Spatio-temporal variation in click production rates of beaked whales: implications for passive acoustic density estimation

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Passive acoustic monitoring has become an increasingly prevalent tool for estimating density of marine mammals, such as beaked whales, which vocalize often but are difficult to survey visually. Counts of acoustic cues (e.g., vocalizations), when corrected for detection probability, can be translated into animal density estimates by applying an individual cue production rate multiplier. It is essential to understand variation in these rates to avoid biased estimates. The most direct way to measure cue production rate is with animal-mounted acoustic recorders. We utilized data from sound recording tags deployed on Blainville's (*Mesoplodon densirostris*, 19 deployments) and Cuvier's (*Ziphius cavirostris*, 16 deployments) beaked whales, in two locations per species, to explore spatial and temporal variation in click production rates. We did not detect spatial or temporal variation within the average click production rate of Blainville's beaked whales when calculated over dive cycles (including silent periods between dives); however, spatial variation was detected when averaged only over vocal periods. Cuvier's beaked whales exhibited significant spatial and temporal variation in click production rates within vocal periods and when silent periods were included. This evidence of variation emphasizes the need to utilize appropriate cue production rates when estimating density from passive acoustic data.

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I. INTRODUCTION

Robust monitoring of the size or density of wild animal populations over time is a prerequisite for making informed management or mitigation decisions: e.g., to prioritize conservation for populations in decline, or for protecting areas with high densities of individuals. It can be challenging to estimate density for marine mammals, particularly for deep diving and oceanic species inhabiting offshore waters. Visual surveys of such species can result in estimates with high uncertainty: brief surfacing intervals and small visual detection ranges limit sample size, and spatial coverage is limited by the high costs of ship-based studies (Barlow, 1999). Passive acoustic monitoring (PAM) allows for the detection of sounds naturally produced by vocalizing animals and provides an alternative means to estimate density (Marques *et al*., 2013). Acoustic surveys can be more cost-effective than visual surveys because PAM is less limited by sea-state, requires less human presence, and can be carried out during both day and night. In the marine environment, acoustic data can be collected by towed or fixed hydrophones (Marques *et al*., 2013) and, most recently, by sound recorders on autonomous vehicles (Klinck *et al*., 2012; Baumgartner *et al*., 2013). PAM-based density estimates have been calculated for a range of cetacean species (e.g., Marques *et al.*, 2009; Marques *et al*., 2011; Martin *et al*., 2013, Fais *et al*., 2016), and the method is also becoming increasingly prevalent in terrestrial ecology, most notably for songbirds (Efford *et al*., 2009), but also for other taxa including amphibians (Stevenson *et al*., 2015) and primates (Heinicke *et al*., 2015).

Acoustic detections from a line transect survey can be used to estimate distances to vocal animals based on target motion analysis and the angle of arrival of their vocalizations received by the recording system (Barlow *et al*., 2013). These distances can then be used within standard methods, such as distance sampling, to estimate animal density (Buckland *et al*., 2001). However, when such data are not available, often PAM frameworks rely on cue-counting density estimation approaches, which require counts of cues (e.g., individual vocalizations) attributed to the study species (Buckland, 2006) and the corresponding cue production rate. The number of cues detected, when corrected for detection probability within the area and timescale monitored, gives the overall cue density (number of cues per unit area and time) for a recording time window. Cue density can then be translated into an estimate of animal density by applying an individual cue production rate multiplier (average number of vocalizations per animal per unit time) (Buckland *et al*., 2001). Unfortunately, due to the cost and difficulty of collecting such data, accurate estimates of cue production rates are unavailable for many cetacean species, while those that have been calculated are often derived from small sample sizes from specific times and locations. For example, Martin *et al*. (2013) presented a preliminary ‘boing’ production rate for minke whales (*Balaenoptera acutorostrata*) based on passively collected data from an acoustic focal follow of a single tracked animal. Cue production rate multipliers obtained from acoustic focal follows using recorders in the habitat of the animals (see also Matthews *et al*., 2001) are useful, but not ideal, due to periods of silence between calls that can lead to focal animals being lost, or calls being missed or mis-attributed.

Animal-mounted sound recording tags offer one of the few reliable methods to sample individual cue production rates in a natural environment (Johnson *et al*., 2009). Continuous recordings of sound and movement made by these tags also enable estimation of vocal production rates as a function of behavior. It should be noted, however, that the relatively short recording time (typically <1 day) of these devices could result in biased estimates of cue production rate if animals are more accessible for tagging in certain behavioral states or locations. Moreover, it is vital to be able to reliably distinguish sounds produced by a tagged animal from those made by conspecifics in order to achieve an accurate cue production rate estimate, free from false positives; however this is not always straightforward, especially in social species (Pérez *et al*., 2016; Arranz *et al.*, 2016; Johnson *et al*., 2009).

Cuvier's (*Ziphius cavirostris*) and Blainville's (*Mesoplodon densirostris*) beaked whales produce broadband echolocation clicks during deep foraging dives at regular intervals of 0.2-0.6 seconds (Johnson *et al*., 2006; Madsen *et al*., 2005). In both species, the regular clicks are interspersed with fast click trains, known as buzzes, indicating attempts to capture prey, and occasional pauses (Johnson *et al*., 2004). Beaked whales perform long silent periods of shallow diving between deep foraging dives (Tyack *et al*., 2006a) and, as a consequence, their overall vocal duty cycles are low: 28% for Cuvier's and 17-19% for Blainville's (Barlow *et al.*, 2013; Arranz *et al.*, 2011). The long silent periods mean that obtaining acoustic cue production rates solely from periods when animals are vocally active (hereafter referred to as vocal periods) would lead to significant underestimation of animal density (Marques *et al.*, 2009). As such, cue rates for use as multipliers in long-term passively collected acoustic density estimates for beaked whales must include both naturally silent and vocal periods (Marques *et al.*, 2009). As discussed, acoustic focal follows are ineffective when focal animals conduct long periods of silence and are easily lost, therefore, acoustic tags provide the most effective method to estimate cue production rates of beaked whales.

An optimal cue for passive acoustic density estimation is a discrete unit that is produced at a rate that is largely independent of external covariates, particularly density, and can be reliably identified, detected and classified (Marques *et al.*, 2013). Sound-recording tags mounted on beaked whales are able to provide reliable click production rates specific to individuals because clicks produced by the tagged animal contain low frequency energy that is absent in far-field clicks from conspecifics (Johnson *et al.*, 2009). Moreover, the clicks can be detected at ranges of several kilometers in quiet conditions (Ward *et al.*, 2008) and have a distinctive frequency modulation, when observed close to the acoustic axis, that distinguishes them from clicks of other toothed whales (Johnson *et al.*, 2006), making them a suitable cue for detection and classification within a passive acoustic framework. Previous cue-based density estimates have been made from acoustic data for Cuvier’s and Blainville’s beaked whales (Moretti *et* al., 2006; Marques *et al.*, 2009; Moretti *et al.*, 2010, Kusel *et* al., 2011; Hildebrand *et* al., 2015). Moretti *et al*. (2006) estimated animal density without using individually-specific cue production rates, while the other studies applied cue rates obtained from limited numbers of acoustic tag deployments, or from previous estimates in the literature.

Cue production rates can vary with context (e.g., Matthews *et al.*, 2001); therefore, to avoid biased density estimates, it is important that rates used as multipliers are appropriate for the time and location of the passive acoustic survey. An ideal cue rate multiplier would be collected from individuals selected at random from the population, concurrently with the passive acoustic survey, and an optimum survey design to collect this secondary data would sample individuals across the entire spatial and temporal range of the intended PAM survey. If the collection of concurrent cue rate data is not possible, statistical models informed by large, reliable datasets must be relied upon to predict the most appropriate cue rate. However, when using models to predict cue rate, it is only reasonable to extrapolate within the range of available covariates, and only when the relationships between cue rate and the main factors affecting cue rate are known.

Data from sound recording tags indicate that click production rates within the echolocation phase of beaked whale foraging dives show substantial fine-scale variation, possibly tracking changing prey density and body turning rates (Madsen *et al.*, 2013). It is not essential that cue production is consistent over short timescales within animals, because it is the *average* cue rate that is of interest and this can be obtained with high precision by sampling over a sufficiently long time period. Nevertheless, consistency in the average rate between individuals is desired as it is typically this value that contributes to the variance (i.e., uncertainty) of the overall average cue rate. Cue production rates could, however, also vary over longer temporal scales and by location, neither of which has been examined in beaked whales. Vocal period click rate is known to vary at a diel scale for other toothed whale species including Risso's dolphins (*Grampus griseus*) (Soldevilla *et al.*, 2010a) and Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) (Soldevilla *et al.*, 2010b), based on data collected by autonomous bottom-mounted hydrophones. There is also evidence that groups of mostly male sperm whales (*Physeter macrocephalus*) in high latitudes off New Zealand conduct longer silent periods between dives than other sperm whale populations with different social structures (e.g. matrilineal groups, which are mainly found in the tropics and sub-tropics (Whitehead, 2002)) suggesting that an average cue production rate for this species could be spatially specific (Douglas *et al.*, 2005).

This study aims to quantify cue production rate metrics, relevant to Blainville's and Cuvier's beaked whales, which are appropriate for passive acoustic density estimation. Using the most comprehensive beaked whale tag dataset available, with a reasonable quantity of samples from two locations for each species, this study tests for spatial and temporal differences that could represent potential sources of bias when estimating cue production rate metrics for beaked whales. The dataset provides the basis for models predicting click production rates for both species, over the four locations and a range of temporal scales.

II. METHODS

Suction-cup sound and movement recording tags (DTAGs, Johnson and Tyack, 2003) were deployed on Cuvier's and Blainville's beaked whales at four sites (Bahamas, Canary Islands, Ligurian Sea and southern California) between 2003 and 2013 (**Table I**). Blainville's beaked whales were tagged in May (11 dives), June (8 dives), August (6 dives), September (12 dives) and October (33 dives). Cuvier's beaked whales were tagged in June (30 dives), July (8 dives) and September (10 dives). Both DTAG2s and DTAG3s were deployed, with 96, 192 or 240kHz acoustic sampling of one (in 2003) or two (all other years) hydrophone channels, and 50Hz or 200Hz sampling of a pressure sensor and three-axis accelerometer (Tyack *et al*., 2006a). Tags were deployed from small rigid-hulled inflatable boats using a 5m long hand-held pole (Johnson *et al*., 2006) and remained attached for a mean of 11.7 hours, ranging from 1.9 to 24.0 hours. Following detachment, the tags were collected from the sea surface *via* VHF radio detection. Data were stored to flash memory in the tag and downloaded upon retrieval (Johnson and Tyack, 2003).

The data utilized in this study were not collected specifically for the analysis of click production rate. In 2010 and 2011, the two Cuvier's beaked whales in southern California were part of a controlled exposure experiment during which they were exposed to mid-frequency active (MFA) sonar. The acoustic behavior of these whales was significantly altered during the exposure (DeRuiter *et al*., 2013), so only the dives prior to the controlled exposure were included in this analysis, hence the low final sample size for southern California (**Table I**). Moreover, incidental MFA sonar was also audible in the remaining 2011 dive (DeRuiter *et al*., 2013), potentially leading to bias, but as this dive was not obviously altered by the sound exposure it was included in the analysis due to the low sample size.

All tagged animals were photographed for photo-ID purposes. No photo-ID matches were found across tag deployments on Cuvier's beaked whales, although individuals can be difficult to distinguish and the possibility of re-tagging within this species cannot be dismissed. In El Hierro, three Blainville's beaked whales were tagged in multiple years; one twice, and two on three occasions (Arranz *et al*., 2011). Cue rate values from each of these animals appeared to be randomly distributed within the range of the other individuals, so each tag deployment was treated as an independent unit.

Acoustic analyses were performed using custom tools from the DTAG toolbox (Johnson, 2014) in MATLAB (The MathWorks, Inc, version R2013a). The vocal period in each dive was defined as the interval from the first to the last click recorded during the dive. These clicks were identified manually by inspection of spectrograms (512 sample FFT (Fast Fourier Transform) with a Hamming window and 50% overlap) formed from successive 15s intervals of the sound recording. Sound data during each vocal period were then passed through a supervised click detector to identify likely clicks from the tagged animal. The detector first applied a bandpass filter (20-60 kHz, covering the frequency range of clicks from both species) and then computed the Hilbert envelope of the filtered sound. Transients above a threshold, adjusted to track the average signal strength in 10 s intervals, were retained as potential clicks. For stereo DTAGs, the angle-of-arrival of each transient was computed from the time difference of arrival of the signal at the two hydrophones in the tag (Johnson *et al.*, 2009). Transients were plotted in a time vs angle-of-arrival display, colored by received level. Trained analysts using this display ascribed clicks to the tagged animal when they had a consistently high received level and came from a consistent angle of arrival. For the 4 monaural tag recordings, transients were plotted in a time vs received level display allowing the generally weaker and more variable clicks from other animals to be readily separated from those of the tagged whale. Selected clicks were subsequently reviewed by visually examining spectrograms to check for missed clicks and false positives. Sounds produced by the tagged animal could be verified in spectrograms as they contained high energy at low frequencies due to the placement of the tag behind the directional sound source and reverberation within the body (Johnson *et al.*, 2009). The result was a vector of times at which clicks were produced by the tagged animal during each dive. Clicks with inter-click interval (ICI) <0.1s were omitted from the analysis to exclude buzzes (Madsen *et al.*, 2005). Buzz clicks are much less likely to be detected by passive acoustic monitoring systems than regular clicks due to their 10-20dB lower source level (Madsen *et al.*, 2013).

A dive cycle was defined as the time between the start of a dive containing a vocal period and the start of the next dive containing a vocal period (sensu Tyack *et al.*, 2006a and Arranz *et al.*, 2011) (**Figure 1**).

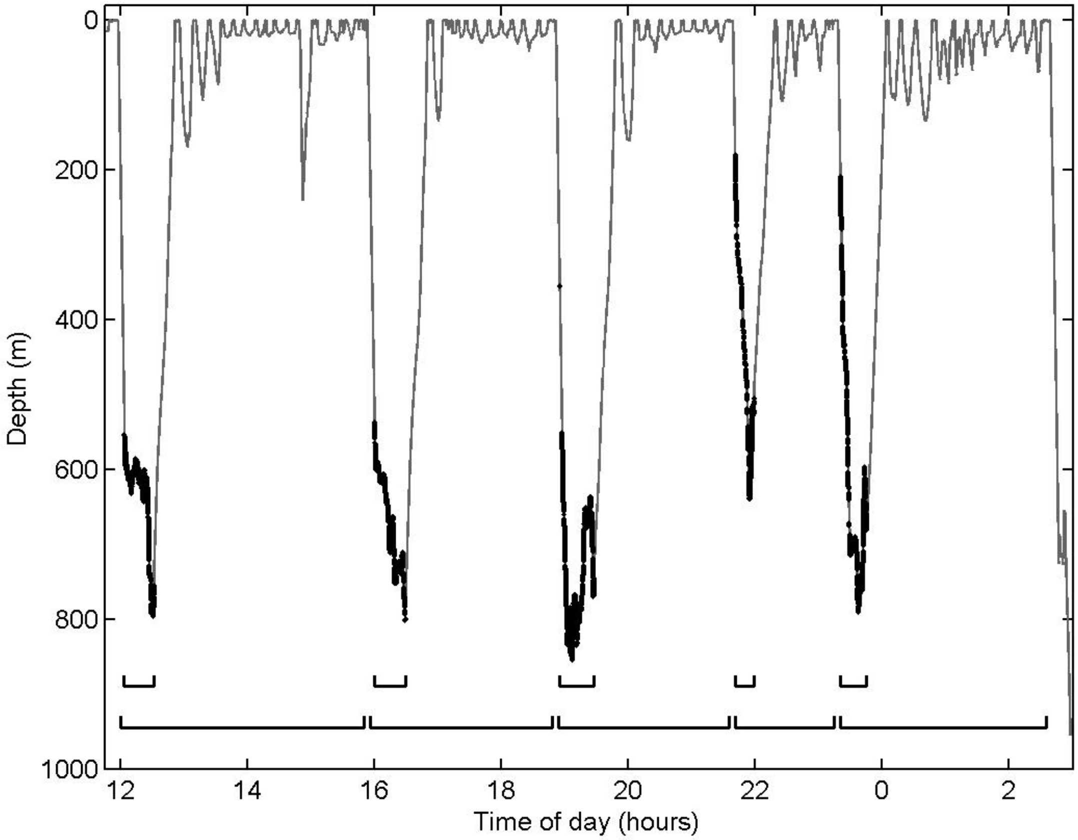

FIGURE 1: Example dive profile of a Blainville's beaked whale tagged in the waters adjacent to El Hierro, Canary Islands. Bold sections indicate the presence of foraging clicks. Shorter, upper markers delineate vocal periods, while lower, longer markers indicate the lengths of individual dive cycles. The final dive featured tag detachment and was not analyzed.

Two click rate metrics were calculated within each dive cycle: (i) the vocal period click production rate, i.e., the number of clicks in a vocal period divided by the vocal period length (in seconds), and (ii) the dive cycle click production rate, i.e., the number of clicks in a vocal period divided by the length of the dive cycle containing this period (in seconds). The sample size of these two metrics differed (**Table I**): in some tag records, the final dive cycle was incomplete due to tag detachment; the final dive cycle length could not be calculated for these records. However, if the final dive contained a complete vocal period the first metric could be calculated.

Although Cuvier's and Blainville's beaked whales are reported rarely to produce sounds outside of deep foraging dives (Tyack *et al*., 2006b; Aguilar de Soto *et al*., 2012), all dives exceeding approximately four body lengths in depth (24m for Cuvier's and 20m for Blainville's) were checked for clicking within 30 seconds before and after their maximum depth. The depth limits were selected graphically from dive profiles to exclude frequent short submersions between respirations which contained confounding surface water noise. 97.5% of dives with maximum depth exceeding 400m contained a vocal period, therefore this threshold was used to define a deep foraging dive. Three dives exceeding 400m were silent, and fives dives with maximum depths shallower than 400m also contained clicking. The impact of these eight anomalous dives on the results will be discussed. Long pauses (of more than a minute) within clicking are rare during deep foraging dives (Tyack *et al*., 2006b), thus all vocal periods were expected to be identifiable by the presence of clicks within the one minute defined analysis window. Deep dives without clicks in the 30-second windows either side of maximum depth were checked throughout their entire duration for unusual vocal activity before being deemed silent.

To investigate spatial and temporal variation in click production rates, and to identify covariates that explained most of the variation present, statistical models were fitted to each of the four click data sets (i.e., two click production rates per species). Clicking rate was not modelled directly, instead, ‘total number of clicks’ was chosen as a Poisson distributed response variable (with a log link function) and an offset, either ‘length of vocal period (seconds)’ or ‘length of dive cycle (seconds)’, was included in the model as appropriate. The model outputs, once converted to the response scale, were thus click production rates per second. Runs tests revealed the presence of weak autocorrelation within model residuals due to longitudinal sampling, i.e., multiple observations of the same animal over time. Generalized Estimating Equations (GEEs) were therefore used in R (version 3.3.1; package ‘geepack’, version 1.2-0 (Højsgaard *et al.*, 2006)), with ‘Tag ID’ specified as the clustering factor, ordered by dive index. An ‘independence’ correlation matrix and robust standard errors were used in light of only weak autocorrelation in click rates between successive dives within individuals (Overall and Tonidandel, 2004; Højsgaard *et al.*, 2006) (see Quick *et al.* (2016) for a similar approach). GEEs are appropriate for data containing a large number of clusters (tag deployments) with relatively few observations (dives or dive cycles) per cluster (Bailey *et al.*, 2013).

Potential covariates of interest were identified *a priori* and checked for collinearity by computing correlograms. Although the DTAG dataset analyzed here is the most comprehensive to date for these two beaked whale species, sample sizes were not large (**Table 1**). Each species was tagged in one location per year, resulting in ‘location’ and ‘year’ being confounded. As the dataset contained two years with a Cuvier’s sample size of one dive, ‘location’ was included as an explanatory covariate rather than ‘year’ in order to generate models using the greatest possible sample sizes per category. Confounding also occurred within the Blainville’s beaked whale data with respect to ’location’ and ‘month’; El Hierro fieldwork was conducted during May, June and

October while the Bahamas were sampled in August, September and October. ‘Month’ was therefore excluded as a covariate within the Blainville’s beaked whale models. Initial explanatory covariates were therefore: location as a factor covariate; month, also as a factor (Cuvier’s only); a binary covariate for whether the dive was the first dive post tag-attachment in order to account for any short-term tagging effects; and time of day of the dive (as a factor covariate comprising six values: night (sun angle below -10° from the horizon), dawn (-10° to +10° sun angle), morning, midday (11am-1pm), afternoon and dusk (+10° to -10° sun angle)). The time of day of the dives breaks down to: morning (5 Blainville’s dives); midday (13 Blainville’s, 3 Cuvier’s dives); afternoon (19 Blainville’s, 17 Cuvier’s dives); dusk (7 Blainville’s, 11 Cuvier’s dives); and night (26 Blainville’s, 17 Cuvier’s dives). These variables were all entered into the models as main effects; due to the relatively small sample sizes, no interaction terms were fitted.

Backwards selection, using marginal ANOVA, from the four (two species with two response variables each) initial full models was used to determine which covariates were significant (i.e., $p \leq 0.05$) and therefore retained in the final models (Zuur *et al*., 2009). Model fit was checked by examining plots of fitted values against observed values, and calculating concordance correlation values (Lin, 1989; Scott-Hayward *et al*., 2013).

III. RESULTS

A total of 118 vocal periods and 106 dive cycles from 35 tag deployments were analyzed from the four study sites (**Table I**). The overall pattern of vocal behavior was similar to that reported by Tyack *et al*. (2006a) for a subset of the same data: deep foraging dives, each containing a vocal period of regular clicking, were interspersed with shallower, silent dives. Three deep dives (maximum depth >400m) were silent: one Cuvier's dive, and two dives by the same Blainville's beaked whale. These three dives were all steep V-shaped dives with no significant bottom phase, occurred directly after deep dives with vocal periods, and were less than half the duration of deep dives with vocal periods.

The vast majority of shallow dives (<400m) were silent, however five of 157 Cuvier's dives with maximum depth between 24m and 400m were not silent. The five shallow dives with clicks occurred during four different tag deployments in Liguria. The number of clicks recorded in each vocal shallow dive ranged from 39 to 219 and clicking persisted for between 180 and 336s. These clicks accounted for approximately 0.45% of the total click production of Cuvier's beaked whales recorded here. As these clicks occurred outside of our definition of vocal periods they were not added to the vocal period click count totals. However, in order to incorporate these additional data, three of these click counts were included in the total counts for their enveloping dive cycles, while the remaining two vocal shallow dives occurred before the first deep dive and corresponding dive cycle in their respective records and so were excluded. All Blainville's dives with maximum depth less than 400m were silent.

The total number of clicks produced during a vocal period ranged from 1001 (during the shortest vocal period of 8mins 46s) to 7558 (during the longest vocal period of 46 mins 18s) for Blainville's beaked whales, and 1387 (during the second shortest vocal period; the shortest vocal period was 23mins 35s and contained 2428 clicks) to 6097 (during the longest vocal period of 54 mins 41s) for Cuvier's beaked whales. A comparison of diving and vocal parameters between the two species and in the four locations (results provided in order for Bahamas and El Hierro in the case of Blainville´s, and for Liguria and southern California for Cuvier´s) indicated that Cuvier's beaked whales clicked at a slower rate (1.67 clicks/sec ± 0.16 and 1.46 clicks/sec ± 0.14) during vocal periods than Blainville's (2.59 clicks/sec ± 0.15 and 2.38 clicks/sec ± 0.06), and tended to perform longer vocal periods (35.2 mins ± 5.7 and 35.1 mins ± 9.1, compared to 29.9 mins ± 5.8 and 24.5 mins ± 2.3) (**Figure 2; Table II**). Values given are mean values with standard deviations weighted by the number of dives in the enveloping tag record. Furthermore, the dive cycle lengths of Cuvier's beaked whales in Liguria (133.0 mins ± 29.8), which represent 90% of the data for this species, were shorter than those of Blainville's beaked whales (181.0 mins ± 53.2 and 145.0 mins ± 31.0), resulting in similar average dive cycle click rates for the two species (0.50 clicks/sec ± 0.06, compared to 0.50 clicks/sec ± 0.11 and 0.43 clicks/sec ± 0.14) (**Figure 3; Table II**). In comparison, the five Cuvier's tagged in southern California performed substantially longer dive cycles (228.0 mins ± 47.4), resulting in an average dive cycle click rate (0.24 clicks/sec ± 0.08) approximately half that of Blainville's, and of the Cuvier's tagged in Liguria (**Figure 3; Table II**). Note that this result should be treated with caution due to the small sample size and potentially confounding MFA sonar exposure. In all cases, between-individual variation was higher in dive cycle click production rates than vocal period click production rates (**Coefficients of variation, Table II**).

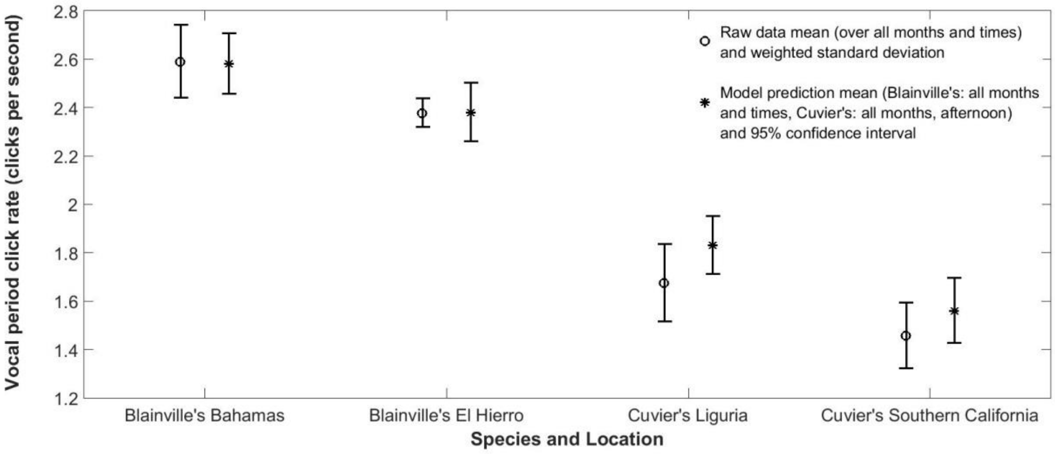

FIGURE 2: Raw and modelled vocal period click production rates (with weighted standard deviation and 95% confidence interval respectively) for both species, and both locations per species. Due to factor covariates in the Cuvier's model, the modelled predictions are appropriate for any of the modelled months, but are only relevant for afternoons.

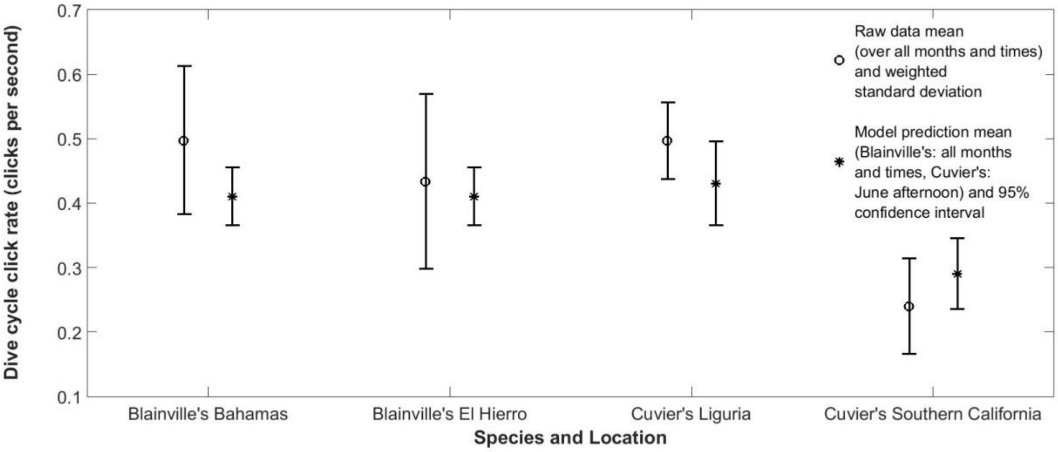

FIGURE 3: Raw and modelled dive cycle click production rates (with weighted standard deviation and 95% confidence interval respectively) for both species, and both locations per

species. Due to factor covariates in the Cuvier's model, the modelled predictions are only relevant for June afternoons.

As anticipated from the raw data (summarized in **Table II**), the models predicted that the vocal period click production rate of Blainville's beaked whales (averaging 2.38 to 2.58 clicks/sec) is approximately twice that of Cuvier's beaked whales (with averages ranging from 1.27 to 1.83 clicks/sec) (**Figure 2; Table III**). However, the dive cycle click rates are very similar between the two species (with averages ranging from 0.29 to 0.52 clicks/sec), excepting the limited data from southern Californian Cuvier's beaked whales (which ranged from 0.18 to 0.35 clicks/sec) (**Figure 3; Table III**). Both the dive cycle and the vocal period click rates for the southern California Cuvier's are notably lower than for the Ligurian whales. While the southern California Cuvier's data from 2011 appears anomalous within the dataset, its removal does not lead to any significant changes in the results due to the small sample size from California. Effect sizes and standard errors were produced on the link scale, and converted to the response scale by exponentiation of the effect size, and via the Delta method for the standard errors (Oehlert, 1992).

Concordance correlation values indicated that the vocal period click production rates were modelled well (Blainville's 0.97, Cuvier's 0.80), while the dive cycle rate models resulted in adequate fits (Blainville's 0.27, Cuvier's 0.35). For both species, location was retained in the GEE models for click rate averaged over vocal period. This suggests that spatial differences in click rate are present within each species, however it must be reiterated that the confound between the location and year covariates means that this could also, or instead, reflect annual differences in vocal period click rate. When the click rates were averaged over dive cycles, location was retained only within the Cuvier’s beaked whale model, implying that on a dive cycle scale, Blainville’s beaked whale click rates are not spatially (or annually) specific.

No further explanatory covariates were retained for either of the two Blainville’s click production rate models. For Cuvier’s beaked whales, time of day was retained in both vocal period and dive cycle click rate models, with month additionally retained in the dive cycle click rate model. There was no evidence for a significant effect of tagging (comparing the first dive post-tagging to later dives) within click production rates for either species.

Within the entire data set for both species, no dives were recorded during dawn and only five dives were recorded during the morning. This gap occurred because most tags were attached during late morning or afternoon and detached before the following morning. The Cuvier’s beaked whale that carried a tag for 24 hours was part of a controlled exposure experiment, and only data from before the experiment were retained. All morning dives were performed by Blainville’s beaked whales; hence the lack of dawn or morning estimates for both of the Cuvier’s click rates (**Table III**).

It was not possible to test directly for long-term temporal effects (i.e., year) due to the small sample sizes within some years and confounding with location; however, exploratory plots indicated the presence of some inter-annual variation within locations in the vocal period and dive cycle click rates of both beaked whale species (**Figure 4**).

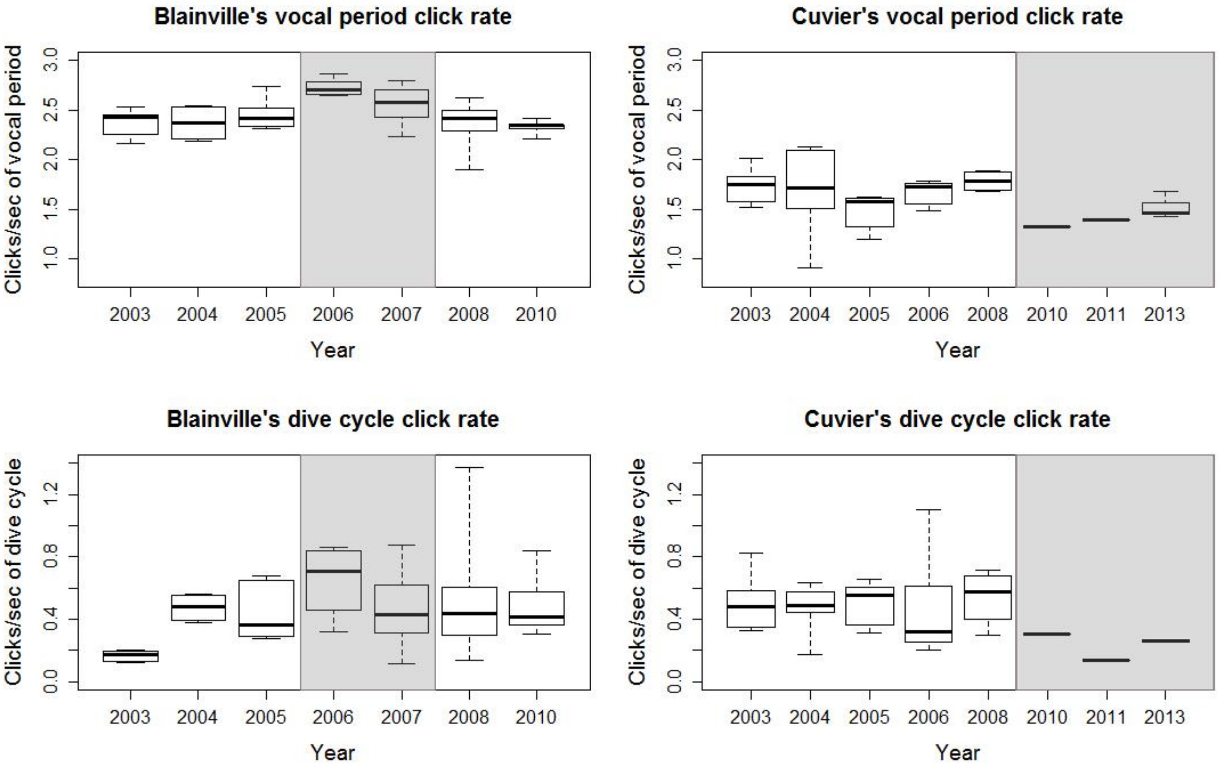

FIGURE 4: Inter-annual variation in vocal period and dive cycle click production rates for Blainville's (left) and Cuvier’s (right) beaked whales. Box plots consist of median, interquartile range and maximum/minimum extremes. In the Blainville’s data, boxes in white areas represent animals tagged in El Hierro and boxes in grey areas (2006 and 2007) indicate tags deployed in the Bahamas. In the Cuvier’s plots, boxes in the white area represent Liguria, and boxes in the grey area (2010, 2011 and 2013) are southern California deployments. See Table I for respective sample sizes. Y axes scales differ between vocal period plots (upper) and dive cycle plots (lower).

IV. DISCUSSION

Acoustic surveys provide a powerful tool to study the occurrence of marine mammals, and may be the most effective way of assessing populations with low probability of visual detection, such as beaked whales (Barlow *et al*., 2013). In a cue-counting density estimation framework, individual whales cannot be distinguished and the number of whales is solely estimated from the number of cues detected. The increasing use of moored hydrophones to study whale occurrence and distribution (Marques *et al*., 2013) emphasizes the need to obtain good quality data on relevant cue production rates to improve the accuracy of cetacean density estimates from acoustic point samples.

A. Cue production rate multipliers for passive acoustic density estimation

A cue-based method to estimate animal density from passive acoustic detections, requires a reliable cue production rate multiplier. Acoustic recording tags offer a practical solution to sample the acoustic behavior of marine mammals in a natural environment providing precise cue production rates from individual animals which are difficult to obtain by other means (Johnson and Tyack, 2003). When tags are deployed at random, concurrent with a passive acoustic survey, tag data can be used to calculate an average population cue rate multiplier that is directly relevant to the survey. However, this is typically not possible and it is often necessary to rely on measurements taken at other times and places. In such cases, it is essential to understand the cue production behavior of the study species, and its variability with context, to establish a reliable cue production multiplier. A large dataset from tag deployments over a range of times, locations and external covariates, allows the development of statistical models for the prediction of cue rate within the range of modelled covariates. Here, GEEs were used to model click production rates of Blainville's and Cuvier's beaked whales, and these models demonstrated that spatial and temporal variation can be present in cue production rates with the potential to bias animal density estimates that do not use specific multipliers.

Cue rates can be quantified in multiple ways and the most appropriate measure for density estimation depends on the acoustic behavior of the species and the monitoring duration of the passive acoustic survey (Marques *et al.*, 2013). For species that produce sound in bouts, such as beaked whales, silent periods must be included in cue rate quantification to avoid underestimation of density. Given their stereotyped diving behavior, dive cycle click rate is therefore the correct metric for acoustic density estimation of beaked whales, as it integrates vocal output over complete behavioral cycles. Vocal period click production rates were presented here for comparison and to help interpret variability in the dive cycle rates.

B. Spatio-temporal variation in beaked whale click production rates

For Blainville's beaked whales, significant variation was present within vocal period click rate, although the confounding between location and year in this dataset meant that spatial variation could not be distinguished explicitly from inter-annual variation. In contrast, the dive cycle click production rate of Blainville's beaked whales, which is directly relevant as a multiplier for density estimation using PAM, was not found to vary significantly over time or space. This lack of statistical significance should not be interpreted as confirmation of lack of biological significance. Although the estimated click rates were very similar between sites, they were enveloped by wide confidence intervals, giving an indication that the rates could potentially vary, but the variation may not be significantly detectable. A larger sample size would provide greater confidence.

The modelled click production rates of Cuvier's beaked whales indicated the presence of significant variation at both vocal period and dive cycle scales. Diel and monthly differences of up to 40% were apparent within both Cuvier's cue production rate metrics, and differences of up to 15 and 30% in click production rate were detected between locations for vocal period and dive cycle click rates respectively. The small sample size in southern California and the confound between location and year in the data lead to some uncertainty, but, irrespective of the cause of variation, its presence indicates that cue rate multipliers for Cuvier's beaked whales should be as specific to the PAM survey as possible in order to estimate animal density reliably.

Temporal variation in Cuvier's click rates occurred at a range of scales. At the finest scale, both vocal period and dive cycle click rates varied with time of day. Deep diving marine mammals, such as beaked whales, target prey near the seafloor (benthic boundary layer) or vertically stratified prey layers that undergo diel migrations through the water column (Benoit-Bird *et al*., 2001; Arranz *et al*., 2011). Beaked whales may change foraging strategy or target different prey species (affecting vocal period rate), or forage at different depths (thus altering transit and recovery time, and therefore dive cycle click rate) depending on the time of day. Baird *et al*. (2008) previously noted diel changes in diving activity of Cuvier's beaked whales, but not in the rate of deep foraging dives, although the sample size was not large enough to test for statistical significance. Arranz *et al*. (2011) noted diel variation in the depth at which Blainville's beaked whales started clicking in deep foraging dives, but no diel change was detected in the depth distribution of clicking time. Here, we found no evidence for diel variation in either of the two click production rates for Blainville's beaked whales.

Cuvier's dive cycle click rate also varied significantly between months, with the fastest rates predicted during June. Month was not a significant covariate to explain variation in Cuvier's vocal period click rate, however, implying that the inter-month differences reflect changes in the length of silent periods between dives. Variation in target prey or seasonal behaviors, such as mating or nursing calves, may drive these changes in diving behavior. The data for Californian Cuvier's beaked whales was particularly limited in its temporal range, however the modelling approach utilized here allowed for specific predictions for click production rates based on features of the Ligurian Cuvier's beaked whale data. It should be reiterated that extrapolation is only recommended within the range of available covariates.

While it was not possible explicitly to distinguish spatial variation from inter-annual variation, spatial differences in cue production rate should not be surprising for allopatric populations. Both the physical environment and its prey resources vary spatially, which can lead to differences in foraging behavior; for example, variation in depth of foraging (often a function of bathymetry) may affect the time available for echolocation-based foraging (due to increased transport time from surface to foraging depth), which may in turn affect the duration of vocal periods. Allopatric populations may also target different prey types with different detection ranges, which would be reflected in inter-click intervals of echolocation-based foraging. Spatial separation may also enable differences to manifest in physiology as well as behavior; populations with naturally larger individuals may click at a different rate due to physiological constraints (Fitch and Hauser, 1995).

Exploratory plots (**Figure 4**) aimed at distinguishing between spatial and inter-annual differences indicated possible variation in click rate between years within locations, perhaps reflecting changes in prey between years, or wider contextual changes, such as El Niño events: 2002/3, 2004/5, 2006/7 and 2009/10 were El Niño years, while 2007/8 and 2010/11 were La Niña years (NOAA Climate Prediction Center, 2015).

External variables, such as anthropogenic sound, can also directly influence the diving behavior and vocal output of odontocetes (Weilgart, 2007; Sivle *et al*., 2012). Marine mammals living in industrialized ocean regions may experience anthropogenic noise pollution that can alter both their vocal output and our probability of detecting their sounds (Weilgart, 2007; Aguilar de Soto *et al*., 2006; Ward *et al*., 2011). Here, both species, in all four locations, experienced varying levels of anthropogenic noise. Sounds from 50kHz fish finders were frequently audible in Blainville's data from El Hierro, while Cuvier's beaked whales in the Ligurian Sea were exposed to high levels of ship traffic, which may affect vocal and dive behavior (Aguilar de Soto *et al.*, 2006). Although dives conducted during controlled sonar exposures were removed from the Californian Cuvier's data, low levels of incidental navy sonar occurred within the southern Californian tag record from 2011 (DeRuiter *et al*., 2013). Cuvier's beaked whales have been reported to increase the interval between foraging dives in response to sonar (DeRuiter et al. 2013), so the increased dive cycle duration observed in the southern California data could have been a result of these sonar exposures. The Blainville's beaked whales tagged around the

Bahamas were within an active naval range and were likely subject to sounds from naval sources (Moretti *et al*., 2014). These whales had a higher vocal period click production rate than Blainville´s from the Canary Islands, which may be explained as an adaptation to different prey (Johnson *et al*., 2008). Here we assumed that site-specific anthropogenic sound sources were absorbed within the 'location' covariate, but further work should investigate the relationship between each type of anthropogenic activity and click production rate

Marques *et al*. (2009) calculated a cue production rate for Blainville's beaked whales from acoustic tag data from five whales tagged in the Tongue of the Ocean, Bahamas in 2005 (a sub-sample of the dataset for the current study). The study calculated a dive cycle click production rate of 0.407 clicks/sec, with a standard error of 0.04 and CV of 9.8%. This estimate is almost identical to the average Blainville's dive cycle click production rate modelled in this study. Moretti *et al*. (2010) utilized the click rate value from Marques *et al*. (2009) for density estimation from a 2008 passive acoustic survey in the same location. The lack of significant temporal variation in Blainville's dive cycle click rates observed in this study corroborates the density estimate calculated by Moretti *et al*. (2010).

Hildebrand *et al*. (2015) calculated dive cycle click production rates for Cuvier's beaked whales across three locations within the Gulf of Mexico by taking the mean proportion of a dive cycle spent clicking and multiplying by the inverse of the average ICI. This method resulted in dive cycle click production rates of 0.45-0.49 clicks/sec (with CV of 0.09 for each value) across the three sites. While these values lie within the range calculated here for this species in the Ligurian Sea, they are greater than any dive cycle click production rate value calculated for southern

Californian Cuvier's, supporting the conclusion that click production rates used for density estimation should ideally be spatially and temporally relevant.

C. Caveats and limitations

Beaked whales often surface and dive in groups (Aguilar de Soto *et al*., 2012) and, like all echolocating animals, have the potential to eavesdrop on the vocalizations produced by conspecifics (Dechmann *et al*., 2009). As such, the acoustic footprint of a group of foraging beaked whales may not increase linearly with group size (Tyack *et al*., 2006b). However, beaked whales apparently produce very few social sounds (Aguilar de Soto *et al*., 2012) and foraging theory suggests that density dependence in an individually-obligated foraging sound should be low (Pyke, 1984). Therefore, the rates calculated here ought not to be strongly influenced by group size.

The short attachment period of suction-cup tags means that there is potential for a significant proportion of the data collected to be biased if the instrumented animal responds to the attachment. To test for this, the models included a covariate for first dive after tagging; its lack of inclusion in the final models implied that first dives were not significantly unusual, suggesting the lack of a strong tagging effect, although the limited sample size means that some effect cannot be ruled out. Similarly, Tyack *et al*. (2006a) did not detect tagging responses in a subset of the same data (N=8). Conversely, Barlow *et al*. (2013) removed all first dive cycles from a dataset that included some of the data here (both species, N=27) due to significantly longer inter-dive intervals immediately subsequent to tagging. Hildebrand *et al*. (2015) also removed first dives from Cuvier's beaked whale tag data (the same Ligurian dataset used here) due to a reduced number of click-positive-seconds. Neither of these effects were detected in the click production rates presented here, however, implying that the effects were not detectable in this larger dataset, or were not directly reflected in click rate.

Here, the raw data informing the models indicated that a greater level of between-individual variation was present within dive cycle click rates compared to vocal period click rates, implying that the length of a dive cycle is not simply proportional to the length of the encompassed vocal period. This resulted in a better model fit for the vocal period model than for the dive cycle model for both species, suggesting that the variation in dive cycle click production rate was not fully explained by the covariates included in the models. As such, any differences that were present, but within the range of natural variation of the data, may not have been detected for this metric. The backwards selection framework using p-values from the GEE was an adequate model selection method to demonstrate that significant spatiotemporal variability was present in the cue production rate estimates, which was the main aim of our study. However, model selection is a broad and active area of research and other approaches could have been implemented. K-fold cross validation is one such criterion-based method (as opposed to using hypothesis testing) that is particularly good at testing a model’s predictive capabilities, as demonstrated by Quick *et al*. (2016).

It is possible that the tagged beaked whales are not representative of the wider populations from which they were sampled. If certain animals, with particular vocal patterns, are more available for tagging, then the click rates calculated will be biased. Extreme bias could occur if highly vocal animals were found via PAM and then tagged. Animals in this study were found relatively close to shore where they were accessible for tagging from small boats and may, in some cases, belong to resident populations (Claridge, 2013; Falcone *et al*., 2009). As a result, the data may not reflect the vocal behavior of animals in off-shore areas. Both beaked whale species are broadly distributed and can be found associated with a variety of bathymetric features including submarine canyons, seamounts, and abyssal plains (Lanfredi *et al.*, 2016). Although vocal production may well be linked with environmental features, there are significant practical and economic difficulties in sampling animals from these offshore domains.

The short periods of clicking observed in a small number of shallow Cuvier's dives reveal that vocal output by beaked whales is not exclusive to deep dives. The purpose of the clicks produced at shallow depth is not clear, but we included the counts of shallow clicks within the dive cycle click rates, despite their rarity. These clicks inherently added to the vocal activity of the Cuvier's beaked whales and would be essentially indistinguishable from regular clicks when detected by passive acoustic survey hydrophones (unlike buzz clicks which can be differentiated by their ICI and reduced source level).

Despite using the most comprehensive beaked whale tag dataset available, confidence in the results of this study is limited by the small sample size. Had a larger data set been available, interaction terms could have been added to the models in order to assess whether the populations displayed independent, and different, responses to each covariate considered (e.g. Soldevilla *et al*., 2010b). However, the small sample size and confounded location and year covariates meant that it would not have been feasible to study interactions with this data set. On a global scale, tagging is a rare event: tags are only deployed in good weather conditions, in certain locations and, so far, only on a limited number of species. However, as more tagging data become available, statistical models, such as those used in this study, will be better able to explore variation in click production rate over space and time. If such models are robust with strong predictive power, then it may be possible to predict location-specific and time-specific cue rates for study areas where tagging is not possible. Predictive models can also inform which time periods are most effective for estimating density: e.g., what time of day, or which month of the year, might yield least variation. Given this, efforts to collate and model tagging studies are particularly valuable.

D. Collecting click production rates: tags and other techniques

Acoustic tag deployments result in reliable individual-oriented data from which cue production rates can be calculated, and, just as importantly, are able to quantify silent intervals when animals will be undetected by a PAM survey. The latter point is particularly pertinent when estimating density of baleen whales, some of which seldom vocalize (e.g. Martin *et al*., 2013). Unlike the stereotyped duty cycles of beaked whales, short term acoustic tags mounted on baleen whales have revealed significant, variable periods of silence. Indeed, Parks *et al*. (2011) noted that 28 of 46 North Atlantic right whales produced no sound during tag deployments with average duration of 4.5 hours. In comparison, the recording durations in the present study were sufficiently long in all cases to include at least one vocal cycle.

Although the limited attachment time of suction cup tags on cetaceans restrict the durations over which individual behavior can be observed with these devices, it is also important to consider the effects of different sampling and sub-sampling routines when collecting cue rates. A large number of short samples on many individuals (as is the case here with many short-term tag deployments) captures variation more reliably than one long term recording from a single animal (Thomisch *et al*., 2015). Furthermore, using a large dataset of real click counts from continuous sampling over entire dive cycles allows for accurate representation of the distributions of the metrics, ensuring models are robust.

As previously mentioned, it is also possible to obtain cue production rates through methodologies other than acoustic tags. Acoustic focal follows allow individual vocalizing animals to be tracked through time and space, resulting in a vocal record similar to that from a short-term acoustic tag. However, such acoustic tracking may involve complex beamforming arrays to maximize range and accuracy (Miller and Tyack, 1998; Von Benda-Beckman *et al*., 2010) as well as frequent movement of recording vessels with the attendant risk of modulating behavior. Moreover, this approach is virtually impossible with animals occurring in large groups, or those that are silent for long periods.

Understanding the vocal behavior of a study species, and the contexts in which a sound cue may be produced, generates possibilities to infer cue rate from other data sources (e.g., Barlow *et al*., 2013). Acoustic tags are ultimately limited by storage capacity; thus they are typically deployed with short-term, non-invasive attachments such as suction-cups. Although longer duration sound recording tags are being developed (Moore *et al*., 2012), most long term tags currently sample movement and depth rather than sound. These time-depth recorders (TDRs) are usually mounted to cetaceans with trans-dermal pins (Andrews *et al*., 2008) and so may have a greater potential for harm than suction cups, but collect long-term movement data from which dive-linked vocal activity can potentially be inferred. For species such as beaked whales with strongly stereotyped vocal behavior, dive durations and inter-dive intervals can be extracted from TDR data and entered into statistical models constructed from acoustic tag data to predict the number of clicks the animals were likely to have produced during these dives, and therefore provide rough estimates of click rates. Although there are dangers in such an approach, it may enable the collection of a much larger sample size than is possible using acoustic tags (e.g., Barlow *et al.*, 2013).

E. Conclusion

This research provided a case-study of vocal cue production rates from Blainville’s and Cuvier’s beaked whales, collected in two sites for each species by acoustic-recording tags, to test for spatial and temporal variability. Cue rates were found to vary significantly by location and over time for Cuvier´s beaked whales, and spatial differences were also detected on a vocal period scale for Blainville´s beaked whales, highlighting the importance of using relevant cue production rates as multipliers within a passive acoustic density estimation framework to reduce bias.

Barlow *et* al. (2013) recommended beaked whales as an ideal species for acoustic density estimation due to the stereotyped nature of their echolocation clicks. This study provides evidence to suggest that even cue rates of species well suited to PAM and acoustic density estimation can vary significantly in relation to a range of explanatory covariates. When densities are estimated from cue counts, cue production rate multipliers should be collected concurrently with the passive acoustic survey from which density will be estimated, and animal-mounted telemetry has proven to be a viable method for collecting this auxiliary data (Marques *et al*., 2013). When it is not possible to collect such data concurrently, a large dataset of acoustic tag records, from a variety of times and locations, can be used to inform a model to predict cue rate multipliers. Click production rate multipliers, collected separately from the PAM survey from which density will be estimated, should be applied with caution, with potential biases recognized and reported.

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REFERENCES

Aguilar Soto, N., Johnson, M., Madsen, P.T., Tyack, P.L., Bocconcelli, A., and Fabrizio Borsani, J. (**2006**). “Does intense ship noise disrupt foraging in deep-diving Cuvier’s beaked whales (*Ziphius cavirostris*)?” *Mar. Mammal Sci.*, **22**, 690-9.

Aguilar de Soto, N., Madsen, P.T., Tyack, P., Arranz, P., Marrero, J., Fais, A., Revelli, E., and Johnson, M. (**2012**). “No shallow talk: cryptic strategy in the vocal communication of Blainville’s beaked whales.” *Mar. Mammal Sci.*, **28**, 75-92.

Andrews, R.D., Pitman, R.L., and Balance, L.T. (**2008**). “Satellite tracking reveals distinct movement patterns for Type B and Type C killer whales in the southern Ross Sea, Antarctica.” *Polar Biol*., **31**, 1461-8.

Arranz, P., DeRuiter, S.L., Stimpert, A.K., Neves, S., Friedlaender, A.S., Goldbogen, J.A., Visser, F., Calambokidis, J., Southall, B.L., and Tyack, P.L. (**2016**). “Discrimination of fast click series produced by tagged Risso’s dolphins (*Grampus griseus*) for echolocation or communication.” *J. Exp. Biol.*, **219**, 2898–907.

Arranz, P., de Soto, N.A., Madsen, P.T., Brito, A., Bordes, F., and Johnson, M.P. (**2011**). “Following a foraging fish-finder: diel habitat use of Blainville’s beaked whales revealed by echolocation.” *PLoS One*, **6**, e28353.

Bailey, H., Corkrey, R., Cheney, B., and Thompson, P.M. (**2013**). “Analyzing temporally correlated dolphin sightings data using generalized estimating equations.” *Mar. Mammal. Sci*., **29**, 123–41.

Baird, R.W., Webster, D.L., Schorr, G.S., McSweeney, D.J., and Barlow, J. (**2008**). “Diel variation in beaked whale diving behavior.” *Mar. Mammal. Sci*., **24**, 630-42.

Barlow, J. (**1999**). “Trackline detection probability for long-diving whales”. In *Marine Mammal Survey and Assessment Methods*, edited by Garner, G.W., Balkema Press, Netherlands. p209-21.

Barlow, J., Tyack, P. L., Johnson, M. P., Baird, R. W., Schorr, G. S., Andrews, R. D., and Aguilar de Soto, N. (**2013**). “Trackline and point detection probabilities for acoustic surveys of Cuvier’s and Blainville's beaked whales,” *J. Acoust. Soc. Am.*, **134**, 2486–96.

Baumgartner, M.F., Fratantoni, D.M., Hurst, T.P., Brown, M.W., Cole, T.V.N., Van Parijs, S.M., and Johnson, M. (**2013**). “Real-time reporting of baleen whale passive acoustic detections from ocean gliders.” *J. Acoust. Soc. Am.*, **134**, 1814-23.

Benoit-Bird, K.J., Au, W.W.L., Brainard R.E., and Lammers, M.O. (**2001**). “Diel horizontal migration of the Hawaiian mesopelagic boundary community observed acoustically.” *Mar. Ecol. Prog. Ser.*, **217**, 1-14.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L., and Thomas, L. (**2001**). *Introduction to distance sampling - estimating abundance of biological populations.* Oxford University Press, Oxford. 448pp.

Buckland, S.T. (**2006**). “Point transect surveys for songbirds: robust methodologies.” *The Auk*, **123**, 345-57.

Claridge, D.E. (**2013**). “Population ecology of Blainville’s beaked whales (*Mesoplodon densirostris*).” Thesis presented for Doctor of Philosophy in Marine Biology at University of St Andrews, Scotland, UK. 313pp.

Dechmann, D.K.N., Heucke, S.L., Giuggioli, L., Safi, K., Voigt, C.C., and Wikelski, M. (**2009**). “Experimental evidence for group hunting via eavesdropping in echolocating bats.” *Proc. Biol. Sci.*, **276**, 2721–8.

DeRuiter, S.L., Southall, B.L., Calambokidis, J., Zimmer, W.M.X., Sadykova, D., Falcone, E.A., Friedlaender, A.S., Joseph, J.E., Moretti, D., Schorr, G.S., Thomas, L., and Tyack, P.L. (**2013**). "First direct measurements of behavioral responses by Cuvier's beaked whales to mid-frequency active sonar." *Biol. Lett.*, **9**, 20130223.

Douglas, L.A., Dawson, S.M., and Jaquet, N. (**2005**). "Click rates and silences of sperm whales at Kaikoura, New Zealand." *J. Acoust. Soc. Am.*, **118**, 523–9.

Efford, M.G., Dawson, D.K., and Borchers, D.L. (**2009**). "Population density estimated from locations of individuals on a passive detector array." *Ecology*, **90**, 2676-82.

Fais, A., Lewis, T.P., Zitterbart, D.P., Álvarez, O., Tejedor, O., and Aguilar Soto, N. (**2016**). "Abundance and distribution of sperm whales in the Canary Islands: can sperm whales in the archipelago sustain the current level of ship-strike mortalities?" *PLoS One*, **11**, e0150660.

Falcone, E.A., Schorr, G.S., Douglas, A.B., Calambokidis, J., Henderson, E., McKenna, M.F., Hildebrand, J., and Moretti, D. (**2009**). "Sighting characteristics and photo-identification of Cuvier's beaked whales (*Ziphius cavirostris*) near San Clemente Island, California: a key area for beaked whales and the military?" *Mar. Biol.*, **156**, 2631–40.

Fitch, W.T., and Hauser, M.D. (**1995**). "Vocal production in nonhuman primates: acoustics, physiology, and functional constraints on "honest" advertisement." *Am. J. Primatol.*, **37**, 191-219.

Heinicke, S., Kalan, A.K., Wagner, O.J.J., Mundry, R., Lukashevich, H., and Kühl, H.S. (**2015**). "Assessing the performance of a semi-automated acoustic monitoring system for primates." *Methods Ecol. Evol.*, **6**, 753-63.

Hildebrand, J., Baumann-Pickering, S., Frasier, K., Trickey, J., Merkens, K., Wiggins, S., McDonald, M., Garrison, L., Harris, D., Marques, T.A., and Thomas, L. (**2015**). "Passive acoustic monitoring of beaked whale densities in the Gulf of Mexico." *Scientific Reports*, **5**, 16343.

Højsgaard, S., Halekoh, U., and Yan, J. (**2006**). "The R package geepack for Generalized Estimating Equations." *J. Stat. Softw*., **15**, 1-11.

Johnson, M.P., and Tyack, P.L. (**2003**). "A digital acoustic recording tag for measuring the response of wild marine mammals to sound." *IEEE J. Ocean. Eng*., **28**, 3–12.

Johnson, M., Madsen, P.T., Zimmer, W.M.X., de Soto, N.A., and Tyack, P.L. (**2004**). "Beaked whales echolocate on prey." *Proc. Biol. Sci*., **271 Suppl**, S383–S386.

Johnson, M., Madsen, P.T., Zimmer, W.M.X., de Soto, N.A., and Tyack, P.L. (**2006**). "Foraging Blainville's beaked whales (*Mesoplodon densirostris*) produce distinct click types matched to different phases of echolocation." *J. Exp. Biol.*, **209**, 5038–50.

Johnson, M., Hickmott, L.S., Aguilar Soto, N., and Madsen, P.T. (**2008**). "Echolocation behaviour adapted to prey in foraging Blainville's beaked whale (*Mesoplodon densirostris*)." *Proc. Roy Soc. B.*, **275**, 133-9.

Johnson, M., de Soto, N.A., and Madsen, P. T. (**2009**). "Studying the behaviour and sensory ecology of marine mammals using acoustic recording tags: a review." *Mar. Ecol. Prog. Ser*., **395**, 55–73.

Johnson, M. (**2014**). DTAG tool box, version 20th August 2014. Retrieved from URL: www.soundtags.st-andrews.ac.uk.

Klink, H., Mellinger, D.K., Klinck, K., Bogue, N.M., Luby, J.C., Jump, W.A., Shilling, G.B., Litchendorf, T., Wood, A.S., Schorr, G.S., and Baird, R.W. (2012). "Near-real-time acoustic monitoring of beaked whales and other cetaceans using a Seaglider^{TM}." *PLoS ONE*, **5**, e36128.

Küsel, E.T., Mellinger, D.K., Thomas, L., Marques, T.A., Moretti, D., and Ward, J. (**2011**). "Cetacean population density estimation from single fixed sensors using passive acoustics." *J. Acoust. Soc. Am.*, **129**, 3610-22.

Lanfredi, C., Azzellino, A., D'Amico, A., Centurioni, L., Rella, M.A., Pavan, G., and Podestà, M. (**2016**). "Key oceanographic characteristics of Cuvier's beaked whale (*Ziphius cavirostris*) habitat in the Gulf of Genoa (Ligurian Sea, NW Mediterranean)." *J. Oceanogr. Mar. Res.*, **4**, 1000145.

Lin, L.I. (**1989**). "A concordance correlation coefficient to evaluate reproducibility." *Biometrics*, **45**, 255-68.

Madsen, P.T., Johnson, M., de Soto, N.A., Zimmer, W.M.X., and Tyack, P. (**2005**). "Biosonar performance of foraging beaked whales (*Mesoplodon densirostris*)," *J. Exp. Biol.*, **208**, 181–94.

Madsen, P. T., de Soto, N. A., Arranz, P., and Johnson, M. (**2013**). "Echolocation in Blainville's beaked whales (*Mesoplodon densirostris*)." *J. Comp. Physiol. A*, **199**, 451–69.

Marques, T.A., Thomas, L., Ward, J., DiMarzio, N., and Tyack, P. L. (**2009**). "Estimating cetacean population density using fixed passive acoustic sensors: an example with Blainville's beaked whales." *J. Acoust. Soc. Am.*, **125**, 1982–94.

Marques, T.A., Munger, L., Thomas, L., Wiggins, S., and Hildebrand, J. A. (**2011**). "Estimating North Pacific right whale *Eubalaena japonica* density using passive acoustic cue counting." *Endanger. Species Res.*, **13**, 163–72.

Marques, T.A., Thomas, L., Martin, S.W., Mellinger, D.K., Ward, J.A., Moretti, D.J., Harris, D., and Tyack, P.L. (**2013**). “Estimating animal population density using passive acoustics.” *Biol. Rev.*, **88**, 287–309.

Martin, S.W., Marques, T.A., Thomas, L., Morrissey, R.P., Jarvis, S., Dimarzio, N., Moretti, D., and Mellinger, D. K. (**2013**). “Estimating minke whale (*Balaenoptera acutorostrata*) boing sound density using passive acoustic sensors.” *Mar. Mammal. Sci.*, **29**, 142–58.

MATLAB R2013a (**2013**), The MathWorks, Inc., Natick, Massachusetts, United States.

Matthews, J., Brown, S., Gillespie, D., Johnson, M., McLanaghan, R., Moscrop, A., Nowacek, D.P., Leaper, R., Lewis, T., and Tyack, P.L. (**2001**). “Vocalization rates of the North Atlantic right whale (*Eubalaena glacialis*)” *J. Cetacean Res. Manag.*, **3**, 271–82.

Miller, P.J. and Tyack, P.L. (1998). “A small towed beamforming array to identify vocalizing resident killer whales (*Orcinus orca*) concurrent with focal behavioral observations.” *Deep-Sea Res. Pt. II.*, **45**, 1389-1405.

Moore, M., Shorter, A., Hurst, T., Bocconcelli, A., Johnson, M., Tyack, P., Rittschof, D., Nowacek, D., and Howle, L. (**2012**). “Improving attachments of non-invasive (type III) electronic data loggers to cetaceans.” Distribution statement, retrieved from URL: http://www.onr.navy.mil/reports/FY14/npmoore.pdf.

Moretti, D., DiMarzio, N., Morrissey, R., Ward, J., and Jarvis, S. (**2006**). “Estimating the density of Blainville’s beaked whale (*Mesoplodon densirostris*) in the Tongue of the Ocean (TOTO) using passive acoustics.” Proceedings of the Oceans’06 MTS/IEEE-Boston, Boston, MA. 5pp.

Moretti, D., Marques, T., Thomas, L., DiMarzio, N., Dilley, A., Morrissey, R., McCarthy, E., Ward, J., and Jarvis, S. (**2010**). “A dive counting density estimation method for

Blainville’s beaked whale (*Mesoplodon densirostris*) using a bottom-mounted hydrophone field as applied to a midfrequency active (MFA) sonar operation.” *Appl. Acoust.*,**71**, 1036–42.

Moretti, D., Thomas, L., Marques, T., Harwood, J., Dilley, A., Neales, B., Shaffer, J., McCarthy, E., New, L., Jarvis, S., and Morrissey, R. (**2014**). “A risk function for behavioral disruption of Blainville’s beaked whales (*Mesoplodon densirostris*) from mid-frequency active sonar.” *PLoS One*, **9**, e85064.

NOAA Climate Prediction Center (**2015**). “Cold and warm episodes by season.” Retrieved from URL: http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears.shtml.

Oehlert, G.W. (1992). “A note on the delta method.” *Am. Stat.*, **46**, 27–9.

Overall, J.E., and Tonidandel, S. (**2004**). “Robustness of Generalized Estimating Equation (GEE) tests of significance against misspecification of the error structure model.” *Biometrical J.*, **46**, 203–13.

Parks, S.E., Searby, A., Célérier, A., Johnson, M. P., Nowacek, D.P., and Tyack, P.L. (**2011**). “Sound production behavior of individual North Atlantic right whales: implications for passive acoustic monitoring.” *Endanger. Species Res.*, **15**, 63–76.

Pérez, J.M., Jensen, F.H., Rojano-Doñate, L., and Aguilar de Soto, N. (**2016**). “Different modes of acoustic communication in deep-diving short-finned pilot whales (*Globicephala macrorhynchus*).” *Mar. Mam .Sci.* doi:10.1111/mms.12344.

Pyke, G.H. (**1984**). “Optimal foraging theory: a critical review.” *Ann. Rev. Ecol. Syst. 1984*, **15**, 523-75.

Quick, N.J., Scott-Hayward, L.A.S., Sadykova, D., Nowacek, D., and Read, A. (**2016**). “Effects of a scientific echo sounder on the behavior of short-finned pilot whales (*Globicephala macrorhynchus*).” *Can. J. Fish. Aquat. Sci*., doi:10.1139/cjfas-2016-0293.

R Core Team (**2015**). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Retrieved from URL: http://www.R-project.org/

Scott-Hayward, L.A.S., Oedekoven, C.S., Mackenzie, M.L., Walker, C.G., and Rexstad, E. (**2013**). "MRSea package (version 0.2.0): statistical modelling of bird and cetacean distributions in offshore renewables development areas." University of St. Andrews: Contract with Marine Scotland: SB9 (CR/2012/05)

Sivle, L.D., Kvadsheim, P.H., Fahlman, A., Lam, F.P., Tyack, P., and Miller, P.J. (**2012**). “Changes in dive behaviour during sonar exposure in killer whales, long-finned pilot whales, and sperm whales.” *Front. Physiol*., **3**, 1-11.

Soldevilla, M. S., Wiggins, S. M., and Hildebrand, J.A. (**2010a**). “Spatial and temporal patterns of Risso’s dolphin echolocation in the Southern California Bight.” *J. Acoust. Soc. Am*., **127**, 124–32.

Soldevilla, M.S., Wiggins, S.M., and Hildebrand, J.A. (**2010b**). “Spatio-temporal comparison of Pacific white-sided dolphin echolocation click types.” *Aquat. Biol.,* **9**, 49–62.

Stevenson, B.C., Borchers, D.L., Altwegg, R., Swift, R.J., Gillespie, D.M., and Measey, G.J. (**2015**). “A general framework for animal density estimation from acoustic detections across a fixed microphone array.” *Methods Ecol. Evol.*, **6**, 38-48.

Thomisch, K., Boebel, O., Zitterbart, D.P., Samaran, F., Van Parijs, S., and Van Opzeeland, I. (**2015**). “Effects of subsampling of passive acoustic recordings on acoustic metrics.” *J. Acoust. Soc. Am*., **138**, 267-78.

Tyack, P.L., Johnson, M., Soto, N.A., Sturlese, A., and Madsen, P.T. (**2006a**). "Extreme diving of beaked whales." *J. Exp. Biol.*, **209**, 4238–53.

Tyack, P.L., Johnson, M.P., Zimmer, W.M.X., Aguilar de Soto, N., and Madsen, P.T. (**2006b**). "Acoustic behavior of beaked whales, with implications for acoustic monitoring." *Oceans 2006*, 1-6.

Von Benda-Beckmann, A.M., Lam, F.P.A., Moretti, D.J., Fulkerson, K., Ainslie, M.A., van IJsselmuide, S.P., Theriault, J., and Beerens, S.P. (**2010**). "Detection of Blainville's beaked whales with towed arrays." *Appl.Acoust.*, **71**, 1027-35.

Ward, J. A., Morrissey, R. P., Moretti, D. J., DiMarzio, N., Jarvis, S., Johnson, M. P., Tyack, P. L., and White, C. (**2008**). "Passive acoustic detection and localization of *Mesoplodon densirostris* (Blainville's beaked whale) vocalizations using distributed bottom-mounted hydrophones in conjunction with a digital tag (DTag) recording." *Can. Acoust*., **36**, 60–6.

Ward, J., Jarvis, S., Moretti, D., Morrissey, R., Dimarzio, N., Johnson, M., Tyack, P., Thomas, L., and Marques, T. (**2011**). "Beaked whale (*Mesoplodon densirostris*) passive acoustic detection in increasing ambient noise." *J. Acoust. Soc. Am.*, **129**, 662-9.

Weilgart, L.S. (**2007**). "A brief review of known effects of noise on marine mammals." *Int. J. Comp. Pysch.*, **20**, 159-68.

Whitehead, H. (**2008**). "Sperm whale (*Physeter macrocephalus*)." In: Perrin, W.F., Würsig, B., and Thewissen, J.G.M. (Eds). *Encyclopedia of Marine Mammals Volume Two*. Burlington, MA: Elsevier, Academic Press. 1352pp.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., and Smith, G.M. (**2009**). *Mixed effects models and extensions in ecology with R.* Springer, New York. 574pp.

TABLES

TABLE I: Overview of the tag deployments (by species, location and year) and total number of vocal periods and dive cycles analyzed in this study. Tag detachment after to the end of a vocal period meant that the total number of complete dive cycles is sometimes lower than the number of vocal periods for the same tag deployment.

[see following page]

Species	**Location**	**Year**	**Tag deployments**	**Vocal periods**	**Dive cycles**
Cuvier's beaked whale (*Ziphius cavirostris*)	**Ligurian Sea, Mediterranean**	2003	2	8	6
		2004	5	18	15
		2005	2	8	7
		2006	2	5	5
		2008	1	4	4
		Total	**12**	**43**	**37**
	Southern California	2010	1	1	1
		2011	1	1	1
		2013	2	3	2
		Total	**4**	**5**	**4**
Blainville's beaked whale (*Mesoplodon densirostris*)	**El Hierro, Canary Islands**	2003	2	7	6
		2004	1	4	4
		2005	4	11	10
		2008	5	17	15
		2010	2	9	8
		Total	**14**	**48**	**43**
	Bahamas	2006	1	4	4
		2007	4	18	18
		Total	**5**	**22**	**22**

TABLE II: Acoustic and dive metrics for Blainville’s and Cuvier’s beaked whales, in two locations per species. Standard deviations, weighted by the number of dive units recorded by each tag, are given in parentheses. Coefficients of variation were calculated from standard deviation divided by the mean for each deployment, both weighted by the number of dives in each tag record. Sample sizes are given in Table I.

[see following page]

Parameter	**Blainville's beaked whales**		**Cuvier's beaked whales**	
	Bahamas	**El Hierro**	**Liguria**	**Southern California**
Mean number of clicks during a vocal period	4628 (913)	3500 (333)	3523 (586)	3046 (717)
Mean vocal period duration (mins)	29.9 (5.8)	24.5 (2.3)	35.2 (5.7)	35.1 (9.1)
Mean dive cycle duration (mins)	181.0 (53.2)	145.0 (31.0)	133.0 (29.8)	228.0 (47.4)
Mean vocal period click rate (clicks/sec)	2.59 (0.15)	2.38 (0.06)	1.67 (0.16)	1.46 (0.14)
Between-tag coefficient of variation in vocal period click rate	5.80%	2.51%	9.59%	9.31%
Mean dive cycle click rate (clicks/sec)	0.50 (0.11)	0.43 (0.14)	0.50 (0.06)	0.24 (0.07)
Between-tag coefficient of variation in dive cycle click rate	23.14%	31.28%	11.98%	30.83%

TABLE III: Modelled click production rates. Different combinations of factor covariates alter the predicted click rates, hence the ranges given below. 95% confidence intervals are given in parentheses.

[see following page]

<table>
<tr><th colspan="3">Blainville’s beaked whale click production rates (clicks/second)</th></tr>
<tr><th></th><th>Bahamas</th><th>El Hierro</th></tr>
<tr><td>Vocal period</td><td>2.58 (2.46-2.71)</td><td>2.38 (2.26-2.50)</td></tr>
<tr><td>Dive cycle</td><td colspan="2">0.41 (0.37-0.46)</td></tr>
<tr><th colspan="3">Cuvier’s beaked whale click production rates (clicks/second)</th></tr>
<tr><th></th><th>Ligurian Sea</th><th>Southern California</th></tr>
<tr><td>Vocal period</td><td>Afternoon: 1.83 (1.71-1.95)
Dusk: 1.49 (1.26-1.75)
Midday: 1.67 (1.50-1.81)
Night: 1.64 (1.52-1.78)</td><td>Afternoon: 1.56 (1.43-1.70)
Dusk: 1.27 (1.07-1.49)
Midday: 1.42 (1.28-1.54)
Night: 1.40 (1.29-1.51)</td></tr>
<tr><td>Dive cycle</td><td>June afternoon: 0.43 (0.37–0.50)
June dusk: 0.52 (0.38-0.72)
June midday: 0.31 (0.24-0.41)
June night: 0.52 (0.40-0.68)
July afternoon: 0.36 (0.32-0.41)
July dusk: 0.44 (0.32-0.61)
July midday: 0.26 (0.19-0.35)
July night: 0.44 (0.34-0.57)
September afternoon: 0.40 (0.37-0.43)
September dusk: 0.48 (0.35-0.66)
September midday: 0.29 (0.22-0.38)
September night: 0.48 (0.37-0.63)</td><td>June afternoon: 0.29 (0.24–0.35)
June dusk: 0.35 (0.26-0.48)
June midday: 0.21 (0.16-0.28)
June night: 0.35 (0.27-0.46)
July afternoon: 0.24 (0.21-0.28)
July dusk: 0.30 (0.22-0.41)
July midday: 0.18 (0.13-0.23)
July night: 0.29 (0.23-0.38)
September afternoon: 0.27 (0.25-0.29)
September dusk: 0.32 (0.24-0.45)
September midday: 0.19 (0.15-0.25)
September night: 0.32 (0.25-0.42)</td></tr>
</table>