whales and target species that likely influence overlap between longlines and pilot whales. Short-finned pilot whales typically forage at depths of 245–1000 m (Quick et al., 2017) and feed on deep-water squid species (Mintzer et al., 2008). Bigeye and yellowfin tuna typically forage in the top 400 m of the water column (Dewar et al., 2011; Howell et al., 2010; Lam et al., 2014), and feed more broadly on squid, cephalopods and mesopelagic fish (Chancollon et al., 2006; Logan et al., 2013; Potier et al., 2007). These differences suggest that pilot whales and species targeted by the longline fishery may use different regions as foraging habitat (in both vertical and horizontal dimensions), and our results suggest that pilot whales and longline fishing effort show seasonal spatial differences in habitat use; the distribution of longline effort was more dispersed relative to the 1000 m isobath than that of pilot whales, though not during fall and winter months. In contrast to longline fishing effort, pilot whale density was consistently highest immediately inshore of the 1000 m isobath. Seasonal patterns in pilot whale-longline overlap influenced POP bycatch rates; the highest bycatch rates primarily occurred in fall and winter months when longline effort shifted inshore and was located in close proximity to the 1000 m isobath.

Two behavioral modes have been observed in pilot whales in this region; most pilot whales typically forage along the 1000 m isobath and in submarine canyons, but individuals occasionally travel into distant waters of the Gulf Stream (Thorne et al., 2017). Most POP bycatch occurred close to the 1000 m isobath, so animals foraging in this area have a higher probability of interacting with the U.S. longline fishery. However, pilot whales foraging in distant Gulf Stream waters travel outside of the U.S. Exclusive Economic Zone and could interact with other longline fleets.

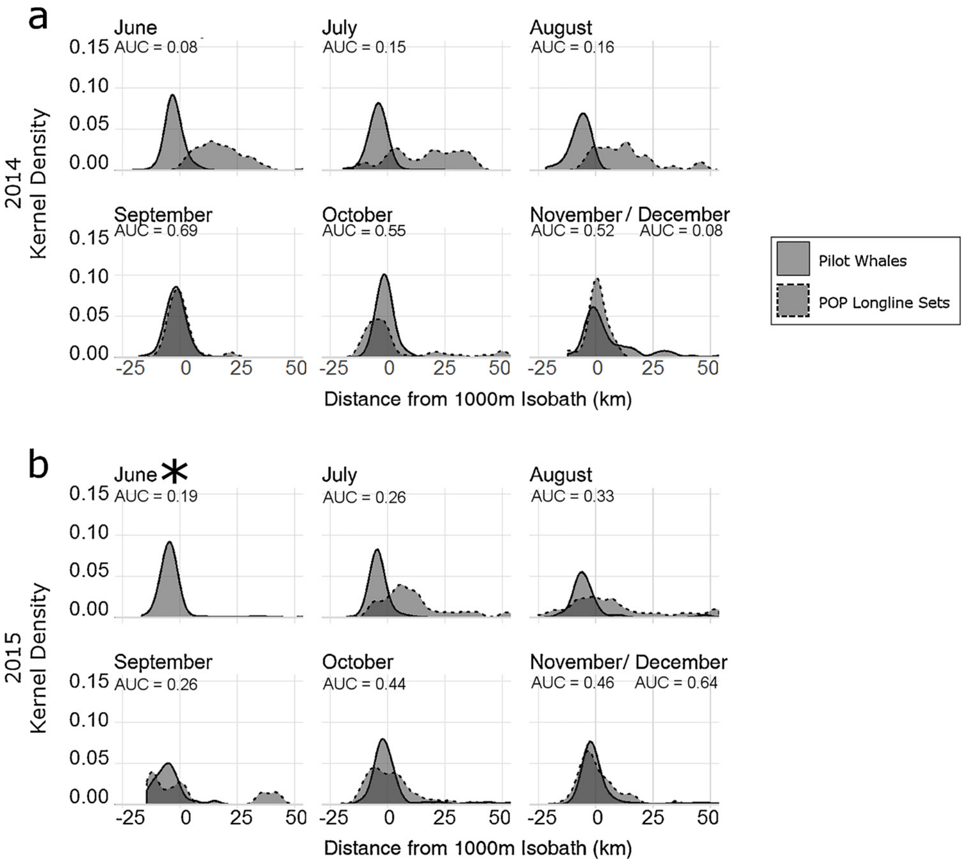

Fig. 7. Kernel density of pilot whale locations and POP longline sets by month from June to December of 2014 (a) and 2015 (b) relative to proximity to the 1000 m isobath. AUC analyses were conducted for all months with both pilot whale transmissions and observed longline sets, but only June through December are shown (with November and December combined) to maintain data confidentiality for months with fewer than 3 observed vessels. June 2015 is denoted with an asterisk because there were fewer than 3 POP longline sets in this month and consequently the distribution of POP longline sets could not be shown. AUC values reflect pilot whale-longline overlap in each month (see Fig. 2). A small proportion of pilot whales made offshore forays into Gulf Stream waters (Thorne et al., 2017) and occurred at distances of up to 475 km from the 1000 m isobath. Here we focus on distributions within 50 km of the 1000 m isobath because 92% of longline effort, and therefore most pilot whale-longline overlap, occurred in this region.

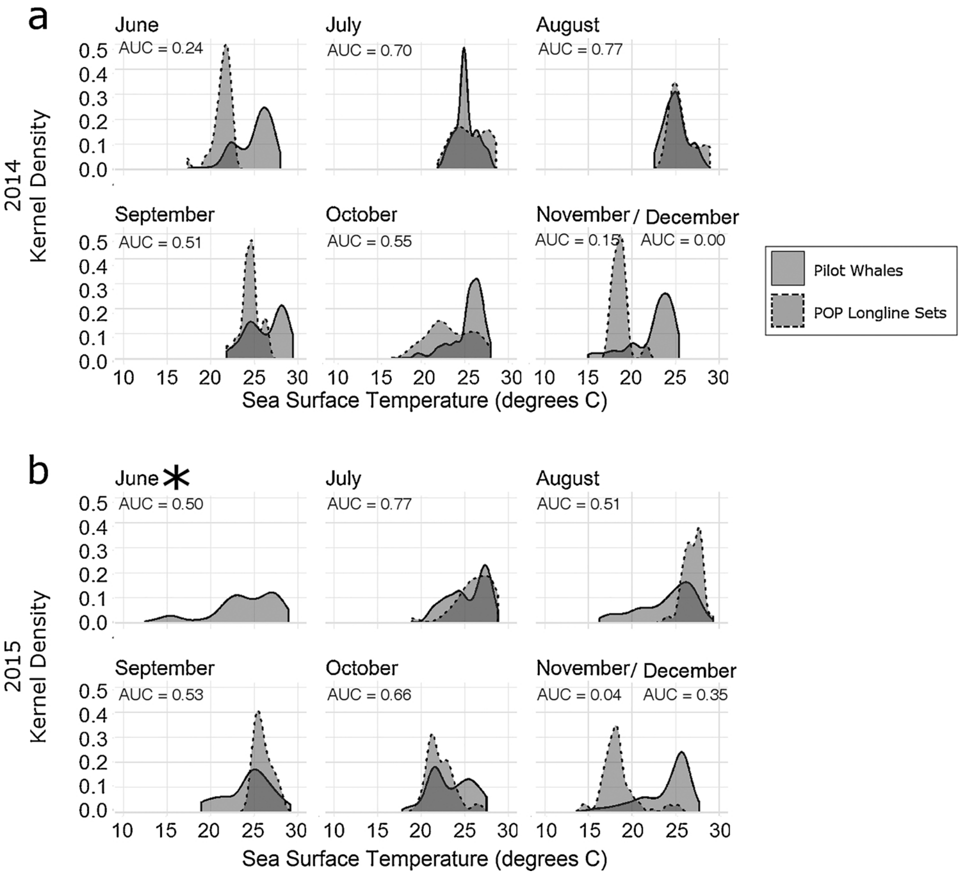

Fig. 8. Kernel density of pilot whale locations and observed longline sets by month from June to December of 2014 (a) and 2015 (b) relative to sea surface temperature. AUC analyses were conducted for all months with both pilot whale transmissions and observed longline sets, but only June through December are shown (with November and December combined) to maintain data confidentiality for months with fewer than 3 observed vessels. June 2015 is denoted with an asterisk because there were fewer than 3 POP longline sets in this month and consequently the distribution of POP longline sets could not be shown. AUC values reflect pilot whale-longline overlap in each month (see Fig. 2).

Prior studies have used static environmental variables to predict the risk of bycatch of marine predators and to highlight important regions for the development of spatial management plans (McClellan et al., 2009; Read and Westgate, 1997). Our analysis of pilot whale-longline overlap and bycatch suggests that shifting fishing effort into deeper waters off the continental shelf, particularly in October through December, might reduce pilot whale bycatch in this pelagic longline fishery. For example, if longline effort was shifted offshore to waters deeper than 1000 m during these months, 56% of the overall POP bycatch could be avoided. Of course, this assumes that pilot whales would not shift their distribution in response. In addition, it is important to note that a shift of this magnitude would strongly impact fishermen, requiring that almost half (47%) of longline sets relocate during these months. Further, shifts in fishing effort could impact bycatch of other protected species in the pelagic longline fishery (Li et al., 2016; Moore et al., 2009; Witzell, 1999), and these impacts should be evaluated before changes to longline effort are recommended or implemented.

Our results suggest that seasonal patterns and dynamic oceanographic variables could be important in further delineating regions with a high risk of bycatch. Longline set characteristics, including the target fish species, are influenced by the presence of mesoscale eddies (Hsu et al., 2015), and the relationship between eddy presence and pilot whale bycatch has not been explored. A more detailed analysis of pilot whale occurrence relative to dynamic variables such as SST, thermal fronts, mesoscale eddies or warm core rings could be used to further delineate smaller high-risk areas for pilot whale bycatch along the 1000 m isobath to decrease the impact of a spatial management approach on the longline fishery. In fall and winter months, bycatch occurred in cool waters relative to the water temperatures where most longline sets occurred. However, the latitudinal distribution of pilot whales may not be well represented by the telemetry dataset in all seasons; while bycatch in fall and winter was typically clustered in either the Southern New England Shelf and Hudson Canyon regions or the Cape Hatteras Region (Fig. 1), there were few pilot whale transmissions in the Southern New England Shelf and Hudson Canyon during these months. Even though few pilot whale tags were transmitting in winter months, pilot whales show consistency in habitat use relative to the shelf break throughout the year (Thorne et al., 2017; shelf break defined therein as the 200 m isobath). Pilot whale bycatch occurred disproportionately in the coldest portions of observed pilot whale distribution during fall and winter months. In the broader telemetry dataset, pilot whales were observed in waters as cool as 9.4 °C but the coolest water temperature where bycatch was recorded was 16.3 °C, suggesting that locations of POP bycatch were generally consistent with our observations of pilot whale occurrence with respect to temperature (Supplementary Fig. 3). Bycatch recorded in cooler temperatures in fall and winter months could be due to the distribution of longline set densities, or a combination of drivers from both longlines and pilot whale latitudinal habitat use along the shelf. Dynamic environmental drivers of pilot whale bycatch merit further investigation.

In other fisheries, near real-time predictive products that combine environmental characteristics of the fishery, the bycaught species, and the occurrence of bycatch have been developed to reduce bycatch risk (Howell et al., 2008). Static and dynamic variables can be integrated with sufficient telemetry data to develop effective near real-time predictive species maps (Hazen et al., 2016), which could be used to inform fishermen of regions to avoid when setting longlines. Ongoing research modeling pilot whale occurrence relative to both static and dynamic variables such as SST will be helpful in developing fine-scale predictions of pilot whale occurrence throughout the year which would allow for a more constrained spatial understanding of potential overlap with longline fishing gear.

POP data represents a critical source of information for understanding patterns of bycatch of protected species, but our results suggest that limitations of both the pilot whale and POP data sets constrain our understanding of pilot whale bycatch in the pelagic longline fishery. The distributions of logbook longline sets and POP longline sets based on SST and distance to the 1000 m isobath were significantly different, indicating that observer coverage is not fully representative of the fishery. Bycatch rates were higher in close proximity to the 1000 m isobath (Table 2), but in comparison to the broader logbook dataset, a higher proportion of POP longline sets occurred farther from the 1000 m isobath (19.4% of logbook sets and 28.2% of POP sets, respectively, occurred more than 15 km from the 1000 m isobath; Table 2, Supplementary Fig. 1). This difference could be due to bias when placing observers on longline vessels or altered fishing behavior when government observers are on board. Bias could be introduced based on non-random observer coverage; for example, some vessels may not comply with observer requirements, may not pass safety inspections, or may be chosen up to four times in a year depending on observer coverage requirements outlined by the Southeast Fisheries Science Center (Keene et al., 2006). Observers are also more likely to be placed on larger vessels that can fish further from the shelf than smaller vessels (McCreary and Poncelet, 2006), which could increase bias in observer effort. If more observer coverage occurred in close proximity to the 1000 m isobath, more bycatch might have been observed. As most pilot whale bycatch recorded in POP longline sets occurred during the winter months when longline sets were constrained to the 1000 m isobath, improving observer effort during these months would improve our understanding of pilot whale bycatch and pilot whale mortality and serious injury. Bias of observer coverage could also be introduced by variation in temporal coverage of longline sets. Observer effort was higher between July and December of 2015 compared to 2014, but there was more variability in the number of POP sets observed in 2015. Observer effort varies throughout the year because effort is based on the amount of fishing effort by quarter; therefore, the number of POP sets depends on how many vessels are fishing (Keene et al., 2006). If the observer quota is met early in a quarter, there may be no observer coverage in subsequent months, creating a bias in effort towards the months earlier in the quarter. Observer effort was variable in fall months (in October through December of 2014, observer effort ranged from 6 to 57 sets per month; and in September through December of 2015, observer effort ranged from 6 to 94 sets per month), which could be a result of the quarterly observer system. Also, fewer longline vessels fish in winter months, so less overall observer coverage is required, and observers may use the same vessel for repeated trips, introducing a source of bias into the POP data (Keene et al., 2006). There was effectively no observer effort in many winter months where longline fishing effort was constrained to the 1000 m isobath (January through April had a total of 11 total POP sets in 2014 and 5 in 2015). POP sets could better represent the broader longline fishery in the context of environmental variables by increasing observer coverage in fall and winter months, which would provide more observations when longline effort shifted towards the 1000 m bathymetric contour and into colder waters during winter months. A more even distribution of observer coverage throughout the year would reduce the seasonal bias which would improve our understanding of pilot whale bycatch.

We investigated spatial drivers of bycatch at the scale of the fishery, but characteristics within the fishery such as bait type or target species could also influence the risk of bycatch. Future investigations of the overlap between pilot whales and pelagic longlines could incorporate environmental and behavioral effects into models simulating the effects of different management strategies on bycatch rates (Harden and Williard, 2012). Before specific scenarios can be investigated, it is important to: 1) distribute observer effort more evenly throughout the year to better understand characteristics of bycatch during months with low longline effort and high potential for pilot whale overlap; 2) better understand the role of dynamic oceanography influencing pilot whale-longline overlap and bycatch; and 3) determine the impact of potential management strategies on the fishery, as well as on other bycatch species.

5. Conclusion

Using novel quantitative methods, we demonstrated that pilot whales and longlines show significant spatial overlap relative to the 1000 m isobath and that overlap was strongly and significantly correlated with observed rates of pilot whale bycatch from the POP. The density of pilot whales and longlines decreased with distance from the 1000 m isobath, and pilot whale bycatch was highest inshore of the 1000 m isobath. We found important, but subtle, differences in the way that pilot whales and longline fishermen are distributed relative to the 1000 m isobath that could be useful in developing mitigation strategies to decrease pilot whale bycatch. Pilot whales primarily occupied habitats just inshore of the 1000 m isobath but longlines were evenly distributed around the 1000 m isobath. Most notably, pilot whales were closely associated with the 1000 m isobath throughout the year, but longline effort shifted inshore and offshore seasonally; as a result, pilot whale-longline overlap also varied seasonally, with the highest bycatch rates typically occurring when longline effort was spatially constrained around the 1000 m isobath. Taken together, our findings highlight the importance of understanding underlying distributions of fishing effort and bycaught species before developing bycatch mitigation strategies. Our results suggest that a spatial management approach could be helpful in reducing pilot whale bycatch in the pelagic longline fishery, though moving fishing effort offshore of the 1000 m isobath would affect a substantial proportion of longline sets. An improved understanding of the relationships between pilot whale bycatch and dynamic variables such as SST may allow high-risk regions for pilot whale bycatch to be further delineated, allowing smaller, more specific regions to be identified to reduce impact on the longline fishery.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.fishres.2018.07.008.

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