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Environmental predictors and temporal patterns of basking shark (*Cetorhinus maximus*) occurrence in the lower Bay of Fundy, Canada

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ABSTRACT

Little is currently known about the population dynamics of basking sharks (*Cetorhinus maximus*) at regional or local scales. Using a long-term sighting database (1994–2012) and photo-identification of individuals, we studied the seasonal and inter-annual patterns in basking shark occurrence and site fidelity in the Bay of Fundy, Canada. Zero-inflated negative binomial models quantified spatial, temporal and environmental predictors of shark sighting rates. The probability of sighting a basking shark increased in August, and in deep water offshore; this may reflect the distribution and availability of calanoid copepod prey. Sea-surface temperature (SST) had no effects on shark sightings, but there was a negative correlation between the North Atlantic Oscillation (NAO) index and shark sightings lagged at two and four years; the former possibly due to the position of the Gulf Stream and the latter likely a result of the lagged influence of the NAO on copepod abundance. The model also showed a significant decline in the occurrence of basking sharks within the Bay of Fundy over the study period. From unique markings on dorsal fins, 98 individual sharks were identified from photographs taken between 1997 and 2012. Four of these individuals were re-sighted in subsequent years, and the longest interval between re-sightings was 9.1 years. These re-sightings suggest some site fidelity by individuals and demonstrate the longevity of some mark-types on the first dorsal fin. This study highlights the role of long-term sightings and photographic records as population assessment tools for regional scale-monitoring of a globally vulnerable species.

1. Introduction

Many coastal and pelagic shark populations, including basking sharks (*Cetorhinus maximus*), are in decline around the world due to anthropogenic threats (Dulvy et al., 2008), such as directed and incidental fisheries (Anonymous, 2002; Compagno, 1984). These threats, in addition to low reproductive and recruitment rates, have led the global basking shark population to be assessed as *Vulnerable* by the International Union for Conservation of Nature (IUCN, 2000). The North Pacific and eastern North Atlantic populations are currently listed as *Endangered* (COSEWIC, 2007; Fowler, 2005), and the Canadian western North Atlantic population is listed as a species of *Special Concern* (COSEWIC, 2009). In the western North Atlantic, basking sharks have been studied along the east coast of the United States (Curtis et al., 2014; Owen, 1984; Skomal et al., 2004, 2009), as well as in Atlantic Canada (Harvey-Clark et al. 1999; DFO, 2008; Siders et al., 2013; Westgate et al., 2014). In the Bay of Fundy, Canada, recent aerial surveys estimated that basking shark abundance is much lower (>85%, Westgate et al., 2014) than previously reported (DFO, 2008), possibly because the earlier estimates were adjusted using a number of untested correction factors relating to the relative visibility of basking sharks compared with North Atlantic right whales (*Eubalaena glacialis*). Nevertheless, basking sharks are frequently seen in near-shore waters of the Bay of Fundy, throughout the summer months, primarily July through October (Siders et al., 2013), offering a unique opportunity to study their distribution, sighting occurrences, and population dynamics in this area.

One approach for examining the occurrences of basking sharks in this region is to model variability in sighting rates from vessel surveys. Count data can be modeled to determine potential predictors – spatial, temporal or environmental – that may be affecting seasonal and inter-annual occurrence. However, ecological count data frequently suffer from high occurrence of zeros, resulting from *true* zeros when individuals are absent due to unsuitable habitat or seasonal cycles of occurrence, or *false* zeros due to imperfect detection or temporary absence (Martin et al., 2005). Accounting for both *true* and *false* zeros is important when dealing with a cryptic species such as basking sharks that may spend 80% of their time below the surface (Westgate et al., 2014).

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Assessment of count data also needs to consider spatial patterns of distribution and environmental factors that may influence the occurrence of basking sharks in the study area. In the Bay of Fundy, Siders et al. (2013) showed that basking sharks display heterogeneous habitat utilization, typically associated with bathymetry, and likely related to prey dynamics — the distribution of basking sharks often mirrors the distribution of their main prey, copepods of *Calanus* spp. (Sims and Quayle, 1998; Sims et al., 2000,b, 2005). *Calanus finmarchicus* is the most abundant copepod in the Bay of Fundy during the summer months (Michaud and Taggart, 2007) and is the most likely prey source for basking sharks in this region. Two key environmental factors which likely influence the abundance and quality of copepods, and the overall ecology of the Bay of Fundy are the North Atlantic Oscillation (NAO), and sea surface temperature (SST) (Cotton et al., 2005). The NAO index provides a relative measure of broad-scale climatic conditions in the northern hemisphere (Hurrell and Deser, 2009) and, in the Gulf of Maine the NAO index is positively correlated with the summer abundance of *C. finmarchicus* at time lags of up to four years (Conversi et al., 2001). SST may also influence basking shark occurrence either directly, with sharks being attracted to warmer waters (Owen, 1984), or indirectly through effects on prey abundance, with winter SST positively and significantly correlated to the summer abundance of *C. finmarchicus* in the Gulf of Maine, when lagged two years (Conversi et al., 2001).

Another approach for studying population dynamics is the use of photographic-identification (photo-identification) techniques. Photo-identification is a non-invasive tool that utilizes unique markings, scars, deformities, pigmentation patterns or fin shape to identify individuals within a species (Sears et al., 1990), allowing researchers to estimate the size, distribution or movement of a population (Wursig and Jefferson, 1990). This method has been used extensively in marine mammal research to estimate population abundance and social structure in whales and dolphins (Matthews et al., 2001; Shane and McSweeney, 1990; Wells, 1991). Photo-identification is now being used on many shark species including grey nurse sharks (*Carcharias taurus*; Bansemer and Bennett, 2008; Barker and Williamson, 2010), white sharks (*Carcharodon carcharias*; Gubili et al., 2009; Chapple et al., 2011) and whale sharks (*Rhincodon typus*; Holmberg et al., 2009; Rowat et al., 2009). Thus far, photo-identification studies on sharks have investigated population abundance (Chapple et al., 2011), population survivability (Rowat et al., 2009), site philopatry, and population movement patterns (Barker and Williamson, 2010).

The objectives of our study were to 1) investigate patterns of occurrence over the summer, and examine environmental factors influencing basking shark sighting rates using a long-term database (1994–2012), and 2) determine whether photo-identification of individual basking sharks in the Bay of Fundy could be a useful tool to estimate occurrences, and site philopatry. We predicted that occurrences would increase in offshore areas (Siders et al., 2013), be correlated with seasonal cycles of prey availability (*C. finmarchicus* typically peak in late summer; Michaud and Taggart, 2007), and be correlated with lagged-effects of the NAO index and SST, which influence regional patterns of copepod abundance in the neighboring Gulf of Maine (Conversi et al., 2001; Fromentin and Planque, 1996). Controlling for seasonal patterns and environmental predictors, we also tested for long-term trends in occurrence over a 19 year period.

2. Materials and methods

2.1. Data collection

This study was carried out in the Bay of Fundy, Canada (Fig. 1). Sightings of basking sharks were recorded from 1994 to 2012 and photographs of dorsal fins were taken when possible. Sightings were recorded by one individual (L. Murison) onboard a 15 m (1994–2004) and a 19 m (2005–2012) whale-watching sailing vessel operating out of North Head, Grand Manan (Fig. 1). A total of 1174 trips were conducted during this time, typically 6 h in duration and covering approximately 40 to 80 km per trip. During each trip, a handheld Global Positioning System (GPS) recorded the position of the vessel approximately every 20 min (1994–2004), or every 10 s (2005–2012). All basking shark encounters from these vessels were opportunistic, and occurred between May and November each year; however, our analysis was limited to July, August and September because there were too few trips during the early summer and late autumn months (May, June, October, November) and sharks were infrequently sighted during these months (11% of trips in June, 0% in other months). From 2008 to 2012, images for photo-identification were also taken from a 4.8 m vessel deployed on dedicated surveys searching for basking sharks. These trips ranged in duration from 1 to 12 h, all within 50 km of Grand Manan.

For each encounter, the location (latitude/longitude), time, weather conditions (visibility, cloud cover, precipitation) and sea state were recorded. From the whale-watching vessels, the approach angle and the side of the dorsal fin photographed were opportunistic since these vessels had limited maneuverability. Onboard the 4.8 m vessel, photographs were taken from both sides of the individual when possible using conventional and later digital photography.

2.2. Temporal trends

To examine temporal trends of shark occurrence in the Bay of Fundy, we used data collected onboard the whale-watching vessels from 1994 to 2012 (see also Siders et al., 2013). The shark sighting rate, defined as the number of sharks sighted per unit effort (SPUE) – with units of effort being 100 km traveled – was used as an index of shark occurrence. The distance traveled for each trip was calculated from the series of GPS positions and used as an index of effort (see below for classification of trip type to account for potential biases associated with trip destination and route). Sea state and visibility can affect the probability of sighting sharks, so shark sighting rates were only calculated for trips with no fog or precipitation, and a mean sea state of Beaufort 3 or less ($n = 776$ trips).

To examine factors influencing the variability of shark occurrence over the summer and across years, we modeled shark occurrence (see the Statistical analysis section) with the following spatial and temporal variables: trip type, month, start time and year. *Trip type* accounted for the variability in habitats covered by vessel trips, since basking sharks in the Bay of Fundy show heterogeneous habitat use (Siders et al., 2013). *Trip type* was classified as either *coastal* (trip stayed along the North or South coastline of the Grand Manan archipelago and within waters shallower than 100 m), or *offshore* (trip ventured east into the Bay of Fundy basin and within waters deeper than 100 m) (Fig. 1). *Month* was included to examine temporal patterns of occurrence. *Start hour* (trip departure time) was used as an index of time of day. *Year* (as a continuous variable) was included to assess long-term trends in sighting rates. After 2004, there was a change from a 15 m to a 19 m sailing vessel, however, the vessels were similar in speed and observer height, and the final model results were qualitatively unchanged when *vessel* was tested as a covariate in the model (i.e. the parameter estimates changed slightly but all factors remained significant in the model); therefore, *vessel* was not included as a predictor.

Principal-component based NAO indices were obtained from the National Center for Atmospheric Research (2015) and linked to trips by year. We used seasonally averaged NAO indices from three periods in each study year: winter (Dec/Jan/Feb), spring (Mar/Apr/May) and summer (Jun/Jul/Aug). Autumn NAO indices (Sep/Oct/Nov) were not considered because preliminary data analysis showed no effect of the 10–12 month lag between the autumn NAO and the following shark sighting period (Jul/Aug/Sep); there is also currently no literature suggesting any autumn NAO effect on ecosystem function. Winter NAO conditions are known to have strong effects on North Atlantic marine ecosystems, including winter NAO indices from up to four years

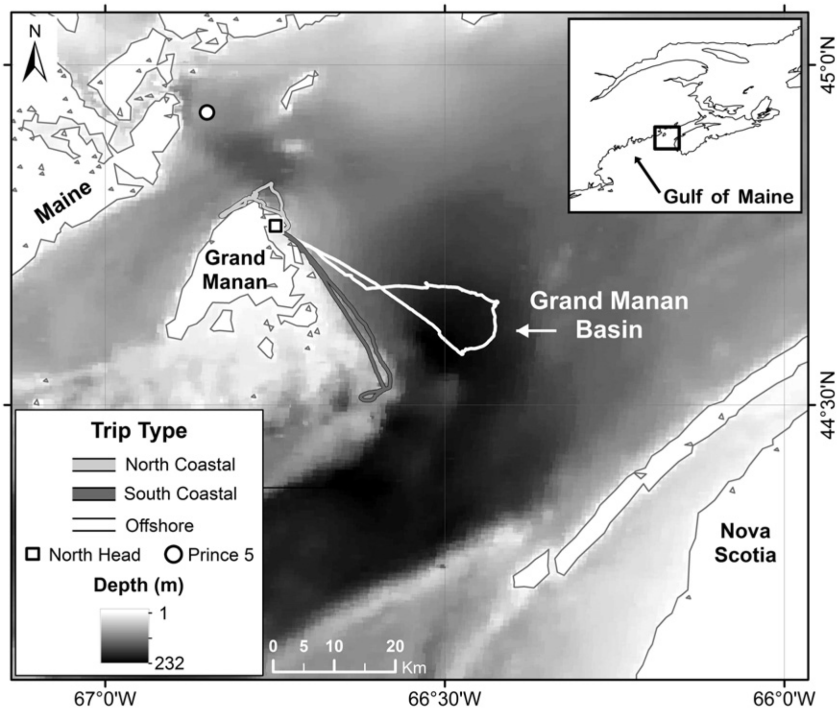

Fig. 1. Study area with respect to Atlantic Canada (inset map) and around Grand Manan Island, Bay of Fundy, Canada (area enlarged). Track lines show examples of the two vessel trip types: Coastal (North coastal or South coastal), and Offshore (into the Grand Manan basin). North Head is the departure location for the commercial whale watching vessels from Grand Manan. Prince 5 is the environmental station operated by the Department of Fisheries and Oceans Canada, from where monthly sea surface temperature (SST) was obtained.

previous (Conversi et al., 2001); therefore, we considered winter NAO of the current year, and lagged up to four years. We did not lag NAO further than four years, as Conversi et al. (2001) examined lagged effects up to seven years, but found effects only up to four years lagged.

The second environmental factor examined was SST. We obtained averaged monthly SST in the top 5 m of the water column from monthly conductivity, temperature and depth (CTD) casts conducted at the Prince 5 station (44.93°N 66.85°W) (Fig. 1) in the lower Bay of Fundy (data accessed from Department of Fisheries and Oceans Canada, http://www.meds-sdmm.dfo-mpo.gc.ca/isdm-gdsi/azmp-pmza/hydro/index-eng.html). We elected to use CTD casts, rather than remote sensing data, because they provided a continuous record from calibrated instruments, and inter-annual variability in summer temperatures at the surface and at depth measured at the Prince 5 station generally reflects inter-annual variability in water column temperature profiles collected from diving basking sharks throughout the Bay of Fundy in the summer (Koopman et al., 2014). Monthly SST data were matched with trips in each year. To examine the effects of winter SST, we also included average monthly winter SST (December to February) lagged up to two years. We did not examine lagged SST further than two years, since no effects were found with longer lags in previous research relating to copepods (Conversi et al., 2001), the primary prey of basking sharks.

2.3. Photo-identification

Photographs captured prior to the transition to digital photography (1994–2006) were taken on slide film, scanned and converted to digital files. All photographs were assessed for quality based on Auger-Methé and Whitehead (1997), with some modifications (Table 1). Individuals with photographs rated 2, 3, or 4 were added to the *Bay of Fundy Basking Shark Catalogue* and assigned an identification number based on the date of initial sighting while photographs of rating 1 were disregarded (Table 1).

Dorsal fins were categorized by their general shape (standard, pyramid, right angle, lobed, conical, tulip, reverse lobed, or unseen), or shape of the apex (rounded, pointed, flat, missing, or unseen), as well as by injuries, markings, scars, deformities or pigmentation patterns on the leading edge, trailing edge, or surface of the fin. These categories were based on methods for photo-identification of basking sharks of western Scottish waters (M. Gore pers. comm.) and allowed individual sharks to be classified by distinguishing markings and features. A side-by-side visual comparison of the images of individuals with similar markings, distinguishing features or fin shapes could then be performed. To ensure accuracy, several researchers (with prior experience in matching animals using photographic analysis) reviewed all potential positive matches before a match was confirmed or rejected.

2.4. Statistical analysis

In ecology, count data frequently suffer from high occurrence of zeros which necessitate the use of zero-inflated modeling approaches (Martin et al., 2005; Zuur et al., 2009). During our study, basking sharks were not observed during 55% of 776 vessel trips, suggesting a high occurrence of zeros, which may be due to both *true* and *false* absences. When both types of zeros occur, zero-inflated negative-binomial (ZINB) models can be used to model both occurrence and abundance simultaneously (Martin et al., 2005), using a binomial model to determine the occurrence of zeros vs. non-zeros, and a count model to determine factors predicting basking shark occurrence (Zuur et al.,

Table 1
Categories for quality of images of basking sharks from the Bay of Fundy. Categories were derived from modifications to Auger-Methé and Whitehead (1997).

Rating	Photograph quality	Description
4	Excellent	All markings and distinguishing features clearly visible. Photographs of *both* sides of the dorsal fin obtained
3	Great	Most markings and distinguishing features seen clearly. Photographs of only *one* side of the dorsal fin obtained
2	Good	Some distinguishing marks and features seen clearly
1	Poor	Distinguishing marks and features cannot be seen clearly. Individual could not be re-identified based on photograph.

2009). Initial modeling with Zero-inflated Poisson models showed a greater variability in the data than expected (i.e. were overdispersed), therefore, we used ZINB models, which introduces parameter θ to account for this overdispersion.

To assess the spatial, temporal and environmental factors that determine the frequency of sharks sighted during vessel trips, we analyzed shark counts as the dependent variable, with individual trips as the unit of analysis, and the log distance traveled per trip as an offset to account for survey effort. All predictor variables were tested in both the count and zero-inflated process model parts. First, we fit a full effects model with all spatial and temporal predictors (*year*, *month*, *start hour*, and *trip type*) as well as summer SST. To minimize the number of NAO variables considered in the model simultaneous, we then tested the improvement of model fit when each of the seven NAO predictor variables (three NAO seasons from the current year – Mar/Apr/May; Jun/Jul/Aug; Dec/Jan/Feb – and winter NAO lagged up to four years) was included in the model. Akaike information criterion (AIC) scores were compared among candidate models to identify the best-fit NAO predictor(s) for further consideration. This was also done for each of the three winter SST predictor variables (winter SST from the current year, and winter SST lagged up to two years). The final ZINB model was constructed using AIC statistics to assess improvement in model fit when dropping non-significant predictor variables from the model (Zuur et al., 2009). This resulted in a backward-stepwise selection of variables that were processed sequentially, removing non-significant predictor variables from either the count or zero-inflated part of the model, until there was no further improvement in the AIC score. Model fit was assessed by examining plots of residuals against fitted data (Zuur et al., 2009), a chi-squared test of the difference in log likelihoods between the fitted model and the null-model (intercept only), and a Vuong test which compares fit of the ZINB model relative to the negative-binomial model (determines whether the predictors in the part of the logit model predicting excessive zeros are statistically significant). Statistical analysis was performed using the *zeroinfl* model (Zeileis et al., 2008) from the package *pcsl* (Jackman, 2012) and *glm.nb* model from the package *MASS* (Venables and Ripley, 2002) in *R* version 12.15.3 (R Core Team, 2012).

3. Results

3.1. Temporal trends

A total of 1295 basking sharks were sighted during 776 trips (mean trips per year = 40.8 ± 7.5 SD) from 1994 to 2012 (Table 2) for a total of 45,170 km traveled (2377 km ± 449 per year). During the trips that did observe sharks (45% of trips), an average of 4 sharks were sighted. The mean number of sharks sighted per unit effort (per 100 km) was 2.7 ± 2.7 animals. Within the 19 year study period, the earliest recorded sighting of a basking shark in the Bay of Fundy was June 26, and the latest was September 28. We saw an overall decline in the occurrence of basking sharks within the Bay of Fundy during our study period, from 5.0 sharks per 100 km during the first 5 years (1994–98), 3.1 in 1999–2003, 1.5 in 2004–08, to 0.9 during the last four years, 2009–12 (Fig. 2, Table 2). One anomaly within this general decline in sightings occurred in 1998, with approximately 13 sharks sighted per 100 km.

The ZINB model of the log shark count indicated five factors responsible for predicting the occurrence of sharks sighted during vessel trips: *year*, *month*, *trip type*, and the *winter NAO index* when shark sightings were lagged two years and four years (Table 3). To account for excess zeros in the data, the binomial process part of the model showed higher probability of a zero count in July relative to August ($p = 0.008$). Several other factors were not statistically significant in the logit part of the model (*winter NAO* lagged four years, $p = 0.112$; *year* effect, $p = 0.070$; and *trip type*, $p = 0.085$) but these variables were retained in the final model because their removal increased AIC scores and, therefore, reduced the model fit. Complementary results were supported with the count process model, which showed a declining shark count over the study period (*year* effect; $p < 0.001$) (Fig. 2), lower shark counts in July relative to August ($p < 0.001$) (Fig. 3), negative effect of *winter NAO* on shark counts at both two-year and four-year lags ($p < 0.001$), and *offshore* trips were likely to observe more sharks than *coastal* trips (*trip type* effect; $p < 0.001$) (Fig. 3). Since the very high number of occurrences of sharks in 1998 may have strongly influenced the *year* effect in the model (Table 2), we reran the model omitting data from 1998. The *year* effect was still significant in the model and the significance of other variables remained unchanged except for *month* which was no longer significant in the binary part of the model and *trip type* which was no longer significant in the count part of the model.

SST (summer, winter, and winter lagged up to two years) was not a significant predictor in either the logit or count part of the model. The final model performed significantly better than the null-model (chi-square test of LogLik; df = 16, $p < 0.001$). The ZINB model was also a significant improvement over the standard negative binomial model (Vuong test-statistic = 4.537, $p < 0.001$) indicating statistically significant predictors in the part of the logit model predicting excessive zero.

Table 2
Summary of trips conducted onboard the whale-watching vessels in July–September, 1994–2012. This includes only those trips with no fog or precipitation and a Beaufort sea state of 3 or less.

Year	Number of trips	Distance traveled (km)	Number of basking sharks sighted	Sightings per unit effort (per 100 km)
1994	38	2316	65	2.8
1995	40	2500	61	2.4
1996	43	2900	114	3.9
1997	47	3035	90	3.0
1998	48	2868	364	12.7
1999	47	2800	61	2.2
2000	39	2285	73	3.2
2001	35	2143	81	3.8
2002	35	2146	82	3.8
2003	30	1845	45	2.4
2004	27	1451	5	0.3
2005	33	1742	44	2.5
2006	53	2937	48	1.6
2007	50	2555	29	1.1
2008	33	2021	43	2.1
2009	48	2578	14	0.5
2010	49	2799	28	1.0
2011	43	2200	23	1.0
2012	38	2049	25	1.2
Total	776	45,170	1295	

3.2. Photo-identification

A total of 129 individual basking sharks were photographed in the Bay of Fundy between 1994 and 2012. From these, 98 unique individuals were identified (photographs of 27 individuals could not be used for photo-identification and four individuals were re-sighted). Plotting the cumulative number of individuals photographed against the cumulative number of unique individuals identified showed a nearly linear relationship ($r^2 = 0.9977$), demonstrating that many new individuals have yet to be identified.

Of the 98 unique individuals, four were re-sighted in later years (Fig. 4; Table 4). Shark A (catalogued as *Fundy-20020819A*) had the longest time interval between sightings, having first been photographed in 2002, then re-sighted nine years later in 2011. Shark B (*Fundy-20060709B*) and Shark C (*Fundy-20080905C*) were both re-sighted after a four year period (2006 and 2010; and, 2008 and 2012, respectively) and Shark D (*Fundy-20080807A*) was re-sighted after a three year period (2008 and 2011).

Table 3
Results of zero-inflated negative binomial (ZINB) model predicting counts of basing sharks encountered during vessel trips (n = 776) in the Bay of Fundy between 1994 and 2012. ZINB models shark encounters with two processes simultaneously: 1) zero-inflated model (binomial, logit link) predicting the probability of obtaining an overabundance of zeros, 2) count process model (negative binomial distribution and log link function) predicting the number of sharks counted. NAO = North Atlantic Oscillation index from the winter (Dec/Jan/Feb) lagged by 2 or 4 years.

Model process	Variable	Coefficient	95% CI	p-Value
Logit (probability of zero count)	NAO (winter 4 year lag)	17.23	−4.02, 38.48	0.112
	Year	−0.30	−0.62, 0.02	0.070
	Month (Jul vs. Aug*)	7.01	1.8, 12.23	0.008
	Month (Sep vs. Aug*)	−6.98	−18.44, 4.49	0.233
	Trip type (offshore vs. coastal*)	−13.24	−28.3, 1.82	0.085
Log (shark count)	NAO (winter 2 year lag)	−0.35	−0.45, −0.25	<0.001
	NAO (winter 4 year lag)	−0.27	−0.42, −0.12	<0.001
	Year	−0.12	−0.15, −0.10	<0.001
	Month (Jul vs. Aug*)	−0.83	−1.12, −0.54	<0.001
	Month (Sep vs. Aug*)	−0.25	−0.55, 0.04	0.093
	Trip type (offshore vs. coastal*)	0.90	0.58, 1.23	<0.001

* Reference category for categorical predictors.

4. Discussion

4.1. Temporal trends

We identified several spatial, temporal and environmental variables that influence the occurrence of basking sharks in the Bay of Fundy, including *trip type*, *month*, *year*, and *winter NAO index* (lagged two and four years). *Trip type* indicated that basking sharks were sighted more frequently on trips to deeper, *offshore* waters than in shallow, *coastal* waters, which corroborates results from Siders et al. (2013). The *offshore* area most commonly frequented by the sailing vessel was the deeper waters of the Grand Manan Basin (Fig. 1) where large patches of *C. finmarchicus* are often found at daytime depths >100 m (Murison and Gaskin, 1989). Therefore, higher shark sighting rates during *offshore* trips in our study area likely reflects shark associations with areas of high copepod abundance (Murison and Gaskin, 1989; Siders et al., 2013). Though the primary prey of basking sharks in this area is typically at depth (Murison and Gaskin, 1989), diving studies nonetheless indicate that individuals spend, on average, 19% of their time near the surface (Westgate et al., 2014), which allows them to be observed and counted from vessels. *Month* was also indicated as significant for predicting basking shark occurrence. During this study, shark sightings peaked in August and early September (Fig. 2). This trend parallels temporal patterns in abundance of *C. finmarchicus* (Murison and Gaskin,

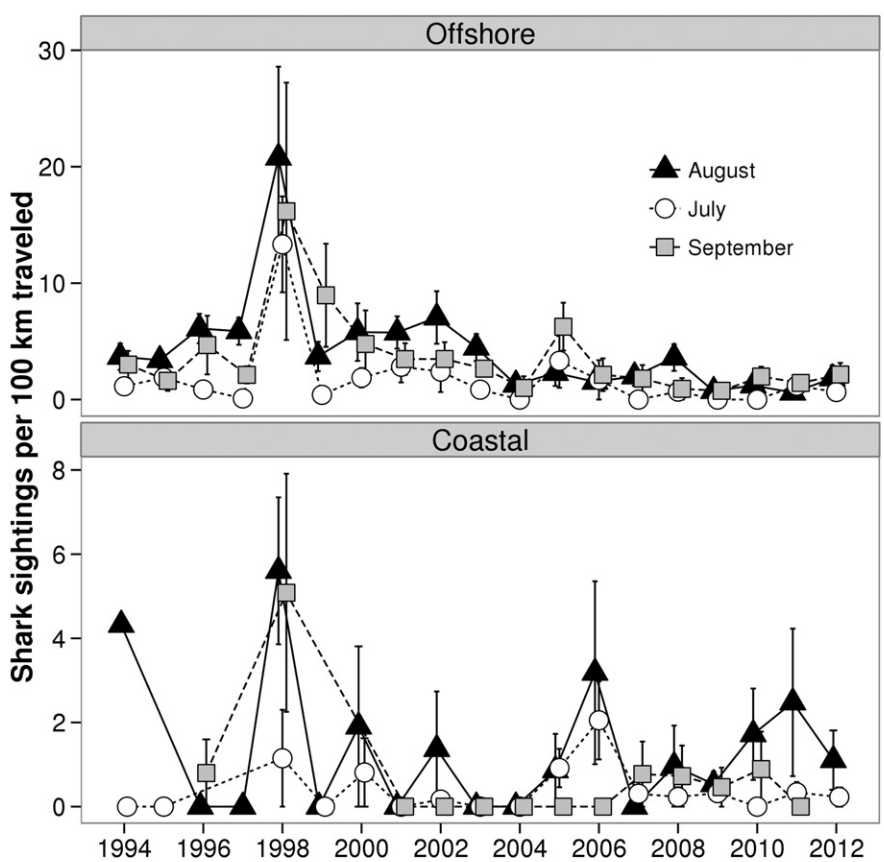

Fig. 2. Seasonal variability in basking sharks observed during vessel trips (n = 776) in the Bay of Fundy, 1994–2012. Points are means ± SE of encounter rates per 100 km traveled, averaged by week (the first Sunday as day 1 of week 1 each year). Means are calculated separately for offshore and coastal trips; note difference in y-axis scales.

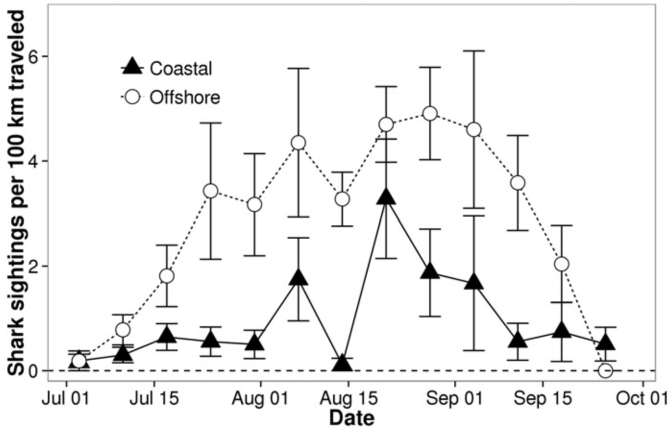

Fig. 3. Seasonal variability in basking sharks observed during vessel trips made offshore and coastal (n = 776) in the Bay of Fundy, 1994–2012. Points are means ± SE of encounter rates per 100 km traveled, averaged across years.

1989), which also peaks in the Bay of Fundy in summer (Michaud and Taggart, 2007, 2011) resulting from warm water temperatures which set up a central gyre over the Grand Manan Basin, trapping zooplankton produced in and transported into the Bay of Fundy through currents (Bumpus and Laurier, 1965; Hachey and Bailey, 1952).

NAO indices were significant predictors of inter-annual variability of shark occurrences in the Bay of Fundy, likely also through associations with *C. finmarchicus* abundance. In the Gulf of Maine, the summer abundance of *C. finmarchicus* was significantly and positively correlated to the NAO when lagged by four years — higher summer abundances of copepods were preceded four years earlier by a more positive winter NAO index (Conversi et al., 2001). Conversely, in our study the four year lagged winter NAO index had a negative effect on shark sighting rates. Though the Bay of Fundy is connected to and often considered to be part of the Gulf of Maine, it is not clear why relative shark sighting rates were lower in the Bay during years of expected higher copepod abundance in the Gulf. One possibility may be that basking sharks are less likely to enter the Bay of Fundy during years when foraging conditions are more favorable in the Gulf of Maine, resulting in lower shark occurrences in the Bay. The seasonal movements of sharks between these two neighboring regions are currently not well understood. Moreover, basking shark diving patterns, in response to copepod abundance and distribution, are not well understood in the Bay of Fundy. Thus, inter-annual variability in shark occurrence, as recorded by sightings at the surface, may partially be attributed to changes in sighting detectability associated with foraging patterns that we were unable to measure from year to year (e.g. more false zeros in some years because more sharks are using deeper waters).

We also observed a two year lagged negative relationship between the winter NAO and the shark sighting rate, but again, the mechanisms behind this correlation are unclear. At two year lags in the Gulf of Maine, it is winter SST, rather than winter NAO, which has a positive effect on the summer abundance of copepods (Conversi et al., 2001) and thus, the shark sighting rate is expected to increase during months (Aug/Sep) that correspond with expected increases in copepod abundances in the Bay two years after a higher winter SST. However, in this study, we found that the winter SST showed no effect on the shark sighting rate. The winter NAO does, however, have a positive two year lagged effect on the environmental conditions in these regions, whereby the Gulf Stream tends to have a more northerly position two years after a positive NAO index (Taylor and Stephens, 1998). Higher latitudes of the Gulf Stream may increase the SST in both the Bay of Fundy and Gulf of Maine by pushing warmer waters north, but the effects of this on the prey base are unknown. Basking shark sightings in the Gulf of Maine have been associated with warmer water temperatures (Owen, 1984; Wilson, 2004), yet we failed to detect any effects of summer SST (or lagged winter SST) on basking shark sighting rates in the Bay of Fundy. Although some clear relationships between NAO, SST and copepod abundance have been observed in the Gulf of Maine (Conversi et al., 2001), these results were from decades prior to our study (1961–1991) and it is uncertain if these associations have persisted or are consistent in the adjacent waters of the Bay of Fundy. Alternatively, temperature at depth, rather than on the surface, may be more important to deep diving animals such as basking sharks, though this hypothesis is untested. Another alternative is that inter-annual occurrences of sharks may also be related to variability in prey quality as recent studies have documented significant seasonal and inter-annual variability in the energetic content of *C. finmarchicus* in the Bay of Fundy (McKinstry et al., 2013). The mechanism behind lagged NAO/SST effects on copepods, and their effects on prey quality, remain untested in the Bay of Fundy, but may be critical factors influencing the seasonal and annual population dynamics of basking sharks.

In additional to spatial, seasonal, and NAO predictors of basking shark occurrence, our results suggest an overall decline in the occurrence of basking sharks in this region over the 19 year study period (Fig. 2; Table 2). The general decline we documented between 1994 and 2003, including the anomalously high SPUE in 1998, mirrors independent basking shark SPUE indices calculated from right whale aerial and boat surveys in the Bay of Fundy from the same time period (DFO, 2008). However, data from right whale surveys during the years 1979, 1987–1992, 1995 as well between 2001 and 2003 also had very low basking shark SPUE, suggesting that current low rates of basking shark occurrences may be more similar to those time periods. Thus, long-term monitoring will be required to assess whether our results represent a true decline or are part of longer cyclical trends. Moreover, since we do not have copepod abundance estimates for the entire 19 year period, we could not compare the shark sighting rates to the actual abundance of their prey. However, there is evidence that prey quality has declined recently in the Bay of Fundy, which may have important consequences on predators feeding on copepods. McKinstry et al. (2013) found significant annual variation in energy content of *C. finmarchicus* between 2006 and 2010, with 2009 and 2010 being the lowest. Given the tight association between basking shark occurrence and the expected distribution of their prey (Siders et al., 2013), it is likely that changes in the abundance, quality and/or spatial and temporal distribution of *C. finmarchicus* may have occurred and are influencing observed trends. In fact, the occurrence of right whales, which also feed on *C. finmarchicus*, in the Bay of Fundy has been very low in recent years (2010–2014; L. Murison, pers observation). Though SPUE indices can be used to monitor long-term population trends in large marine animals (Weir et al., 2007), it is currently unknown whether the observed decline in basking shark sightings in the Bay of Fundy is an indicator of a larger population decline or merely a reflection of local changes in abundance, possibly caused by deficiency in their local prey source and movement of sharks to other areas.

4.2. Photo-identification

Photo-identification has previously been shown to be an effective non-invasive research tool to study a wide range of marine animals (e.g. Matthews et al., 2001; Wells, 1991; Wursig and Jefferson, 1990). Within the Bay of Fundy, we were able to show some evidence of site fidelity by four individuals, with the longest interval between sightings being 9.1 years. Prior to our study, the longest documented interval between sightings for a basking shark using photo-identification was 3.1 years (in the coastal waters off south-west England) (Sims et al., 2000a,b). Re-sighting only four individuals out of the 98 identified sharks suggests that the use of photo-identification techniques alone may not be adequate to study the demographics of this population. Westgate et al. (2014) recently documented mean population abundance of basking sharks in the lower Bay of Fundy around 580

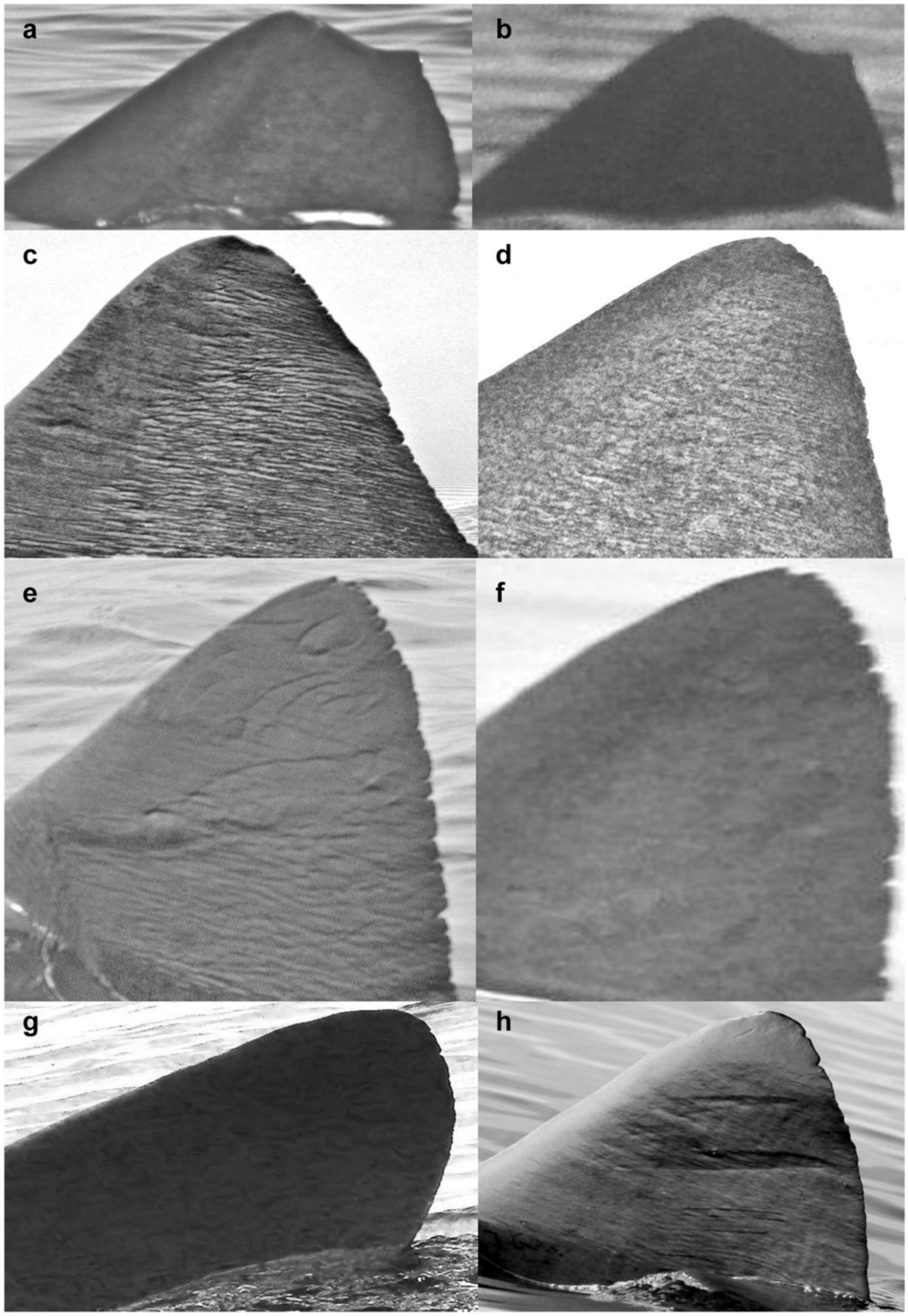

Fig. 4. Four individual basking sharks photographed in the Bay of Fundy, and re-sighted in subsequent years. a) Shark A (*Fundy-20020819A*) initially sighted August 19, 2002; b) Shark A re-sighted September 9, 2011; c) Shark B (*Fundy-20060709B*) initially sighted July 9, 2006; d) Shark B re-sighted August 14, 2010; e) Shark C (*Fundy-20080807C*) initially sighted August 7, 2008; f) Shark C re-sighted September 9, 2011; g) Shark D (*Fundy-20080905A*) initially sighted September 5, 2008; h) Shark D re-sighted August 19, 2012. In some pairs of images it is difficult to see all of the markings used in the matching process because of differences in fin angles and because fin matches were made with images enlarged on computer monitors, allowing greater scrutiny at higher image resolution.

Table 4
Time interval between initial sighting and re-sighting of four basking sharks in the Bay of Fundy, as well as distinguishing features that made it possible to match them within the Bay of Fundy Basking Shark Catalogue.

Shark	Catalogue ID	Initial sighting	Re-sighting	Interval (years)	Identification characteristics
A	Fundy-20020819A	19/08/2002	09/09/2011	9.1	Apex missing
					Lobed trailing edge
B	Fundy-20060707B	07/07/2006	14/08/2010	4.1	Nick on apex
					Rough surface
					Pattern of nicks along trailing edge
C	Fundy-20080905C	05/09/2008	19/08/2012	4.0	Distinct two nicks near apex on edge
D	Fundy-20080807A	07/08/2008	09/09/2011	3.1	Conical fin shape
					Scar on left surface
					Nick on apex

individuals (95% CI: 198 to 1482) which suggests that the low re-sighting rates are not because the population is quite large but rather maybe due to limited inter-annual site fidelity of individual sharks or high inter-seasonal rates of turnover of individuals which may also be driving differences in SPUE discussed above. There is currently no evidence suggesting that the Bay of Fundy basking sharks comprise a discrete population, thus, instantaneous population estimates (Westgate et al., 2014) coupled with high turnover rates, could mean that total number of individual sharks using this region may differ from the Westgate et al. estimates if individuals are arriving and departing frequently. Detailed studies of individual residency times would be required to test this hypothesis in order to determine total annual numbers of basking sharks using the lower Bay of Fundy over any given summer.

Our study did, however, highlight the longevity of some mark-types and scars on the first dorsal fin of basking sharks, which allowed for the re-identification of individuals. Though limited in its ability to provide specific data on population demographics, photo-identification, when used in conjunction with other population assessment tools can provide unique data on individual site fidelity. With increased effort in obtaining high-quality photographs of individuals, we could begin broad-scale comparisons with the Basking Shark Photo-ID Catalogue in the eastern North Atlantic, to further explore the possible mixing of individuals between regions (Gore et al., 2008).

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References

Anonymous, 2002. Proposal to Include the Basking Shark (*Cetorhinus maximus*) in Appendix II of the Convention on International Trade in Endangered Species (CITES) (Santiago, Chile).
Auger-Methé, M., Whitehead, H., 1997. The use of natural markings in studies of long-finned pilot whales (*Globicephala melas*). Mar. Mamm. Sci. 23, 77–93.
Bansemer, C.S., Bennett, M.B., 2008. Multi-year validation of photographic identification of grey nurse sharks *Carcharias taurus*, and applications for non-invasive conservation research. Mar. Freshw. Res. 59, 322–331.
Barker, S.M., Williamson, J.E., 2010. Collaborative photo-identification and monitoring of grey nurse sharks (*Carcharias taurus*) at key aggregation sites along the eastern coast of Australia. Mar. Freshw. Res. 61, 971–979.
Bumpus, D.F., Laurier, L., 1965. Circulation on the continental shelf off eastern North America between Newfoundland and Florida. Serial Atlas of the Marine Environment — Folio 7. American Geographical Society.
Chapple, T.K., Jorgensen, S.J., Anderson, S.D., Kanive, P.E., Klimley, A.P., Botsford, L.W., Block, B.A., 2011. A first estimate of white shark, (*Carcharodon carcharias*), abundance off Central California. Biol. Lett. 7, 581–583.
Compagno, L.J.V., 1984. Sharks of the world. Hexanchiformes to Lamniformes. FAO Fisheries Synopsis No. 124. Vol. 4. FAO, Rome (Part 1).
Conversi, A., Piontkovski, S., Hameed, S., 2001. Seasonal and interannual dynamics of *Calanus finmarchicus* in the Gulf of Maine (Northeastern US shelf) with reference to the North Atlantic Oscillation. Deep-Sea Res. II 48, 519–530.
Core Team, R., 2012. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria 3-900051-07-0 (URL http://www.R-project.org/).
COSEWIC, 2007. COSEWIC Assessment and Status Report on the Basking Shark (*Cetorhinus maximus*) Pacific Population, in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa (vii + 34 pp. http://www.sararegistry.gc.ca/status/status_e.cfm. Accessed 5 February 2013).
COSEWIC, 2009. COSEWIC Assessment and Status Report on the Basking Shark (*Cetorhinus maximus*) Atlantic Population, in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa (viii + 56 pp. Available from: http://www.sararegistry.gc.ca/status/status_e.cfm. Accessed 5 February 2013).
Cotton, P.A., Sims, D.W., Fanshawe, S., Chadwick, M., 2005. The effects of climate variability of zooplankton and basking shark (*Cetorhinus maximus*) relative abundance off southwest Britain. Fish. Oceanogr. 14 (2), 151–155.
Curtis, T.H., Zeeman, S., Summers, E.L., Cadrin, S.X., Skomal, G.B., 2014. Eyes in the sky: linking satellite oceanography and biotelemetry to explore habitat selection by basking sharks. Anim. Biotelem. 2, 12.
DFO, 2008. Status of Basking Sharks in Atlantic Canada. (p. 4 Can Sci Advis Sec Sci Advis Rep 2008/036). Department of Fisheries and Oceans, Dartmouth, NS.
Dulvy, N.K., Baum, J.K., Clarke, S., Compagno, L.J., Cortés, E., Domingo, A., Fordham, S., Fowler, S., Francis, M.P., Gibson, C., Martinez, J., Musick, J.A., Soldo, A., Valenti, S., 2008. You can swim but you can't hide: the global status and conservation of oceanic pelagic sharks and rays. Aquat. Conserv. 18, 459–482.
Fowler, S.L., 2005. *Cetorhinus maximus*. IUCN 2012. IUCN Red List of Threatened Species. Version 2012.2 (http://www.iucnredlist.org. Accessed 5 February 2013).
Fromentin, J.M., Planque, B., 1996. *Calanus* and environment in the eastern North Atlantic. II. Influence of the North Atlantic Oscillation on *C. finmarchicus* and *C. helgolandicus*. Mar. Ecol. Prog. Ser. 134, 111–118.
Gore, M.A., Rowat, D., Hall, J., Gell, F.R., Ormond, R.F., 2008. Transatlantic migration and deep mid-ocean diving by basking sharks. Biol. Lett. 4, 385–398.
Gubili, C., Johnson, R., Gennari, E., Oosthuizen, W.H., Kotze, D., Meyer, M., Sims, D.W., Jones, C.S., Noble, L.R., 2009. Concordance of genetic and fin photo identification in the great white shark, *Carcharodon carcharias*, off Mossel Bay, South Africa. Mar. Biol. 156, 2199–2207.
Hachey, H.B., Bailey, W.B., 1952. The general hydrography of the waters of the Bay of Fundy. Fish. Res. Board Canada Manuscript Rept. No. 455 (62 pp.).
Harvey-Clark, C.J., Stobo, W.T., Helle, E., Mattson, M., 1999. Putative mating behaviour in basking sharks off the Nova Scotia coast. Copeia 3, 780–782.
Holmberg, J., Norman, B., Arzoumanian, Z., 2009. Estimating population size, structure, and residency time for whale sharks *Rhincodon typus* through collaborative photo-identification. Endanger. Species Res. 7, 39–53.
Hurrell, J.W., Deser, C., 2009. North Atlantic climate variability: the role of the North Atlantic Oscillation. J. Mar. Syst. 78, 28–41.
IUCN, 2000. IUCN Red List of Threatened Species. IUCN — The World Conservation Union, Gland Switzerland, and Cambridge, UK.
Jackman, S., 2012. Package 'pscl'. http://cran.r-project.org/web/packages/pscl/.
Koopman, H.N., Westgate, A.J., Siders, Z.A., Cahoon, L.B., 2014. Rapid subsurface ocean warming in the Bay of Fundy as measured by free-swimming basking sharks. Oceanography 27, 14–16.
Martin, T.G., Wintle, B.A., Rhodes, J.R., Kuhnert, P.M., Field, S.A., Low-Choy, S.J., Tyre, A.J., Possingham, H.P., 2005. Zero tolerance ecology: improving ecological inference by modeling the source of zero observations. Ecol. Lett. 8, 1235–1246.
Matthews, J.N., Steiner, L., Gordon, J., 2001. Mark-recapture analysis of sperm whale (*Physeter macrocephalus*) photo-id data from the Azores (1987–1995). J. Cet. Res. Manag. 3, 219–226.
McKinstry, C.A.E., Westgate, A.J., Koopman, H.N., 2013. Annual variation in the nutritional value of Stage V *Calanus finmarchicus*: implications for right whales and other copepod predators. Endanger. Species Res. 20, 196–204.
Michaud, J., Taggart, C.T., 2007. Lipid and gross energy content of North Atlantic right whale food, *Calanus finmarchicus*, in the Bay of Fundy. Endanger. Species Res. 3, 77–94.
Michaud, J., Taggart, C.T., 2011. Spatial variation in right whale food, *Calanus finmarchicus*, in the Bay of Fundy. Endanger. Species Res. 15, 179–194.
Murison, L.D., Gaskin, D.E., 1989. The distribution of right whales and zooplankton in the Bay of Fundy, Canada. Can. J. Zool. 67, 1411–1420.
National Center for Atmospheric Research Staff (Eds). Last modified 13 Jan 2015. "The Climate Data Guide: Hurrell North Atlantic Oscillation (NAO) Index (PC-based)." Retrieved from https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-pc-based.
Owen, R.E., 1984. Distribution and Ecology of the Basking Shark *Cetorhinus maximus* (Gunnerus 1765). (M.Sc. Thesis). University of Rhode Island, Kingston, RI.
Rowat, D., Speed, C.W., Meekan, M.G., Gore, M.A., Bradshaw, C.J., 2009. Population abundance and apparent survival of the *Vulnerable* whale shark *Rhincodon typus* in the Seychelles aggregation. Oryx 43, 591–598.
Sears, R., Williamson, M., Wenzel, F.W., Berube, M., Gendron, D., Jones, P., 1990. Photographic identification of the blue whale (*Balaenoptera musculus*) in the Gulf of St. Lawrence, Canada. Rep. Int. Whal. Comm. (Spec. Iss. 12), pp. 335–342.
Shane, S.H., McSweeney, D., 1990. Using photo-identification to study pilot whale social organization. Rep. Int. Whal. Comm. (Spec. Iss. 12), pp. 259–263.
Siders, Z., Westgate, A.J., Johnston, D.W., Murison, L.D., Koopman, H.N., 2013. Seasonal variation in the spatial distribution of basking sharks (*Cetorhinus maximus*) in the lower Bay of Fundy, Canada. PLoS ONE 8 (12), e82074.
Sims, D.M., Quayle, V.A., 1998. Selective foraging behaviour of basking sharks on zooplankton in a small-scale front. Nature 393, 460–464.
Sims, D.W., Speedie, C.D., Fox, A.M., 2000a. Movements and growth of a female basking shark re-sighted after a three year period. J. Mar. Biol. Assoc. UK 80, 1141–1142.

Sims, D.W., Southall, E.J., Quayle, V.A., Fox, A.M., 2000b. Annual social behaviour of basking sharks associated with coastal front areas. Proc. R. Soc. Lond. 267, 1897–1904.
Sims, D.W., Southall, E.J., Tarling, G.A., Metcalfe, J.D., 2005. Habitat-specific normal and reverse diel vertical migration in the plankton-feeding basking shark. J. Anim. Ecol. 74, 755–761.
Skomal, G.B., Wood, G., Caloyianis, N., 2004. Archival tagging of a basking shark, *Cetorhinus maximus*, in the western North Atlantic. J. Mar. Biol. Assoc. UK 84, 795–799.
Skomal, G.B., Zeeman, S.I., Chrisholm, J.H., Summers, E.L., Walsh, H.J., McMahon, K.W., Thorrold, S.R., 2009. Transequatorial migrations by basking sharks in the Western Atlantic Ocean. Curr. Biol. 19, 1019–1022.
Taylor, A.H., Stephens, J.A., 1998. The North Atlantic Oscillation and the latitude of the Gulf Stream. Tellus A 50, 134–142.
Venables, W.N., Ripley, B.D., 2002. Modern Applied Statistics with S. Fourth ed. Springer, New York.
Weir, C.R., Stokin, K.A., Pierce, G.J., 2007. Spatial and temporal trends in the distribution of harbour porpoises, white-beaked dolphins and minke whales off Aberdeenshire (UK), north-west North Sea. J. Mar. Biol. Assoc. UK 87, 327–338.
Wells, R.S., 1991. The role of long-term study in understanding the social structure of a bottlenose dolphin community. In: Pryor, K., Norris, K.S. (Eds.), Dolphin Societies: Discoveries and Puzzles. University of California Press, Berkeley, pp. 199–225.
Westgate, A.J., Koopman, H.N., Siders, Z.A., Wong, S.N.P., Ronconi, R.A., 2014. Population density and abundance of basking sharks (*Cetorhinus maximus*) in the lower Bay of Fundy, Canada. Endanger. Species Res. 23, 177–185.
Wilson, S.G., 2004. Basking shark (*Cetorhinus maximus*) schooling in the southern Gulf of Maine. Fish. Oceanogr. 13, 283–286.
Wursig, B., Jefferson, T.A., 1990. Methods of photo-identification for small cetaceans. Rep. Int. Whal. Comm. (Spec. Iss. 12), pp. 43–52.
Zeileis, A., Kleiber, C., Jackman, S., 2008. Regression models for count data in R. J. Stat. Softw. 27 (8) (http://www.jstatsoft.org/v27/i08/. Accessed 7 March 2013).
Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R. Springer Science + Business Media, New York, NY.