Deep-Sea Research I 91 (2014) 10–16

Contents lists available at ScienceDirect

Deep-Sea Research I

journal homepage: www.elsevier.com/locate/dsri

Seasonal occurrence of sperm whales (*Physeter macrocephalus*) around Kelvin Seamount in the Sargasso Sea in relation to oceanographic processes

Sarah N.P. Wong *, Hal Whitehead

Department of Biology, Dalhousie University, 1355 Oxford Street, Halifax, NS, Canada B3H 4J1

ARTICLE INFO

Article history:
Received 3 March 2014
Received in revised form
13 May 2014
Accepted 16 May 2014
Available online 2 June 2014

Keywords:
Sperm whales
Kelvin Seamount
New England Seamount Chain
Seasonal distribution
Gulf Stream

ABSTRACT

Sperm whales (*Physeter macrocephalus*) are widely distributed in all oceans, but they are clumped geographically, generally in areas associated with high primary and secondary productivity. The warm, clear waters of the Sargasso Sea are traditionally thought to be low in productivity, however recent surveys have found large numbers of sperm whales there. The New England Seamount Chain bisects the north-western portion of the Sargasso Sea, and might influence the mesoscale eddies associated with the Gulf Stream; creating areas of higher productivity within the Sargasso Sea. We investigated the seasonal occurrence of sperm whales over Kelvin Seamount (part of the New England Seamount Chain) and how it is influenced by oceanographic variables. An autonomous recording device was deployed over Kelvin Seamount from May to June 2006 and November 2006 to June 2007. A total of 6505 hourly two-minute recordings were examined for the presence of sperm whale echolocation clicks. Sperm whales were more prevalent around Kelvin in the spring (April to June: mean=51% of recordings contained clicks) compared to the winter (November to March: mean=16% of recordings contained clicks). Sperm whale prevalence at Kelvin was related to chlorophyll-*a* concentration four weeks previous, eddy kinetic energy and month. The mesoscale activity associated with the Gulf Stream and the Gulf Stream's interaction with the New England Seamount Chain likely play an important role in sperm whale occurrence in this area, by increasing productivity and perhaps concentration of cephalopod species.

1. Introduction

Studies of the spatial and temporal distribution of marine predators can be used to identify biologically diverse "hotspots" and inform management and conservation (Worm et al., 2003; Sydeman et al., 2006). Identifying the oceanographic processes driving the distribution and abundance of marine predators leads to a better understanding of this fluid and dynamic habitat. Species richness and abundance can be related to sea surface temperature (Worm et al., 2005), primary productivity (Whitehead et al., 2010) and prominent bathymetric features such as seamounts, islands and slope (Worm et al., 2003; Morato et al., 2008, 2010). The distribution and abundance of top marine predators is also associated with areas of increased productivity due to mesoscale activity, such as fronts (Haney, 1986; Podesta et al., 1993), which aggregate prey (Schneider, 1990; Olson et al., 1994), and cyclonic eddies, as indicated by negative sea surface height anomalies (SSHA) (Teo and Block, 2010), which can lead to increased primary and secondary productivity (Yoder, 1985). Oceanic processes associated with major currents, such as upwelling, also aggregate top predators (Block et al., 2011).

Sperm whales (*Physeter macrocephalus*) are one of the most widely distributed cetaceans in the world, found in all oceans from the equator to the pack ice of both poles (Rice, 1989). They are an important oceanic predator (Whitehead, 2003), feeding mainly on meso- and bathypelagic cephalopods. Within their wide distribution, sperm whales are clumped geographically. Previous research has found that sperm whale distribution is associated with areas of high primary or secondary productivity (Gulland, 1974; Jaquet and Whitehead, 1996; Jaquet et al., 1996) and topographic features, such as depth and slope (Pirotta et al., 2011). Sperm whales were associated with warm-core rings of the Gulf Stream (Waring et al., 1993; Griffin, 1999), cyclonic eddies in the Gulf of Mexico (Ortega-Ortiz and Mate, 2006), frontal zones (Gannier and Praca, 2007) in the Mediterranean Sea and negative SSHA (Biggs et al., 2006) in the Gulf of Mexico.

Recent surveys (Wong, 2012) have found large numbers of sperm whales in the Sargasso Sea and historically, this area supported a lucrative whaling industry for sperm whales (Townsend, 1935; Smith et al., 2012). The Sargasso Sea lies in the middle of the North

* Corresponding author. Tel.: +1 902 494 3723; fax: +1 902 494 3736.
E-mail address: snpwong@dal.ca (S.N.P. Wong).

http://dx.doi.org/10.1016/j.dsr.2014.05.001
0967-0637/

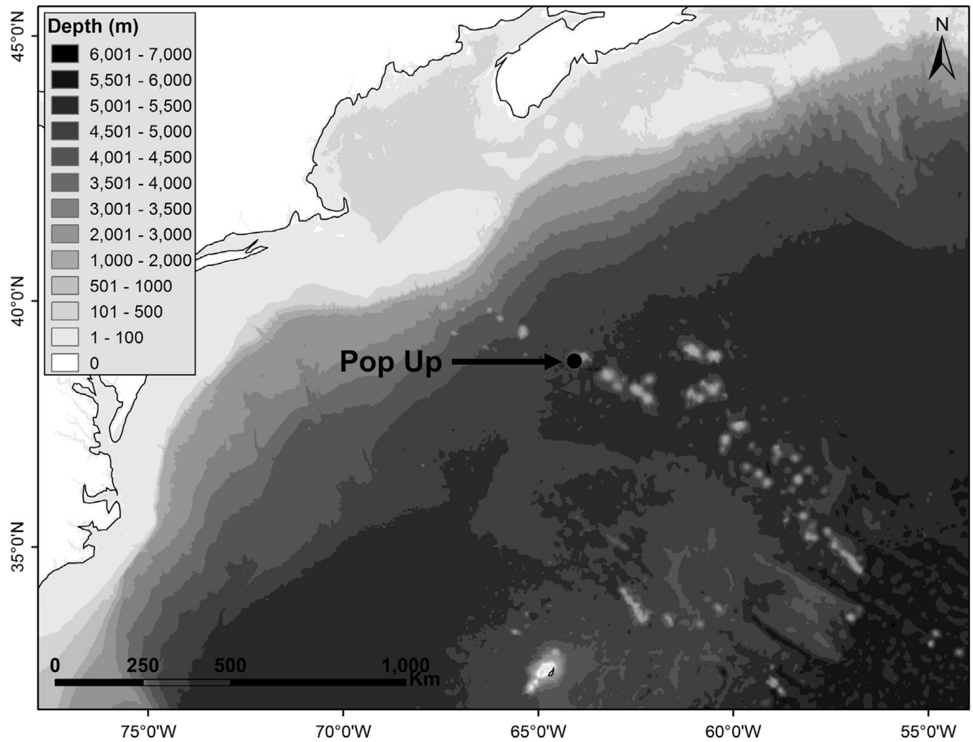

Fig. 1. Study area location showing the New England Seamount Chain and Kelvin seamount in the Northwest Atlantic Ocean, where an autonomous acoustic recording device (pop-up) was deployed to examine seasonal sperm whale prevalence in this area.

Atlantic and is bordered by ocean currents, particularly the Gulf Stream to its west. The warm, clear water of the Sargasso Sea was described as some of the poorest on earth (Blackburn, 1981), however, the northern part of the Sargasso Sea experiences increased productivity due to the presence of eddies, rings and meanders associated with the Gulf Stream (Ortner et al., 1978; McGillicuddy et al., 1998). Oceanic fronts, currents and bathymetry are some factors influencing the distribution and abundance of squid (O'Dor, 1992; Bakun and Csirke, 1998). Thus, eddies, fronts, meanders, and cold-core rings associated with the Gulf Stream may influence the occurrence of sperm whales in this area.

Prominent bathymetric features are also found in the Sargasso Sea, such as the New England Seamount Chain, whose major peaks rise as much as 4000 m above the abyssal plain (Fig. 1). Seamounts result in increased turbulence, mixing and mesoscale eddies, which transport nutrients into the euphotic zone, thereby increasing local production (Wolanski and Hamner, 1988; Oschlies and Garçon, 1998). Several studies have shown an association of marine predators with seamounts, such as large tuna, billfishes and sharks (Worm et al., 2003; Morato et al., 2008), common dolphins (*Delphinus delphis*) (Morato et al., 2008), Cory's shearwaters (*Calonectris diomedea*) (Morato et al., 2008) and beaked whales (Johnston et al., 2008).

Much of what is known about factors driving sperm whale distribution is the result of research conducted in water bodies partially enclosed by land, such as gulfs or seas (Jaquet and Gendron, 2002; Gannier and Praca, 2007; Praca et al., 2009; Pirotta et al., 2011) or in pelagic systems near islands (Morato et al., 2008). With the exception of sperm whale research conducted in the Pacific Ocean (Jaquet and Whitehead, 1996; Jaquet, 1999), and limited offshore work in the Atlantic Ocean (Waring et al., 1993), very little is known about how oceanographic variables influence the distribution of sperm whales in the open ocean and whether their distribution varies seasonally. Furthermore, since oceanic processes vary over temporal scales ranging from seconds to centuries and range spatially from millimeters to thousands of kilometers (Halley 2005), it is important to take spatial and temporal scale into account in studies of marine ecosystems (Schneider, 2001; Pinaud and Weimerskirch, 2007; Pirotta et al., 2014) as there is often a spatial–temporal mismatch between the environmental proxies used to model the distribution of both prey and predators and the actual mechanisms driving it (Grémillet et al., 2008). Previous research has demonstrated the scale-dependent distribution of sperm whales in the Pacific (Jaquet, 1996; Jaquet and Whitehead, 1996).

As a result of extreme weather conditions (hurricanes in the summer and fall, followed by winter storms), it is difficult to conduct vessel-based surveys in the Sargasso Sea outside of the spring season, thus seasonal variability of sperm whale occurrence in this area is unknown. Autonomous recording devices can overcome the difficulties of weather and remoteness and provide the opportunity to examine the prevalence of sperm whales in this little-studied area throughout the year. These devices have been used successfully to monitor the abundance and habitat use of other marine mammals elsewhere (Soldevilla et al., 2011). Although the depth of this area (over 5000 m) makes it difficult to survey using submersible recording devices, Kelvin Seamount, part of the New England Seamount Chain, provides a perfect platform on which to deploy an autonomous recording unit. Since the New England Seamount chain strongly influences the trajectory of the Gulf Stream (Richardson, 1981), deployment on Kelvin Seamount provides an opportunity to examine whether this interaction plays an important role in the distribution and abundance of sperm whales in the Sargasso Sea. Our objective was to examine the seasonal occurrence of sperm whales over Kelvin Seamount and relate their prevalence to oceanographic conditions.

2. Methods

2.1. Data collection and preparation

An autonomous acoustic recording device (Cornell Bioacoustics Research Program, Ithaca, NY) hereafter referred to as a "pop-up", was deployed on Kelvin Seamount (approx: 38° 48′N; 64° 05′W; Fig. 1) four times between May 2006 and June 2007 (1st deployment: 11 May to 2 June 2006, 2nd: 2–21 June 2006, 3rd: 2 November, 2006 to 5 May 2007, 4th: 5 May to 20 June 2007). Due to logistical constraints and severe weather, it was not possible to deploy the pop-up for a second winter (November–May) or from July to November therefore, temporal variability could only be examined from November to June. The pop-ups recorded for two minutes every hour at frequencies up to 5 KHz (first and second deployment), 10 KHz (third deployment) or 25 khz (fourth deployment). All recordings covered the range of sperm whale vocalizations (Madsen et al., 2002).

Weekly composite chlorophyll-*a* concentration (as a proxy for primary productivity) and sea surface temperature (SST) data were downloaded from Aqua-MODIS satellite images (http://oceancolor.gsfc.nasa.gov/) for the period of study. Aqua-MODIS images provide chlorophyll-*a* concentrations in mg m^{-3} and SST in degrees Celsius at a resolution of 4×4 km^2 pixels. Chlorophyll-*a* and SST images were imported into a Geographic Information System (Idrisi Andes Edition). Sea surface height anomaly (SSHA) and geostrophic velocity anomaly data were downloaded from Aviso's global sea surface height products (http://www.aviso.oceanobs.com/en/data/products/sea-surface-height-products/global/index.html) at a resolution of 28.7×28.7 km^2. These data were derived from merged satellite altimetry measurements of four altimeters (Jason-1, ENVISAT/ERS, GEosat Follow-On and Topex/Poseidon interlaced). Eddy kinetic energy (EKE) is a measure of turbulence and flow of a region and can be used to identify where mesocale eddies and meanders are common and also identify the presence of major currents, such as the Gulf Stream (Teo and Block, 2010). EKE was calculated using the following formula:

$$EKE = 1/2x(U^2 + V^2)$$

where U and V are zonal and meridian geostrophic currents components, respectively.

The location of the pop-up was digitized and a “real time” value for chlorophyll-*a* concentration, SST, SSHA and EKE was calculated for that pixel. SST slope (as an indicator of the presence of fronts) was also calculated for that pixel using the Idrisi SURFACE function which determines the slope of a cell based on the cell resolution and the values of the immediate neighboring cells (Rook's case procedure) (Eastman, 2006). To investigate local oceanographic conditions at multiple scales and to reduce the amount of missing chlorophyll-*a* and SST data due to cloud cover, the following values were calculated for quadrants 12×12 km^2, 20×20 km^2, 36×36 km^2, 68×68 km^2, 132×132 km^2 and 260×260 km^2 centered around the pop-up: arithmetic mean chlorophyll-*a* concentration, mean SST, mean SST slope and standard deviation of SST (as a measure of ocean temperature variability). A temporal lag between sperm whale occurrence and SST and chlorophyll-*a* concentration is expected, given the time needed for primary productivity to transfer to top predators (Jaquet, 1996; Croll et al., 2005), as physical processes might either aggregate prey or enhanced primary productivity may indirectly result in high abundance of prey over time (Hunt et al., 1999). Thus, the values of chlorophyll-*a* concentration and SST were also calculated for one to eight weeks previous.

2.2. Data analysis

Pop-up recordings were converted to AIFF files and analyzed using Raven Pro 1.3 (Bioacoustics Research Program, Cornell Lab of Ornithology). Each two-minute recording was examined acoustically and visually (using its spectrogram) for the presence of sperm whale clicks. These clicks are used primarily in echolocation and communication and are arranged in various patterns: usual clicks, slow clicks, creaks and codas. The majority of clicks detected were usual clicks, which are thought to function primarily in searching echolocation and are a long train of regularly spaced clicks (0.5–1.0 s) that can last for several minutes (Whitehead and Weilgart, 1990; Madsen et al., 2002).

To examine the seasonal occurrence of sperm whales around Kelvin Seamount, we calculated a weekly prevalence of sperm whales (expressed as a proportion), defined as: (number of two-minute recordings per week in which sperm whales (clicks) were detected)/(number of two-minute recordings per week), for each month. A Kruskal Wallis test was used to compare the prevalence of sperm whales among months using weekly prevalence of sperm whales as the unit of analysis. Months were grouped into two seasons: spring (April–June) and winter (November–March) and the mean prevalence of sperm whales for winter and spring were compared using a Mann–Whitney U Test.

We modeled the response variable (weekly prevalence of sperm whales) using a Generalized Linear Model (McCullagh and Nelder, 1989) in *R*. Proportional data was modeled with a binomial distribution and logit link function (Lewis, 2004). Our model included the following variables: month (treated as a factor), chlorophyll-*a* concentration, SST, SST slope, SST standard deviation, SSHA and EKE. Including all the covariates at the different spatial and temporal scales would have resulted in instability due to the collinearity between the variables. Therefore, an ad hoc procedure was performed to select the most appropriate spatial and temporal (lag) scale to use in the final model. First, we ran correlation tests on the different spatial scales for chlorophyll-*a* and SST, to identify whether they were correlated and if it was appropriate to use the scale which had the least missing data. Due to the small sample size, second-order Akaike's Information Criterion (AICc) approach was used to evaluate the covariates at different temporal lags (Burnham and Anderson, 2002). To determine which temporal lag to use in the final model, we ran models (GLM) containing the covariate at each temporal lag and used the lag with the lowest AICc score in the final model. Once the appropriate spatial and temporal scales were selected, a full model was fitted. We used a manual backward stepwise approach. At each step, a series of reduced models (containing all variables but one) were fitted and the model with the lowest AICc score was used in the following step. This procedure was continued until removal of any variable caused the AICc score to increase.

3. Results

A total of 6505 hourly, 2-min recordings from 11 May to 21 June, 2006 and 2 November, 2006 to 20 June, 2007 were examined. Mean weekly prevalence of sperm whales was significantly higher in spring (mean $\pm$ SD $= 0.51 \pm 0.21$) compared to winter (mean $\pm$ SD $= 0.16 \pm 0.08$) (Mann–Whitney U Test: $n_1 = 17$, $n_2 = 20$, $U = 20.000$ $z = -4.572$, $p < 0.001$). There were strong differences in prevalence of sperm whales among months (Fig. 2; Kruskal–Wallis $H(7) = 23.407$, $p = 0.001$). Tukey post-hoc comparisons of the eight months indicated that the prevalence of sperm whales in May (mean $\pm$ SD $= 0.56 \pm 0.23$) and June (mean $\pm$ SD $= 0.58 \pm 0.18$) was significantly higher than the winter months (January: mean $\pm$ SD $= 0.17 \pm 0.14$, $p_{May} = 0.005$, $p_{June} = 0.004$; February: mean $\pm$ SD $= 0.18 \pm 0.07$, $p_{May} = 0.006$, $p_{June} = 0.004$; March: mean $\pm$ SD $= 0.19 \pm 0.06$, $p_{May} = 0.009$, $p_{June} = 0.006$; November: mean $\pm$ SD $= 0.15 \pm 0.07$, $p_{May} = 0.003$, $p_{June} = 0.002$; December: mean $\pm$ SD $= 0.11 \pm 0.04$, $p_{May} = 0.001$, $p_{June} = 0.001$). There was no significant difference between the prevalence of sperm whales in April (mean $\pm$ SD $= 0.31 \pm 0.11$) compared to May ($p = 0.189$) and June ($p = 0.132$) (Fig. 2).

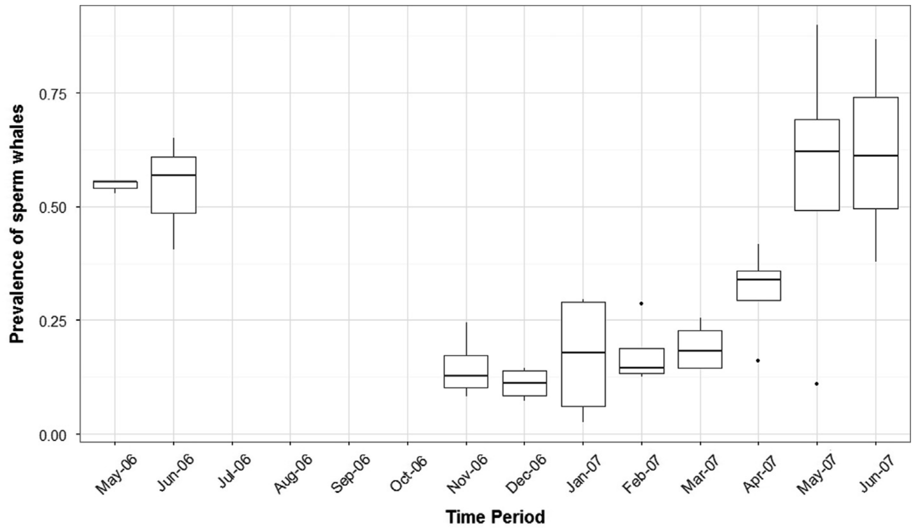

Fig. 2. Monthly prevalence of sperm whales (mean ± SE) from an autonomous recording device deployed on Kelvin Seamount (approx: 38048′N; 64005′W) from May to June 2006 and November 2006 to June 2007. Prevalence of sperm whales is number of two-minute recordings per week in which sperm whales were detected/number of two-minute recordings per week. Box plots show the median, the first and third quartile (lower and upper hinges), whiskers extend to 1.5*IQR (inter-quartile range) and outliers plotted as points. No recordings were made in July–October, 2006.

Table 1
Relationship between mean values of chlorophyll-*a* concentration and sea-surface temperature at 132 × 132 km^2 and other spatial scales.

Scale	r^2	n	p
Mean chlorophyll-a			
In cell (km)	0.782	23	< 0.001
12 km	0.804	23	< 0.001
20 km	0.841	23	< 0.001
36 km	0.896	23	< 0.001
68 km	0.967	23	< 0.001
Mean sea-surface temperature			
In cell	0.938	34	< 0.001
12 km	0.945	34	< 0.001
20 km	0.963	34	< 0.001
36 km	0.968	34	< 0.001
68 km	0.990	34	< 0.001

Pop-up recordings produced 37 weeks of data, which were linked to satellite derived oceanographic data. Due to poor satellite coverage, chlorophyll-*a* data could not be obtained for four weeks (17–23 May, 2006, 25 January to 1 February, 2007, 6–13 March, 2007, 14–21 March, 2007). These weeks were excluded from the analysis, resulting in a sample size of 33 weeks. Averaging chlorophyll-*a* concentration in the cell and over 12 × 12 km^2, 20 × 20 km^2, 36 × 36 km^2 and 68 × 68 km^2, was not always possible due to poor satellite coverage. However, mean chlorophyll-*a* concentration and mean SST at these scales were strongly correlated with values at 132 × 132 km^2 (Table 1). Thus, values for chlorophyll-*a* concentration, SST, SST standard deviation and SST slope were taken at the 132 × 132 km^2 scale were included in the model to retain the maximum sample size of 33 weeks. This scale is roughly 66 km away from the pop-up location and is about the distance a sperm whale could cover in a day (Whitehead, 2003).

The ad hoc procedure evaluating the different temporal lags for chlorophyll-*a* and the SST covariates resulted in the following temporal lags with the lowest AICc score: chlorophyll-*a* concentration at a 4 week lag, SST at a 8 week lag, SST slope at a 2 week lag and SST SD in real time. Therefore, the final Generalized Linear model included month (as a factor) and the following covariates: mean chlorophyll-*a* concentration 4 week lag, SST 8 week lag, SST slope 2 week lag, SST standard deviation in real-time, SSHA and EKE. The final model, after variable selection using AICc scores, retained month, chlorophyll-*a* at a 4 week lag and EKE as the best predictors to explain the weekly prevalence of sperm whales. Autocorrelation function (ACF) plots of model residuals found no temporal autocorrelation. There was a significant positive relationship between prevalence of sperm whales and chlorophyll-*a* concentration at a 4 week lag (Spearman correlation: r_s=0.682, n=17, p=0.003) (Fig. 3) and prevalence of sperm whales and EKE (Spearman correlation: r_s=0.578, n=17, p=0.015) (Fig. 4).

4. Discussion

This is the first study to examine the contemporary temporal variability of sperm whale occurrence in the western North Atlantic Ocean. The occurrence of sperm whales around Kelvin Seamount is variable from November to April, with greater numbers occurring in the spring (April to June: 51%) compared to the winter months (November to March: 16%). While our conclusions can only be drawn by one season of winter data, the seasonal variability of sperm whale occurrence was also noted historically. From 1780 to 1920, commercial whaling ships sighted sperm whales in the northwest portion of the Sargasso Sea more frequently in the spring and summer months than the winter months, with very low sightings from December to February (see figures in Smith et al., 2012). We were not able to examine summer occurrence of sperm whales in this area since pop-ups were not deployed between July and October.

Few studies have examined the seasonal variability of sperm whale distribution and what factors might be driving seasonal occurrence. In the Gulf of California, sperm whales remain in the same areas throughout the year, but change their aggregative behavior, reflecting changes in prey availability (Jaquet and Gendron, 2002). However, seasonal variability in the distribution of male sperm whales off South Island, New Zealand, exists: whales are more limited to deep canyons in the summer, but more evenly distributed in the winter, possibly due to changes in prey (Jaquet et al., 2000). That sperm whales were heard so frequently during the spring around Kelvin Seamount suggests that food availability in this area is quite high during this time.

Since it was not possible to measure the relationship between sperm whales and their prey directly, we used environmental parameters, tested at different spatial scales, as proxies for prey

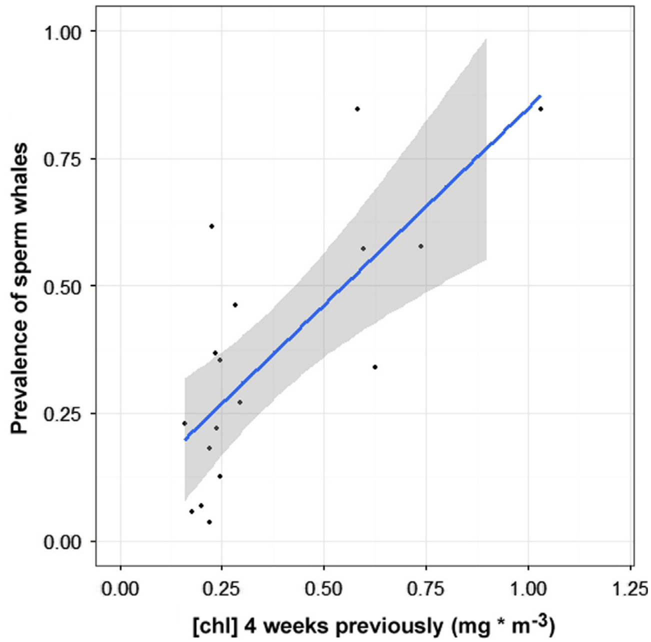

Fig. 3. Relationship between mean prevalence of sperm whales and mean chlorophyll-*a* concentration (mg m^{-3}) in an area 66 km from pop-up (deployed on Kelvin Seamount). Prevalence of sperm whales is the number of two-minute recordings per week in which sperm whales were detected/number of two-minute recordings per week.

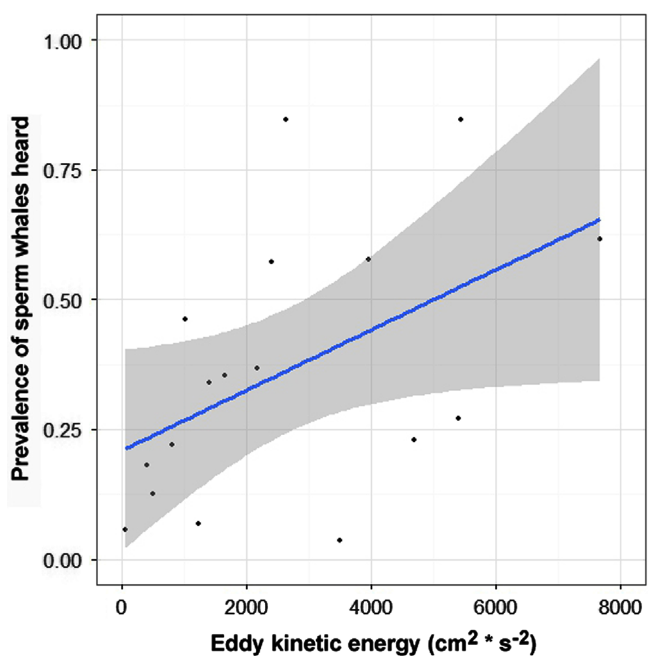

Fig. 4. Relationship between mean prevalence of sperm whales and eddy kinetic energy (cm^2 s^{-2}) around the pop-up (deployed on Kelvin seamount). Prevalence of sperm whales is the number of two-minute recordings per week in which sperm whales were detected/number of two-minute recordings per week.

availability to provide insight into the large difference in temporal distribution between spring and winter months. In this study, month, chlorophyll-*a* concentration four weeks previously and eddy kinetic energy best explained the variation in sperm whale occurrence, using an AICc approach. Previous studies examining the relationship between odontocete densities and chlorophyll-*a* concentration have also found temporal lags of four weeks (Soldevilla et al., 2011), though sperm whale studies in the Gulf of Mexico found an even shorter lag of two weeks (O'Hern and Biggs, 2009). Our finding that primary production is a predictor variable for sperm whale occurrence is consistent with other studies in the Pacific (Jaquet and Whitehead, 1996) and the Mediterranean Sea (Praca et al., 2009). However, it has been demonstrated the correlations between measures of primary productivity such as chlorophyll-*a* concentration are higher for mid-trophic level communities than high-trophic level communities, like sperm whales (Renner et al., 2012).

There was a significant, positive relationship between prevalence of sperm whales and chlorophyll-*a* concentration four weeks previously (Fig. 3) and EKE (Fig. 4). Areas with high EKE indicate high variability and are defined by increased turbulence associated with eddies, fronts and Gulf Stream meanders (Stammer and Wunsch, 1999; Venaille et al., 2011). These turbulent and/or boundary areas may attract and concentrate a wide range of prey and associated predators. Mesoscale activity can lead to important hotspots for enhanced phytoplankton activity (Falkowski et al., 1991; McGillicuddy et al., 1998) and fronts are important oceanographic features that aggregate prey and marine megafauna (Schneider, 1990; Olson et al., 1994; Bost et al., 2009; Raymond et al., 2010). Indeed, the distribution of some squid species is influenced by EKE (Chen et al., 2011). Consequently, sperm whales may also be attracted to these productive habitats as a result of the increased probability of finding prey. For example, aggregations of sperm whales in the northwestern Mediterranean Sea coincide with the presence of SST fronts (Gannier and Praca, 2007). Gulf Stream mesoscale eddies also influence the distribution of other top predators. For example, higher swordfish (*Xiphius gladius*) catch rates are found in the vicinity of thermal fronts (Podesta et al., 1993), tuna species aggregate in frontal systems (Laurs, et al., 1984), and seabird densities at eddies are much higher at thermal fronts than in adjacent shelf and Gulf Stream waters (Haney, 1986).

Although the diet of sperm whales in the Sargasso Sea is not known, some research indicates that it includes the giant squid (*Architeuthis dux*), *Cycloteuthis sirventi* and *Histioteuthis* spp. (Wong, 2012). Very little is known about the deep-water squid species in this area, however, the Gulf Stream plays an important role in some other well-known squid species. For example, short-finned squid (*Illex illecebrosus*) use the Gulf Stream to facilitate their migration (O'Dor and Coelho, 1993; Bakun and Csirke, 1998; Mann and Lazier, 2006). Bakun and Csirke (1998) proposed that adults spawn at the northern edge of the Gulf Stream and egg masses, hatchlings and paralarvae drift north in the warm waters of the Gulf Stream (O'Dor and Coelho, 1993). The increased productivity as a result of Gulf Stream meanders and eddies, combined with the seasonal life cycles of cephalopods likely plays an important role in the prey of sperm whales in this area.

There is evidence that a seasonal cycle exists for the Gulf Stream position, with more northerly locations in the summer/fall and more southerly locations in the winter/spring (Tracey and Watts, 1986). This corresponds to transport, which is lower in the summer/fall and higher in the winter/spring (Tracey and Watts, 1986). Examining the relationship between sea surface temperature in real time and month suggests that the Gulf Stream is further south in parts of the winter, since temperatures over the seamount are cool (~16 °C). If mesoscale eddies are driving sperm whale distribution, then the fact that mesoscale variability is less in the winter might explain the corresponding lower sperm whale occurrence at this time of year. Winter movements of sperm whales in the Sargasso Sea are not known, and our pop-up recordings provide the first and only available data on sperm whale occurrence in the Sargasso Sea during this time of year.

While it is clear that the Gulf Stream influence contributes to the large prevalence of sperm whales in this area during the spring, the seamount chain itself may also play an important role in sperm whale distribution in the region. Worm et al. (2003)

stressed the importance of prominent topographic features in food stressed areas, such as the open ocean. Skov et al. (2008) found that sperm whales had higher affinities to cross-seamount or cross-frontal structures along the mid-Atlantic Ridge. The New England Seamounts influence the Gulf Stream trajectory, with large-amplitude meanders beginning at the New England Seamount Chain and small, localized eddies at individual seamounts (Richardson, 1981). Thus, the interaction between the Gulf Stream and the New England Seamount Chain may also influence sperm whales in this area.

5. Conclusions

Overall, our data show strong seasonal variability in sperm whale occurrence around Kelvin Seamount in the Sargasso Sea between November and June, with sperm whale occurrence being significantly higher in the spring (51%) than the winter (16%). Month, chlorophyll-*a* concentration with a four week temporal lag and eddy kinetic energy can best explain this pattern. Our approach also addressed the issues associated with scale and modeling the distribution of marine top predators. Local oceanographic conditions around the New England Seamount Chain and seasonal changes in mesoscale variability are likely driving the temporal distribution of sperm whales in this area. It appears that the effects of the Gulf Stream are important to sperm whale distribution in this region.

Acknowledgments

Many thanks to H. Moors for logistical support with the pop-ups and W. Krkoska and K. White from Cornell Lab of Ornithology for technical support. Thank you to all *Balaena's* crew members, especially R. Ronconi and M. Janikowski for help in the winter deployment. Thanks to C. Gómez-Salazar, R. Ronconi, M. Lewis, B. Worm and two anonymous reviewers for their comments and suggestions on the manuscript. Funding was provided by Okeanos-Foundation for the Sea, Operating and Equipment Grants to H. Whitehead from the Natural Sciences and Engineering Research Council of Canada (NSERC) and the Whale and Dolphin Conservation Society. S.Wong was supported by an Natural Sciences and Engineering Research Council of Canada Postgraduate Scholarship (PGS-D), Dalhousie University and the Patrick Lett Fund. Research was carried out under Dalhousie Animal Care and Use Committee approved protocols 04–006, 05–136, 07–145 and 08–138.

References

Bakun, A., Csirke, J., 1998. Environmental processes and recruitment variability In: Rodhouse, P.G., Dawe, E.G., O'Dor, R.K. (Eds.), Squid recruitment dynamics: the genus *Illex* as a model, the commercial *Illex* species and influneces on variability. Food and Agriculture Organization of the United Nations, Rome, pp. 105–124.

Biggs, D.C., Engelhaupt, D., Gordon, J., Jaquet, N., Jochens, A., Johnson, M., Leben, R., Mate, B.R., Miller, P., Ortega-Ortiz, J.G., Thode, A., Tyack, P.L., Wormuth, J.H., Wursig, B., 2006. Sperm Whale Seismic Study in the Gulf of Mexico: Summary Report, 2002–2004. Texas A&M University, Texas.

Blackburn, M., 1981. Low latitude gyral regions. In: Longhurst, A.R. (Ed.), Analysis of Marine Ecosystems. Academic Press, New York, pp. 3–29.

Block, B.A., Jonsen, I.D., Jorgensen, S.J., Winship, A.J., Shaffer, S.A., Bograd, S.J., Hazen, E.L., Foley, D.G., Breed, G.A., Harrison, A.-L., Ganong, J.E., Swithenbank, A., Castleton, M., Deward, H., Mate, B.R., Shillinger, G.L., Schaefer, K.M., Benson, S.R., Weise, M.J., Henry, R.W., Costa, D.P., 2011. Tracking apex marine predator movements in a dynamic ocean. Nature 475, 86–90.

Bost, C.A., Cotte, C., Bailleul, F., Cherel, Y., Charrassin, J.B., Guinet, C., Ainley, D.G., Weimerskirch, H., 2009. The importance of oceanographic fronts to marine birds and mammals of the southern oceans. J. Mar. Syst. 78, 363–376.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multi-Model Inference: A Practical Information-Theoretic Approach. Springer, Berlin Heidelberg New York.

Chen, X.J., Tian, S.Q., Liu, B.L., Chen, Y., 2011. Modeling a habitat suitability index for the eastern fall cohort of *Ommastrephes bartrami*i in the central North Pacific Ocean. Chin. J. Oceanol. Limnol. 29, 493–504.

Croll, D.A., Marinovic, B., Benson, S., Chavez, F.P., Black, N., Ternullo, R., Tershy, B.R., 2005. From wind to whales: trophic links in a coastal upwelling system. Mar. Ecol.-Prog. Ser. 289, 117–130.

Eastman, J.R., 2006. IDRISI Andres Guide to GIS and Image Processing. Clark Labs, Clark University, Worcester p. 327.

Falkowski, P.G., Ziemann, D., Kolber, Z., Bienfang, P.K., 1991. Role of Eddy pumping in enhancing primary production in the ocean. Nature 352, 55–58.

Gannier, A., Praca, E., 2007. SST fronts and the summer sperm whale distribution in the north–west Mediterranean Sea. J. Mar. Biol. Assoc. UK 87, 187–193.

Grémillet, D., Lewis, S., Drapeau, L., van Der Lingen, C.D., Huggett, J.A., Coetzee, J.C., Verheye, H.M., Daunt, F., Wanless, S., Ryan, P.G., 2008. Spatial match-mismatch in the Benguela upwelling zones: should we expect chlorophyll and sea-surface temperature to predict marine predator distributions? J. Appl. Ecol. 45, 610–621.

Griffin, R.B., 1999. Sperm whale distributions and community ecology associated with a warm-core ring off Georges Bank. Mar. Mammal Sci. 15, 33–51.

Gulland, J.A., 1974. Distribution and abundance of whales in relation to basic productivity. In: Schevill, W.E. (Ed.), The Whale Problem. Harvard University Press, Cambridge, pp. 27–52.

Halley, J.M., 2005. Comparing aquatic and terrestrial variability: at what scale do ecologists communicate? Mar. Ecol.-Prog. Ser. 304, 274–280.

Haney, J.C., 1986. Seabird affinities for Gulf-stream frontal eddies-responses of mobile marine consumers to episodic upwelling. J. Mar. Res. 44, 361–384.

Hunt, G.L.J., Mehlum, F., Russel, R.W., Irons, D., Decker, M.B., Becker, P.H., 1999. Physical processes, prey abundance, and the foraging ecology of seabirds. In: Adams, N.J., Slotow, R. (Eds.), Proceedings of the 22nd International Ornithological Congress. BirdLife South Africa, Durban, pp. 2040–2056.

Jaquet, N., 1996. How spatial and temporal scales influence understanding of sperm whale distribution: a review. Mammal Rev. 26, 51–65.

Jaquet, N., 1999. Movements, distribution and feeding success of sperm whales in the Pacific Ocean, over scales of days and tens of kilometers. Aquat. Mammals 25, 1–13.

Jaquet, N., Dawson, S., Slooten, E., 2000. Seasonal distribution and diving behavior of male sperm whales off Kaikoura: foraging implications. Can. J. Zool. 78, 407–419.

Jaquet, N., Gendron, D., 2002. Distribution and relative abundance of sperm whales in relation to key environmental features, squid landings and the distribution of other cetacean species in the Gulf of California, Mexico. Mar. Biol. 141, 591–601.

Jaquet, N., Whitehead, H., 1996. Scale-dependent correlation of sperm whale distribution with environmental features and productivity in the South Pacific. Mar. Ecol.-Prog. Ser. 135, 1–9.

Jaquet, N., Whitehead, H., Lewis, M., 1996. Coherence between 19th century sperm whale distributions and satellite derived pigments in the tropical Pacific. Mar. Ecol.-Prog. Ser. 145, 1–10.

Johnston, D.W., McDonald, M., Polovina, J., Domokos, R., Wiggins, S., Hildebrand, J., 2008. Temporal patterns in the acoustic signals of beaked whales at Cross Seamount. Biol. Lett. 4, 208–211.

Laurs, R.M., Fiedler, P.C., Montgomery, D.R., 1984. Albacore tuna catch distributions relative to environmental features observed from satellites. Deep-Sea Res. Pt. I 31, 1085–1099.

Lewis, K.P., 2004. How important is the statistical approach for analyzing categorical data? A critique using artificial nests. Oikos 104, 305–315.

Madsen, P.T., Payne, R., Kristiansen, N.U., Wahlberg, M., Kerr, I., Mohl, B., 2002. Sperm whale sound production studied with ultrasonic time/depth-recording tags. J. Exp. Biol. 205, 1899–1906.

Mann, K.H., Lazier, J.R.N., 2006. Dynamics of Marine Ecosystems: Biological–Physical Interactions in the Oceans. Blackwell Publishing, Maine, USA.

McCullagh, P., Nelder, J.A., 1989. Generalized Linear Models. Chapman and Hall, New York.

McGillicuddy, D.J., Robinson, A.R., Siegel, D.A., Jannasch, H.W., Johnson, R., Dickeys, T., McNeil, J., Michaels, A.F., Knap, A.H., 1998. Influence of mesoscale eddies on new production in the Sargasso Sea. Nature 394, 263–266.

Morato, T., Hoyle, S.D., Allain, V., Nicol, S.J., 2010. Seamounts are hotspots of pelagic biodiversity in the open ocean. Proc. Natl. Acad. Sci. USA 107, 9707–9711.

Morato, T., Varkey, D.A., Damaso, C., Machete, M., Santos, M., Prieto, R., Pitcher, T.J., Santos, R.S., 2008. Evidence of seamount effect on aggregating visitors. Mar. Ecol.-Prog. Ser. 357, 23–32.

O'Dor, R.K., 1992. Big squid in big currents. S. Afr. J. Mar. Sci. 12, 225–235.

O'Dor, R.K., Coelho, M.L., 1993. Big squid, big currents, and big fisheries. In: Okutani, T., O'Dor, R.K., Kubodera, T. (Eds.), Recent Advances in Cephalopod Fisheries Biology. Tokai University Press, Tokyo, pp. 385–396.

O'Hern, J.E., Biggs, D.C., 2009. Sperm whale (*Physeter macrocephalus*) habitat in the Gulf of Mexico: satellite observed ocean color and altimetry applied to small-scale variability in distribution. Aquat. Mammals 35, 358–366.

Olson, D.B., Hitchcock, G.L., Mariano, A.J., Ashjian, C.J., Peng, G., Nero, R.W., Podesta, G.P., 1994. Life on the edge: marine life and fronts. Oceanography 7, 52–60.

Ortega-Ortiz, J.G., Mate, B.R., 2006. Sperm whales in a subtropical, mesoscale upwelling system: temporal variability. Eos Trans. AGU 87 (36) (Ocean Science Meeting Suppl., Abstract OS11A-04).

Ortner, P.B., Wiebe, P.H., Haury, L., Boyd, S., 1978. Variability in zooplankton biomass distribution in Northern Sargasso Sea – contribution of Gulf-stream cold core rings. Fish. B-NOAA 76, 323–334.
Oschlies, A., Garçon, V., 1998. Eddy-induced enhancement of primary production in a model of the North Atlantic Ocean. Nature 394, 266–269.
Pinaud, D., Weimerskirch, H., 2007. At-sea distribution and scale-dependent foraging behavior of petrels and albatrosses: a comparative study. J. Anim. Ecol. 76, 9–19.
Pirotta, E., Matthiopoulos, J., MacKenzie, M., Scott-Hayward, L., Rendell, L., 2011. Modelling sperm whale habitat preference: a novel approach combining transect and follow data. Mar. Ecol.-Prog. Ser. 436, 257–272.
Pirotta, E., Thompson, P.M., Miller, P.I., Brookes, K.L., Cheney, B., Barton, T.R., Graham, I.M., Lusseau, D., 2014. Funct. Ecol. 28, 206–217.
Podesta, G.P., Browder, J.A., Hoey, J.J., 1993. Exploring the association between swordfish catch rates and thermal fronts on United-States Longline grounds in the Western North-Atlantic. Cont. Shelf Res. 13, 253–277.
Praca, E., Gannier, A., Das, K., Laran, S., 2009. Modelling the habitat suitability of cetaceans: example of the sperm whale in the northwestern Mediterranean Sea. Deep-Sea Res. Pt. I 56, 648–657.
Raymond, B., Shaffer, S.A., Sokolov, S., Woehler, E.J., Costa, D.P., Einoder, L., Hindell, M., Hosie, G., Pinkerton, M., Sagar, P.M., Scott, D., Smith, A., Thompson, D.R., Vertigan, C., Weimerskirch, H., 2010. Shearwater foraging in the Southern Ocean: the roles of prey availability and winds. Plos One 5 (6), e10960.
Renner, M., Arimitsu, M.L., Piatt, J.F., 2012. Structure of marine predator and prey communities along environmental gradients in a glaciated fjord. Can. J. Fish. Aquat. Sci. 69, 1–17.
Rice, D.W., 1989. Sperm whales (*Physeter macrocephalus*). In: Ridgeway, S.H., Harrison, R. (Eds.), Handbook of Marine Mammals. Academic Press, London, pp. 177–233.
Richardson, P.L., 1981. Gulf-stream trajectories measured with free-drifting buoys. J. Phys. Oceanogr. 11, 999–1010.
Schneider, D.C., 1990. Seabirds and fronts - a brief overview. In: Brekke, A. (Ed.), Polar Research, vol. 8; 1990, pp. 17–21.
Schneider, D.C., 2001. The rise of the concept of scale in ecology. Bioscience 51, 545–553.
Skov, H., Gunnlaugsson, T., Budgell, W.P., Horne, J., Nottestad, L., Olsen, E., Soiland, H., Vikingsson, G., Waring, G., 2008. Small-scale spatial variability of sperm and sei whales in relation to oceanographic and topographic features along the Mid-Atlantic Ridge. Deep-Sea Res. Pt. II 55, 254–268.
Smith, T.D., Reeves, R.R., Josephson, E.A., Lund, J.N., 2012. Spatial and seasonal distribution of American whaling and whales in the age of sail. Plos One 7, e34905, http://dx.doi.org/10.1371/journal.pone.0034905.
Soldevilla, M.S., Wiggins, S.M., Hildebrand, J.A., Oleson, E.M., Ferguson, M.C., 2011. Risso's and Pacific white-sided dolphin habitat modeling from passive acoustic monitoring. Mar. Ecol.-Prog. Ser. 423, 247–267.
Stammer, D., Wunsch, C., 1999. Temporal changes in eddy energy of the oceans. Deep-Sea Res. Pt. II 46, 77–108.
Sydeman, W.J., Brodeur, R.D., Grimes, C.B., Bychkov, A.S., McKinnell, S., 2006. Marine habitat "hotspots" and their use by migratory species and top predators in the North Pacific Ocean: introduction. Deep-Sea Res. Pt. II 53, 247–249.
Teo, S.L.H., Block, B.A., 2010. Comparative influence of ocean conditions on yellowfin and Atlantic bluefin tuna catch from longlines in the Gulf of Mexico. Plos One 5, e10756, http://dx.doi.org/10.1371/journal.pone.0010756.
Townsend, C.H., 1935. The distribution of certain whales as shown by logbook records of American whaleships. Zoologica 19, 1–52.
Tracey, K.L., Watts, D.R., 1986. On Gulf Stream meander characteristics near Cape Hatteras. J. Geophys. Res. C 91, 7587–7602.
Venaille, A., Vallis, G.K., Smith, K.S., 2011. Baroclinic turbulence in the ocean: analysis with primitive equation and quasigeostrophic simulations. J. Phys. Oceanogr. 41, 1605–1623.
Waring, G.T., Fairfield, C.P., Ruhsam, C.M., Sano, M., 1993. Sperm whales associated with Gulf stream features off the north-eastern USA shelf. Fish. Oceanogr. 2, 101–105.
Whitehead, H., 2003. Sperm Whales: Social Evolution in the Ocean. The University of Chicago Press, Chicago.
Whitehead, H., O'Brien, K., Worm, B., 2010. Diversity of deep-water cetaceans and primary productivity. Mar. Ecol.-Prog. Ser. 408, 1–5.
Whitehead, H., Weilgart, L., 1990. Click rates from sperm whales. J. Acoust. Soc. Am. 87, 1798–1806.
Wolanski, E., Hamner, W.M., 1988. Topographically controlled fronts in the ocean and their biological nature. Science 241, 177–181.
Wong, S.N.P., 2012. A Pelagic Paradox: The Ecology of a Top Predator in an Oceanic Desert (Ph.D. thesis). Dalhousie University, Halifax, Canada (147 pp.).
Worm, B., Lotze, H.K., Myers, R.A., 2003. Predator diversity hotspots in the blue ocean. Proc. Natl. Acad. Sci. USA 100, 9884–9888.
Worm, B., Sandow, M., Oschlies, A., Lotze, H.K., Myers, R.A., 2005. Global patterns of predator diversity in the open oceans. Science 309, 1365–1369.
Yoder, J.A., 1985. Environmental control of phytoplankton production on the Southeastern U.S. continental shelf. In: Atkinson, L.P., Menzel, D.W., Bush, K.A. (Eds.), Oceanography of the Southwestern U.S. Continental Shelf. American Geophysical Union, Washington, D.C., pp. 93–103.