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Surfacing characteristics and diving behaviour of blue whales in Sri Lankan waters

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ABSTRACT

Surfacing behaviour and dive characteristics were quantified from focal follows of individual blue whales between January–March 2012 and 2013. During this period individual whales were followed from small boats to observe their surfacing patterns and breathing behaviour. Data on time at first surface, length of surface interval, number of blows, final dive time and whether or not the whale 'fluked up' before a deep dive were recorded. A step-wise modelling approach was used to estimate a number of surfacing characteristics: mean Inter-Breath Interval (IBI), bout duration and the number of surfacings in a bout. First, dives were classified as either surface dives or deep dives based on the occurrence of arching or fluking behaviour at the surface prior to a deep dive. The mean IBI of surface dives was 17.6 s (SD = 26.14) and for deep dives, 640.3 s (SD = 214.38). To account for temporal dependence between dive types, a first-order Markov chain was used to estimate the transition probability between dive types. Time series of dive types were then simulated, using Monte Carlo methods, while accounting for heterogeneity in IBI of the different dive types. The mean IBI of blue whales in Sri Lanka, obtained from the Monte Carlo methods, was 84.7 s (SD = 11.17). The mean bout duration was 145 s (SD = 28.31), with the mean number of breaths per surface bout being 9.3 (SD = 1.43). Whales also lifted their tail flukes out of the water on 55% of terminal dives, which is considerably more frequent than elsewhere in the world. These results significantly advance our understanding of blue whales in Sri Lankan waters. More specifically, this information is essential for the calculation of precise abundance estimates as it informs the detection probability parameters for line transect surveys. In this way it will help formulate better management decisions related to the conservation of this population.

1. Introduction

Many wild animals are elusive or inhabit a hostile environment making it difficult if not impossible to observe them as they undertake critical activities such as feeding, breeding or escaping predators. Yet if we are to understand the pressures on a population or species, we need to be able to appropriately interpret the aspects of their lives that we can observe. For air breathing marine vertebrates such as whales, dolphins, seals, and turtles the need to breathe forces them to return frequently to the surface where we can at times observe them in their natural environment. Quantifying this behaviour provides a powerful tool for interpreting different aspects of their life history and also provides us with a means of increasing precision in any estimates of abundance of populations.

The issue of surface visibility applies to a range of taxa whose abundance is assessed through direct counts. Aerial and ship-board surveys have been widely used to estimate abundances and population sizes for various marine species (Forney et al., 1995; Marsh and Saalfeld, 1989; Rowat et al., 2009; Sims et al., 2005). The importance of collecting surfacing and diving behaviour data to calculate availability correction factors for increasing the precision of abundance estimates has been highlighted through numerous studies (Heide-Jørgensen et al., 2010a, 2010b, 2012; Sims et al., 2005; Thomson et al., 2012, 2013). Correction factors account for the amount of time an animal is unavailable or undetectable at the surface and allow for the adjustment of otherwise negatively biased abundance estimates (Marsh and Sinclair, 1989).

Diving duration and surfacing behaviour have been examined for many of the great whales including fin whales *Balaenoptera physalus* (Kopelman and Sadove, 1995), minke whales *Balaenoptera acutorostrata* (Stern, 1992), grey whales *Eschrichtius robustus* (Harvey and Mate, 1984), bowhead whales *Balaena mysticetus* (Krutzikowsky and Mate, 2000; Würsig et al., 1984), humpback whales (Baird et al., 2000; Gulesserian et al., 2011) and blue whales *Balaenoptera musculus* off Monterey Bay, California (Lagerquist et al., 2000), using observations of surfacing data or satellite derived data. Given the precarious state of

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many whale populations obtaining precise measurements of observable behaviours is an essential step in improving our understanding of their ecology. Studies of surfacing and diving habits also provide useful information for management of these populations. This information is critical for calculating detection probabilities, through precise estimates of the proportion of time whales are visible at the surface (Dorsey et al., 1989; Würsig et al., 1984) and thereby adjusting shipboard and aerial counts to provide accurate abundance estimates (Doi, 1974; Hiby and Hammond, 1989).

Data for the calculation of these correction factors are generally derived from tags deployed on individual animals. Tag-derived data offers the opportunity to collect high resolution information on individual whales' diving behaviour continuously, over long periods of time and distances, accounts for diurnal variation and in many cases reduces the bias due to the presence of a research vessel in the vicinity. Despite the disadvantage of having to recover archival tags to retrieve data, they provide fine-scale information about critical sub-surface behaviours such as foraging that cannot be collected through visual surveys (Johnson and Tyack, 2003). The limitations associated with visually collecting dive data such as the necessity for calm weather, good visibility, the fact that data collection is limited to daylight hours and the short-term nature of the data sets likely biases correction factors as has been shown in studies that compared tag data vs. visual data (Harvey and Mate, 1984; Lagerquist et al., 2000).

Blue whales in the northern Indian Ocean are thought to be a subgroup of the pygmy blue whales (*B. musculus* spp.). They possess a different acoustic call (Alling and Payne, unpublished) and are five metres shorter than their Antarctic counterparts (Mikhalev, 2000). Unlike blue whales in other ocean basins, they do not undertake poleward migrations to feed, but remain in low-latitude waters year-round with a part of their population remaining resident in Sri Lankan waters (Afsal et al., 2008; Alling et al., 1991; Branch et al., 2007; de Vos et al., 2012; Ilangakoon, 2006). This population is at risk of ship strike, as prime blue whale habitat lies adjacent to some of the most heavily used shipping lanes in the world (Kaluza et al., 2010). Yet at present, relatively little data is available on the ecology of blue whales in Sri Lankan waters. The aim of this paper is to quantify the diving and surfacing characteristics of this population of blue whales. While we acknowledge that the use of telemetry is a necessary step to refine the results provided through this study, it represents the first attempt to quantify three important surfacing parameters which are essential to any attempts to estimate abundance of this potentially isolated population, and thereby assess its conservation status.

2. Methods and materials

2.1. Study site

The study site was located off the southern coast of Sri Lanka (Fig. 1). Blue whales are regularly sighted in high numbers within these waters with the Northeast monsoon from January to March providing ideal conditions for observing and documenting blue whale behaviour.

2.2. Boat based surveys

Data on blue whale surfacing intervals and dive characteristics were systematically recorded through focal follows conducted between January–March 2012 and 2013 off southern Sri Lanka. In both seasons dedicated research platforms were used for the surveys. Two observers were seated 1–2 m above water level and scanned for blue whales. The focal sampling technique used was adapted from Altmann (1974).

Once a whale was sighted the boat would attempt to approach the whale. At a distance of 50 m, if the whale was travelling, the boat would slow and turn to match the speed and direction of the whale. If the whale was circling and displaying high turning rates typical of feeding whales, the boat was positioned on the outer side of the circle to ensure that the whale's behaviour remained undisturbed. Whenever possible photo-identification images were taken of the individuals being followed. Once photos had been taken, the boat was moved to within 100 m of the whale. To minimise the possibility that some surfacings in a sequence would be missed, the boat was kept within 100 m of the whale and travelled at the same speed and in the same direction as the surfacing whale. Effort was also made to locate the 'footprint' of the terminal dive in a surfacing sequence. The boat was then manoeuvred on to the footprint and a GPS location taken. During a focal follow the following data were gathered: number of individuals, behaviour, time of first surfacing, time of each subsequent blow and time of final blow measured to the nearest second, whether or not the whale 'fluked up' before a deep dive and GPS location of foot print.

To describe the diving and surfacing characteristics of blue whales in Sri Lankan waters, it was necessary to first distinguish between different dive types. Previous studies have shown that blue whale dives can be separated into relatively shorter surface dives (IBI = 22.0 s, SD = 4.7) and relatively longer deep dives (IBI = 635.6 s, SD = 405.4) (de Vos et al., 2011). A 'fluke up' dive constituted of the whale lifting its tail flukes out of the water before a deep dive and a non-

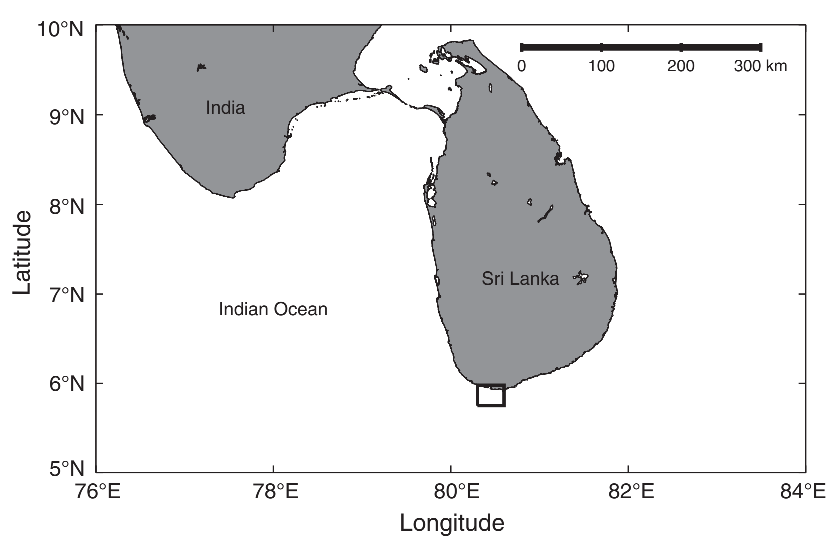

Fig. 1. Location of study site off southern Sri Lanka (black box).

fluke up dive comprised of a 'high arch' dive where the whale arched its back steeply before sinking below the surface prior or a 'lazy fluke' where the whale skimmed the surface of the water with its tail fluke prior to the deep dive. Time series of Inter-Breath Intervals (IBI) were estimated as the time between two surfacings in a focal follow. Based on this, all dives preceded by a high arch, lazy fluke or fluke were classified as deep dives and all other dives classified as surface dives.

A typical dive cycle of a blue whale is a series of surface dives followed by a deep dive. The time period between the first surfacing after a deep dive and the last surfacing before the next deep dive was called a surfacing bout. Based on this classification of dives, a number of metrics were estimated to describe the diving and surfacing characteristics of the blue whales during a follow: mean IBI, bout duration and number of surfacings in a bout.

In the event that a whale watch boat (or multiple) was present within 300 m of a surfacing whale, the research vessel would maintain a distance of 300 m from the whale and only document fluking behaviour. No other metrics were gathered during these encounters due to the risk of missing surfacings in the presence of multiple boats.

2.3. Data analysis

To obtain unbiased estimates of mean IBI, both surface dives and deep dives need to be recorded with the same probability. If the data sampling is more likely to record one of the two dive types, this can lead to the mean IBI estimates either being positively (if more deep dives are recorded) or negatively (if more surface dives are recorded) biased. While surface dives within a bout are relatively easy to record from the same individual, the long duration of deep dives often makes it hard to predict where and when the whale will surface after the dive. When several whales are present in the same area (off Sri Lanka at times up to ten individuals) the chances of confusing the focal whale with another whale, and thus missing the surfacing time, is also relatively high. As a result, many focal follows ended up constituting only a single dive cycle, and some just a single surfacing bout. To overcome this sampling bias when estimating mean IBI of the follow, the temporal dependence between dive types within follows was estimated, using a first-order Markov chain (Caswell, 2001; Guttorp, 1995). The time series data of dive types, one for each follow, were first compiled into two-way contingency tables of preceding dive type versus succeeding dive type (Christiansen et al., 2010; Lusseau, 2003) using R (R Development Core Team, 2013). If a follow ended with a high arch or a fluke (indicating the transition from a surfacing dive to a deep dive), an additional transition from surfacing dives to deep dives was added to the contingency table to reduce any sampling bias from missing the longer deep dives. For the same reason, a transition from deep dives to surfacing dives was also added, since a deep dive was never observed directly following another deep dive in this dataset. Transition probabilities from preceding to succeeding dive types were then calculated using the following equation (Lusseau, 2003):

$$P_{ij} = \frac{\alpha_{ij}}{\Sigma_{j=1}^{n} \alpha_{ij}}, \Sigma_{j=1}^{n} P_{ij} = 1$$

where i is the preceding dive type, j is the succeeding dive type, n is the total number of dive types (i.e. two), a_{ij} is the number of transitions observed from dive types i to j, and P_{ij} is the transition probability from i to j in the Markov chain. To test whether or not the estimated contingency table differed from a theoretical distribution, a goodness of fit test was performed using Pearson's chi-squared test in R.

To estimate the surfacing metrics (mean IBI, bout duration and number of surfacings in a bout), Monte Carlo methods were used to simulate individual time series (follows) of dive types based on the transition probability matrix obtained from the Markov model. The methods are the same as those described in Christiansen et al. (in press). 1000 simulations were run. First, an empty vector of dive types was created in R, with each empty value representing a sampling unit to which a dive type and duration (i.e. IBI), were randomly assigned. The initial dive type was arbitrarily categorised as a surface dive. The next dive type was then randomly chosen based on the transition probability matrix obtained from the Markov chain model. This procedure was repeated for the entire vector. To account for the heterogeneity in duration of dive types (i.e. the variation in IBI) a duration was assigned to each dive type by randomly selecting with replacement an IBI from the "distribution" of IBIs obtained from the raw data. Each dive assigned as a surface dive was given a random IBI from the "distribution" of IBIs classified as surface dives, while each dive assigned as a deep dive was given a random IBI from the "distribution" of IBIs classified as deep dives. After allocating dive types, and durations of dive types, the first 100 dives in the time series were removed as a burn-in period so that each simulation began with a randomly chosen dive type. The time series was then cut at an upper limit of 7 h, which represents the time between the earliest (07:50:50) and latest (15:18:55) recordings in a day, rounded to the nearest hour, to avoid extrapolation. From the resulting time series, the mean IBI, bout duration and number of surfacings per bout were estimated. This was done for each simulation, so that a density distribution around each surfacing metric was obtained.

The frequency of fluking in relation to non-fluking (high arch or lazy fluke dives) was estimated from the raw data. A chi-square test was performed to observe if blue whales fluked up less in the presence of whale watch boats (<300 m). We also tested if the duration of deep dives differed when preceded by fluking behaviour compared to arching behaviour using linear models in R.

All analyses were carried out on data from solitary individuals, to avoid potential behavioural biases resulting from social interactions of pairs/groups.

3. Results

Data were collected on 29 days during two field seasons between January and March of 2012 and 2013. During this period a total of 2175 IBIs were recorded (surface dives = 2144, deep dives = 31) from a total of 211 follows. The mean IBI of blue whales was 17.6 s (SD = 26.14) during surface dives and 640.3 s (SD = 214.38) during deep dives.

The transition probability between dive types, estimated from the Markov chain, was significantly different from a theoretical distribution ($x^2 = 33.79$, df = 1, $p < 0.0001$). A blue whale performing a surface dive had an 87.9% (1887 of 2146 transitions) probability of performing another surface dive, and a 12.1% (259 of 2146 transitions) probability of changing to a deep dive. Since two deep dives never succeeded each other, the probability of changing from deep dive to surface dive was 100% (259 of 259 transitions).

The mean IBI of blue whales in Sri Lankan waters obtained from the Monte Carlo methods was 84.7 s (SD = 11.17) (Fig. 2), which is equivalent to a respiration rate (number of surfacings/follow duration) of 0.72 breaths sec^{-1} (SD = 0.094). The mean bout duration was 145 s (SD = 28.31), with the mean number of surfacings per bout being 9.3 (SD = 1.43) (Fig. 2).

55% (136 of 246) of all deep dives were preceded by fluking behaviour, with the remaining 42% being preceded by a high arch and 3% being preceded by a lazy fluke. There was no significant difference in the proportion of animals who fluked up in the presence of whale watch boats compared to those who fluked up in the absence of whale watch boats ($x^2 = 3.32$, df = 1, $p > 0.05$). There was also no difference in the duration of deep dives following fluking behaviour compared to non-fluking behaviour ($F_{1,29} = 0.021$, $P = 0.887$), although the sample size was quite small (n = 31 deep dives).

Mean IBI obtained from the model data was higher than that calculated using the raw data while mean bout duration and mean number of breaths per surfacing bout were comparable between both techniques (Table 1).

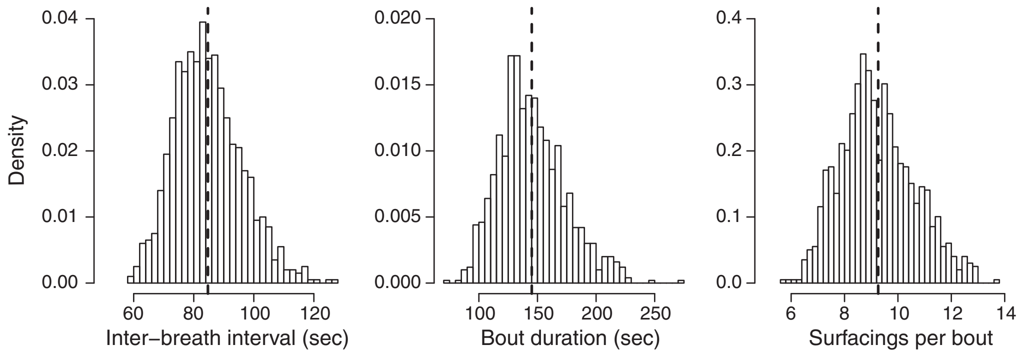

Fig. 2. Density distributions of blue whale IBI, bout duration and number of surfacings per bout. The mean of each surface metric is indicated by the dashed vertical line. The density distributions were derived from 1000 simulated follows, each representing a seven-hour long time series.

4. Discussion

The mean IBI of blue whales in Sri Lankan waters calculated using the Monte Carlo methods, was 84.7 s (SD = 11.17). This is considerably higher than if mean IBI was estimated directly from the raw data, which gives an estimate of 26.5 s (SD = 82.19). This difference highlights the importance of taking the temporal dependence between dive types into consideration when estimating surface mean IBI, or else the resulting mean IBI will be strongly negatively biased. The temporal dependence was however less important when estimating the mean bout duration and the number of surfacings within bouts. Our Monte Carlo estimate of mean bout duration was 145 s (SD = 28.31) compared to 167 s (SD = 68) when estimated directly from the raw data. The mean number of breaths per surfacing bout, estimated from the Monte Carlo methods, was 9 (SD = 1.3) compared to 11 (SD = 3.7) when estimated directly from the raw data. That the main discrepancy was between mean IBI and not bout duration or number of surfacings within bouts makes sense given that the main sampling bias was on the probability of recording deep dives and not surface dives within bouts.

Blue whales off southern Sri Lanka were seen breathing between 3 and 20 times (average 11) at the surface over a 29–421 s period. The reason for the shortest surface time is unclear. Following this period at the surface the whales would dive for an average of 640 s. In general, this suggests that blue whales off Sri Lanka follow similar surfacing/dive cycles to those in the North Atlantic where blue whales were seen breathing at the surface 6–20 times over a 50–300 s period followed by dives that extended from 300 to 900 s (COSEWIC, 2002).

It is important to highlight however, that diving and surfacing characteristics likely vary between foraging periods and travelling periods, and diurnally (Klinowska, 1986; Lagerquist et al., 2000). In the north Pacific, feeding dives averaged 9.8 min (SD = 2 min) with surface recovery times ranging from 16 s to 6.7 min and a mean of 10 surfacings (SD = 3) (Goldbogen et al., 2011). Sims et al. (2005) predict that basking shark abundance (*Cetorhinus maximus*) is over/underestimated by at least ten-fold in the absence of bias reduction for habitat specific Diel Vertical Migratory patterns. For turtles in Shark Bay, Western Australia, correction factors were highly heterogeneous, and found to vary between different diving behaviours and associated environmental conditions highlighting the need to consider spatiotemporal variation in diving when estimating abundance (Thomson et al., 2012, 2013).

Blue whales in Sri Lankan waters were observed 'fluking up' 55% of the time. This contrasts with blue whales in the north Atlantic, where fluking up is exhibited only by specific individuals and is observed only 15–20% of the time (COSEWIC, 2002). Within Sri Lankan waters, this behaviour was not individual specific and showed no obvious pattern. Ilangakoon and Sathasivam (2012) state that the blue whales on the south coast of Sri Lanka fluked up on "approximately 70%" of the dives while dives without fluking were associated with hurried behaviours resulting from disturbances caused by whale watching boats. This implies that non-fluke up diving occurred 30% of the time and only resulted from vessel related disturbances. We did not find this to be the case in our study as non-fluke up dives occurred 45% of the time and were not significantly associated with the presence of other vessels within 300 m. A fluke up dive was always followed by a deep dive but not necessarily one of longer duration. This suggests that individuals were not diving deeper following a 'fluke up' dive as is also supported by our model results.

Most methods of abundance estimation rely heavily on cue counting. Knowledge of dive times is important to estimate the amount of time a whale spends submerged and undetectable for counting as it allows for more accurate abundance estimations. Not accounting for the temporal dependence in dive types leads to an underestimation of IBI, which subsequently leads to an underestimation of density and ultimately abundance. In this study, the results obtained for the surfacing and diving characteristics of blue whales off southern Sri Lanka are comparable with those obtained for blue whales elsewhere in the northern hemisphere. Besides its use in survey calibration, this data can also be used to measure responses to potential threats, such as vessel traffic and sound sources and to examine foraging behaviour in relation to anthropogenic presence and presence of other species.

Surfacing characteristics and dive data gathered through visual surveys have inherent shortcomings. The presence of the research vessel in the vicinity of the whale may cause a bias in the data that has not been accounted for through this study. Our data was collected only during daylight hours and therefore does not account for diurnal variations in behaviour, though population surveys are generally conducted

Table 1
Table comparing estimations of surfacing characteristics from raw vs. model data derived using the Monte Carlo method.

Surfacing characteristic	Raw data					Model	
	Min	Max	Mean	SD	n	Mean	SD
IBI (sec)	1	1326	26.5	82.19	2175	84.7	11.17
Bout duration (sec)	29	421	167	68	142	145	28.31
Surfacings per bout	3	20	11	3.7	148	9.3	1.43
Duration of deep dive (sec)	137	1326	641	214	31	N/A	N/A

during daylight hours. The risk of missing surfacings, the inability to collect data in the presence of multiple animals due to confusion between the focal animal and others, the inability to collect data in the presence of multiple vessels at close range that move unpredictably, the inability to work in sea conditions exceeding Beaufort Sea State 3 (this is also impacted by the height of the observer platform and therefore the vessel being used), and the ability to collect surfacing data reliably over only one cycle because the long duration of a deep dive makes it hard to predict where and when a whale will surface are all acknowledged disadvantages. The use of archival tags such as D-tags that collect sub-surface and acoustic data from the whale and its surroundings (Johnson and Tyack, 2003) would provide insight into the interactions between the whales and anthropogenic influences such as high-intensity sounds and vessel traffic and enable the calculation of more precise correction factors. However, despite the short-comings associated with the visual techniques described here, it is the first attempt to quantify these variables for blue whales in Sri Lankan waters and provides a baseline from which estimates of abundance can be conducted with considerably increased precision, an important first step to informing conservation and management of this unique population.

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