Vol. 23: 177–185, 2014
doi: 10.3354/esr00567

ENDANGERED SPECIES RESEARCH
Endang Species Res

Published online March 10

Population density and abundance of basking sharks *Cetorhinus maximus* in the lower Bay of Fundy, Canada

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ABSTRACT: The conservation status of basking sharks *Cetorhinus maximus* in eastern Canadian waters is not clearly understood, in part because population densities and abundances have not been recently estimated. On September 11, 2009 and 2011, aerial surveys of basking sharks were conducted in the lower Bay of Fundy, Canada. Flyover tests of a wooden shark silhouette revealed that basking sharks were visible to a depth of 5 m. The proportion of time basking sharks were estimated between 0 and 5 m depth (availability bias) was 19% based on 1252 h of time-depth recorder data from 13 free-swimming sharks. During the 2 surveys, 26 sharks were sighted. Using the program Distance, availability bias corrected densities of 0.0513 sharks km^{-2} (2009, 95% CI = 0.0188 to 0.1402) and 0.0598 sharks km^{-2} (2011, 95% CI = 0.0358 to 0.1001) were reported. This corresponds to abundance estimates of 542 sharks (2009, 95% CI = 198 to 1482) and 632 sharks (2011, 95% CI = 377 to 1058) occupying a 10 570 km^2 area in the lower Bay of Fundy. Abundance was far lower than previously estimated using indirect methods and untested assumptions (Bay of Fundy = 4200 sharks). Previously published habitat suitability models for basking sharks in the Bay of Fundy predict heterogeneous habitat use, which would lower the overall abundance estimate. This lower population estimate for the Bay of Fundy, coupled with a very limited capacity to respond to significant levels of anthropogenic mortality, raises concerns about the conservation status of eastern Canadian basking sharks.

KEY WORDS: Basking shark · Bay of Fundy · Abundance · Population · Diving behaviour · Time-depth recorder

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INTRODUCTION

Shark populations around the world have been decimated by decades of over-fishing (Baum et al. 2003, Dulvy et al. 2008). This loss of abundance and diversity has resulted in cascading consequences to ecosystems (Myers et al. 2007, Ferretti et al. 2010). Recovery efforts for many animal populations rely on effective management, which begins with robust estimations of current abundance and distribution (Dulvy et al. 2008). Population estimates for various shark species and populations have typically been generated using fisheries data (Musick et al. 1993, Wirsing et al. 2006), although photo-identification (Holmberg et al. 2009, Rowat et al. 2009a, Chapple et al. 2011),

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boat (Williams et al. 2010) and aerial surveys have also been employed (Rowat et al. 2009b).

In marine systems, population densities can be estimated using line-transect surveys (Buckland et al. 2001). This technique has been used to estimate densities of a wide variety of marine species, including sirenians (Pollock et al. 2006), cetaceans (Barlow & Forney 2007) and seabirds (Ronconi & Burger 2009). One of the obstacles involved in using this technique is determining the *availability* bias, or the proportion of time diving animals are available to be counted, as they spend unknown proportions of time underwater. Availability bias can be estimated in a number of ways (Laake et al. 1997, Slooten et al. 2006), including collection of detailed information on the diving behaviour of the species being surveyed.

Basking sharks *Cetorhinus maximus* are the second largest fish in the world and are found circumglobally in temperate and tropical oceans (Compagno 2002, Skomal et al. 2009). Many basking shark populations have been diminished by historically high directed catches and an unknown level of bycatch in fisheries (Francis & Duffy 2002, Southall et al. 2005, DFO 2008). Like most sharks, basking sharks are extremely sensitive to exploitation because of slow growth, late maturity, limited productivity and low population abundance (Sims 2008). Additionally, robust estimates of population densities are lacking for most regions. These factors combined have prompted the IUCN to list basking sharks as 'Vulnerable' as they face a high risk of extinction in the wild (IUCN 2004). The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) recently assessed eastern Canadian basking sharks as a species of 'special concern' (COSEWIC 2009).

Basking sharks are found off both coasts of Canada, but, to date, limited work has been conducted on these populations (DFO 2008). In the Bay of Fundy, basking sharks congregate during summer months to feed on rich zooplankton blooms, making it an important regional study site (COSEWIC 2009). Sighting records have shown that sharks are typically present in the Bay of Fundy between May and October (Siders et al. 2013).

The current population estimate for Atlantic Canada is 10 125 basking sharks, with no error estimate. This region was defined as the waters around Newfoundland, the Gulf of St. Lawrence and Scotian Slope, and the Bay of Fundy (DFO 2008). While estimates for the non-Fundy habitats were made using data collected during aerial surveys, the Bay of Fundy estimate (4200) was based on sightings recorded during aerial-and boat-based surveys for western North Atlantic right whales *Eubalaena glacialis*, which were then adjusted using a number of untested correction factors relating to the relative visibility of basking sharks compared with right whales (DFO 2008). It is uncertain to what degree this 2008 Bay of Fundy estimate reflects the actual number of basking sharks that utilize this area during summer.

The present study aimed to produce the first empirical estimates of basking shark densities for the Bay of Fundy during summer time using line-transect surveys. In order to assess availability bias we also collected 1252 h of diving data from 13 free-swimming basking sharks to quantify the percentage of time they spend at various depths. Lastly, we used a wooden model 'shark' to measure how deep a basking shark could be seen from the aerial survey height of 305 m.

MATERIALS AND METHODS

Surveys

The geographic area of interest, defined here as the lower Bay of Fundy, is shown in Fig. 1. The delineations of this area (10 570 km^2) were arbitrar-

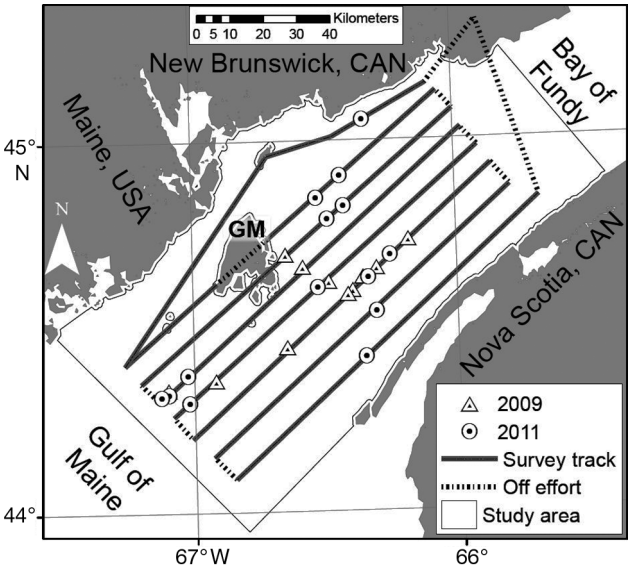

Fig. 1. Lower Bay of Fundy, Canada, showing the distribution of transects flown during surveys for basking sharks *Cetorhinus maximus* conducted on September 11, 2009 and 2011. The spatial distribution of basking shark sightings in 2009 (triangles) and 2011 (circles) is also shown. The area bounded by the thin black line delineates the study area and represents 10 570 km^2. GM: Grand Manan

ily defined by 2 parallel lines located at the ends of the track-lines and a perpendicular line running southeast from Brier Island, Nova Scotia, with a 1 km buffer from shore. Two aerial surveys were conducted, the first on September 11, 2009 and the second on September 11, 2011. Recent habitat modeling of basking sharks in the Bay of Fundy (Siders et al. 2013) revealed that the highest densities of animals were predicted in August and September. Weather conditions on both survey days were similar (winds <15 km h^{-1}, 20+ km visibility). The surveys were conducted between 11:00 and 17:00 h (Eastern Standard Time) in a high-wing, twin engine Cessna 337 which flew at an altitude of 305 m, a speed of 204 km h^{-1} and had a flying time of approximately 8 h. The survey was designed to equally divide effort over the whole study area. During each survey, 10 legs were flown representing 990 km of tracklines (Fig. 1). Seven parallel legs covered most of the lower Bay of Fundy and were each 125 km in length and separated by 10 km. There were 3 additional return legs that flew up the Grand Manan channel and then along the SE shore of New Brunswick, and these were 70, 20 and 25 km in length, respectively. Basking shark sightings were not recorded between transects or while flying over Grand Manan (Fig. 1). For both flights, 2 observers scanned, and a third person recorded data. The vertical angle to each sighting was recorded to the nearest 5° increment by looking through a 5 × 50 cm clear plastic strip marked from 0° (on trackline) to 90° (horizon) that hung in the window. The sighting boards were later calibrated using a clinometer, and a correction factor was applied to all recorded angles. The plane was equipped with bubble windows so sightings were possible even directly under the plane. Environmental conditions (sea state, glare) were also recorded as they changed.

Availability bias

To record the proportion of time sharks were visible, and their potential travel speeds (the latter in order to assess possible double counting), we used data collected from time-depth recorders (TDR) that were deployed on 13 basking sharks during August and September, 2008 to 2013 (see Table 1). All sharks were tagged in the lower Bay of Fundy from a 7 m skiff. Tags were attached to surface-swimming sharks via a 2 m monofilament tether that was attached to a small barb that was pushed through the trailing edge of the dorsal fin. Tag release was facilitated using steel/magnesium galvanic linkages which corroded in seawater. After tag release the barb and tether were free to detach from the shark. The tag consisted of a TDR (Mk.8 or Mk.10, Wildlife computers), a satellite transmitter (Wildlife Computers) and a small VHF radio (Holohil Systems), all potted in a buoyant epoxy matrix. The TDR is an archival logger and needs to be recovered to access the data; floating tags were found and recovered using VHF telemetry after traveling to the general location provided by the satellite transmitter. The TDR was programmed to log time, depth, speed and water temperature every second. Analysis of dive records was conducted using Wildlife Computers software. Proportion of time at depth and average travel speeds were calculated in MATLAB 7.14 (The MathWorks). We also analyzed depth profiles for evidence of diurnal behaviour by comparing time at depth, binned every 20 m from 0 to 220 m, between day and night recordings using a Wilcoxon signed-rank test with normal approximation.

Subsurface sharks can be visually detected from the air, so we needed to verify the maximum depth at which sharks could be seen. To do this we constructed a 'shark-like' silhouette model out of plywood (approximately 1.5 × 3.0 m) and painted it grey-brown to mimic the colouration of a live basking shark. The weighted silhouette was suspended in the water on 1.5 cm nylon line by 2 large buoys at depths ranging from 1 to 6 m. The silhouette was flown over by an airplane (Piper Seneca) at a similar height and speed to those used on the actual surveys, and an observer recorded the depth at which the silhouette was no longer visible. This experiment was conducted with multiple flyovers, approximately 2 km from the shore of Grand Manan in September 2012 in an area in which basking sharks are commonly observed. Weather conditions were similar to those on the actual survey days.

Density

One form of the line-transect equation for abundance (N) is:

$$N = \frac{A \times n}{2L \times \mathrm{ESW} \times g(0)} \quad (1)$$

where A is the size of the study area (km^2), n is the number of animals seen, L is the length of transect lines surveyed (km), ESW is the effective strip width (km) and $g(0)$ is the probability of seeing animals

directly on the trackline (please refer to Buckland et al. 2001 for a complete explanation of distance sampling equations). In distance sampling analysis a basic assumption is that all sharks on the transect line are detected: $g(0) = 1$, where $g(0)$ is the probability of detecting sharks at distance zero. There are 2 reasons why sharks may not be detected: (1) availability bias (animals are missed because they are submerged) and (2) perception bias (visible animals are missed for other reasons, e.g. sea state, observer error). While we were able to provide estimates of the availability bias from the TDR and flyover records, we were not able to examine perception bias. Hence, in our abundance equation the term $g(0)$ reflects only the interaction of availability bias. Although variable, Dawson et al. (2008) concluded that perception bias estimates for cetaceans are usually >0.9. We predict that perception values for basking sharks would also be high because they are very large, slow-moving animals that contrast sharply with the surrounding water.

Because of the low number of sightings, data were not truncated prior to analysis nor were any sightings removed from the records. Because of low sample sizes, data were pooled and global estimates of ESW were made in the program Distance 6.0 (Thomas et al. 2010) using the conventional distance sampling (CDS) routine. Encounter rates (n/L) for each year were also calculated using Distance. Distance uses several key function and series expansion terms for modeling the detection function. The following models and series expansion terms were run: uniform model (with cosine or simple polynomial or hermite polynomial expansion), half-normal (with cosine or simple polynomial or hermite polynomial) and hazard-rate models (with cosine or simple polynomial expansion). Model fit and ranking were assessed within Distance using Akaike's information criterion with a correction for small samples sizes (AICc) (Burnham & Anderson 2002). Final model goodness-of-fit was assessed using a Kolmogorov-Smirnov test (Buckland et al. 2001). Individual density and abundance estimates were calculated outside Distance using the global ESW estimate and n/L calculations from each year. Coefficients of variation (CV) for density (D) and abundance (N) were calculated using the CVs from each variable element:

$$\mathrm{CV}(D,N) = \sqrt{[\mathrm{CV}^2(N/L) + \mathrm{CV}^2(\mathrm{ESW}) + \mathrm{CV}^2\ g(0)]} \quad (2)$$

Log normal confidence intervals (CI) for small sample sizes were calculated following Buckland et al. (2001). Abundance CIs were derived directly from the density calculations.

RESULTS

Surveys

During the aerial surveys we recorded 12 basking sharks in 2009 and 14 in 2011 (Fig. 1). The mean (±SD) detection distance from the trackline was 378 ± 244 m. Sea state remained below Beaufort 2 for all but the last 2 legs of the 2011 survey. Glare was present but never obscured the entire field of view.

Availability bias

All deployed tags were recovered, usually within a day of being released from the shark. The 13 individual deployments ranged between 21 and 126 h, and overall we obtained 1252 h of diving information. Fig. 2 shows examples of 2 complete diving records from Bay of Fundy basking sharks and illustrates some of the variation that was present in the records. Depth selection in 20 m bins from 0 to 220 m did not differ significantly between day and night for pooled depth recordings from all sharks (Wilcoxon signed rank-test, $W = 47$, $p = 0.5693$). Individual deployments

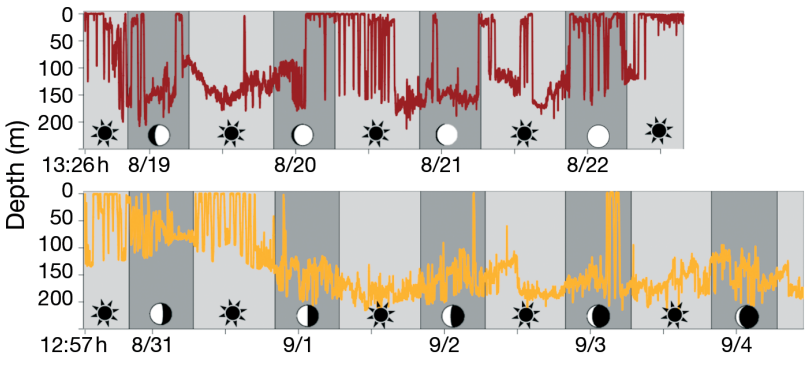

Fig. 2. *Cetorhinus maximus*. Diving records from 2 individual basking sharks collected in the Bay of Fundy in 2010. Symbols and shading indicate day and night periods (with moon phase). Time of deployment is shown, and dates (month/day) are indicated at midnight. Upper panel: Animal A (Aug 18, 2010) showed a pattern that was typical of most of the basking sharks we observed. Lower panel: Animal B (Aug 30, 2010) was atypical and showed prolonged periods of time at depth. A lack of obvious diurnal behaviour was noted in all diving records ($p > 0.05$)

did not show significant difference in depth distributions between day and night either (p-value ranged from 0.1783 to 1 across deployments). This meant we could use all the diving data in the availability bias analysis. The overall frequency distribution of depths from all individuals is shown in Fig. 3. We also calculated the proportion of time each individual shark spent in specific depth bins between 0 to 1, 0 to 2 and 0 to 5 m (Table 1). Because the individual deployment times were not equal, we pooled the results for each depth range across all individuals to obtain an overall mean, weighted by tag deployment duration. These represent the depth-specific availability bias estimates for basking sharks in the Bay of Fundy. The results of the flyover test revealed that the shark silhouette was clearly visible 5 m below the surface, but became much more difficult to see at 5.5 m. Therefore, we assumed that only sharks that were swimming in the upper 5 m of the water column were visible from the aircraft. The mean (±SD) time spent between these depths for all tagged sharks was 19 ± 13% (Table 1); therefore, all density estimates were rescaled by a factor of 0.19 ($g[0]$) to account for sharks below 5 m.

Average speeds for individuals ranged between 0.10 and 0.64 m s^{-1}, and the overall weighted average was 0.32 ± 0.30 m s^{-1}.

Table 1. *Cetorhinus maximus*. Proportion of time spent by Bay of Fundy basking sharks in depth bins between 0–1, 0–2, and 0–5 m recorded using time-depth recorders. Animal ID reflects date of tag deployment (month, day, year). Deployments ranged between 21.8 and 126.4 h. The mean is the weighted average of all deployments with its associated standard deviation

Animal ID	Length of deployment (h)	Depth bins 0–1 m	0–2 m	0–5 m
Sep 05 08	21.8	0.22	0.30	0.38
Sep 12 09	46.8	0.34	0.42	0.52
Aug 18 10	98.4	0.10	0.17	0.21
Aug 28 10	114.1	0.01	0.06	0.11
Aug 30 10	118.2	0.04	0.04	0.05
Sep 09 10	114.7	0.03	0.12	0.17
Aug 19 12a	82.9	0.16	0.22	0.28
Aug 19 12b	108.4	0.05	0.13	0.21
Aug 25 12	104.4	0.05	0.13	0.20
Aug 18 13	106.2	0.08	0.19	0.26
Aug 20 13	126.4	0.01	0.06	0.11
Aug 27 13	107.4	0.04	0.06	0.09
Sep 21 13	102.0	0.04	0.21	0.33
Mean ± SD		0.06 ± 0.1	0.13 ± 0.11	0.19 ± 0.13

Density

The model with the lowest AICc scores was the uniform model with cosine expansion. The results of the Kolmogorov-Smirnov test showed no significant difference (D = 0.1300, p = 0.7717) between the cumulative distribution function and the empirical distribution function, indicating a good model fit (Buckland et al. 2001). Perpendicular sighting distances and the fitted uniform detection function are shown in Fig. 4. ESW was 622.1 m (CV: 6.74%), which translates to an effective survey area of 1232 km^2. Encounter rates (n/L) for 2009 and 2011 were 0.0121 (CV: 46.6%) and 0.0141 (CV: 15.9%), respectively. Density estimates corrected for availability bias (0.19; Table 1) were 0.0513 sharks km^{-2} (CV: 51.0%, 95% CI: 0.0188 to 0.1402) for 2009 and 0.0598 sharks km^{-2} (CV: 26.0%, 95% CI: 0.0358 to 0.1001) for 2011. This translates to an overall abundance estimate of 542 (CV: 51.0%, 95% CI: 198 to 1482) sharks in 2009 and 632 (CV: 26.0%, 95% CI: 377 to 1058) sharks in 2011.

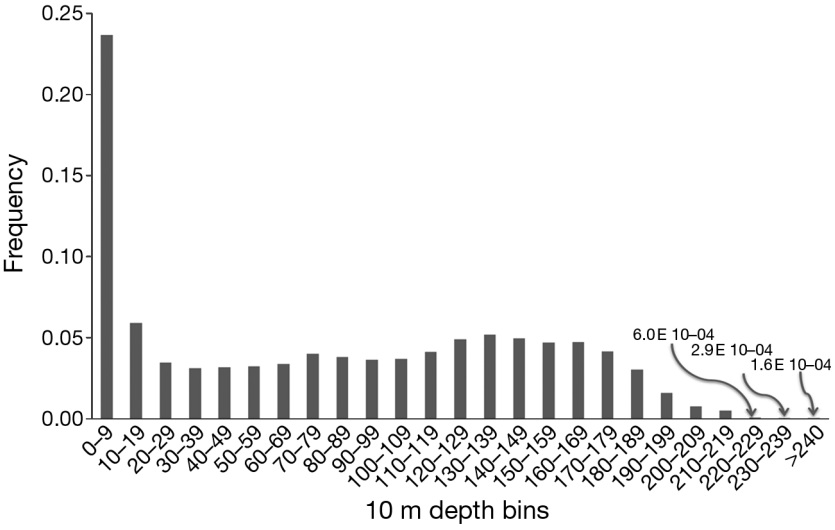

Fig. 3. *Cetorhinus maximus*. Distribution of 10 m depth bins from dives made by basking sharks in the Bay of Fundy. Data are the pooled results from 1252 h of time-depth recorder data from 13 sharks

DISCUSSION

These results represent the first empirical density estimates of basking sharks in the Bay of Fundy. The global probability function fitted the data well even though the sample sizes were small. Our abundance estimates for 2009 and 2011

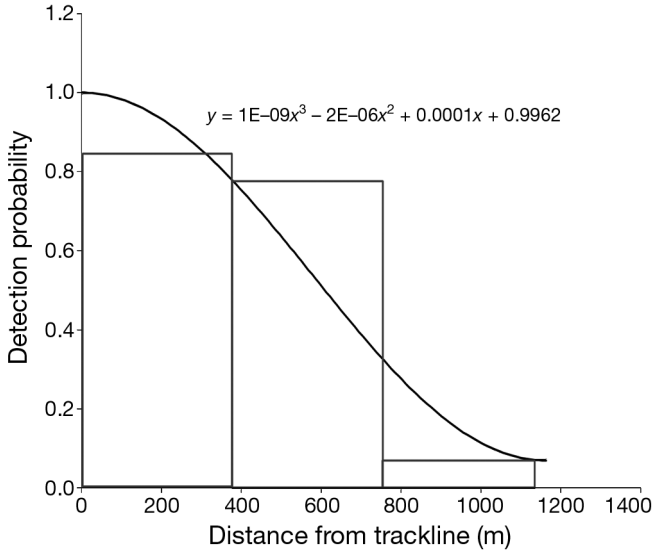

Fig. 4. *Cetorhinus maximus*. Perpendicular sighting distances (n = 26) made on basking sharks in the lower Bay of Fundy, Canada. The fitted probability function is a uniform model with cosine adjustment

were quite similar, but 85% lower than previous population estimates (i.e. ~600 sharks rather than 4200 [DFO 2008]) even though a more conservative availability bias adjustment was applied (0.19 [present study] vs. 0.36 [DFO 2008]). The DFO (2008) study reported that the ratio of basking shark sightings to right whale sightings from 10 yr of Bay of Fundy surveys was 0.17; with an average of 123 right whales observed per year, this corresponds to an average of 21 sharks. The DFO (2008) reasoned that because differences exist in observer bias and relative sightability, basking sharks should be 200 times more difficult to observe, meaning there were 4200 sharks (DFO 2008). The present results (even though from just 2 surveys) refine the previous estimates as they were based on empirical counts and standard line-transect techniques and analyses. We were also able to present measures of variation and confidence in our estimates. If the actual number of basking sharks was more in line with the previous DFO (2008) estimate, then we would have expected to have more sightings during the surveys. For example, if there were 4200 basking sharks in the bay (10 570 km^2) and if our availability bias (0.19) is reliable, there should be 798 sharks visible throughout the entire study area from the aircraft at any given time. If we look at the number of sharks that would be present in our effective survey area (1232 km^2), this number drops to 93 sharks, which is still much higher than the average sightings per survey reported here (13 sharks). This supports the idea that the population as censused in 2009 and 2011 was much smaller than previously estimated.

When the average abundance estimates from this study (587, CI: 288 to 1270) are added to those from Newfoundland (558, CI: 116 to 2694) and the Gulf of St. Lawrence/Scotian slope (5367, CI: 3636 to 7922) (DFO 2008) (all obtained using similar aerial line-transect techniques), the estimated population size for eastern Canadian basking sharks is 6512 (CI: 4040 to 11 886). The non-Fundy estimates used an availability bias estimate of 0.36; if the times spent at the surface were more similar to those of Fundy basking sharks, then the overall estimates would increase.

The abundance estimates presented here likely over-estimate the true number of basking sharks in the Bay of Fundy. In a recent basking shark habitat suitability model, Siders et al. (2013) showed that suitable habitat was largely restricted to the deeper waters of the Bay of Fundy. The heterogeneous spatial distribution of our sightings (Fig. 1) also supports the idea that habitat is not uniformly utilized. Abundance estimates rely on a good understanding of the utilized habitat and will be inflated if only a portion is used. We therefore recommend using the lower boundary of the abundance confidence interval until a better understanding of habitat use emerges. We also recommend that future surveys be stratified, with increased effort in the central deep-water portions of the Bay of Fundy and less effort closer to shore. If habitat use outside of the Bay of Fundy is also heterogeneous, then this suggests that the population estimate for eastern Canadian waters could also be inflated.

The average unadjusted density estimates from the Bay of Fundy (0.01 sharks km^{-2}) are much higher than those obtained from aerial surveys that were conducted around Newfoundland/Labrador (0.0001 sharks km^{-2}) and the Gulf of St. Lawrence (0.003 sharks km^{-2}) (DFO 2008). They are also greater than the highest densities recorded from the adjoining Gulf of Maine (0.006 sharks km^{-2}) (Owen 1984). Densities on the Scotian shelf (0.007 sharks km^{-2}) were the highest reported outside the Bay of Fundy, and examination of the distribution of these sightings (see Fig. 2, in DFO 2008) suggests that this was being driven largely by a cluster of sightings near the Emerald Basin (DFO 2008), a purported mating ground (Harvey-Clark et al. 1999). The seasonally high densities observed in the Bay of Fundy support the contention that this area represents important foraging habitat for eastern Canadian basking sharks (COSEWIC 2009).

While there was some degree of individual variation in our availability bias estimates (Table 1, Fig. 2), these results were collected over a 5 yr period from 13 individuals with average deployment times of 4 d. We believe that these data provide the best estimates of availability bias for Bay of Fundy basking sharks at the present time, while recognizing that only 2% of the estimated population has been tagged. It is worth noting that our estimates are lower than the estimates (time at surface = 36%) in previous abundance calculations (DFO 2008) that were from Sims et al. (2003). These differences relate to regionally specific foraging strategies; Sims et al. (2003) collected data from basking sharks in UK waters, where basking sharks target surface swarms of zooplankton (Sims et al. 2005), whereas the present data were obtained from sharks that spend most of their time foraging on deep-water zooplankton layers (Murison & Gaskin 1989, Siders et al. 2013) (Table 1, Fig. 3). These differences highlight the risk of over- or underestimating densities when availability bias is not clearly understood. While other methods exist to estimate this parameter, including shore-based, helicopter, or boat behavioural observations (Slooten et al. 2006), we deployed TDRs because they collect data over longer time frames and provide a better picture of average behaviour for animals that are not obliged to surface for respiration. In addition, in our case, it would have been nearly impossible to utilize an observational approach, since basking sharks spend little time at the surface (Table 1) and are relatively uncommon. It is important to note that, while the TDR data provided a description of basking shark diving behaviour, to calculate suitable availability bias estimates it was also necessary to quantify how deep a shark could be observed from the air. Differences in the maximum depth of visibility directly affect the availability bias values (Table 1); this illustrates the importance of using a cut off that is appropriate for the area being surveyed. For practical reasons, in our flyover experiment we used a non-moving model that was smaller than a typical shark (3 m vs. 8 m) and a region of ocean that was both well mixed and turbulent. Because water clarity, object size and movement all influence an object's sightability from the air, we view 5 m as a conservative estimate of maximum depth of visibility for Bay of Fundy basking sharks. In future efforts it would be optimal to collect maximum depth of visibility data from various locations throughout the survey area using towable, life-size models.

The survey design was constrained by the 8 h flight time of the aircraft and the desire to maximize coverage of the lower Bay of Fundy in a single day. The separation of transect lines in any survey should be such that potential double sightings of the same individual are minimized. In our case, transects were spaced 10 km apart, meaning that an individual shark would have to travel at least that far to be recounted. Examining sightings data from both years (Fig. 1) shows that there were few cases in which that might occur, given that swim speeds of <2 km h^{-1} were typical and flying times for each transect were on the order of 40 min. Changes in perception bias (shark present but not seen) can also influence survey results, but, unfortunately, we had no way to fully evaluate this. Both observers had similar numbers of sightings at similar distances, suggesting that observer efficiency was similar.

Sea state remained favourable throughout both surveys (Beaufort 1 to 2), with the exception of the final 2 legs of the 2011 survey during which sea state deteriorated to a Beaufort value of 3 to 4. A shark was observed on the last transect that day (Fig. 1), which shows these very large animals can be visible in higher sea states. Glare presented a problem in both our surveys, partially reducing sightability. Generally, glare was restricted to the back portion (4 to 6 o'clock) of one viewing field when travelling northeast and the front portion (12 to 2 o'clock) of one during southwest transects. To be missed, a shark would have had to surface in the glare field either before (aircraft flying southwest) or after (aircraft flying northeast) flyover. Most sightings in non-glare conditions revealed sharks at the surface for the entire flyover. Given this, we reasoned that sightings were possible even when glare was present.

These new results are based on 2 surveys conducted 2 yr apart in which a low number of sharks were observed. Ideally, additional surveys should be completed, preferably closer together, to increase confidence in the results. It would also be beneficial to use a larger aircraft with an extended flying time so 2 counting teams (to address perception bias) and additional transects (to improve spatial coverage) could be used. As with any survey of this kind there is a level of uncertainty in the estimates that must be considered. We do feel our new results are more compatible with those from the other regions of Atlantic Canada which were collected using similar techniques.

Our data suggest that basking shark abundance in the Bay of Fundy is much lower than previously thought. This highlights the need to use a precautionary approach when managing this species. Bask-

ing sharks have an extremely limited reproductive capacity and cannot withstand even low levels of anthropogenic mortality (Sims 2008). The lack of significant recovery in the western Canadian population, after near eradication in the 1950s, suggests that population recovery can be very slow. While we do not know the population trajectory of eastern Canadian basking sharks, after years of sustained high levels of mortality in fisheries (DFO 2008), the population is undoubtedly still depleted.

Acknowledgements. The project was supported by the PADI Foundation, Canadian Wildlife Federation, New Brunswick Wildlife Trust Fund, Shell's Fuelling Change program, the Garfield-Weston Foundation and the Royal Caribbean Cruise Lines Ocean Fund. We thank Laurie Murison and the Grand Manan Whale and Seabird Research Station for sightings data and logistical assistance. All tagging was done under scientific research permits issued through the Department of Fisheries and Oceans Canada (2009: License No. 322858; 2010–12: License No. 325842) and animal care and use permits (2008-007, A1112-006) vetted through the University of North Carolina Wilmington. The manuscript was improved by the generous comments of 2 anonymous reviewers.

LITERATURE CITED

Barlow J, Forney KA (2007) Abundance and population density of cetaceans in the California Current ecosystem. Fish Bull 105:509–526

Baum JK, Myers RA, Kehler DG, Worm B, Harley SJ, Doherty PA (2003) Collapse and conservation of shark populations in the Northwest Atlantic. Science 299: 389–392

Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (2001) Introduction to Distance sampling: estimating abundance of biological populations. Oxford University Press, Oxford

Burnham KP, Anderson DR (2002) Model selection and multi-model inference: a practical information-theoretic approach. Springer-Verlag, New York, NY

Chapple TK, Jorgensen SJ, Anderson SD, Kanive PE, Klimley AP, Botsford LW, Block BA (2011) A first estimate of white shark, *Carcharodon carcharias*, abundance off Central California. Biol Lett 7:581–583

Compagno JV (2002) Sharks of the world. An annotated and illustrated catalogue of shark species known to date, Vol 2. Bullhead, mackerel and carpet sharks (Heterodontiformes, Lamniformes and Orectolobiformes). FAO species catalogue for fishery purposes, No. 1, Food and Agriculture Organization, Rome

COSEWIC (Committee on the Status of Endangered Wildlife in Canada) (2009) COSEWIC assessment and status report on the basking shark *Cetorhinus maximus*, Atlantic population, in Canada. COSEWIC, Ottawa. www.sararegistry.gc.ca/virtual_sara/files/cosewic/sr_Basking%20Shark_0810_e1.pdf (accessed November 2012)

Dawson S, Wade P, Slooten E, Barlow J (2008) Design and field methods for sighting surveys of cetaceans in coastal and riverine habitats. Mammal Rev 38:19–49

DFO (Department of Fisheries and Oceans) (2008) Status of basking sharks in Atlantic Canada. Can Sci Advis Sec Sci Advis Rep 2008/036, DFO, Ottawa

Dulvy NK, Baum JK, Clarke S, Compagno LJV and others (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

Ferretti F, Worm B, Britten GL, Heithaus MR, Lotze HK (2010) Patterns and ecosystem consequences of shark declines in the ocean. Ecol Lett 13:1055–1071

Francis MP, Duffy C (2002) Distribution, seasonal abundance and bycatch of basking sharks (*Cetorhinus maximus*) in New Zealand, with observations on their winter habitat. Mar Biol 140:831–842

Harvey-Clark CJ, Stobo WT, Helle E, Mattson M (1999) Putative mating behavior 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. Endang Species Res 7:39–53

IUCN (International Union for the Conservation of Nature and Natural Resources) (2004) IUCN Red List of Threatened Species. IUCN, Gland

Laake JL, Calambokidis J, Osmek SD, Rugh DJ (1997) Probability of detecting harbor porpoise from aerial surveys: estimating g (0). J Wildl Manag 61:63–75

Murison LD, Gaskin DE (1989) The distribution of right whales and zooplankton in the Bay of Fundy, Canada. Can J Zool 67:1411–1420

Musick JA, Branstetter S, Colvocoresses JA (1993) Trends in shark abundance from 1974 to 1991 for the Chesapeake Bight region of the U. S. Mid-Atlantic coast. NOAA Tech Rep 115, NMFS Sept 1993

Myers RA, Baum JK, Shepherd T, Powers SP, Peterson CH (2007) Cascading effects of the loss of apex predatory sharks from a coastal ocean. Science 315:1846–1850

Owen RE (1984) Distribution and ecology of the basking shark *Cetorhinus maximus* (Gunnerus, 1765). Master's dissertation, University of Rhode Island, Kingston, RI

Pollock KH, Marsh HD, Lawler IR, Alldredge MW (2006) Estimating animal abundance in heterogeneous environments: an application to aerial surveys for dugongs. J Wildl Manag 70:255–262

Ronconi RA, Burger AE (2009) Estimating seabird densities from vessel transects: distance sampling and implications for strip transects. Aquat Biol 4:297–309

Rowat D, Speed CW, Meekan MG, Gore MA, Bradshaw CJ (2009a) Population abundance and apparent survival of the Vulnerable whale shark *Rhincodon typus* in the Seychelles aggregation. Oryx 43:591–598

Rowat D, Gore MA, Meekan MG, Lawler IR, Bradshaw CJ (2009b) Aerial survey as a tool to estimate whale shark abundance trends. J Exp Mar Biol Ecol 368:1–8

Siders ZA, Westgate AJ, Johnston DW, Murison LD, Koopman HN (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 DW (2008) Sieving a living: a review of the biology, ecology and conservation status of the plankton feeding basking shark *Cetorhinus maximus.* Adv Mar Biol 54:171–220

Sims DW, Southall EJ, Richardson AJ, Reid PC, Metcalfe JD (2003) Seasonal movements and behaviour of basking sharks from archival tagging: no evidence of winter hibernation. Mar Ecol Prog Ser 248:187–196

Sims DW, Southall EJ, Tarling GA, Metcalfe JD (2005) Habitat-specific normal and reverse diel vertical migration in the plankton-feeding basking shark. J Anim Ecol 74: 755–761

Skomal GB, Zeeman SI, Chisholm JH, Summers EL, Walsh HJ, McMahon KW, Thorrold SR (2009) Transequatorial migrations by basking sharks in the western Atlantic Ocean. Curr Biol 19:1019–1022

Slooten E, Dawson S, Rayment W, Childerhouse S (2006) A new abundance estimate for Maui's dolphin: What does it mean for managing this critically endangered species? Biol Conserv 128:576–581

Southall EJ, Sims DW, Metcalfe JD, Doyle JI and others (2005) Spatial distribution patterns of basking sharks on the European shelf: preliminary comparison of satellite-tag geolocation, survey and public sightings data. J Mar Biol Assoc UK 85:1083–1088

Thomas L, Buckland ST, Rexstad EA, Laake JL and others (2010) Distance software: design and analysis of distance sampling surveys for estimating population size. J Appl Ecol 47:5–14

Williams R, Okey TA, Wallace S, Gallucci VF (2010) Shark aggregation in coastal waters of British Columbia. Mar Ecol Prog Ser 414:249–256

Wirsing AJ, Heithaus MR, Dill LM (2006) Tiger shark (*Galeocerdo cuvier*) abundance and growth in a subtropical embayment: evidence from 7 years of standardized fishing effort. Mar Biol 149:961–968

Editorial responsibility: Robert Harcourt, Sydney, Australia

Submitted: January 25, 2013; Accepted: November 6, 2013
Proofs received from author(s): February 7, 2014