Evaluating inter-annual relative abundance of leatherback sea turtles in Atlantic Canada

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ABSTRACT: We opportunistically assessed the relative abundance of leatherback sea turtles *Dermochelys coriacea* over 14 yr in a foraging area off the coast of Nova Scotia, Canada. We conducted haphazard, unmarked, non-linear transects (HUNTs) for leatherbacks from a vessel with an observation tower, recording the time and location of all sightings concurrent with opportunistic sampling of turtles in support of other research objectives. We calculated the sightings per unit effort (SPUE) and standardized it using both a generalized linear model (GLM) and a generalized additive model (GAM) accounting for variables that may have affected detectability. During the monitoring period, a total of 179 HUNTs occurred and 564 leatherbacks were sighted, with annual average nominal SPUE (leatherbacks h^{-1} ± SE) fluctuating from a low of 0.02 ± 0.02 in 2005 to a high of 0.69 ± 0.15 in 2014. Both standardization approaches indicated no significant linear effect of year (GLM: p = 0.16, GAM: p = 0.17), suggesting that although the relative abundance of leatherbacks at this field site exhibits high inter-annual variability, it is likely stable. We present preliminary estimates of absolute abundance in years where a spatial component provided by vessel GPS tracks in a subset of HUNTs allowed for the use of spatial modelling techniques. These data suggest Canadian waters may have the highest density of foraging leatherbacks reported across the species' range, providing further evidence of the importance of this region to leatherback conservation.

KEY WORDS: Abundance · Trends · Platform of opportunity · Sea turtle · CPUE standardization · Spatial models

INTRODUCTION

Assessing population abundance is a fundamental component of wildlife management and key to evaluating the success of conservation efforts for species at risk. Unfortunately, it is seldom a straightforward exercise. A reliance on visual detection methods for enumeration of individuals can be obscured by species' habitat (e.g. subterranean, marine, or aquatic species or those that inhabit dense vegetative cover, etc.), the time of the day when the species is active (e.g. nocturnal and crepuscular species), species size, appearance, behaviour, and spatial distribution. For both terrestrial species (e.g. birds, bats, anurans and insects; Blumstein et al. 2011) and marine species (e.g. fish, invertebrates and cetaceans; Rountree et al. 2006, Mellinger et al. 2007) that produce vocalizations, passive stationary autonomous acoustic surveys are an option for evaluating diversity and abundance, but the scales at which they are effective are limited. Active acoustic sampling with echosounders presents an alternative sampling technique, which also enables enumeration of non-vocalizing species and has been used successfully with several invertebrate and vertebrate marine organisms (Medwin & Clay 1997). For all acoustic methods, it is usually impossible to count every individual; thus, estimating abundance becomes a

more realistic objective (Schwarz & Seber 1999). Widely distributed and long-lived animals such as sea turtles present additional challenges to assessing abundance or trends in abundance over time (Seminoff & Shanker 2008).

In population assessments of sea turtles, terrestrial-based approaches (e.g. the counting of nesting females, nests, or body pits) are the most commonly used metrics to estimate abundance (Heppell et al. 2003, National Research Council 2010, Katsanevakis et al. 2012). However, despite the obvious logistical advantages terrestrial (vs. in-water) surveys present, there are numerous disadvantages inherent in using nesting beach-based observations to assess population dynamics (Heppell et al. 2003, Seminoff & Shanker 2008). First, the methodology and monitoring effort can differ greatly among nesting beach projects, making compilations of (or comparisons based on) this data challenging (Heppell et al. 2003). Even within projects, methodologies may change over time, making determination of trends in abundance complicated (Heppell et al. 2003). Second, converting nest number estimates to individual abundance estimates requires knowledge of several demographic parameters, such as the following: clutch frequency, length and number of re-migration intervals, nest site fidelity, and nesting success. These conversion parameters can vary across sub-populations; however, calculations do not always consider site-specific values, some, or all of which may not even be available (SWOT Scientific Advisory Board 2011). Furthermore, because of individual and sub-population variation in re-migration intervals, any assessment of trends must be based on long-term datasets (Heppell et al. 2003, Seminoff & Shanker 2008). Finally, nest counts only reflect the adult breeding female component of the population and disregard adult male and juvenile cohorts (Heppell et al. 2003, Seminoff & Shanker 2008). The key sea turtle demographic parameters required to convert to an estimate of total population abundance remain debatable for many species. For example, age at maturity, generation length, survivorship across life stages, and adult and hatchling sex ratios are not clearly defined for leatherbacks (Eckert et al. 2012).

In contrast to nesting beach-based studies, in-water sea turtle research projects in foraging areas offer the potential to monitor a broader cross-section of a species' population and may include adult males, females, and juveniles. Evaluating in-water population abundance of large air-breathing marine vertebrates such as cetaceans and sea turtles traditionally involves relatively costly aerial and/or shipboard surveys (Bjorndal & Bolten 2000, Heppell et al. 2003, Evans & Hammond 2004, Dawson et al. 2008, National Research Council 2010).

Ariel surveys along strip or line transects have the largest geographic scope and can allow for estimates of relative and absolute abundance and density (Marsh & Sinclair 1989a, Shoop & Kenney 1992, Epperly et al. 1995, Cardona et al. 2005, Gomez de Segura et al. 2006, Benson et al. 2007, Jean et al. 2010, Seminoff et al. 2014). The precision of abundance estimates is improved when metrics of species surfacing behaviour inform the application of area-specific correction factors (Pollock et al. 2006, Fuentes et al. 2015). However, aerial surveys are often impractical because of their high cost, variable species detectability (resulting from animal behaviour, environmental conditions, and observer skills), and potential misidentification of species (National Research Council 2010), especially if the survey was primarily designed for marine mammals (Marsh & Sinclair 1989a). Some of these drawbacks can be resolved by incorporating photography (Taylor & Kenney 2014) or conducting *a priori*-designed surveys from vessels (Beavers & Ramsey 1998, Eguchi et al. 2007, Tripathy 2013). Yet vessel survey costs can still be limiting, particularly as vessel size (and associated operating costs) increase (Evans & Hammond 2004, Dawson et al. 2008). Snorkelling or towed-diver strip transect surveys present simpler approaches to estimating abundance from sightings (Roos & Pelletier 2005, Kolinski et al. 2006, Mancini et al. 2015, Stadler et al. 2015). These may be more cost-effective than aerial or large vessel-based surveys, but they are restricted to a smaller spatial scale and are most feasible for species having life history stages involving foraging in shallow coastal waters, where individuals can be relatively easily detected.

Assessment of sea turtle abundance is also possible in projects that incorporate directed captures of individuals with unique identifiers (i.e. flipper tags or passive integrated transponders), using capture-mark-recapture (CMR) methods (for a review of CMR see Pine et al. 2003), provided that recapture rates are high enough. In addition to supporting abundance estimation, CMR studies have the benefit of allowing for concomitant estimates of other demographic parameters such as survivorship and sex ratios (Chaloupka & Limpus 2001) or size-class distributions (Redfoot & Ehrhart 2013). If recapture rates are relatively low but a measure of effort is also recorded, then catch per unit effort (CPUE, normally associated with fisheries biology) can be calculated and used to assess relative abundance (León & Diez 1999, Witherington 2002,

Bresette et al. 2010, Metz & Landry 2013). In CPUE analysis, it is assumed that CPUE is proportional to absolute abundance; however, this may not always hold true (Beverton & Holt 1993, Harley et al. 2001). For example, CPUE may remain high even while actual abundance declines (i.e. hyperstability) due to increasing efficiency of the 'catcher' or an alteration in aggregating behavior by the target species. Alternatively, CPUE may lower while actual abundance increases (i.e. hyperdepletion) due to an alteration in entrapment gear avoidance behaviour by the target species and an associated decrease in catchability. Benefits of the CPUE approach include positive species identification and the capacity to address multiple research objectives with additional sampling (e.g. stock identification via blood or tissue collection) while individuals are captured. CPUE analysis can also be conducted with sightings data only (Eberhardt et al. 1979), sightings data followed by directed captures (Bresette et al. 2010), or with fishery-dependent data (i.e. by-catch; Casale et al. 2007, Pons et al. 2010, Minami et al. 2013). Additionally, spatial modelling techniques combined with sightings data from platforms or ships of opportunity can be used in lieu of standardized surveys and are increasingly being employed to estimate abundances of cetaceans (Hedley et al. 1999, Hedley & Buckland 2004, Williams et al. 2006, Miller et al. 2013).

In waters of the Atlantic Ocean off the coast of Canada, the leatherback sea turtle *Dermochelys coriacea* is listed as Endangered (Species at Risk Act 2002). Satellite tracking suggests that this area supports one of the highest seasonal densities of foraging adult and sub-adult leatherbacks in the NW Atlantic (James et al. 2006b). Leatherbacks in this region originate from numerous nesting beaches throughout the western Atlantic (Stewart et al. 2013), where, in the last decade, there have been detections of stable or increasing nesting trends (Dutton et al. 2005, Girondot et al. 2007, Fossette et al. 2008, McGowan et al. 2008, Stewart et al. 2011, Rivas et al. 2015; however, also see Troëng et al. 2004). It is important to assess whether or not in-water abundance trends of leatherbacks are consistent with these nesting-beach derived trends. We investigated potential changes in relative abundance of leatherbacks estimated from opportunistic sightings per unit effort (SPUE) data obtained during 14 yr of in-water research at a field site off Nova Scotia, Canada. Additionally, we calculated preliminary estimates of absolute abundance at the field site in years where GPS-based vessel tracks provided a spatial component to surveys allowing for the use of spatial modelling techniques.

MATERIALS AND METHODS

Study site

Research was conducted at a field site in temperate continental shelf waters off the NE tip of Cape Breton Island, Nova Scotia, Canada (approximately 47° N, 60° W). This site is proximate to the shelf break, where the Laurentian Channel exits the Gulf of St. Lawrence. Leatherback satellite telemetry research has indicated that this site represents part of a larger seasonal high-use foraging area for this species (James et al. 2005a, 2006b). Therefore, we consider seasonal leatherback occurrence at this site to be representative of the species' broader occurrence in Canadian waters and, as such, it exists as an index area for leatherback monitoring and sampling activities. Dedicated leatherback fieldwork began at the site in 1999; however, effort data was not consistently recorded until 2002. Thus, we restrict our analysis of SPUE data to the years 2002–2015. Omitting these initial years is likely beneficial, as it allowed field team personnel to become experienced and efficient at detecting leatherbacks and, therefore, should remove some variability due to observer experience in the SPUE trend analysis. The timing of field work corresponded to periods of peak leatherback occurrence in coastal areas of Nova Scotia previously identified from patterns of sightings reported by the public (James et al. 2006b, 2007). Field operations were conducted annually during late summer; however, exact dates for years included in the SPUE analysis varied slightly from year to year (2002: Aug 24 to Sep 16; 2003: Aug 21 to Sep 14; 2004: Aug 24 to Sep 10; 2005: Sep 6 to Sep 19; 2006: Aug 13 to Sep 15; 2007: Aug 23 to Sep 21; 2008: Aug 12 to Sep 14; 2009: Aug 20 to Sep 12; 2010: Aug 11 to Sep 3; 2011: Aug 19 to Sep 2; 2012: Jul 28 to Sep 3; 2013: Aug 17 to Sep 24; 2014: Aug 12 to Sep 1; 2015: Aug 19 to Sep 6).

Surveys

We observed leatherbacks from vessels during haphazard unmarked non-linear transect surveys (HUNTs; Bresette et al. 2010). Surveys are an integral part of a larger study of the biology of leatherbacks in Canadian Atlantic waters (James et al. 2005b, 2006b, 2007, Stewart et al. 2013, Wallace et al. 2014, 2015), which includes tagging of live-captured turtles and deployment of archival data loggers on free-swimming turtles. Length of HUNTs in distance and time were not pre-determined and were haphazard with regards to

vessel course decisions. HUNTs were conducted from similar types of ~10 m commercial fishing vessels (Cape Island style), outfitted with 2 m tall observation towers mounted on the wheelhouse roof (observers were ~5 m above the water), and under relatively similar weather and sea state conditions (Beaufort sea state ≤4), with at least 2 experienced observers present. During each HUNT we recorded the time and location of all leatherback sightings, live-captured and sampled turtles opportunistically, and recorded the duration of the HUNT and the number of observers present. Additionally, in a subset of HUNTs (55%), a handheld GPS unit recorded the location of the vessel at minimum 4 min intervals resulting in full (46% of HUNTs) or partial vessel tracks (9% of HUNTs).

Sea surface temperature

Sea surface temperature (SST) may help explain variability in leatherback behaviour and distribution within (Sherrill-Mix et al. 2008) and between years (James et al. 2007, Benson et al. 2011). Therefore, we assessed SST associated with HUNTs to allow for correction of seasonal differences in the timing of HUNTs across years. Daily SST data during HUNTs was obtained from the NOAA Optimum Interpolation 1/4 degree cell resolution daily advanced very high resolution radiometer (AVHRR) SST images. These images used Pathfinder AVHRR data through December 2005, and operational AVHRR data thereafter, and correct for satellite biases using *in situ* data from ships and buoys (Reynolds et al. 2007). The SST data corresponding to HUNT dates were extracted as the average value of the cells falling within a minimum convex polygon (MCP) containing 100% of all available vessel GPS track points (excluding areas over land) collected throughout the study. HUNTs without vessel tracks occurred within the same general area as those with tracks; therefore, the MCP should be reflective of the overall study site. Calculations were conducted using the statistical software R (R Core Team 2014), with the package 'adehabitatHR' (Calenge 2006) to create the MCP and the package 'raster' (Hijmans 2014) to extract average SST values. To assess the accuracy of the satellite-derived SST values, we compared them to SST as measured on the survey vessels using a microprocessor-based hand-held thermometer connected to a stainless steel type 'T' thermocouple probe (model TJ36-CPSS; Omega Engineering) on a subset of days (n =

39 d). The satellite-derived SST values calculated for the study site were positively correlated to mean daily SST as measured on the survey vessel (Pearson's correlation coefficient = 0.62, p < 0.001).

Wind speed

Wind speed was used to represent sea state and, therefore, one index of visibility conditions (Evans & Hammond 2004). Wind speed data was obtained on an approximately hourly basis from the nearest Environment Canada Meteorological Service of Canada weather station located on St. Paul's Island (World Meterorological Organization [WMO] identifier 71418, ~41 km NbW from center of the study site MCP). Although this station is just outside the study site, wind speed data from this station should be reflective of the overall relative conditions at the study site. Wind speed corresponding to each specific HUNT date was calculated as the average value of all records on a given date.

SPUE analysis

To assess potential trends in relative abundance of leatherbacks at our study site, we used 3 different methods. All analyses were conducted using the statistical software R (R Core Team 2014) with an α level of 0.05, and means ± SE are reported unless stated otherwise.

Sea turtle CPUE data is often presented as the number of turtles per hour or per unit area searched (León & Diez 1999, Bjorndal & Bolten 2000, Witherington 2002, Bresette et al. 2010). The first method we used represented a similar approach. HUNT duration was incorporated into SPUE directly, and SPUE was defined as the total number of leatherbacks sighted or captured per HUNT, divided by HUNT duration (no. of leatherbacks h^{-1}). We then calculated the annual relative abundance as the annual mean SPUE. Annual values were normally distributed (Shapiro-Wilk test of normality, p > 0.05), and we assessed annual trends in SPUE by testing for a year effect as a continuous variable using linear regression. This method can identify potential trends in a nominal SPUE while accounting for duration but does not account for the influence of other factors that may affect leatherback detectability.

To remove the impact of factors other than abundance on catch rate, CPUE data is often standardized in fisheries research. The application of generalized

linear models (GLMs) and generalized additive models (GAMs, an extension of GLMs allowing the linear predictor to vary on unknown smooth functions of the predictors; Hastie & Tibshirani 1986) are the most common approaches for this purpose (Maunder & Punt 2004, Venables & Dichmont 2004). Therefore, we chose to standardize sightings per unit effort (SPUE; number of leatherbacks sighted or captured per HUNT) using both a GLM (Method 2), and a GAM (Method 3), that accounted for the effects of factors that may affect detectability (Evans & Hammond 2004), including the number of observers present, SST, and wind speed (i.e. sea state), while using the log of the duration of the HUNT as an offset (Maunder & Punt 2004).

Initial exploration of the dataset using a GLM with a Poisson error distribution indicated overdispersion; therefore, the negative binomial distribution was used in both the GLM and the GAM approaches (Maunder & Punt 2004) using the packages 'MASS' (Venables & Ripley 2002) and 'mgcv' (Wood 2011), respectively. In the GLM approach we selected the variables for the standardization model using an information–theoretic approach (Burnham & Anderson 2002). We used the package 'MuMIn' (Barton 2014) to compare models with all possible 2-way combinations of variables (model subset selection) and retained terms in the standardization GLM found in the top models with the lowest second-order Akaike information criteria (i.e. ΔAICc < 2). In the GAM approach we selected the variables for the standardization model using automatic smoothness selection with null space penalization and restricted maximum likelihood (Marra & Wood 2011). This method allows smoothing terms to be penalized to zero and essentially dropped from the model and does not suffer from the uncertainty inherent in stepwise selection and model subset selection (Marra & Wood 2011). Any term penalized to zero was removed from the GAM standardization model, which was modelled without penalization. In both of these approaches, a categorical year effect was retained in the standardization model, regardless of the results of the selection procedure, because it was the quantity of interest (Maunder & Punt 2004). Standardized annual SPUE was predicted using the median values of the variables selected (Maunder & Punt 2004). The standardized annual SPUE from both approaches were normally distributed (Shapiro-Wilk test of normality, p > 0.05), and annual trends were assessed using linear regression with a year effect as a continuous variable.

Preliminary absolute abundance estimates

Although we suggest the above method is appropriate for assessing annual relative abundance and trends using SPUE data, due to the lack of a spatial component it does not allow for an estimate of the actual number of leatherbacks at the study site. To accurately estimate absolute abundance, researchers traditionally use design-based strip or line transect sampling within the distance sampling framework (Buckland et al. 2004). However, recent developments combing spatial models with distance-sampling data (density surface models: DSM) have allowed for the assessment of absolute abundance from undesigned surveys (Hedley et al. 1999, Hedley & Buckland 2004, Miller et al. 2013), such as those obtained from ships of opportunity (Williams et al. 2006). To obtain preliminary estimates of absolute abundance of leatherbacks at the site in each year, we used a similar approach using HUNTs with vessel GPS tracks. However, because we did not estimate distance from the vessel to each sighted leatherback, we could not use traditional line transect distance-sampling methods to calculate a detection function. Instead, we used a strip transect approach similar to the DSM approach for strip transects suggested by Hedley & Buckland (2004; their Eq. 3.3) with the assumptions that (1) we did not detect leatherbacks beyond 1 km on either side of the vessel, and (2) we did not miss any within this distance (a standard strip transect assumption; Katsanevakis et al. 2012). This strip width was chosen because it is the maximum distance at which we estimate we are able to sight leatherbacks from the survey vessel. Considering there are currently no estimates of leatherback absolute abundance in any northern NW Atlantic foraging area, we believe the preliminary estimate derived for the study site off Cape Breton Island provides important context.

DSMs are often a 2-stage process whereby the detection function is fit first using estimated distances to sighted animals and then given the detection function, fitting a spatial model using a GAM (Miller et al. 2013). Factors that account for detectability are often incorporated into the first stage (Marques & Buckland 2003), but since we could not fit a detection function, we chose to incorporate factors that may impact detectability directly into the DSM. Thus, we used a combination of spatial (i.e. SST) and non-spatial covariates (i.e. number of observers), essentially combining a similar stan-

dardization method as previously described for the SPUE analysis, with spatial influences, in 1 step. The DSM dataset contained all HUNTs with GPS-based vessel tracks across all years. Because the measure of effort was now spatial and not temporal, this resulted in a loss of data, as not all years or HUNTs included in the SPUE analysis at our field site had vessel tracks.

Our first step in developing the DSM was to split each vessel track into contiguous segments. Segment length in DSMs are chosen arbitrarily but should be small enough such that neither density of objects, nor covariate values, vary appreciably within a segment (Miller et al. 2013). We chose a segment length of 5 km but also explored models using 2 and 10 km segment lengths and found little difference in the resulting abundance estimates. We then modelled the total number of leatherbacks sighted or captured per segment as a sum of the smooth functions of the same covariates that accounted for detectability as in the above SPUE analysis: SST, wind speed, and the number of observers present. This time, SST was extracted as the mean value of the AVHRR data for each segment, but wind speed remained as the daily average because it was not spatially variable, nor did all hours have values, and we did not want to further decrease the resolution of the dataset. We also included a bivariate smooth function for the locations of the midpoint of each segment, expressed as northing and easting, to account for the isotropic nature of the smoother (Miller et al. 2013). Since we were using all available data, year was included as a categorical parametric term.

The models also included an offset term. DSM offset terms for line transect data usually include segment length multiplied by effective strip width and the estimated probability of detection (Eq. 3.4 in Hedley & Buckland 2004), as estimated by the detection function. The probability of detection can be divided into the probability an observer misses a visible animal (perception bias) and the probability that an animal is not visible but present (i.e. under the surface, availability bias; Marsh & Sinclair 1989b). Perception bias is often incorporated by modelling distance data and, although less frequently applied, there are numerous methods to incorporate availability bias into the detection function, including using animal-informed information (Laake & Borchers 2004, Pollock et al. 2004, Fuentes et al. 2015). Considering leatherbacks in this area spend a lot of their time submerged (James 2006a, Wallace et al. 2015), we

decided to incorporate a term for availability bias into our offset. Thus, our offset was the product of the length of the segment multiplied by the width of the strip and the mean proportion of time spent at the surface by leatherbacks (0.385) at our study site. The mean surface time value we used was obtained from high-resolution archival dive data collected from leatherbacks at this field site (n = 21, deployment length range; 55.5 to 212.7 min) during the daytime in 2008, 2009, 2010, 2011 and 2013 (Wallace et al. 2015). The value represents the mean proportion of time spent at the surface for the duration of the deployment across all individuals. We chose to use the 0.385 surface time value derived from high-resolution archival data loggers rather than from satellite tag-derived values (e.g. James et al. 2006a), as the archival data was obtained from leatherbacks within the study site during the same time period (season and daylight hours) as HUNTs. In our DSM we assume this surface time value remains constant across time and space.

We selected final terms for the DSM by initially fitting a GAM using automatic smoothness selection with null space penalization and restricted maximum likelihood (Marra & Wood 2011) and using a negative binomial distribution (Miller et al. 2013) using the package 'mgcv' (Wood 2011). Any term penalized to zero was removed from the final DSM, which was modelled without penalization. To use the final DSM to predict abundance over the study site, we created a 1 km grid covering a MCP bounding all HUNTs (Miller et al. 2013). We then predicted abundance for each grid cell in each year separately using the final DSM and a new dataset containing year (valued as the year of interest), median values of all other covariates in each dataset, and the midpoints of each cell. Cell area was incorporated into the offset term (rather than segment area). The absolute abundance of leatherbacks in each year was estimated as the sum of the predicted cell values (Miller et al. 2013). Confidence intervals of the abundance estimates were calculated using variance propagation (Wood 2006). This method uses the distribution of the parameters in the GAM to simulate model coefficients and then uses them to generate replicate (1000) abundance estimates, and it is the recommended method to obtain variance estimates in DSM models (Miller et al. 2013). However, we note that these estimates do not include the uncertainty inherent in the calculation of the mean value of surface time incorporated into the offset term in the models.

RESULTS

SPUE

The minimum convex polygon encompassing all available survey vessel track points had an area of 1503.6 km² (Fig. 1), and a total of 564 leatherbacks were sighted or captured at our field site in years where effort was consistently recorded (n = 14; 2002–2015; Fig. 2). A total of 179 HUNTs occurred across these years (median: 11.5 HUNTs yr^{-1}; range: 5–23 HUNTs yr^{-1}), with a median duration of 6.6 h (range: 2.3–15.5 h), and a median of 4 observers present (range: 2–13 observers). Median SST during HUNT dates was 17.5° C (range: 12.8–21.0° C), and median daily average wind speed on HUNT dates was 23.4 km h^{-1} (range; 6.9–52.0 km h^{-1}).

The overall mean SPUE (no. of leatherbacks h^{-1}) at the field site was 0.38 ± 0.09; ranging from a low of 0.02 ± 0.02 in 2005, to a high of 0.69 ± 0.15 in 2014 (Table 1). There was no significant linear effect of year (β = 0.02, 95% CI [−0.005, 0.04], p = 0.11, overall model r² = 0.20) on SPUE (no. of leatherbacks h^{-1}). When expressing SPUE as the number of leatherbacks per HUNT, the annual average nominal SPUE (no. of leatherbacks per HUNT) at the field site ranged from a low of 0.2 ± 0.2 in 2005 to a high of 6.2 ± 2.0 in 2014 (Fig. 3A). Both the GLM and GAM standardization models included all terms contained within the initial global models since either all variables were present in the top models (GLM, ΔAICc < 2; Table 2) or no terms were penalized to zero (GAM; Table 3). The GLM standardized SPUE
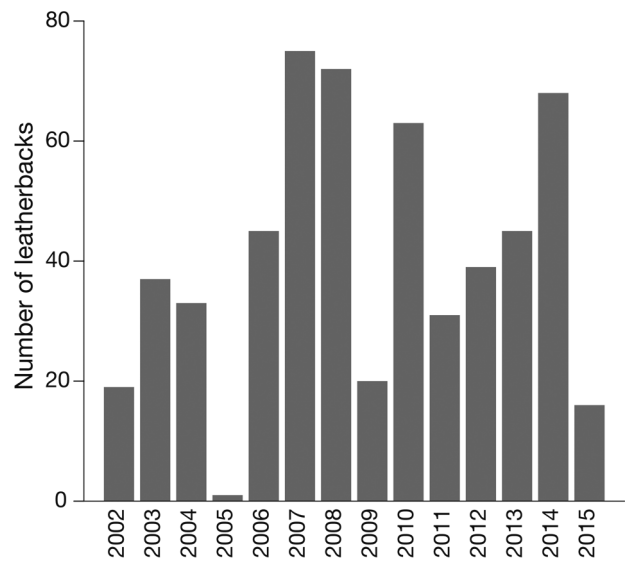

Fig. 2. Total numbers of leatherback sea turtles *Dermochelys coriacea* sighted or captured in each year (2002–2015) at the study site
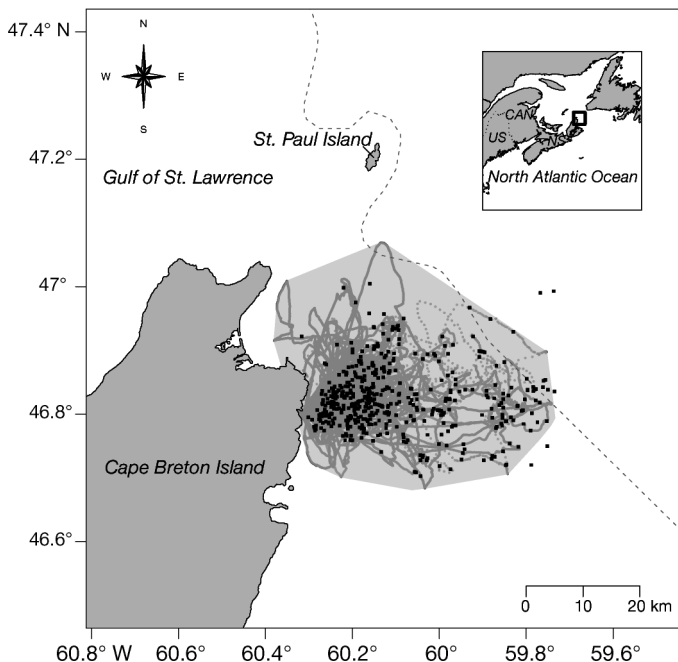

Fig. 1. Study site off the NE tip of Cape Breton Island, Nova Scotia (NS) as represented by a minimum convex polygon (MCP; light grey) encompassing 100% of vessel GPS track points (grey circles) recorded by handheld GPS units during a subset of haphazard, unmarked, non-linear transects (HUNTs) (from 2006 to 2010 and 2012 to 2015). Squares: leatherback sea turtle sightings or captures (2002–2015). Dashed line: 200 m isobath; inset: general location of site in Atlantic Canada
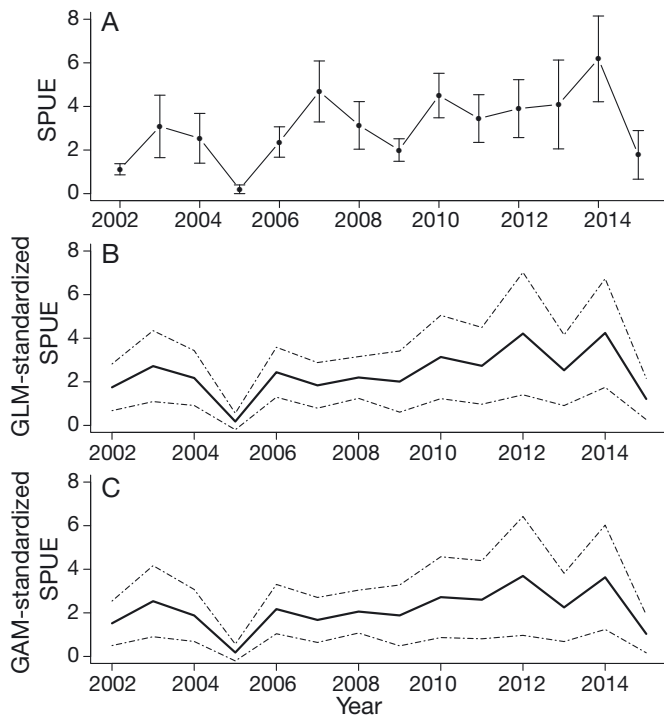
Table 1. Mean annual nominal sightings per unit effort (SPUE) (no. of leatherbacks sighted or captured h^{-1}) at the study site with annual coefficient of variation (CV or relative standard error, SE/mean; Dawson et al. 2008)

Year	Mean SPUE (no. h^{-1})	CV
2002	0.20	0.23
2003	0.35	0.34
2004	0.27	0.38
2005	0.02	1.00
2006	0.34	0.25
2007	0.48	0.22
2008	0.43	0.31
2009	0.24	0.24
2010	0.52	0.25
2011	0.43	0.24
2012	0.54	0.27
2013	0.45	0.39
2014	0.69	0.22
2015	0.14	0.58

Fig. 3. Mean (±SE) (A) annual nominal sightings per unit effort (SPUE) (no. of leatherbacks sighted or captured per haphazard, unmarked, non-linear transect [HUNT]), (B) generalized linear model (GLM)-standardized SPUE and (C) generalized additive model (GAM)-standardized SPUE at the study site across 14 yr. Solid trend lines: standardized SPUEs; dot-dashed lines: 95% confidence limits. Both standardization approaches accounted for the effects of wind speed, number of observers, and sea surface temperature (SST) with the log of the duration of HUNT included as an offset in models. Predictions were made using median values of these variables at this site in these 14 yr

(no. of leatherbacks per HUNT) fluctuated annually, ranging from a low of 0.18 ± 0.19 in 2005 to a high of 4.24 ± 1.27 in 2014 (Fig. 3B), and there was no significant linear effect of year (β = 0.10, 95% CI [−0.04, 0.25], p = 0.16, overall model r^2 = 0.16). The GAM standardized SPUE (no. of leatherbacks per HUNT) fluctuated annually, ranging from a low of 0.18 ± 0.20

Table 3. Generalized additive model (GAM) standardization model selection summary. Variables were selected from the terms not penalized to zero in this initial GAM fit using automatic smoothness selection with null space penalization and restricted maximum likelihood (Marra & Wood 2011). The model investigated the effects of year (categorical parametric), wind speed, number of observers and sea surface temperature (SST) on sightings per unit effort, with the log of the duration of haphazard, unmarked, non-linear transect as an offset. Year was retained in the final standardization model regardless of significance because it was the term of interest; final model was fit without penalization. Model overall r^2 = 0.40; second order Akaike information criterion = 746.2

Term	df or edf (smooths)	χ^2	p
Parametric terms:			
Year	13	15.2	0.295
Smooth terms:			
s(Wind speed)	1.95	11.4	0.001
s(No. of obs.)	0.93	1.89	0.124
s(SST)	1.02	2.24	0.099

in 2005 to a high of 3.69 ± 1.39 in 2012 (Fig. 3C), and there was no significant effect of year (β = 0.09, 95% CI [−0.04, 0.21], p = 0.17, overall model r^2 = 0.15).

Preliminary absolute abundance estimates

Initial model fitting with null space penalization did not result in the removal of any terms from the DSM model (Table 4). Assuming a 1 km strip width, absolute abundance estimates ranged from 18.3 ± 0.5 leatherbacks in 2015 to 569.5 ± 20.3 in 2007 (Table 5). The resultant abundance map (Fig. 4) indicates regions of high leatherback abundance near the 200 m isobath. We reiterate that these are preliminary estimates of absolute abundance considering the ad hoc nature of the assumed strip width; that only a subset of HUNTs had vessel tracks; and that the spatial survey coverage of the entire study area varied from year to year (Table 5).

Table 2. Variable selection for the generalized linear model (GLM) standardization model was determined from the terms present in the top models (Akaike information criteria, ΔAICc < 2) of all possible 2-way combinations of variables (wind speed, number of observers [obs], sea surface temperature [SST], and year, using the log of the duration of haphazard, unmarked, non-linear transects [HUNTS] as an offset) with sightings per unit effort (SPUE) as the response variable in a GLM fit with the negative binomial distribution. Year was retained in the standardization models because it was the term of interest

Model	df	AICc	ΔAICc	Akaike weight
SPUE ~ 1 + Wind speed + No. of obs. + offset(log(Duration))	4	734.9	0.00	0.347
SPUE ~ 1 + Wind speed + No. of obs. + SST + offset(log(Duration))	5	735.2	0.28	0.302
SPUE ~ 1 + Wind speed + offset(log(Duration))	3	735.9	0.93	0.218

DISCUSSION

The relative abundance of leatherbacks at our study site over the last 14 yr exhibits high inter-annual variability but appears to be stable, as there were no significant linear effects of year on nominal annual SPUE (leatherbacks h^{-1}) or standardized SPUE (leatherbacks per HUNT). Although non-significant, taking into account that the linear effect

of year was positive using all methods, and never significantly negative, it seems improbable that leatherbacks are decreasing in relative abundance in this

Table 4. Density surface model (DSM) selection summary. Variables were selected for the DSM model as the terms not penalized to zero in this initial generalized additive model fit using automatic smoothness selection with null space penalization and restricted maximum likelihood (Marra & Wood 2011). Total number of leatherbacks per segment was modelled with the effects of year (categorical parametric), wind speed, number of observers, sea surface temperature (SST), a bivariate term for the easting (E) and northing (N) midpoint locations of the segment, and with the log of segment area multiplied by mean leatherback surface time (0.386) as the offset term. Year was retained in the final DSM regardless of significance because estimates of abundance in each year were desired and it was the term of interest; final model was fit without penalization. Model overall r^2 = 0.16 and second order Akaike information criterion = 1460.0

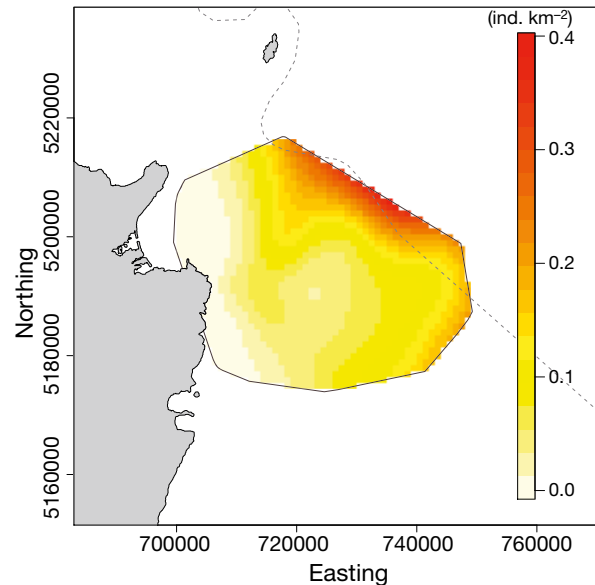| Term	df or edf (smooths)	χ^2	p
Parametric terms:			
Year	8	47.6	<0.001
Smooth terms:			
s(Wind speed)	3.34	24.4	<0.001
s(No. of obs.)	2.22	20.9	<0.001
s(SST)	5.30	24.3	<0.001
s(N, E)	14.2	67.7	<0.001

Fig. 4. Preliminary estimates of leatherback abundance in 2014 per 1 km grid cell at the study site. Estimates represent the predicted abundance in each grid cell from a density surface model (DSM) that incorporated the midpoint of each grid cell, year valued as the year of interest, median values of all other covariates in each dataset, and including cell area into the offset term rather than segment area. Because we fit the DSM using all available data with categorical parametric terms for year without any interaction with the bivariate smoothes for grid cell midpoint (northing and easting), the spatial relationship remains the same across all years with only the absolute values of predicted abundances changing. Dashed line: 200 m isobath

Table 5. Preliminary estimates (est.) of annual leatherback absolute abundance at the study site using a 1 km (likely maximum distance at which leatherbacks were sighted) ad hoc assumed strip width. Estimates determined from the sum of the predicted abundances of each cell in a 1 km grid overlaid on a minimum convex polygon (MCP) of survey vessel GPS track points. Predicted abundances for each cell in each year were made using the midpoint of each grid cell, year valued as the year of interest, median values of all other covariates in the dataset, and incorporating cell area into the offset term rather than segment area. Confidence intervals (95%; in brackets) of the abundance estimates were calculated using variance propagation (Wood 2006, Miller et al. 2013). Density estimates calculated by dividing the abundance estimate by the area of the MCP (1503.6 km^2) and converting this to an estimate per 100 km^2. HUNT: haphazard, unmarked, non-linear transect. No vessel GPS tracks available for 2011

Year	Abundance est. [95% CI]	Density est. (ind. 100 km^{-2})	Proportion of HUNTs with vessel tracks	Proportion of overall MCP covered by annual MCP
2006	125 [119–130]	8.3	0.75	0.44
2007	570 [530–609]	37.9	0.94	0.58
2008	80 [76–84]	5.3	0.75	0.78
2009	137 [128–14]	9.1	0.55	0.38
2010	52 [50–55]	3.5	0.47	0.38
2011	–	–	0	–
2012	135 [127–142]	9.0	0.90	0.38
2013	56 [53–58]	3.7	1.0	0.35
2014	149 [142–155]	9.9	1.0	0.21
2015	18 [17–19]	1.2	1.0	0.74

area. When considering conservation objectives, the lack of any support for a decreasing trend is encouraging. Considering the population using this site is composed of individuals originating from numerous nesting beaches throughout the NW Atlantic (James et al. 2007, Stewart et al. 2013), our results are consistent with the stable or, in some cases, increasing trends reported for leatherbacks at several nesting sites in the NW Atlantic in the last decade (Dutton et al. 2005, Girondot et al. 2007, Fossette et al. 2008, McGowan et al. 2008, Stewart et al. 2011, Rivas et al. 2015). However, it should be noted that the stable or increasing nesting trends at some sites is not necessarily uniform throughout all the western Atlantic leatherback nesting areas (e.g. Troëng et al. 2004). The stable index of relative abundance found at our site may be due to the inclusion of adults and sub-adults of both sexes (James et al. 2007), combined with the amalgamation of varying demographics of different nesting stocks throughout the western Atlantic (Stewart et al. 2013).

The stable relative abundance of leatherbacks reported here for the period 2002–2015 must be interpreted with caution, as it reflects data collected opportunistically at one site only and the relative density of leatherbacks outside of the study area is not understood. For these reasons, we cannot extrapolate our findings to the broader North Atlantic leatherback population. Additionally, CPUE studies inherently assume that CPUE is proportional to actual abundance, which may not always hold true (Beverton & Holt 1993, Harley et al. 2001). Increases in efficiency of the techniques used could result in an apparent increase or maintenance of a level CPUE while actual abundance is decreasing (i.e. 'hyperstability'; Katsanevakis et al. 2012). Although it is possible that the field team became increasingly efficient at detecting leatherbacks throughout the duration of the study, we suggest that, by excluding the first 3 yr of data from the SPUE analysis, we have accounted for any drastic improvements in detectability associated with enhanced field team turtle sighting skills. We also expect that in the first 3 yr of at-sea research, the field team would have had enough time to hone their techniques and become efficient at detecting leatherbacks. Furthermore, throughout the duration of the study, the sampling period remained relatively constant; there was consistency in the core members of the field team; and the survey vessel, associated equipment, and scientific protocols did not change appreciably. The coefficient of variation (CV) of our surveys was less than 1 in all but one year (Table 1) and mostly in the range of what is considered good

(~0.3; Dawson et al. 2008). Yet, regardless of our efforts to standardize important elements of our methodology, sea turtles often cluster in space and time. Furthermore, because research objectives were not limited to evaluating turtle abundance but also involved sampling turtles, surveys often targeted discrete areas where earlier work yielded relatively high turtle densities. Both factors can lead to a non-linear relationship between CPUE and actual abundance (Beverton & Holt 1993). Nevertheless, although our sampling regime ideally would have been random in space and time, to possibly support broader inferences, non-random sampling with consistent methodology can be valuable to assess annual trends in sea turtle abundance at specific sites (Bjorndal & Bolten 2000, National Research Council 2010).

The only other multi-year assessment of relative abundance of leatherbacks in a temperate foraging area corresponded to aerial surveys off the coast of California, USA (1990 to 2003), where no trend was found (Benson et al. 2007). However, Benson et al. (2007) did find a positive relationship between leatherback relative abundance and average annual Northern Oscillation Index (NOI) values, suggesting that positive NOI might be favorable for gelatinous prey production off the coast of California. Unfortunately, comparable data regarding the distribution or trends in abundance of jellyfish within the NW Atlantic are not available. Gibbons & Richardson (2009) did not identify any environmental variables with a significant influence on the long-term inter-annual variation in abundance of jellyfish in shelf waters of the North Atlantic. However, they used continuous plankton recorder (CPR) data, and the relevance of such sampling as a tool for assessing distribution of scyphozoan jellyfish, including *Cyanea capillata*, the primary prey of leatherbacks at our study site (Wallace et al. 2015), is debatable. In NE Atlantic shelf waters of the North Sea, Lynam et al. (2005) found that abundance of scyphozoan jellyfish was related to climate indices, such as the North Atlantic Oscillation Index (NAOI), but the response was contrasting in different regions. Considering these results, and a lack of data near our study site, we did not investigate any variables that could influence jellyfish biomass in our study. However, as leatherbacks are likely capable of tracking prey distributions (Houghton et al. 2006), habitat conditions specific to our site could cause independence from any trends in the broader North Atlantic leatherback population and could possibly explain some of the intra-annual variation we observed.

Abundance and distribution of scyphozoans in shelf regions of the NE Atlantic (Irish Sea) can vary greatly between years and sub-regions (Bastian et al. 2014). If such variability in jellyfish abundance and distribution exists in the region of our study area, it may result in fewer turtles remaining in areas of low jellyfish density, leading to low detectability. For example, we speculate that in 2005, when there was only one leatherback sighted at our field site, jellyfish prey density was relatively low and most leatherbacks therefore proceeded through the area and into the Gulf of St. Lawrence prior to the start of our turtle surveys. Further research investigating jellyfish distribution and densities at this field site is critical to understanding leatherback distribution in the region.

To our knowledge, no comparable SPUE data exist for leatherbacks in other foraging areas. In-water census methods have been used for other sea turtle species (e.g. snorkelling surveys for hawksbill sea turtles, *Eretmochelys imbricata*, represented as the number of turtles h^{-1}; León & Diez 1999, Bjorndal & Bolten 2000); however, meaningful comparisons to our results are not evident because of divergent survey protocols, and different species, habitats, life history traits, and demographics.

Despite using opportunistic methodology, with its inherent limitations, we have confidence in our preliminary estimates of annual abundance at our study site because when we divide them by its area, we obtain density estimates (mean, 9.8 leatherbacks per 100 km^2) within the realm (albeit higher) of those reported from standardized aerial surveys (range 0.1 to 3.3 leatherbacks per 100 km^2; Shoop & Kenney 1992, Benson et al. 2007). Our higher estimate is not surprising when we consider that opportunistic sightings and satellite telemetry has revealed that this region is one of the most important foraging areas for leatherbacks in the NW Atlantic (James et al. 2006). At this site, even when we exclude the possible high value outlier in 2007, the mean annual preliminary abundance estimate converts to 6.2 leatherbacks per 100 km^2. This represents the highest in-water density of leatherbacks reported to date, consistent with designation of Canadian waters as critical foraging habitat for this species. However, it is important to note that all of the annual relative and preliminary absolute abundance estimates presented here represent average seasonal snapshots. They may actually be underestimates if residency times at the study site are shorter than seasonal field operations. We suspect this could be the case, as satellite telemetry data has revealed that leatherbacks tagged early in the season in this same area often move northwards into

the southern Gulf of St. Lawrence (James et al. 2005a,b, 2006a, and M.C.J. unpubl. data), and GPS tracks collected by high-resolution data loggers attached to leatherbacks at the study site are often linear (Wallace et al. 2015), indicating directed horizontal movements. Additionally, if we double the post hoc assumed strip width (and assume we did not detect leatherbacks beyond 2.0 km on either side of the vessel), the corresponding abundance estimates (50% of what is reported here) would still represent the highest in-water density of leatherbacks reported anywhere. Considering there are currently no estimates of leatherback absolute abundance in any northern NW Atlantic foraging area, we believe the preliminary estimate derived for our study site provides important context.

Our results further emphasize the significance of Canadian waters, and research and conservation efforts there, to North Atlantic leatherbacks. It is possible that at our study site, tens — if not hundreds — of leatherbacks are present on any given day in late summer. Although highly fluctuating, we found the relative abundance of leatherbacks at this site to be stable from 2002 to 2015. This result is important because this foraging population includes adults and sub-adults of both sexes (James et al. 2007) and represents all principal nesting stocks throughout the western Atlantic (Stewart et al. 2013). Our results complement nesting beach-based abundance assessments and highlight the value of in-water population assessments.

This study used turtle sightings data collected opportunistically while searching for leatherbacks in support of other research objectives to facilitate assessment of trends in relative abundance and estimate absolute abundance. Therefore, this work highlights the value of recording both observer effort and sightings data in the course of long-term research projects and the merit of non-randomized surveys with reasonable spatial coverage (Williams et al. 2006). The methods applied here could be used to assess relative and absolute abundances of other surfacing marine species sighted from ships of opportunity (e.g. ferries, cruise ships, freighters and fishing boats), or from research vessels where other science objectives take priority and preclude more systematic surveys. Furthermore, this study was posited on a sightings dataset derived from long-term monitoring. Increasingly, scientists and resource managers are recognizing the importance of long-term monitoring to successful marine management (Day 2008, Katsanevakis et al. 2011), including assessment of population trends among long-lived, late-maturing

species with long generation times, such as cetaceans and turtles. Only through long-term monitoring programs can we detect changes in species' abundance (Thomas 1996) and evaluate potential relationships with environmental and anthropogenic stressors (Magurran et al. 2010). Continued monitoring of leatherbacks at high latitude foraging areas, including this site and others is, therefore, vital to making informed conservation decisions for this endangered species. Recognizing these and other benefits, systematic monitoring of leatherback abundance is now occurring at a second long-term field site off the coast of Nova Scotia, with comparable data collection protocols in place, and will hopefully provide future insight into the applicability of the present results to the broader leatherback foraging region.

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