

# Towed passive acoustic monitoring complements visual survey methods for Heaviside's dolphins *Cephalorhynchus heavisidii* in the Namibian Islands Marine Protected Area

T Gridley<sup>1,2,3\*±</sup>, MJ Martin<sup>4,5,6±</sup>, J Slater<sup>7</sup>, J-P Roux<sup>8,9</sup>, RJ Swift<sup>10</sup> and SH Elwen<sup>2,3,4</sup>

<sup>1</sup> Centre for Statistics in Ecology, Environment and Conservation, Department of Statistical Sciences, University of Cape Town, Cape Town, South Africa

<sup>2</sup> Department of Botany and Zoology, Stellenbosch University, Stellenbosch, South Africa

<sup>3</sup> Sea Search Research and Conservation NPC, Cape Town, South Africa

<sup>4</sup> Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Pretoria, South Africa

<sup>5</sup> Wildlife Conservation Society Canada, Whitehorse, Yukon, Canada

<sup>6</sup> Department of Biology, University of Victoria, Victoria, British Columbia, Canada

<sup>7</sup> Department of Biodiversity and Conservation Management, Cape Peninsula University of Technology, Cape Town, South Africa

<sup>8</sup> Lüderitz Marine Research, Ministry of Fisheries and Marine Resources, Lüderitz, Namibia

<sup>9</sup> Current affiliation: SEACODE and Namibia Nature Foundation, Lüderitz, Namibia

<sup>10</sup> Sea Mammal Research Unit, School of Biology, University of St Andrews, St Andrews, Scotland, United Kingdom

± These authors are equal contributors to this work

\* Corresponding author, e-mail: [tessgridley@yahoo.co.uk](mailto:tessgridley@yahoo.co.uk)

## Abstract

The genus *Cephalorhynchus* contains four dolphin species, of which three are classified as Near Threatened or Endangered and one subspecies is close to extinction. Understanding the species' abundance, distributions and habitat preferences is necessary for effective management to prevent further population declines. Heaviside's dolphin *C. heavisidii* is endemic to the Benguela ecosystem off southwest Africa, and like other *Cephalorhynchus* species these dolphins produce narrowband high-frequency (NBHF) echolocation clicks with a centroid frequency around 125 kHz. We conducted dedicated visual and acoustic line-transect surveys within and adjacent to the Namibian Islands Marine Protected Area in 2012–2014. Acoustic data were processed in the passive acoustic monitoring software PAMGuard, using the default porpoise click detector and classifier to identify NBHF echolocation clicks. Click detection and classification in PAMGuard included a large excess of false positives, which were easily identified by manual verification of events, and ultimately provided 52 definite detections. The acoustic methods provided data in offshore areas and

during overnight periods, but were imperfect and not suitable for ecologically important shallow coastal areas. While demonstrating the utility of passive acoustic monitoring in line-transect surveys targeting *Cephalorhynchus* species, the study shows that both visual and acoustic methods were needed to collect data throughout the range of Heaviside's dolphin.

**Keywords:** click detection and classification; echolocation; encounter rate; line-transect survey; narrowband high-frequency clicks; PAMGuard; southwestern Atlantic

## Introduction

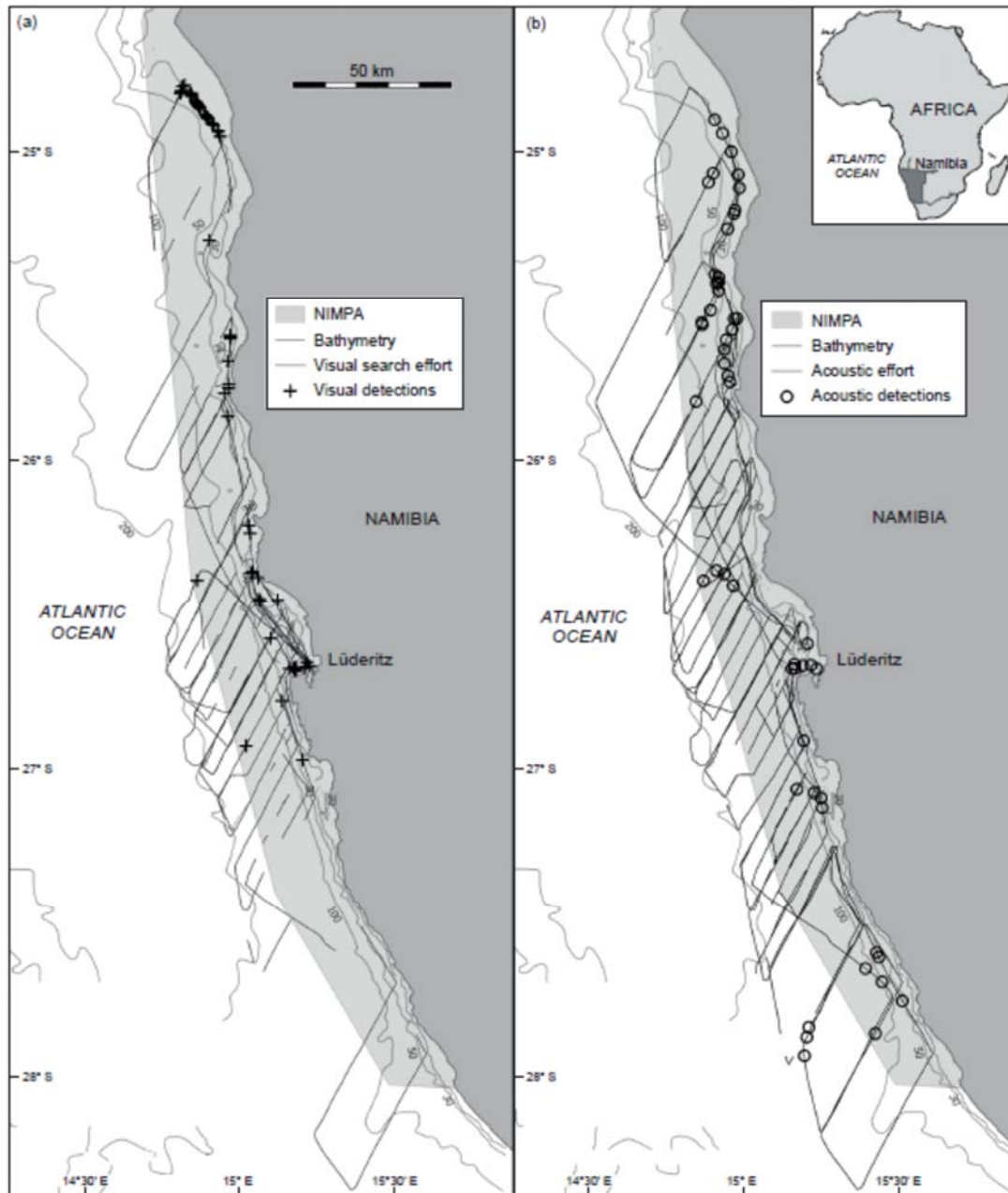
Four species of dolphin comprise the genus *Cephalorhynchus* and are distributed in cool-temperate coastal waters of the Southern Hemisphere (Pichler et al. 2001). The Chilean dolphin *C. eutropia* is classified as Near Threatened (Heinrich and Reeves 2017) and Hector's dolphin *C. hectori* as Endangered (Reeves et al. 2013a). The subspecies *C. hectori maui* (Maui's dolphin) is assessed as Critically Endangered (Reeves et al. 2013b) and is close to extinction (Slooten et al. 2006; Baker et al. 2013). Although arguably the least well-known of the genus, Heaviside's dolphin *C. heavisidii* appears comparatively abundant, particularly in the southern part of its range (Elwen et al. 2009; Gopal et al. 2016). However, this species was recently reclassified from Data Deficient to Near Threatened in global assessments, partly because of uncertainty regarding its overall population structure, abundance and anthropogenic threats (Elwen and Gopal 2018).

Understanding the abundance, density, distribution and habitat preferences of dolphins in the genus *Cephalorhynchus* is necessary for effective management to prevent further population declines. However, the small body sizes and group sizes (Dawson 2018) of all *Cephalorhynchus* species can make them cryptic to detection with visual surveys. Passive acoustic monitoring (PAM) of naturally occurring echolocation clicks offers an alternative detection mode (Gillespie and Chappell 2002; Mellinger et al. 2007). PAM has several advantages over visual detection in that animals can be detected 24 hours a day, in poor weather conditions and when submerged (Zimmer 2011). For cryptic marine mammals whose vocal behaviour is understood, acoustic monitoring can increase the number of detections when compared with visual-only detection methods (Barlow and Taylor 2005). Consequently, PAM is increasingly used to generate information on rare and endangered cetacean species (e.g. Gerrodette and Rojas-Bracho 2011; Richman et al. 2014).

All *Cephalorhynchus* species produce narrowband, high-frequency (NBHF) echolocation clicks (Dawson and Thorpe 1990; Götz et al. 2010; Kyhn et al. 2010; Morisaka et al. 2011; Martin et al. 2018), with a waveform, centroid frequency, bandwidth and duration strikingly similar to the echolocation clicks produced by most porpoises (genus *Phocoena*) (Møhl and Andersen 1973; Au 1997; Morisaka and Connor 2007). This makes them particularly amenable to PAM using click detection and click classification criteria originally developed for the harbour porpoise *P. phocoena* (Gillespie and Chappell 2002). Static (moored) acoustic monitoring devices designed for odontocete detection (T-POD and C-POD monitors; Chelonia Ltd, UK) have been used successfully to investigate the occurrence and density of Heaviside's and Hector's dolphins (Rayment et al. 2009b; Leeney et al. 2011). Although capable of monitoring continuously for long periods, static devices have limited spatial resolution unless they are deployed in extensive arrays.

Incorporating PAM into line-transect surveys (Buckland and Turnock 1992) offers an alternative method for understanding the distribution of cetaceans and for generating estimates of abundance and density (Marques et al. 2012). Most simultaneous visual and acoustic line-transect surveys for NBHF species have targeted porpoise species, notably harbour porpoises in European waters (Gillespie et al. 2005; Booth et al. 2013) and the vaquita *P. sinus* in the Gulf of California (Gerrodette et al. 2011). These studies have commonly used the open-source software PAMGuard (Gillespie et al. 2008; [www.pamguard.org](http://www.pamguard.org)) and its precursor RainbowClick (International Fund for Animal Welfare, [www.ifaw.org](http://www.ifaw.org)) to automatically detect porpoise clicks in real-time and *post hoc*. During detection, clicks are localised using ‘time of arrival differences’ (TOAD) of pulses detected on two hydrophone elements arranged in a linear formation and towed behind the research vessel. The perpendicular distance of vocalising individuals or groups from the survey track line can be estimated from multiple click detections that occur close in time and space using target motion analysis. Although this method has generated considerable data on the occurrence of *Phocoena* species (e.g. Gillespie et al. 2005; Gerrodette et al. 2011; Booth et al. 2013), to the authors’ knowledge no studies have conducted dedicated acoustic line-transect ship surveys for *Cephalorhynchus* species.

This methodological report arises from a series of dedicated visual and acoustic line-transect ship-based surveys for dolphins in Namibia. Here, we focus on click detection and classification for Heaviside’s dolphin, which is endemic to the Benguela ecosystem off the west coast of southern Africa (Findlay et al. 1992; Gopal et al. 2016). The range of this species is limited to coastal and shelf waters (primarily depths of <100 m: Elwen et al. 2006; De Rock et al. 2019), where it is exposed to several unquantified human threats, including bycatch and prey depletion by fisheries and disturbance from unregulated marine ecotourism (Elwen and Gopal 2018). Heaviside’s dolphins produce directional echolocation clicks characterised by a mean centroid frequency of 125 kHz, root-mean-square (RMS) bandwidth of 15 kHz (–3 dB), duration (–10 dB) of 74  $\mu$ s, and mean apparent source level (ASL) of 173 dB re 1  $\mu$ Pap-p (Morisaka et al. 2011). The echolocation click and spectral parameters are similar to values previously reported for harbour porpoises as well as other species of *Cephalorhynchus* (Au et al. 1999; Kyhn et al. 2009, 2010, 2013). We investigated whether PAMGuard software with the default ‘porpoise’ click detection and click classification settings would detect Heaviside’s dolphins. We assessed differences in detection range relative to detection mode and the influence of environmental conditions (Beaufort sea state and water depth) on detection. For abundance estimates and a discussion of the distribution of Heaviside’s dolphins as revealed by the full series of NIMPA surveys, see Martin et al. (2020).



**Figure 1:** During surveys of Heaviside's dolphins in the Namibian Islands Marine Protected Area (NIMPA), survey effort on systematic, transit and opportunistic lines (dark grey lines), shown by detection mode. (a) Visual-survey effort, with locations of visual detections. (b) Acoustic-survey effort, with locations of acoustic detections

## Materials and methods

### *Survey design*

Data were collected between March and May of 2012 to 2014 during simultaneous visual and passive acoustic line-transect surveys within and adjacent to the recently established Namibian Islands Marine Protected Area (NIMPA) in southern Namibia (Figure 1). The NIMPA comprises a coastal strip spanning approximately three degrees of latitude with an

average width of 30 km. It includes 11 offshore islands and islets, extending from Hollamsbird Island (24°38' S, 14°31' E) in the north to Sinclair Island (27°40' S, 15°31' E) in the south (Currie et al. 2009). Surveys were performed as a collaboration with Namibia's Ministry of Fisheries and Marine Resources (MFMR), using their dedicated 22-m Lüderitz-based research vessel the RV *!Anichab*. All surveys departed and returned to Lüderitz, with data collection continuing overnight when weather conditions allowed or with occasional overnight stops to take shelter under adverse conditions. Our study design incorporated systematic survey lines that ran from areas with an expected high density of Heaviside's dolphins in the nearshore, to areas of expected low density offshore (Best 2007; De Rock et al. 2019). Surveys were conducted at a relatively constant speed of 8–10 knots and with survey lines designed to head into (220°) and away from (40°) the predominant swell, running from coastal waters to the 200-m isobath. As this study compares detectability between two survey modes, we used data from all survey effort (dedicated transect lines, transit passages and opportunistic transect lines) throughout the study, where the same survey protocols were applied.

### ***Visual-survey data collection***

Visual surveys for all cetacean species were conducted during daylight hours, generally between 06:00 and 17:00 (UCT+02:00). Prior to survey commencement, visual observers were trained in estimating distance using objects at a known distance from the vessel. At the start of each survey, standard information was collected on the sighting conditions, including Beaufort sea state (BF, 0–6), wind direction and speed (knots), swell height (m), cloud cover (out of 8) and sight ability (an overall index of the sighting conditions, out of 5). Information on sighting conditions was updated every 30 min, and whenever conditions changed. The visual-survey design consisted of two observers, stationed on either side of the vessel and searching from the transect line to 90° port or starboard. Searches were conducted with 8×42 binoculars and the naked eye, and observers rotated every 30 min to minimise fatigue. Where possible, photographs were used to confirm species identification. Observers used VHF radios to communicate all sightings information to the data logger, for real-time entry using Logger 2010 software developed by the International Fund for Animal Welfare (Gillespie et al. 2010). Observers reported the distance and bearing to the dolphin group (distance estimated by eye, and bearing with an angle board), and the group sizes as 'best,' 'high' and 'low' estimates of the number of individuals present. Visual data were collected throughout all daylight hours whenever survey conditions were favourable (BF 1–5, no mist or fog).

### ***Acoustic-survey data collection***

When possible, acoustic data were collected using a custom-built linear hydrophone array, which recorded continuously when deployed. The array was deployed when surveying in waters exceeding a depth of 30 m and it was extended 380 m behind the vessel, positioned approximately 10 m deep in the water column when the vessel was underway. The hydrophone array consisted of a 3-m oil-filled streamer section containing three hydrophone elements (HS150; Sonar Research and Development Ltd, Beverley, UK), with sensitivities of –204 dB re 1 V/μPa and a flat frequency response (±2 dB) from 1 Hz to 160 kHz. Data collected from the first and second hydrophones separated by 25 cm in the linear configuration were used. Amplified signals were digitised at a 500-kHz sampling rate through a National Instruments Digital Acquisition sound card (USB-X6356,

<http://www.ni.com>), with a high-pass filter (2-pole Butterworth) at 400 Hz and a low-pass filter (1-pole Butterworth) at 200 kHz. All recordings were made using PAMGuard 1.13.03, which limited file sizes to 655 MB (equivalent to 5 min 35 s of recording time), and were saved at a 16-bit resolution directly to the hard drive of a Dell XPS laptop.

### ***Acoustic classification in PAMGuard***

Acoustic-data analysis took place offline following initial data screening. Files influenced by extreme electrical noise on one or both channels were removed from subsequent analyses. Analysis was conducted in the PAMGuard mixed mode using a high-pass pre-filter at 10 kHz (4-pole Butterworth) and a bandpass trigger filter set between 100 kHz and 160 kHz (4-pole Butterworth). Clicks were detected using a standard trigger threshold set at 10 dB. Click classification took place in the PAMGuard viewer mode using the default 'porpoise' settings to classify Heaviside's dolphin clicks based on pre-defined click parameters. Clicks were automatically classified as porpoise—hereafter referred to as NBHF clicks—if there was a difference of >5 dB in energy between the 100–150 kHz 'test band' compared with the 40–90 kHz 'control band,' together with the peak and mean frequency occurring within the test band.

Acoustic events were defined as all classified clicks occurring within a time-window of 4 min 5 s. This time-window was identified using the speed of the vessel (8 knots) and a maximum radial detection distance of 500 m, estimated for an animal echolocating at a stationary location on the horizontal plane (Rayment et al. 2009a; Gerrodette et al. 2011). Based on these values it would take 4 min 5 s for the research vessel to approach and fully pass through the radial detection distance of echolocating dolphin(s). Encounters separated by more than this time-limit were assumed to be from separate dolphin groups. In practice, most events were discrete and concluded within a much shorter time-frame. All events and standard information concerning the time, number of clicks and inter-click interval (ICI) per event were automatically stored in a linked database. Based on the PAMGuard click classification, acoustic events were scored as (1) definite Ch ('Ch'), (2) probable Ch ('PrCh') or (3) possible Ch ('PCh'), by the analysts (MM, TG, JS), according to the PAMGuard criteria shown in Table 1. Therefore, although the detection and classification of clicks was automated, information on the total number of clicks in each event, click-energy distribution across both hydrophone channels, and the respective click-bearing and click-waveform characteristics, were reviewed through the built-in features of PAMGuard and used by the analysts to classify acoustic events. 'Definite Ch' and 'probable Ch' events were assigned based on the number of NBHF clicks identified in PAMGuard, where five clicks was used as a threshold between the two categories (Gerrodette et al. 2011). Two additional categories were created for false-positive click classification, attributed to either the wrong species ('FP-WS') or noise interference ('FP-N'). Broadband dolphin clicks, such as those produced by the dusky dolphin *Lagenorhynchus obscurus* (Au and Würsig 2004), can extend up to and beyond the characteristic frequency band of NBHF clicks (Au 1993) and occasionally they can be misclassified as NBHF (i.e. porpoise) (Gillespie and Chappell 2002). However, such events have a very small proportion of overall clicks classified as NBHF when compared with broadband clicks within the encounter (Gillespie and Chappell 2002). Confident assignment of false-positive events that were attributed to noise was also necessary, as even after preliminary data-screening there were still intermittent recording periods with excessive

noise on one channel, which triggered the NBHF classifier. Events classified as ‘FP-N’ were identified through careful visual inspection of the clicks’ waveform and frequency spectra in the PAMGuard viewer.

**Table 1:** From acoustic surveys of Heaviside’s dolphins *Cephalorhynchus heavisidii* in the Namibian Islands Marine Protected Area, summary of criteria used to identify and categorise click events detected within PAMGuard viewer mode, and the criteria applied during manual verification through inspection of the sound ‘.wav’ file. NBHF = narrowband high-frequency clicks

Code	Term	PAMGuard criteria	Manual analyst confirmation	Manual analyst refutation
Ch	Definite Ch	Events with $\geq 5$ NBHF clicks and a corresponding waveform and frequency spectra that conform to NBHF click characteristics, such as: typically contain no energy below 100 kHz, narrow bandwidth (approx. <15 kHz [-3 dB]), polycyclic waveform, and duration >100 $\mu$ s (Au 1997)	(i) Sightings of <i>C. heavisidii</i> within the ‘matched’ time-window and/or (ii) Visual inspection of ‘.wav’ files confirms ‘Ch’ clicks through spectral and waveform characteristics conforming to NBHF clicks	Visual inspection of ‘.wav’ files indicates the spectral and waveform characteristics do not conform to NBHF click characteristics
PrCh	Probable Ch	Events with <5 NBHF clicks and a corresponding waveform and frequency spectra, which through visual assessment conform to NBHF click characteristics	As above	As above
PCh	Possible Ch	Events with $\geq 1$ NBHF clicks with low amplitude and/or a corresponding waveform that did not conform well to NBHF click characteristics. Classified clicks often occurred at similar time-bearing positions with one or more non-classified clicks, which, upon inspection, also contained energy in the 125 kHz frequency band, indicative of a low-amplitude detection. Such information was used to distinguish these possible ‘Ch’ click events from false-positive events	As above	As above
FP-WS	False positive: wrong species	Events where a very small proportion of the overall clicks were NBHF and the remaining were broadband dolphin clicks	(i) Sightings of dusky dolphins <i>Lagenorhynchus obscurus</i> within the ‘matched’ time-window, and/or (ii) Visual inspection of ‘.wav’ files confirms broadband dusky dolphin clicks through spectral and waveform characteristics (Au and Würsig 2004)	(i) Visual inspection of ‘.wav’ files confirms noise interference (i.e. ‘FP-N’), or (ii) Visual inspection of ‘.wav’ files confirms NBHF clicks. Most likely to arise in a mixed-species group, where NBHF clicks are poorly represented as compared with numerous higher-amplitude broadband clicks
FP-N	False positive: noise	Events with $\geq 1$ NBHF clicks that fulfilled at least one of the following criteria: (i) occurred coincidentally with broadband noise, often occurring at a constant bearing of 90°; (ii) had an erratic waveform that did not follow the characteristic sinusoidal waveform of NBHF clicks; (iii) contained energy in the 125 kHz frequency band only on one channel	Visual inspection of ‘.wav’ files confirms noise interference	Visual inspection of ‘.wav’ files identifies clear ‘Ch’ click trains (i.e. true positive)
F-N	False negative	No NBHF clicks classified in PAMGuard	Visual inspection of ‘.wav’ files confirms NBHF clicks within the ‘matched’ time-window. Indicates clicks did not meet PAMGuard detection thresholds	Visual inspection of ‘.wav’ files fails to detect NBHF clicks (i.e. true negative). This indicates that the animal(s) were acoustically quiet, out of acoustic detection range, or their clicks did not propagate well to the hydrophone array

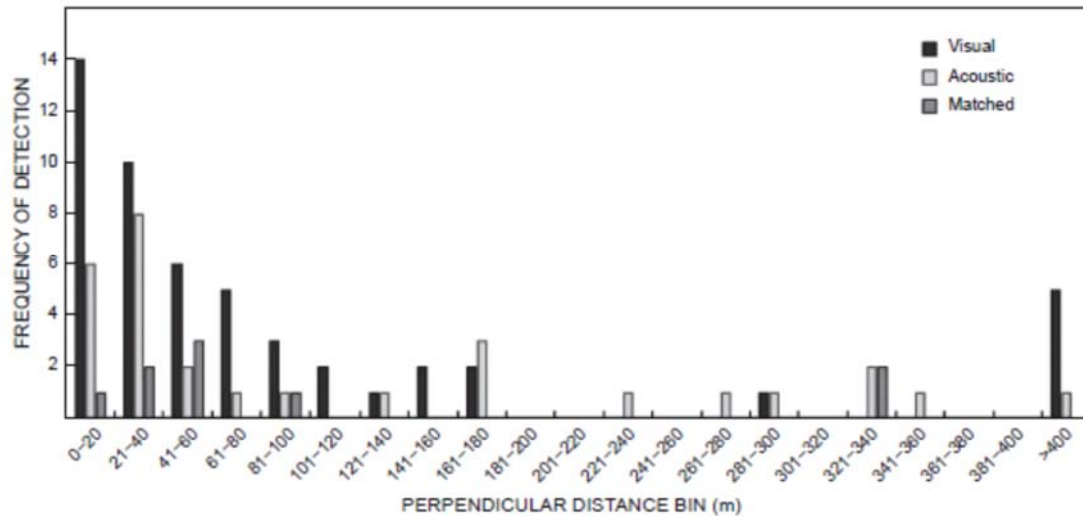
We verified our PAMGuard-based event classification through manual verification of the underlying sound files in the spectrogram and waveform displays of Adobe Audition CC

(Adobe Systems Inc., setting: 512-point FFT, Hamming window). All classified acoustic events and a subset (~40%) of the 'FP-N' events were assessed by inspecting the sound files containing these events. We also cross-referenced all acoustic events assigned as 'Ch,' 'PrCh,' 'PCh' and 'FP-WS' with the visual-sightings data to determine matched detections. The criteria for matching followed Richman et al. (2014), whereby the time and radial distance of the visual sighting, vessel speed, distance between the visual and acoustic platforms, and time of acoustic detection were considered during matching decisions. However, some exceptional circumstances required deviation from this approach because Heaviside's dolphins were occasionally encountered in loose aggregations of multiple, small separate groups. These were treated as discrete encounters in the sightings database. However, through the acoustic-detection mode, such aggregations were detected as extended acoustic events lasting several minutes longer than single-group acoustic detections. In these unusual cases, matching decisions were based on careful inspection of the visual and acoustic event information, including localisation of click-trains. Where necessary, the encounter was aggregated to a conservative estimate for matched detections.

### ***Detection modes***

Detections of Heaviside's dolphins were compared by mode (visual, acoustic or matched) to investigate differences that might influence survey efficiency and future survey-design criteria. The perpendicular distance from the transect line at the time of detection was estimated for all visual detections and, wherever possible, for acoustic events. Acoustic detections were localised in PAMGuard using the signal time of arrival differences by applying the 2D 'Simplex' target-motion-localisation algorithm. Differences in detection distance for visual and acoustic detections were tested statistically using a nonparametric one-way ANOVA (Kruskal–Wallis test). The influence of wind conditions (measured on the Beaufort scale, ranging from 0 to 6) on encounter rates (detection events per hour) was examined by scaling the number of detections made by each survey mode (visual and acoustic) by the respective amount of survey effort during each sea state. Finally, we investigated the depth at detection for each mode. As most detection distances were within 200 m of the research vessel (Figure 2), the vessel location at the initial time of detection was used as a location proxy from which water depth at detection was calculated. Depth values were calculated in QGIS, derived from the freely available GEBCO Atlas (2014, [www.gebco.net](http://www.gebco.net)), at a resolution of 15 arc-second intervals (roughly 400 × 400 m resolution at the latitude of the study area).





**Figure 2:** Graphical summary of the estimated perpendicular detection distances by detection mode (visual, acoustic or matched), obtained during surveys of Heaviside’s dolphins in the Namibian Islands Marine Protected Area

## Results

Data were collected over 34 survey days (31 with acoustic effort) and we report the results of 167 h 53 min of dedicated visual survey effort and 278 h 57 min of acoustic survey effort (Figure 1). Combined visual and acoustic survey effort amounted to 107 h 3 min. Heaviside’s dolphins were encountered engaged in a range of behaviours and would frequently approach the vessel to bow ride. Approximately 67% of the Heaviside’s dolphin groups exhibited attractive-responsive movement, as their aspect was directed towards (i.e. they were swimming towards) the vessel on visual detection. Best estimates of group size based on the 72 confirmed visual detections were generally small, with a mean of 4 dolphins (SD 6) observed per encounter. Although not corrected for covariates which might influence detection, Figure 1 indicates spatial aggregation and a preference for inshore waters for Heaviside’s dolphin. Depth-at-detection ranged from 13 to 158 m, with the farthest-offshore detections at 21 km (visual) and 46 km (acoustic) from shore. Overall encounter rates were 0.43 groups h<sup>-1</sup> (visual) and 0.19 groups h<sup>-1</sup> (acoustic).

### ***Acoustic classification of Heaviside’s dolphin signals in PAMGuard***

In total, 640 NBHF click events were identified in PAMGuard, ranging from 1 to 4 054 NBHF clicks per event (mean: 24 [SD 203], mode 1). Of these, 52 (8%) NBHF click events were identified as definite Heaviside’s dolphin (‘Ch’), 10 (2%) as probable Heaviside’s dolphin (‘PrCh’), and 46 (7%) as possible Heaviside’s dolphin (‘PCh’). The number of NBHF clicks per ‘Ch’ event ranged from 5 to 727 (mean: 88 [SD 139], mode 7). In some cases, the ‘PCh’ events contained a high number of NBHF clicks (range 1–93). However, by applying the predetermined event criteria specified in Table 1, confidence in these events being ‘Ch’ was low. All 52 ‘Ch’ events identified in PAMGuard were manually verified as true positive detections by examining the associated ‘.wav’ sound-file data. The number of ‘PrCh’ events was low, and most (7 out of 10) were confirmed as ‘Ch’ through verification using the supporting sound files. For ‘PCh’ detections, only 22% (10) were confirmed as true ‘Ch’ and the rest retained the ‘PCh’ classification or were re-classified as false positives. Events classified as ‘FP-WS’ were easily identified through inspection of PAMGuard outputs and

manually verified. When cross-checked against the sightings data, 23 out of 24 FP-WS events (96%) were confirmed as dusky dolphins (Table 2). Although numerous ( $n = 508$ ), the false-positive events caused by noise (FP-N) were identified through PAMGuard with ease (Table 2).

**Table 2:** Classification of PAMGuard detection events (right column) recorded during acoustic surveys of Heaviside’s dolphins. The shaded values on the diagonal show the number of events identified in PAMGuard that remained in each category following manual verification. Values to the left and right indicate reclassification of events into new categories following manual verification, with the column header indicating the reclassified category. Final category sizes following manual verification are shown in the bottom row. The number of ‘FP-N’ events verified manually ( $n = 197$ ) is a subsample of the total identified in the dataset ( $n = 508$ ). See Table 1 for abbreviation codes

	Ch	PrCh	PCh	FP-WS	FP-N	Identified in PAMGuard
Ch	52	0	0	0	0	52
PrCh	7	0	3	0	0	10
PCh	10	0	24	0	12	46
FP-WS	1	0	0	23	0	24
FP-N	1	0	3	1	192	197 (508)
Manually verified	71	0	30	24	204	

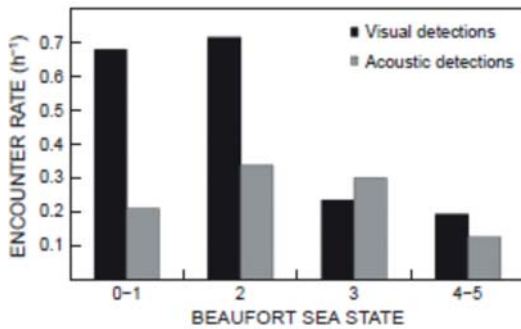
### **Detection-mode comparisons**

Of the ‘Ch’ acoustic detections, 29 (56%) could be localised in PAMGuard using time-of-arrival differences of the NBHF signals on the array elements, providing an estimated perpendicular distance of the dolphin group from the transect line. Localisation failed when successive bearing angles could not be determined, usually caused by a low number of clicks in the acoustic event. There was no significant difference in estimated detection distance from the transect line between the visual ( $n = 51$ ) and acoustic modes (Kruskal–Wallis:  $\chi^2 = 0.60$ ,  $df = 1$ ,  $p = 0.438$ , visual mean: 121 m [SD 214], acoustic mean: 128 m [SD 154]). In general, visual and acoustic perpendicular-detection distances were <200 m from the transect line, with the majority of detections <100 m away (Figure 2). Very few visual or acoustic detections ( $n = 6$ ) exceeded 400 m.

The influence of the Beaufort sea state on encounter rates was assessed for the visual and acoustic modes (Table 3). Where effort was low, encounter rates fluctuated, and rates were calculated for pooled data at the extremes (i.e. BF 0/1, and BF 4/5) for visualisation. A strong negative relationship in the visual-detection encounter rates with increasing sea state was observed, decreasing more than 6-fold from BF 0/1 to BF 4/5 (Table 3; Figure 3). The relationship between the acoustic encounter rate and sea state (BF 0–5) was not monotonic, as the highest group encounter rates occurred in BF 2 and BF 3 (Table 3; Figure 3). Encounter rates varied much more between sea states for visual detection (range in encounter rates across sea states = 0.72) than for acoustic detection (range = 0.28).

**Table 3:** The encounter rate (ER = number of detections per hour of survey effort, by Beaufort sea state [BF] code) for Heaviside’s dolphins in the Namibian Islands Marine Protected Area. Values in parentheses show corrected counts where two matched detections were characterised by multiple visual detections occurring close in time and space

BF	Visual mode			Acoustic mode		
	No. of detections	Effort (h)	ER (no. h <sup>-1</sup> )	No. of detections	Effort (h)	ER (no. h <sup>-1</sup> )
0	1	6.2	0.16	5	10.8	0.46
1	16	18.9	0.85	1	17.6	0.06
2	36 (34)	50.5	0.71 (0.67)	19	56.3	0.34
3	10 (7)	42.6	0.23 (0.16)	17	56.7	0.30
4	5	38.6	0.13	5	52.0	0.10
5	4	7.8	0.51	4	18.4	0.22
6	–	–	–	1	3.6	0.27



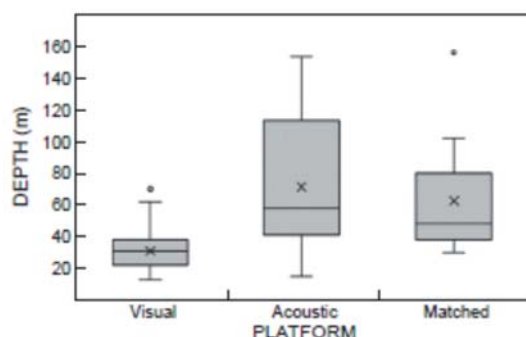
**Figure 3:** Graphical summary of the effort-corrected detection rates, as a function of Beaufort sea state and detection mode, obtained during surveys of Heaviside’s dolphins in the Namibian Islands Marine Protected Area

Spatial partitioning in the data collection by detection mode was driven by survey-depth considerations. This arose from logistical constraints as the hydrophone array could not be deployed in water <30 m deep. Visual-only survey effort therefore predominantly occurred in shallow nearshore waters, where Heaviside’s dolphins are known to aggregate (Elwen et al. 2006), whereas acoustic monitoring was concentrated in deeper waters farther from shore. Consequently, more groups of Heaviside’s dolphins were detected visually ( $n = 72$ , corrected to 67 following aggregation: see Methods section) than acoustically ( $n = 52$ ), and the overall visual-encounter rate was more than double the acoustic-encounter rate (Table 4). Visual only detections occurred in shallower water depths (mean: 31 m [SD 11]) compared with the acoustic-only detections (mean: 71 m [SD 42]) (Figure 4). Temporal partitioning in data collection occurred as acoustic recordings continued overnight when visual observations were not possible. Although sparse, during simultaneous detection effort there were nine matched detections and the acoustic mode was slightly more effective than the visual mode, with five acoustic-only detections and two visual-only detections (Table 4).

**Table 4:** Summary of overall detections and encounter rates (ER = number of detections per hour of survey effort by survey mode [visual or acoustic]), and during simultaneous survey effort, for groups of Heaviside’s dolphins in the Namibian Islands Marine Protected Area. Detections are subdivided between hours of daylight (06:00–17:00) and nighttime (17:01–05:59)

Platform	Total no. of detections	Day/night detections	Effort (h)	ER (no. h <sup>-1</sup> )
<i>All effort</i>				
Visual platform	72	72/0	167.9	0.43
Acoustics platform	52	21/31	279.0	0.19
<i>Simultaneous effort</i>				
Matched	9*		107.1	0.08
Visual only (acoustic missed)	2		107.1	0.02
Acoustic only (visual missed)	5		107.1	0.05

\*In two cases there were multiple visual detections matched with one acoustic event because of clustered sightings. In these cases, the group of visual detections was counted as a single match for this assessment



**Figure 4:** Estimated water depth for Heaviside’s dolphins when detected visually, acoustically or by both modes simultaneously, in the Namibian Islands Marine Protected Area. Boxes represent the depth interquartile range, within which the median depth value is depicted by a horizontal line and the mean depth is indicated with an ‘x’; outliers are represented as dots

## Discussion

The application of line-transect-survey methodology using passive acoustic monitoring (PAM) has flourished in recent years and is being more regularly applied for NBHF-clicking odontocetes (e.g. SCANS 2008; Gerrodette et al. 2011; Fleming et al. 2018). This has been facilitated by technological advances and the greater affordability of sophisticated acoustic equipment capable of high sampling rates (i.e. 250 kHz and above). To our knowledge this is the first study to implement PAM during line-transect surveys for any dolphin of the genus *Cephalorhynchus*, using PAMGuard software to facilitate the click-classification process. The NIMPA series of surveys are the only simultaneous visual and acoustic line-transect cetacean surveys conducted in Namibian waters and within the Benguela ecosystem, and the approach remains rare within Africa as a whole (but see Braulik et al. 2018 for a recent example).

Automated detection and classification methods have greatly facilitated click-data processing (Gillespie et al. 2008), with concurrent developments in statistical methodology to help generate density and abundance estimates from combined visual and acoustic data sources (Marques et al. 2012). Although we hoped to fully automate our analysis pipeline, the high false-positive rate encountered in our dataset prevented this from being fully achieved. Therefore, we used a combined approach of automated detection and classification of NBHF clicks in PAMGuard and a decision-rule process, following Rayment et al.

(2011). The 'Ch' events were classified based on the number of NBHF clicks detected, the click characteristics and the proportion of NBHF to broadband clicks (when applicable) using built-in features of PAMGuard. Although not fully automated, manual verification through careful inspection of the recordings indicated that this approach worked well for our data, which included false positives generated from sporadic periods of electrical noise interference and detections of broadband-clicking species. Regarding efficiency and accuracy, this combined approach was about three-times faster than a fully manual approach and increased confidence in the dataset. It could be easily adapted for similar datasets analysed in PAMGuard.

We attribute the higher encounter rate from visual (0.43 groups h<sup>-1</sup>) over acoustic (0.19 groups h<sup>-1</sup>) modes to the difference in areas surveyed with the two methods. Visual effort was more concentrated in nearshore areas where the hydrophone could not be towed, and acoustic effort was concentrated in deeper waters where Heaviside's dolphins are less prevalent (Best 2007; De Rock et al. 2019). This is also reflected in the corresponding depth-at-detection data, whereby the average visual-detection depth was ~40 m shallower than the average acoustic-detection depth (Figure 4). These differences were minimised in the final analyses for abundance estimation (Martin et al. 2020) by using only the dedicated parallel-transect legs which ran perpendicular to this density gradient (as suggested by Thomas et al. 2010).

An offshore movement of Heaviside's dolphins in the late afternoon/evening has been observed in the southern Benguela (Elwen et al. 2006). As visual surveys are rarely possible overnight (although thermal imaging and infrared may be applied; see Verfuss et al. [2018] for a review), acoustic monitoring provides the best option for maximising detection rates and understanding diurnal patterns in distribution (e.g. Temple et al. 2016) and behaviour (e.g. Leeney et al. 2011). In this study, 60% of acoustic detections took place at night, providing important information on the nocturnal and offshore distribution of Heaviside's dolphins. There were relatively few detections during periods of simultaneous visual- and acoustic-data collection; however, examination of these data demonstrated missed detections for both modes. Missed detections may be explained by the distance separating the platforms as well as the attractive responsive-movement behaviour of animals towards the ship's bow and potentially away from the acoustic platform. Given these results, combining both detection modes clearly increased the overall survey efficiency.

The acoustic-detection range during vessel-based surveys depends on the signal's source level, vessel speed and environmental covariates (e.g. depth, topography, salinity, ambient noise), some of which were not quantified in this study. Although our maximum acoustic-detection distance from localised calls was 687 m, all other detection distances were under 350 m, supporting our assumed maximum radial-detection distance of 500 m. We found no perceivable difference in the visual and acoustic perpendicular-detection range from the transect line, with average values of 121 m and 128 m, respectively. In fact, there were more visual detections exceeding a 400-m perpendicular distance from the track line ( $n = 5$ ) compared to acoustic detections ( $n = 1$ ). Reported maximum acoustic-detection ranges for large-bodied, broadband-clicking species such as the sperm whale *Physeter macrocephalus* far exceed possible visual ranges (Leaper et al. 1999). However, NBHF species produce

highly directional clicks with comparatively low source levels compared with large odontocetes such as sperm whales (Richardson et al. 1995). Combined with increased signal attenuation of high-frequency sounds, this can result in short transmission distances for NBHF clicks. Thus, in calm conditions the visual-detection distance may exceed the acoustic-detection distance (Akamatsu et al. 2001; this study), which can result in a narrow effective-strip-width (ESW) for the acoustic-survey mode (Gerrodette et al. 2011; Fleming et al. 2018). Acoustic detections at short range could also be influenced by behavioural changes and responsive movement in reaction to the approaching vessel. We often observed Heaviside's dolphins approaching the research vessel to engage in bow-riding. Responsive movement prior to detection is problematic in distance-sampling as animals are assumed to be located independently from the track line (Thomas et al. 2010). Such behaviour can cause a peak in detections at close distances and influence the choice of detection function, with the potential to inflate subsequent estimates of abundance from line-transect distance sampling if not accounted for. This responsive behaviour has been documented for other *Cephalorhynchus* species, including Hector's dolphins in New Zealand (DuFresne et al. 2001) and Commerson's dolphins in Patagonia, Argentina (Iñíguez and Tossenberger 2007). A double-platform observer approach is recommended as a better option to fit the shape of the detection function (Buckland et al. 2015). Because of responsive movement, in our subsequent estimates of abundance (Martin et al. 2020), we did not use the perpendicular distances generated from target-motion analysis in the acoustic detections. Instead we applied the relatively novel approach of incorporating the visual and acoustic-detection data as independent observer platforms using a mark-recapture trial configuration, assuming full independence, to better fit the detection function and address the issue of boat-attraction (see Martin et al. 2020 for full details).

Visual detection of cetaceans may be reduced by both availability bias, such as when animals are below the surface, and perception bias (Marsh and Sinclair 1989), such as that caused by poor sea conditions, which is especially important when surveying small cetaceans (e.g. Palka 1996; Barlow 2015). The use of PAM could help reduce both categories of bias and increase detection rates—but only if cetaceans are vocalising within detection range. Our visual data indicated a reduced encounter rate with increasing BF sea state (BF 1 to 4). Acoustic-detection rates varied less with environmental condition and had a different distribution, with the greatest encounter rates during BF 2 and 3. However, there were exceptions, including a Heaviside's dolphin detection by both survey modes during a BF 5 sea state (relatively far from shore, at 156 m deep), demonstrating the value of data collection even in adverse weather conditions.

Comparing the acoustic behaviour between species of *Cephalorhynchus* and *Phocoena* can facilitate efficient development of appropriate acoustic-classification approaches. PAMGuard allowed for rapid processing of the high-frequency acoustic data. During the verification stage, 100% of definite 'Ch' events identified in PAMGuard viewer mode were confirmed through inspection of the associated sound files. The similarity in echolocation-click characteristics between NBHF species is therefore high enough that classification parameters developed for porpoise species can identify NBHF clicks of Heaviside's dolphins. In addition, trials using T-POD monitors have found that the standard 'NBHF' settings can be used for detecting *Cephalorhynchus* species. (Rayment et al. 2009a; Leeney et al. 2011).

However, detailed characterisation of at least two species of *Cephalorhynchus* (Commerson's and Heaviside's dolphins) have found unusual click types and production rates (Reyes Reyes et al. 2015; Martin et al. 2018, 2019). For example, Heaviside's dolphins produce some burst-pulse sounds and click-trains with lower centroid frequencies (median: 119.5 kHz and 110.8 kHz, respectively) and broader bandwidths (median bandwidth [-10 dB]: 79.9 kHz and 75.4 kHz, respectively) than their standard NBHF clicks (Martin et al. 2018). Burst-pulse production is tightly linked to socialising group behaviour and to a lesser degree foraging behaviour (Martin et al. 2019). Whether these unusual, pulsed sounds would be classified as NBHF clicks remains to be tested, but any click classification based on energy-band comparison (as used in PAMGuard and in C-POD detection) may be compromised. Nonetheless, for Heaviside's dolphins, the production of burst-pulse and broadband click-trains is fortunately coupled with regular NBHF clicks (Martin et al. 2019), so this unusual acoustic behaviour might not influence dolphin-detection probability. However, this example underlies the importance of thorough investigation into the vocal behaviour of target species, before generalising across species classifiers.

## Conclusions

Overall, the results strongly support combined methods to maximise spatial and temporal survey coverage for Heaviside's dolphins. In nearshore waters, logistical constraints meant that visual methods were more applicable and more effective, while passive acoustic monitoring enabled greater survey coverage offshore, in poor weather conditions and at night. Future surveys should also consider deployment of acoustic equipment on smaller research vessels which can conduct acoustic-survey work within nearshore waters. Our results demonstrate that the automated click-detection and click-classification algorithm developed principally for porpoise species (genus *Phocoena*) could be applied to acoustic data for Heaviside's dolphins.

## Acknowledgements

This work is part of a collaborative project between the Namibian Dolphin Project (operated by Sea Search Research and Conservation, registered South African NPC, 2015/392325/08), the SEACODE research group, and Namibia's Ministry of Fisheries and Marine Resources (MFMR, Ecosystem Section). We would like to thank all staff, volunteers, interns and students who assisted with data collection and we are indebted to C Grobler (MFMR Lüderitz Marine Research) for her support in coordinating the surveys, and Sacky Jason (Captain) and the crew of the RV *Anichab* for their contribution and help. Financial support for equipment and logistics was provided by the Nedbank Go Green Fund (Namibia) and the Rufford Small Grants Society. TG was supported by the University of Pretoria Vice Chancellor's postdoctoral fellowship, a Claude Leon Fellowship, and the University of Stellenbosch. MJM was supported by a Fulbright U.S. Research Fellowship, a National Geographic Society Explorers Grant in conjunction with the Waitt Foundation (#38115), and a University of Pretoria doctoral scholarship. RS was supported by the Scientific Committee on Oceanic Research (SCOR) Visiting Scholars Program. SE was supported by a research fellowship from the University of Pretoria and a Research Career Advancement Fellowship from the National Research Foundation (South Africa).

## ORCID

Simon Elwen: <https://orcid.org/0000-0002-7467-6121>

Tess Gridley: <https://orcid.org/0000-0003-0925-5782>

Morgan J Martin: <https://orcid.org/0000-0002-3556-6632>

Jean Paul Roux: <https://orcid.org/0000-0001-5883-2342>

Jeff Slater: <https://orcid.org/0000-0002-4412-6081>

Rene Swift: <https://orcid.org/0000-0003-0462-3187>

## References

Akamatsu T, Wang D, Wang K, Wei Z. 2001. Comparison between visual and passive acoustic detection of finless porpoises in the Yangtze River, China. *The Journal of the Acoustical Society of America* 109: 1723–1727. doi: 10.1121/1.1356705

Au WWL. 1993. *The sonar of dolphins*. New York: Springer-Verlag.

Au WWL. 1997. Echolocation in dolphins with a dolphin–bat comparison. *Bioacoustics – The International Journal of Animal Sound and its Recording* 8: 137–162.

Au WWL, Würsig B. 2004. Echolocation signals of dusky dolphins (*Lagenorhynchus obscurus*) in Kaikoura, New Zealand. *The Journal of the Acoustical Society of America* 115: 2307–2313. doi: 10.1121/1.1690082

Au WWL, Kastelein RA, Rippe T, Schooneman NM. 1999. Transmission beam pattern and echolocation signals of a harbor porpoise (*Phocoena phocoena*). *Journal of the Acoustical Society of America* 106: 3699–3705. doi: 10.1121/1.428221

Baker CS, Hamner RM, Cooke J, Heimeier D, Vant M, Steel D, Constantine R. 2013. Low abundance and probable decline of the critically endangered Maui’s dolphin estimated by genotype capture–recapture. *Animal Conservation* 16: 224–233. doi: 10.1111/j.1469-1795.2012.00590.x

Barlow J. 2015. Inferring trackline detection probabilities,  $g(0)$ , for cetaceans from apparent densities in different survey conditions. *Marine Mammal Science* 31: 923–943. doi: 10.1111/mms.12205

Barlow J, Taylor BL. 2005. Estimates of sperm whale abundance in the northeastern temperate Pacific from a combined acoustic and visual survey. *Marine Mammal Science* 21: 429–445. doi: 10.1111/j.1748-7692.2005.tb01242.x

Best PB. 2007. *Whales and dolphins of the southern African subregion*. Cambridge, UK: Cambridge University Press.

Booth C, Embling C, Gordon J, Calderan SV, Hammond PS. 2013. Habitat preferences and distribution of the harbour porpoise *Phocoena phocoena* west of Scotland. *Marine Ecology Progress Series* 478: 273–285. doi: 10.3354/meps10239

Braulik GT, Kasuga M, Wittich A, Kiszka JJ, MacCaulay J, Gillespie D et al. 2018. Cetacean rapid assessment: an approach to fill knowledge gaps and target conservation across large data deficient areas. *Aquatic Conservation: Marine and Freshwater Ecosystems* 28: 216–230. doi: 10.1002/aqc.2833



- Buckland ST, Turnock BJ. 1992. A robust line transect method. *Biometrics* 48: 901–909. doi: 10.2307/2532356
- Buckland ST, Rexstad E, Marques TA, Oedekoven CS. 2015. *Distance sampling: methods and applications*. London: Springer.
- Currie H, Grobler K, Kemper J. 2009. *Namibian Islands' Marine Protected Area*. Windhoek, Namibia: Ministry of Fisheries and Marine Resources.
- Dawson SM. 2018. *Cephalorhynchus dolphins: C. heavisidii, C. eutropia, C. hectori, and C. commersonii*. In: WürsigB, ThewissenJGM, KovacsKM (eds), *Encyclopedia of marine mammals* (3rd edn). London: Academic Press. pp 166–172.
- Dawson SM, Thorpe CW. 1990. A quantitative-analysis of the sounds of Hector's dolphin. *Ethology* 86: 131–145. doi: 10.1111/j.1439-0310.1990.tb00424.x
- De Rock P, Elwen SH, Roux JP, Leeney RH, James BS, Visser V et al. 2019. Predicting large-scale habitat suitability for cetaceans off Namibia using MinxEnt. *Marine Ecology Progress Series* 619: 149–167. doi: 10.3354/meps12934
- DuFresne S, Dawson S, Slooten E. 2001. Line-transect survey of Hector's dolphin abundance between Timariu and Long Point, and effect of attraction to survey vessel. *DOC Science Internal Series No 1*. Wellington, New Zealand: Department of Conservation.
- Elwen S, Gopal K. 2018. *Cephalorhynchus heavisidii*. The IUCN Red List of Threatened Species 2018: e.T4161A50352086.
- Elwen SH, Meÿer MA, Best PB, Kotze PGH, Thornton M, Swanson S. 2006. Range and movements of female Heaviside's dolphins (*Cephalorhynchus heavisidii*), as determined by satellite-linked telemetry. *Journal of Mammalogy* 87: 866–877. doi: 10.1644/05-MAMM-A-307R2.1
- Elwen SH, Reeb D, Thornton M, Best PB. 2009. A population estimate of Heaviside's dolphins, *Cephalorhynchus heavisidii*, at the southern end of their range. *Marine Mammal Science* 25: 107–124. doi: 10.1111/j.1748-7692.2008.00246.x
- Findlay KP, Best PB, Ross GJB, Cockcroft VG. 1992. The distribution of small odontocete cetaceans off the coasts of South Africa and Namibia. *South African Journal of Marine Science* 12: 237–270. doi: 10.2989/02577619209504706
- Fleming AH, Yack T, Redfern JV, Becker EA, Moore TJ, Barlow J. 2018. Combining acoustic and visual detections in habitat models of Dall's porpoise. *Ecological Modelling* 384: 198–208. doi: 10.1016/j.ecolmodel.2018.06.014
- Gerrodette T, Rojas-Bracho L. 2011. Estimating the success of protected areas for the vaquita, *Phocoena sinus*. *Marine Mammal Science* 27: E101–E125. doi: 10.1111/j.1748-7692.2010.00449.x
- Gerrodette T, Taylor BI, Swift R, Rankin S, Jaramillo-Legorreta AM, Rojas-Bracho L. 2011. A combined visual and acoustic estimate of 2008 abundance, and change in abundance since 1997, for the vaquita, *Phocoena sinus*. *Marine Mammal Science* 27: E79–E100. doi: 10.1111/j.1748-7692.2010.00438.x

- Gillespie D, Chappell O. 2002. An automatic system for detecting and classifying the vocalisations of harbour porpoises. *Bioacoustics –the International Journal of Animal Sound and its Recording* 13: 37–61.
- Gillespie D, Berggren P, Brown S, Kuklik I, Lacey C, Lewis T et al. 2005. Relative abundance of harbour porpoises (*Phocoena phocoena*) from acoustic and visual surveys of the Baltic Sea and adjacent waters during 2001 and 2002. *Journal of Cetacean Research and Management* 7: 51–57.
- Gillespie DM, Mellinger DK, Gordon JO, McLaren D, Redmond PA, McHugh R et al. 2008. PAMGUARD: semiautomated, open source software for real-time acoustic detection and localisation of cetaceans. *The Journal of the Acoustical Society of America* 30: 54–62.
- Gillespie D, Leaper R, Gordon J, Macleod K. 2010. An integrated data collection system for line transect surveys. *Journal of Cetacean Research and Management* 11: 217–227.
- Gopal K, Elwen S, Plön S. 2016. A conservation assessment of *Cephalorhynchus heavisidii*. In: Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT (eds), *The Red List of mammals of South Africa, Swaziland and Lesotho*. Pretoria and Johannesburg, South Africa: South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa. pp 1–7.
- Götz T, Antunes R, Heinrich S. 2010. Echolocation clicks of free-ranging Chilean dolphins (*Cephalorhynchus eutropia*) (L). *The Journal of the Acoustical Society of America* 128: 563–566. doi: 10.1121/1.3353078
- Heinrich S, Reeves RR. 2017. *Cephalorhynchus eutropia*. The IUCN Red List of Threatened Species 2017: e.T4160A50351955.
- Iñiguez M, Tossenberger V. 2007. Commerson's dolphins (*Cephalorhynchus commersonii*) off Ría Deseado, Patagonia, Argentina. *Aquatic Mammals* 33: 276–285. doi: 10.1578/AM.33.3.2007.276
- Kyhn LA, Jensen FH, Beedholm K, Tougaard J, Hansen M, Madsen PT. 2009. Feeding at a high pitch: source parameters of narrow band, high-frequency clicks from echolocating off-shore hourglass dolphins and coastal Hector's dolphins. *Journal of Experimental Biology* 213: 1940–1949. doi: 10.1242/jeb.042440
- Kyhn LA, Jensen FH, Beedholm K, Tougaard J, Hansen M, Madsen PT. 2010. Echolocation in sympatric Peale's dolphins (*Lagenorhynchus australis*) and Commerson's dolphins (*Cephalorhynchus commersonii*) producing narrow-band high-frequency clicks. *Journal of Experimental Biology* 213: 1940–1949. doi: 10.1242/jeb.042440
- Kyhn LA, Tougaard J, Beedholm K, Jensen FH, Ashe E, Williams R, Madsen PT. 2013. Clicking in a killer whale habitat: narrow-band, high-frequency biosonar clicks of harbour porpoise (*Phocoena phocoena*) and Dall's porpoise (*Phocoenoides dalli*). *PLoS ONE* 8: e63763. doi: 10.1371/journal.pone.0063763
- Leaper R, Gillespie D, Papastavrou V. 1999. Results of passive acoustic surveys for odontocetes in the Southern Ocean. *Journal of Cetacean Research and Management* 2: 187–196.
- Leeney RH, Carslake D, Elwen SH. 2011. Using static acoustic monitoring to describe echolocation behaviour of Heaviside's dolphins (*Cephalorhynchus heavisidii*) in Namibia. *Aquatic Mammals* 37: 151–160. doi: 10.1578/AM.37.2.2011.151

Marques TA, Thomas L, Martin SW, Mellinger DK, Ward JA, Moretti DJ et al. 2012. Estimating animal population density using passive acoustics. *Biological Reviews of the Cambridge Philosophical Society* 88: 287–309. doi: 10.1111/brv.12001

Marsh H, Sinclair FD. 1989. Correcting for visibility bias in strip transect aerial surveys of aquatic fauna. *The Journal of Wildlife Management* 53: 1017–1027. doi: 10.2307/3809604

Martin MJ, Gridley T, Elwen SH, Jensen FH. 2018. Heaviside's dolphins (*Cephalorhynchus heavisidii*) relax acoustic crypsis to increase communication range. *Proceedings of the Royal Society B: Biological Sciences* 285: article 20181178.

Martin MJ, Elwen SH, Kassanje R, Gridley T. 2019. To buzz or burst-pulse? The functional role of Heaviside's dolphin, *Cephalorhynchus heavisidii*, rapidly pulsed signals. *Animal Behaviour* 150: 273–284. doi: 10.1016/j.anbehav.2019.01.007

Martin MJ, Gridley T, Roux J P, Elwen SH. 2020. First abundance estimates of Heaviside's (*Cephalorhynchus heavisidii*) and dusky (*Lagenorhynchus obscurus*) dolphins off Namibia using a novel visual and acoustic line transect survey. *Frontiers in Marine Science* 7: article 555659. doi: 10.3389/fmars.2020.555659

Mellinger D, Stafford K, Moore SE, Dziak B, Matsumoto H. 2007. An overview of fixed passive acoustic observation methods for cetaceans. *Oceanography (Washington, D.C.)* 20: 36–45. doi: 10.5670/oceanog.2007.03

Møhl B, Andersen S. 1973. Echolocation: high-frequency component in the click of the harbour porpoise (*Phocoena ph. L.*). *The Journal of the Acoustical Society of America* 54: 1368–1379. doi: 10.1121/1.1914435

Morisaka T, Connor RC. 2007. Predation by killer whales (*Orcinus orca*) and the evolution of whistle loss and narrow-band high frequency clicks in odontocetes. *Journal of Evolutionary Biology* 20: 1439–1458. doi: 10.1111/j.1420-9101.2007.01336.x

Morisaka T, Karczmarski L, Akamatsu T, Sakai M, Dawson S, Thornton M. 2011. Echolocation signals of Heaviside's dolphins (*Cephalorhynchus heavisidii*). *Journal of the Acoustical Society of America* 129: 449–457. doi: 10.1121/1.3519401

Palka D. 1996. Effects of Beaufort sea state on the sightability of harbour porpoises in the Gulf of Maine. *IWC Report No. 46*: Cambridge, UK: International Whaling Commission. pp 575–582.

Pichler FB, Robineau D, Goodall RN, Meyer MA, Olivarria C, Baker CS. 2001. Origin and radiation of Southern Hemisphere coastal dolphins (genus *Cephalorhynchus*). *Molecular Ecology* 10: 2215–2223. doi: 10.1046/j.0962-1083.2001.01360.x

Rayment W, Dawson S, Slooten L. 2009a. Trialling an automated passive acoustic detector (T-POD) with Hector's dolphins (*Cephalorhynchus hectori*). *Journal of the Marine Biological Association of the United Kingdom* 89: 1015–1022. doi: 10.1017/S0025315409003129

Rayment W, Dawson S, Slooten L. 2009b. Use of T-PODs for acoustic monitoring of *Cephalorhynchus* dolphins: a case study with Hector's dolphins in a marine protected area. *Endangered Species Research* 10: 333–339. doi: 10.3354/esr00189

Rayment W, Dawson S, Scali S, Slooten L. 2011. Listening for a needle in a haystack: passive acoustic detection of dolphins at very low densities. *Endangered Species Research* 14: 149–156. doi: 10.3354/esr00356

Reeves RR, Dawson SM, Jefferson TA, Karczmarski L, Laidre K, O’Corry-Crowe G et al. 2013a. *Cephalorhynchus hectori*. The IUCN Red List of Threatened Species 2013: e.T4162A44199757.

Reeves RR, Dawson SM, Jefferson TA, Karczmarski L, Laidre K, O’Corry-Crowe G et al. 2013b. *Cephalorhynchus hectori* ssp. *maui*. The IUCN Red List of Threatened Species 2013: e.T39427A44200192 .

Reyes Reyes MV, Iñíguez MA, Hevia M, Hildebrand JA, Melcón ML. 2015. Description and clustering of echolocation signals of Commersons dolphins (*Cephalorhynchus commersonii*) in Bahía San Julián, Argentina. *The Journal of the Acoustical Society of America* 138: 2046–2053. doi: 10.1121/1.4929899

Richardson WJ, Greene CR, Malme CI, Thomson DH. 1995. *Marine mammals and noise*. London: Academic Press.

Richman NI, Gibbons JM, Turvey ST, Akamatsu T, Ahmed B, Mahabub E et al. 2014. To see or not to see: investigating detectability of Ganges River dolphins using a combined visual-acoustic survey. *PLoS ONE* 9: e96811. doi: 10.1371/journal.pone.0096811

SCANS-II. 2008. Small cetaceans in the European Atlantic and North Sea. Final report to the European Commission on project LIFE04 NAT/GB/000245. Fife, Scotland: University of St Andrews.

Slooten E, Dawson S, Rayment W, Childerhouse S. 2006. A new abundance estimate for Maui’s dolphin: what does it mean for managing this critically endangered species? *Biological Conservation* 128: 576–581. doi: 10.1016/j.biocon.2005.10.013

Temple AJ, Tregenza N, Amir OA, Jiddawi N, Berggren P. 2016. Spatial and temporal variations in the occurrence and foraging activity of coastal dolphins in Menai Bay, Zanzibar, Tanzania. *PLoS ONE* 11: e0148995. doi: 10.1371/journal.pone.0148995

Thomas L, Buckland ST, Rexstad EA, Laake JL, Strindberg S, Hedley SL et al. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology* 47: 5–14. doi: 10.1111/j.1365-2664.2009.01737.x

Verfuss UK, Gillespie D, Gordon J, Marques TA, Miller B, Plunkett R et al. 2018. Comparing methods suitable for monitoring marine mammals in low visibility conditions during seismic surveys. *Marine Pollution Bulletin* 126: 1–18. doi: 10.1016/j.marpolbul.2017.10.034

Zimmer WMX. 2011. *Passive acoustic monitoring of cetaceans*. Cambridge, UK: Cambridge University Press.