Mark–recapture of individually distinctive calls—a case study with signature whistles of bottlenose dolphins (*Tursiops truncatus*)

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Robust abundance estimates of wild animal populations are needed to inform management policies and are often obtained through mark–recapture (MR) studies. Visual methods are commonly used, which limits data collection to daylight hours and good weather conditions. Passive acoustic monitoring offers an alternative, particularly if acoustic cues are naturally produced and individually distinctive. Here we investigate the potential of using individually distinctive signature whistles in a MR framework and evaluate different components of study design. We analyzed signature whistles of common bottlenose dolphins, *Tursiops truncatus*, using data collected from static acoustic monitoring devices deployed in Walvis Bay, Namibia. Signature whistle types (SWTs) were identified using a bout analysis approach (SIGnature IDentification [SIGID]—Janik et al. 2013). We investigated spatial variation in capture by comparing 21 synchronized recording days across four sites, and temporal variation from 125 recording days at one high-use site (Aphrodite Beach). Despite dolphin vocalizations (i.e., echolocation clicks) being detected at each site, SWTs were not detected at all sites and there was high variability in capture rates among sites where SWTs were detected (range 0–21 SWTs detected). At Aphrodite Beach, 53 SWTs were captured over 6 months and discovery curves showed an initial increase in newly detected SWTs, approaching asymptote during the fourth month. A Huggins closed capture model constructed from SWT capture histories at Aphrodite Beach estimated a population of 54–68 individuals from acoustic detection, which overlaps with the known population size (54–76 individuals—Elwen et al. 2019). This study demonstrates the potential power of using signature whistles as proxies for individual occurrence and in MR abundance estimation, but also highlights challenges in using this approach.

Key words: abundance estimation, Africa, bioacoustics, capture–recapture, conservation, fixed sensors, individual identity, passive acoustic monitoring, population estimation, SoundTrap

Management policies of wild animal populations often require robust estimates of abundance (Thompson et al. 1998). One commonly used method to estimate the abundance and survival of wild animal populations is mark–recapture (MR). During MR abundance estimation, information on the number of marked individuals within a population and their proportional presence in subsequent sampling events is used (Seber 1982). Site fidelity, movement patterns, and social structure also can be obtained through MR (Norris and Dohl 1980; Whitehead 1997). MR methods can be applied to animals bearing artificial marks such as brands or tags, or natural markings such as scarring or color patterns, and more

recently by incorporating acoustic methods (e.g., Dudgeon et al. 2015).

Understanding populations through acoustic monitoring is recognized as a growing field with potential for further development (see reviews by Blumstein et al. 2011; Marques et al. 2013). Acoustic monitoring is particularly useful in the aquatic environment where sound propagation is more efficient than on land and animals spend large portions of time out of view under water. Passive acoustic monitoring increasingly is being used to study cetacean populations, and is particularly powerful for investigating species presence, distribution, and temporal patterns in site attendance over long time frames (e.g., Clark and Clapham 2004; Simon et al. 2010; Thomisch et al. 2019). Cue-based methods using spatially explicit capture–recapture (SECR) have been applied to acoustic data to estimate density of marine mammal populations (Martin et al. 2013). An alternative applicable to populations where individuals have individually distinctive sound types (see Marques et al. 2013) is an acoustic MR approach.

Many species have individually distinctive call types (see Terry et al. 2005), mostly resulting from by-product distinctiveness generated through morphological variation (so-called "voice" features). In some rare examples, distinctive calls are acquired through vocal production learning forming designed individual signatures (Boughman and Moss 2003; Sayigh et al. 2007). Common bottlenose dolphins (*Tursiops truncatus*) have developed a sophisticated acoustic repertoire to exploit their underwater environment and produce a wide variety of sounds including broadband echolocation clicks, broadband burst-pulsed sounds, and frequency-modulated narrowband whistles (Popper 1980). One of the most studied calls is the bottlenose dolphin signature whistle: a learned, individually distinctive whistle type that broadcasts the identity of the whistle owner (Janik and Sayigh 2013). Over 50 years of dedicated research has generated an understanding of the development, function, and stability of signature whistles (Caldwell et al. 1990; Janik and Sayigh 2013). Bottlenose dolphins are capable of producing whistles from their first day of life, but the frequency modulation and stereotypy of signature whistles tends to develop within the first year of life (Caldwell and Caldwell 1979). Once formed, signature whistles remain stable for at least 12 years (Sayigh et al. 1990; dos Santos et al. 2005) and likely remain stable over the individual's lifetime. By transmitting individual identity information, signature whistles function as contact calls used to maintain group cohesion (Janik and Slater 1998). Signature whistles account for around 50% of all whistles produced by free-ranging dolphins, although the rates of emission vary widely with behavioral context (Cook et al. 2004). Bottlenose dolphin signature whistles can be identified reliably in recordings of freely interacting bottlenose dolphins using a bout analysis approach termed SIGnature IDentification (SIGID; Janik et al. 2013).

Through an understanding of the spatial and temporal changes in detection of signature whistles of free-ranging animals, these whistles could be used in a MR framework, generating information on individual habitat range, population abundance, and even group social structure (Terry et al. 2005; Janik et al. 2013; Gowans 2019). Using static acoustic monitoring (SAM) to capture acoustic cues in a MR framework has benefits over traditional photographic methods of MR—collecting continuous data regardless of time or weather, as well as being less obtrusive and potentially more cost-effective (Stevenson et al. 2015). Further, deploying an array of fixed hydrophones with an additional spatial component could allow density estimation using a SECR approach (Borchers and Efford 2008). However, survey design for acoustic methods is poorly explored; in particular, the role of sensor deployment and location (Marques et al. 2013).

This study aims to test whether signature whistles can be used to monitor dolphins in a MR framework and understand some of the potential biases that may occur, as well as identify issues to consider in future study design. For this, we assess signature whistle capture variability at four sites within the known range of the coastal bottlenose dolphin population in Walvis Bay, Namibia, and analyzed the capture variability over a long-term deployment at one site. We then applied MR models to the long-term deployment data to test the feasibility of using signature whistles for estimating abundance of a wild animal population by comparing results to existing photographic MR estimates.

MATERIALS AND METHODS

Data were collected from January to July 2016 in Walvis Bay (22°54′S, 14°29′E), Namibia (Fig. 1). Walvis Bay is a north-facing bay and the only embayment of significant size (approximately 10 × 10 km) along the central Namibian coastline. The bottlenose dolphin population numbers fewer than 100 individuals, with a maximum of 82 individuals estimated in any 3-month season (Elwen et al. 2019). It is the only inshore population of common bottlenose dolphins along the southern African coastline (Best 2007). The population is estimated to range approximately 1,000 km along the coastline between Möwe Bay (19°21′S, 12°41′E) to the north of Walvis Bay and Lüderitz (26°35′S, 15°07′E) to the south, but with the majority of sightings within the central ~400 km of that span, and generally occurring close to shore in less than 15-m water depth (Elwen et al. 2019). Walvis Bay is roughly central within the dolphin's range and provides core habitat with both resting and foraging opportunities (T. Gridley, pers. obs., 2008–2019).

Within Walvis Bay, long-term passive acoustic monitoring took place January to July 2016 as part of a larger project with associated boat-based survey work. The focus of the project was to investigate the impact on the dolphin population from construction of a ~2-km-long jetty, on the northeastern side of Walvis Bay. Hydrophones were deployed across the east side of the Bay (Fig. 1) at four locations; Aphrodite Beach—a site 4.5 km north of the construction site where dolphins are observed regularly, inshore at the oil jetty, offshore at the oil jetty (which was an active construction site), and at the western side of a recently completed land reclamation project for a
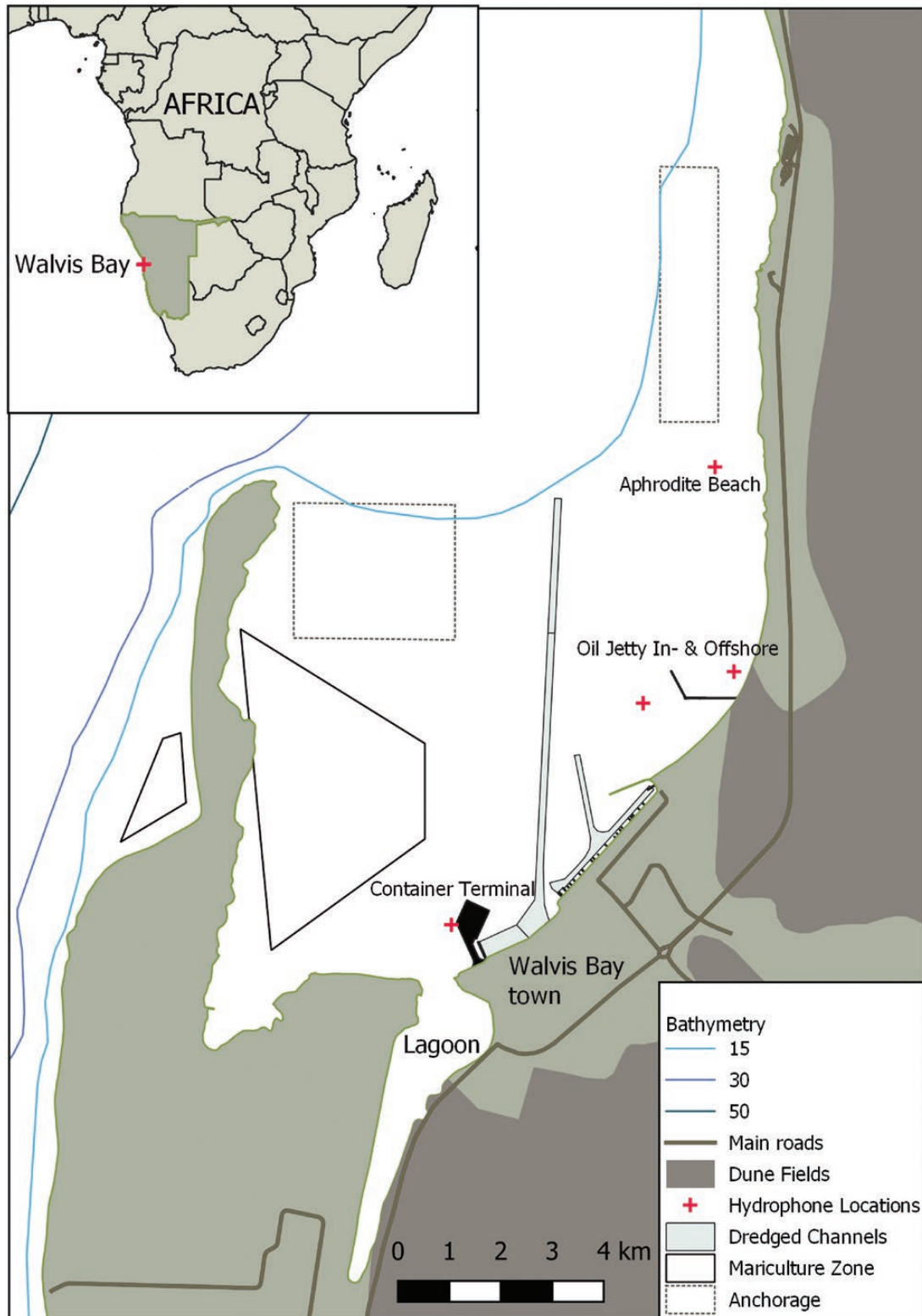
Fig. 1.—The locations of the four hydrophones deployed in Walvis Bay, Namibia, to collect long-term data on the presence of individual common bottlenose dolphins from January to July 2016.

container terminal. Recordings were made using SoundTrap hydrophones (one standard model 300STD, sensitivity −184.8 V/μPa and three high frequency model 300HF, sensitivity −184.3 to −187.9 V/μPa, Ocean Instruments Ltd., Auckland, New Zealand). Recorders sampled data at 96 kHz with a flat frequency response (± 3 dB) between 20 Hz and 48 kHz and duty cycle set to record 10 min on – 10 min off (i.e., 50% sampling rate). Most deployments lasted 3 weeks per month with

gaps between deployments necessary for downloading data and recharging the hydrophone units.

Long-term spectral averages (LTSAs) were used to visualize the acoustic data from each deployment. These were created using Triton (Scripps Whale Acoustic Lab 2016), a MATLAB program (MathsWorks 2012) with a 5-s time average and 50-Hz frequency bin. The first 7 s of each 10 min recording interval contained calibration tones of the hydrophones and were removed from analysis. LTSAs allowed visualization of each deployment in a single figure enabling efficient review of the data. LTSAs were inspected manually in 30-min time windows, searching for high-energy vocal events representing echolocation clicks (settings used: Hanning window, 512 FFT, 75% overlap). Such click trains are easily identifiable in the LTSAs as transient periods of broadband sound containing high-frequency energy. Acoustic encounters were then verified by more detailed inspection of the associated .wav file, using the expand function in Triton to view the files in 5-s time windows. Encounters were considered to have ended if no further vocalization was identified for three consecutive 10 min acoustic files (spanning 1 h of real time at the 50% sampling rate).

Identification of signature whistle types.—Previous studies have demonstrated the reliability of visual methods in signature whistle identification (Janik 1999), particularly when agreement consensus is achieved among multiple observers. We therefore used visual classification and categorization to identify "captures" and new signature whistle types (SWTs). Here, SWTs are likely signature whistles identified though the SIGID method applied to data sets from wild populations. Whistles were identified as a unit of one continuous contour (either as a single element or repeated, connected multiloops), or multiple, repeated, disconnected loops with intervals of silence between 0.03 and 0.25 s ("disconnected multiloops"—Esch et al. 2009). All whistles identified in the recordings were graded following Kriesell et al. (2014) according to the signal-to-noise ratio (SNR; 1: signal is faint but visible on the spectrogram, 2: signal is clear and unambiguous, 3: signal is prominent and dominates). All whistles of SNR 2/3 in the data set were extracted using Raven Pro (Center for Conservation Bioacoustics 2014) as short .wav files containing only the whistle and analyzed to determine which were SWTs. Whistles were compared to the SWT catalog created for the Walvis Bay population by Kriesell et al. (2014; updated in 2016 by the Namibian Dolphin Project) using acoustic data collected during boat-based focal group follows (Mann 1999). If the candidate whistle matched a SWT from the catalog it was counted as a "capture" of that SWT, and the associated date, time, and location were documented. No match could mean that the whistle is a nonsignature whistle or variant, or may be a SWT not yet in the Walvis Bay catalog (Janik et al. 2013). To examine this possibility, stereotyped and repeatedly emitted whistles that did not match any SWTs in the existing catalog were analyzed further using the SIGID method (Janik et al. 2013). New SWTs were identified when whistles were produced in a bout containing a minimum of four whistles of the same type (i.e., same frequency modulation pattern), if

at least once in the bout 75% or more of the whistles (i.e., minimum 3 out of 4) were produced within 1–10 s of each other. All whistles in the data set of SNR 2/3 therefore either were: (1) matched to the existing catalog; (2) added to the catalog using SIGID; or (3) found to not be a SWT and removed from further analysis. The matching then was verified by two experienced observers who were given files containing the .wav extracts of the SWTs created by the first observer. For this, all repetitions of a SWT identified across the whole data set were opened in the groupings designated by the first observer. SWTs were viewed side by side in the spectrogram view of Raven, allowing cross-comparison of contour shape. To be conservative and ensure reliability of identification, any whistles where consensus was not reached by the observers were removed from the analysis.

Although vocal copying has been identified in bottlenose dolphins, copies often are imperfect and more variable than the original signature whistle (Janik 2000; King et al. 2013) and may overlap it. Where copying was identified through overlapping signals of a similar contour shape, we followed Kriesell et al. (2014) and identified the second, overlapping whistle as the copy and discounted it from further analysis. There still may have been vocal copying where contours did not overlap in time. However, for the purposes of this MR approach, SWTs were counted as present at the encounter level, so any SWT copies involved in addressing or matching interactions that replicated the owner's whistle would not affect the detection of the owner's SWT, or consequently the overall results.

Spatial variation in SWT detection.—We investigated the variability in SWT capture at the four different recording sites using data from a single deployment period of 21 days (13 June to 5 July 2016). This deployment occurred during winter, when dolphin encounter rates in the bay are higher (Elwen et al. 2019). We compared the number of acoustic encounters at each site, encounter duration, the number of encounters with SWTs detected, the number of SWTs captured at each site, and recaptures among sites. Acoustic encounter duration was calculated cumulatively from the active recording time and omitted the 10 min that the hydrophone was dormant.

Temporal variation in SWT presence.—We analyzed in more detail the variation in detection of SWTs over 6 months at the high-capture site (Aphrodite Beach) to investigate a number of questions relevant to study design and the capture probability of animals, which may potentially bias this type of study. We investigated population closure by generating a discovery curve of SWTs over 125 recording days (six deployments) from the high-use site (Aphrodite Beach). Open populations are characterized by a steady increase in cumulative captures over time; closed populations are represented by a plateau where increases in capture effort return no or few new individuals (see Wilson et al. 1999). As different recapture frequencies can affect model outputs, we investigated capture heterogeneity at both the encounter and whistle repetition level by comparing the number of recaptures of SWTs and repeats of each SWT between encounters. To see how length of recording and acoustic activity

may influence models, time was calculated from the beginning of the acoustic encounter to the first whistle emission that could clearly be attributed to each SWT. The total number of SWTs detected per encounter was compared using Pearson's correlation with (1) the time within each encounter to first detect all SWTs present and (2) acoustic encounter duration (analysis retained one apparent outlier, details below). These results have implications for the duty cycle settings used for extending recording duration during hydrophone deployments.

MR methods using signature whistles.—We generated an exploratory MR abundance estimate through SWT capture using the long-term data from Aphrodite Beach and compared this to a recently published photographic MR estimate of this population (Elwen et al. 2019). The data naturally fell into six capture occasions each representing a deployment ranging from 10 to 21 days with weeklong periods between capture occasions in which the population could theoretically mix. Following Elwen et al. (2019) and supported by visual assessment of the SWT discovery curve (Fig. 2), we assumed population closure over this time period and interpret the results of the analysis as representing the number of animals using the study site over the duration of the sampling period. We used the conditional likelihood methods developed by Huggins (1989), which are recommended due to their flexibility and ability to include covariates (e.g., sex—Manly et al. 2005; Conn et al. 2011) and in the absence of covariates, are equivalent to "full likelihood" models (Lukacs 2016). Analysis was conducted in Program MARK

(White and Burnham 1999; Cooch and White 2010) using the RMark interface (Laake and Rexstad 2008). As the capture process was completely passive there was no reason to expect a behavioral change between initial and later captures so, c (recapture probability) was set equal to p (initial capture probability) throughout (Parra et al. 2006; Nicholson et al. 2012). We fitted a suite of models to explore which combination of parameters best described the data including: the null model, models allowing for capture probability to vary over time, for two mixtures of capture heterogeneity, and for a full model that allowed for capture heterogeneity and for capture probability to vary over time. Model fit was assessed using the Akaike Information Criteria corrected for small samples sizes (AICc).

RESULTS

Between 1 January and 5 July 2016, 4,419 h of underwater recordings were made over 125 days at four sites in Walvis Bay. Across the 6 months and four sites, there were 204 acoustic encounters, 50 of which contained SWTs. From these encounters, 53 SWTs were identified; 40 were in the existing catalog and 13 were newly identified as SWTs following the SIGID method (Janik et al. 2013) and subsequently added to the Walvis Bay catalog (Table 1).

Spatial variation.—The monthlong data sets obtained simultaneously at the four sites were compared. Although all four mooring sites fall within areas regularly used by bottlenose
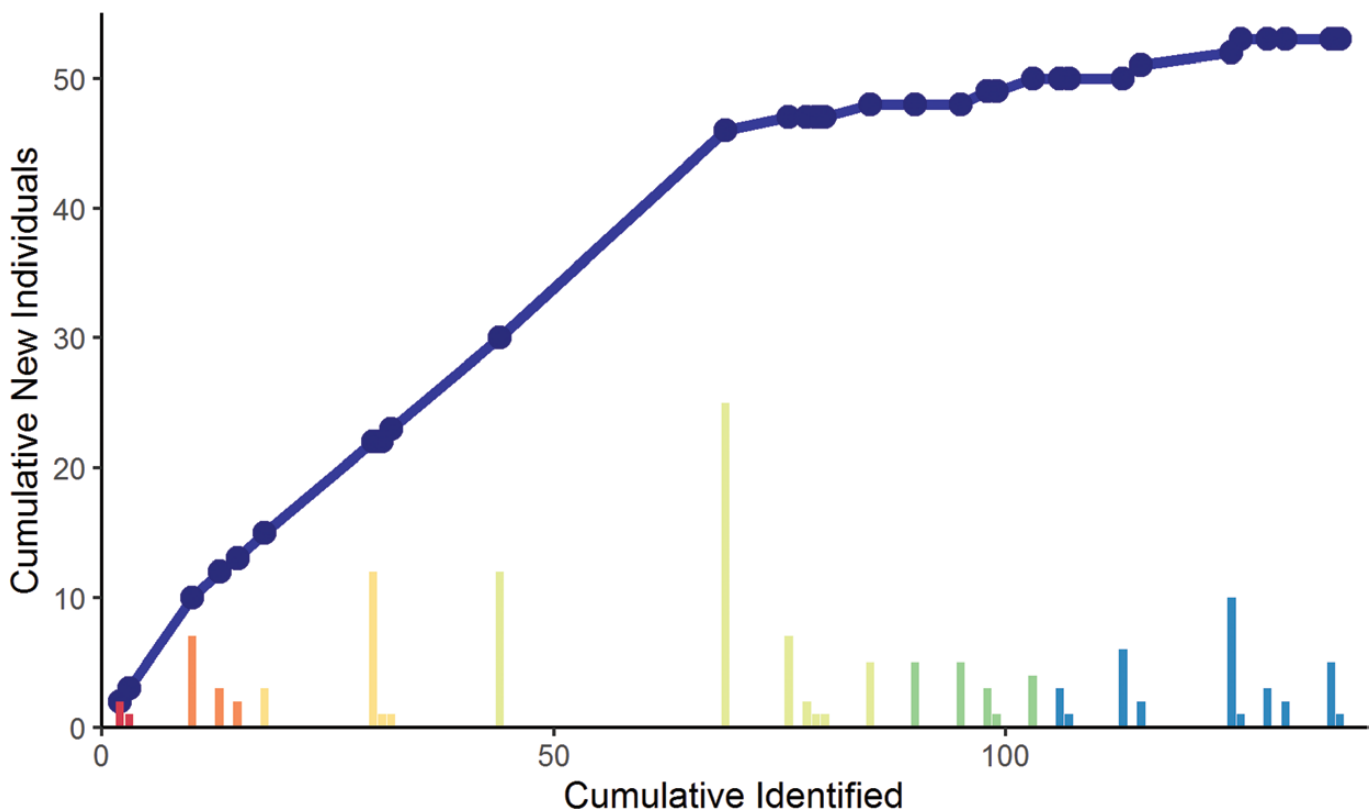

Fig. 2.—Discovery curve showing detection of new signature whistle types (SWTs) belonging to common bottlenose dolphins at the Aphrodite Beach site in Walvis Bay, Namibia, against the cumulative number of SWT identifications. Bars represent acoustic encounters and are colored by deployment ($n = 6$; spanning January to July 2016).

Table 1.—Data collected from long-term hydrophone deployments at four sites in Walvis Bay, Namibia, showing number of acoustic encounters and signature whistle types (SWTs) detected from common bottlenose dolphins. The hydrophones were deployed six times at Aphrodite Beach from January to July 2016; further hydrophones were deployed simultaneously at the three other sites during the sixth deployment period (June).

Site	Deployment period	Number of acoustic encounters	Cumulative encounter duration in minutes (mean) over deployment	Number of acoustic encounters with SWTs detected (%)	Number of individually distinctive SWTs detected
Aphrodite Beach	1 (January)	11	230 (21)	3 (27)	3
Aphrodite Beach	2 (February)	14	290 (21)	4 (28)	11
Aphrodite Beach	3 (March)	12	170 (14)	5 (41)	14
Aphrodite Beach	4 (April)	39	1,230 (32)	13 (33)	39
Aphrodite Beach	5 (May)	23	550 (24)	6 (26)	15
Aphrodite Beach	6 (June)	62	1,610 (26)	15 (24)	21
Oil jetty—inshore	6 (June)	27	660 (24)	3 (11)	3
Oil jetty—offshore	6 (June)	4	120 (30)	1 (25)	7
Container terminal	6 (June)	12	310 (26)	0 (0)	0

dolphins (see figure 1 in Elwen et al. 2019), there was substantial spatial variability in the number of acoustic encounters at each site (Table 1). Dolphin presence was acoustically detected at Aphrodite Beach ($n = 62$) substantially more often than the other three sites (oil jetty—inshore, $n = 27$; oil jetty—offshore, $n = 4$; container terminal, $n = 12$). The cumulative encounter duration for deployments, which was calculated from the active recording time omitting 10 min periods of silence in the duty cycle, varied considerably among sites and deployments (range 120 – 1,610 min, Table 1, June data only). This was driven largely by the number of encounters, and the mean encounter duration was similar among sites and deployments, ranging from 24 to 30 cumulative recording minutes. In total, 25 SWTs were captured during the 21 simultaneous recording days across the four sites. One SWT was captured at three sites, four SWTs were captured at two sites, and the remainder (20) were captured at one site only. No SWTs were captured at all four sites.

Long-term deployment.—During the long-term deployment at Aphrodite Beach, 53 SWTs were discovered with most of them detected in the fourth deployment (April). The discovery rate of captured SWTs over the study period shows a clear asymptote after deployment four (Fig. 2), suggesting closure of the population during the 6-month study period. There was considerable variability in the capture probability of SWTs (Fig. 3). Of the 53 SWTs identified, 43% ($n = 23$) were captured only once, whereas the majority (57%, $n = 30$) were recaptured twice or more. Of the 30 SWTs that were recaptured, 90% ($n = 27$) occurred over more than one capture occasion (deployment period).

There was one outlying encounter that should be noted that began at 2140 h on 23 April and ended at 0110 h on 24 April. The encounter lasted 110 cumulative recording minutes (i.e., the encounter spanned 210 min with every other 10 min recorded). In this instance it took 100 recording minutes to identify all 26 SWTs produced within the encounter. When this encounter was excluded, the number of SWTs captured ranged from 1 to 12 per encounter (mean = $3.34 \pm SE$ 0.62, $n = 45$ encounters) with all SWTs captured within the first 30 cumulative recording minutes in most (80%) of encounters (Fig. 4a). There was a weak positive correlation between the time taken within the encounter to detect all SWTs present and

the number of SWTs captured ($r = 0.391$, $n = 46$, $P < 0.01$) (Fig. 4a), yet there was no significant relationship ($r = 0.281$, $n = 46$, $P = 0.059$) between the duration of an acoustic encounter and the number of SWTs captured (Fig. 4b). We found that the number of whistle repeats of each SWT ranged widely for encounters. From 1 to 50 whistle repeats per encounter (mean = $8.0 \pm SE$ 0.8, $n = 152$; Fig. 5) were found, indicating substantial variation in vocal behavior between individuals and encounters.

MR methods using signature whistles.—The two best-fitting MR models were those allowing for capture heterogeneity and time-varying capture probability, or only the latter. Although the most complex model was the best fitting (175 individuals, 95% $CI = 55$–5,770), we rejected it because a large number of the parameters did not converge and the SE was very large (828.6). All parameters in the second best fitting (time-varying capture probability only) fitted well and the SE was reasonable. The estimated total population size from this model was 58 (95% $CI = 54$–68, $SE = 3.04$) calculated from 53 SWTs over six capture occasions at Aphrodite Beach.

DISCUSSION

The use of naturally occurring, individually distinctive signature whistles within a MR framework first was suggested several years ago (Terry et al. 2005; Janik et al. 2013) but to our knowledge has remained untested. Here we demonstrated the ability to generate MR abundance estimates from 6 months of passive acoustic monitoring of bottlenose dolphin signature whistles. Estimates are comparable with existing estimates from standard boat-based photographic-identification studies in the area (Elwen et al. 2019). This approach shows great promise for future applications. Our results highlight some of the challenges and strengths that should be considered in more detail. Notably, there was strong spatial variation in the detection of SWTs within Walvis Bay, but no clear temporal biases, and no clear relationship between encounter duration and number of SWTs detected. Some of the patterns observed are common to all MR studies of free-ranging animals, while others derive from the use of SWTs as "marks." We discuss these in more detail below.
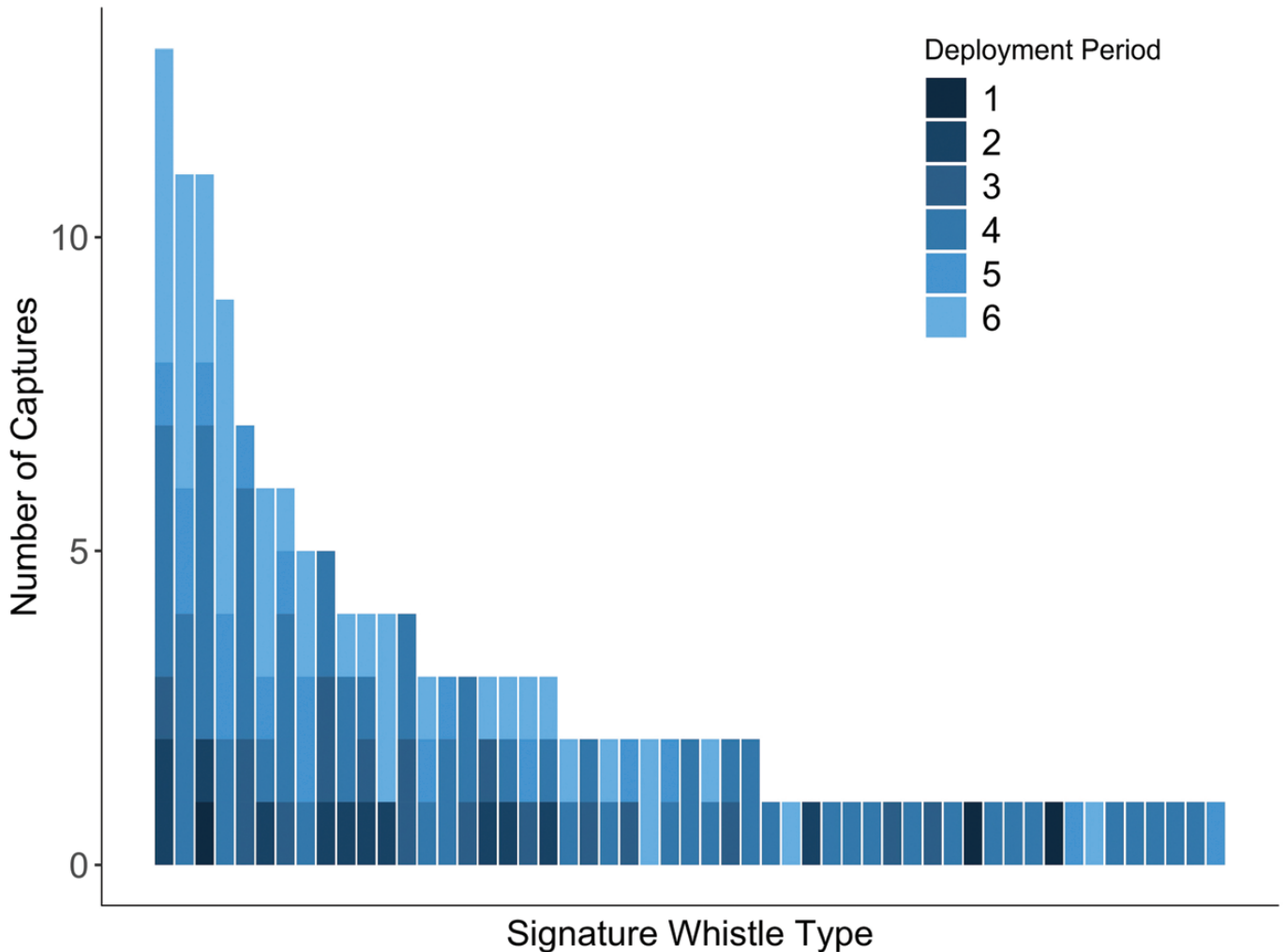
Fig. 3.—Encounter heterogeneity of 53 signature whistle types (SWTs) of common bottlenose dolphins at the Aphrodite Beach site in Walvis Bay, Namibia. Bars show the total number of times a SWT was encountered; color corresponds to the hydrophone deployment the encounter occurred in. Hydrophones were deployed six times from January to July 2019, each deployment lasting 10–21 days.

Closed-population MR analysis, as we have used above for comparability with existing estimates (Elwen et al. 2019), is applied widely in the study of free-ranging dolphins to calculate survival and abundance parameters. These model types are reliant on several core assumptions including that: identifying marks are distinctive and consistently identified, sampling occasions are independent, animals mix randomly between occasions, and all animals have a chance of being caught. The distinctiveness of signature whistles and ability to identify them have been addressed in detail elsewhere (Sayigh et al. 2007; Janik et al. 2013; Kriesell et al. 2014). The requirements for sample independence and limited capture heterogeneity can be addressed partially through good study design and increasingly through analytical approaches. Recent developments in MR theory offer more flexibility than older approaches, as well as the calculation of other metrics such as population density. For instance, SECR models are particularly useful for studies using arrays of "traps" (Efford et al. 2009). SECR can account both for capture heterogeneity as well as situations where animals are next to the sensor but not detected (Stevenson et al.

2015). These models recently have been adapted to work with data collected in continuous time, such as from camera-trap surveys (Borchers et al. 2014), thereby foregoing the need for independent sampling events. SECR models allow density estimates to be obtained using multiple "proximity sensors" such as acoustic detectors, camera traps, or hair snares (Efford et al. 2009), and if applied to signature whistle MR, could be particularly useful for rapid assessment surveys of new study areas. Regarding capture of individuals, a common problem in studies using proximity detectors such as acoustic methods or camera traps is the issue of optimal trap placement (Marques et al. 2013). The placement of "traps" must be linked to the needs and designs of each study. Burton et al (2015) noted that many camera-trap studies focusing on density estimation place sensors to maximize detection probability such as on roads and trails. This approach likely biases density upwards and is not appropriate for modeling of occupancy or richness across a habitat, where an unbiased sample of the full range of habitat features present is needed (Wearn et al. 2013). The results of our study have shown the large differences in detection that
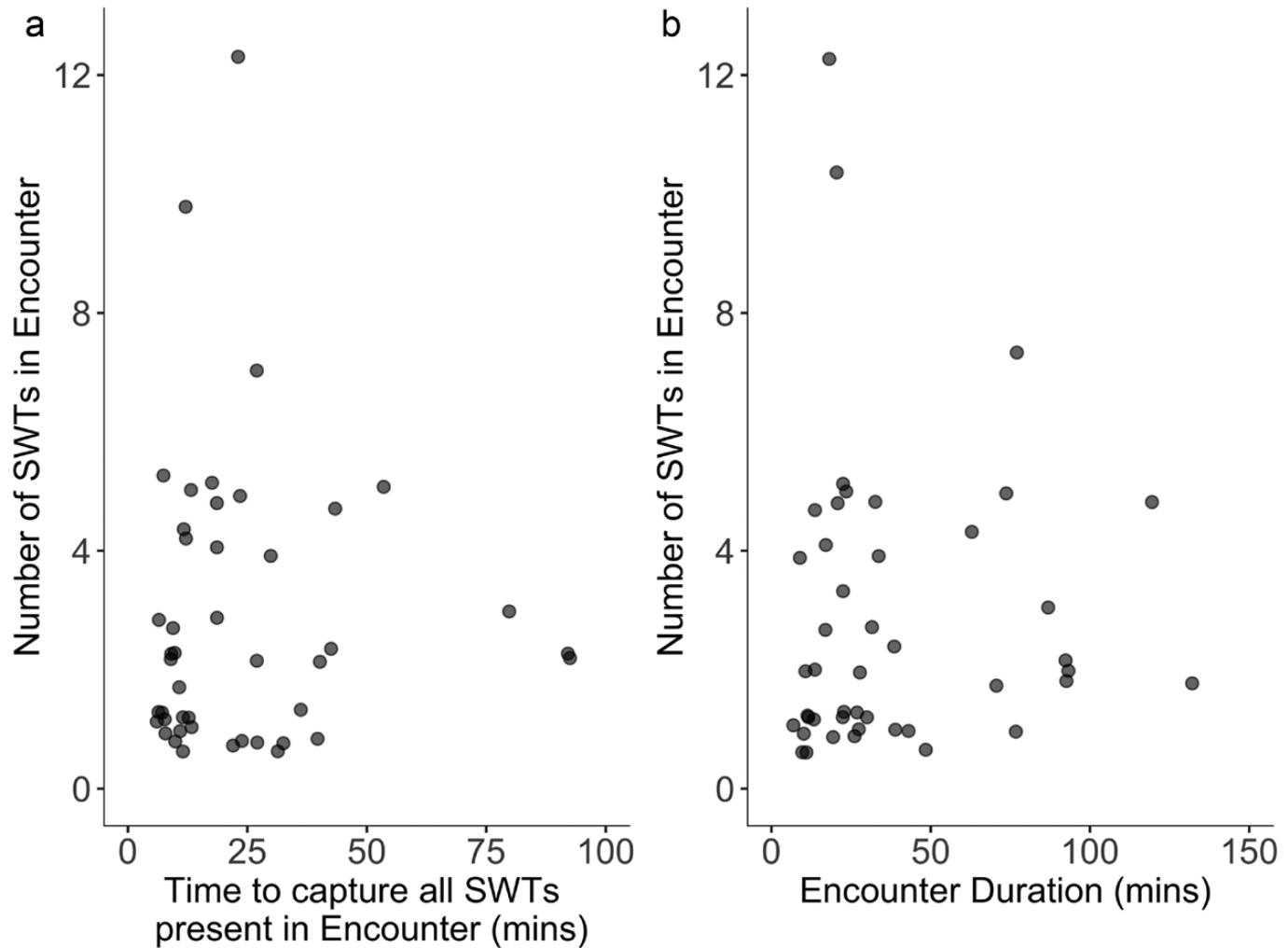
Fig. 4.—The duration of acoustic encounters of common bottlenose dolphins, and the number of signature whistle types (SWTs) detected from moored hydrophones in Namibia from January to July 2016. Each point corresponds to an acoustic encounter, with a single outlier point omitted from each plot (26 signature whistles captured in 100 min within a 110 min long encounter). Figure (a) shows the time into the encounter required to detect all SWTs present; (b) shows the total encounter duration and the number of SWTs detected.

can occur across habitats within a single study area either when using overall dolphin presence (presence of vocalizations) or the presence of individual dolphins (from signature whistles).

As signature whistles are cohesion calls, their production varies with behavior (Janik and Slater 1998; Cook et al. 2004). They are exchanged prior to groups combining at sea (Janik and Slater 1998; Quick and Janik 2012) and often are used by mothers and calves to facilitate reunions (Smolker et al. 1993; King et al. 2016). The production and likelihood of detecting SWTs therefore will be affected by the behavior and composition of the group when in detection range of the hydrophone. As dolphin behavior typically varies in different habitats (Hanson and Defran 1993; Hastie et al. 2004), it is likely that differences in SWT detection are driven at least in part by differential habitat use. Our results clearly highlight the importance of hydrophone location on detection probability, with at least five times more SWT detections at Aphrodite Beach than at other sites during the period in which all hydrophones were

compared, despite the furthest two sites being less than 10 km apart. Overall differences in the detection of dolphin presence were not unexpected, because Aphrodite Beach long has been recognized as a high-use site for this population (Elwen et al. 2019); the three other hydrophones were located at lower use sites, so differences in detections likely reflect overall differences in use of different portions of the bay. More striking, and of greater importance, is the difference in the detection of SWTs at each site, relative to overall animal presence. Notably, no SWTs were detected at the container terminal on any of the 12 occasions during which dolphin vocal presence was detected. Therefore, when placing hydrophones for MR, it is important not only to identify a site in which the animals regularly occur and vocalize, but one where they regularly emit the individually distinctive call being studied.

During the 6-month deployment at Aphrodite Beach, 30 of the 53 SWTs identified were captured more than once, including during different capture occasions (deployments),
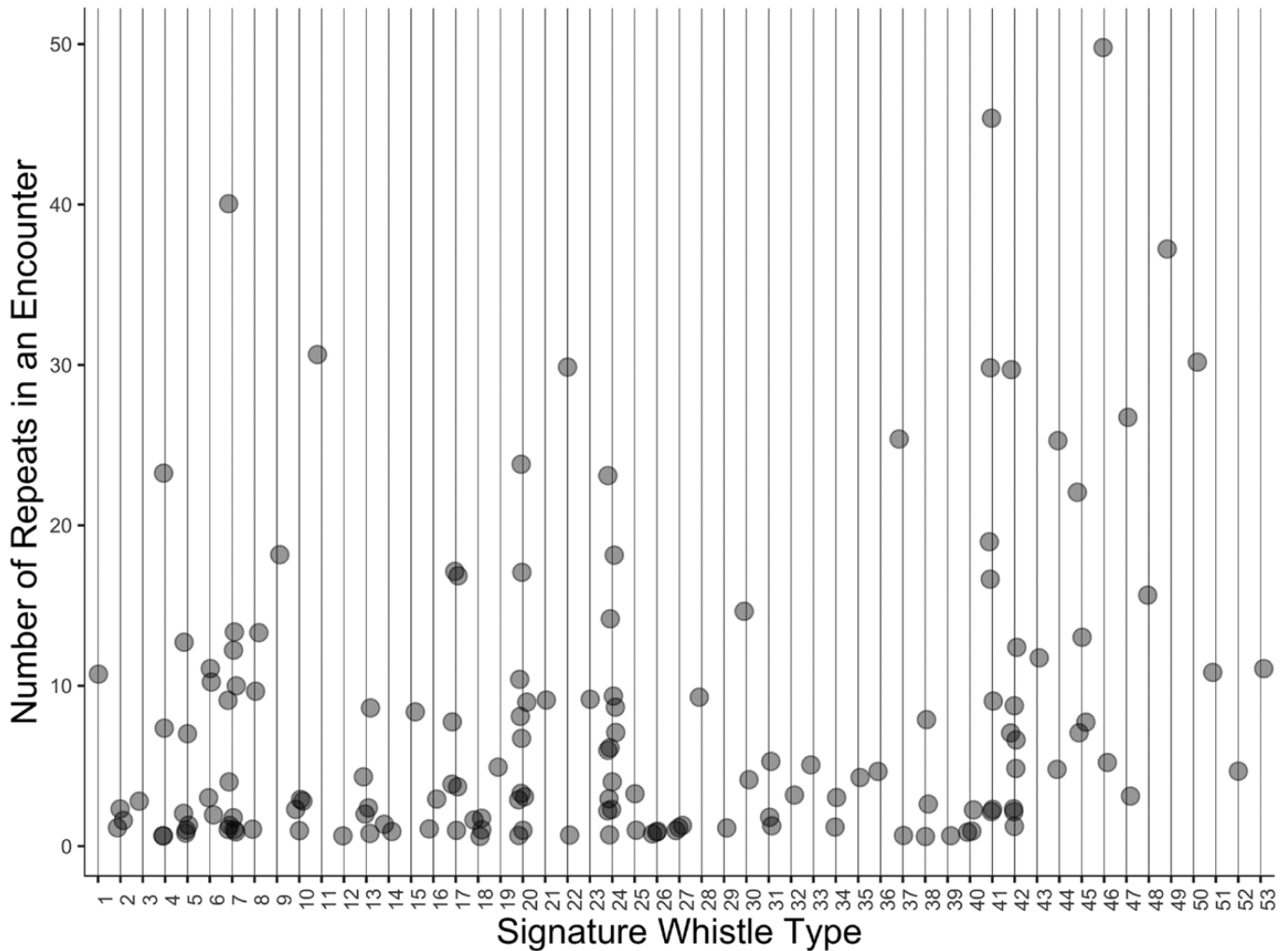
Fig. 5.—Capture heterogeneity of signature whistle types (SWTs) of common bottlenose dolphins detected during long-term acoustic monitoring from moored hydrophones in Namibia from January to July 2016. Each vertical gray line represents a SWT identified within the study (SWT identification 1–53). Points correspond to a detection of that SWT and the number of repeats in the encounter when it was detected.

with six captured in four or five deployments and 23 captured in just one. Such heterogeneity in recaptures of individuals is typical of MR studies of free-ranging dolphins, with a few individuals captured many times and many captured only a few times (Smith et al. 2013; James et al. 2015; Elwen et al. 2019). As with boat-based photographic studies, these differences in individual recaptures may reflect differences in individual use of the study area. Capture heterogeneity to some extent can be dealt with analytically, notably in closed-population models as above, or using SECR methods (Marques et al. 2013). Ideally, however, a study estimating abundance should be designed to maximize recaptures and ensure a good understanding of the likely scale of the study area relative to the population range (Hammond 1986). Regardless of any violation of the assumptions of MR models, the information gained on individual presence, timing, and area use, that is available from using signature whistles, is useful for a range of biological-, conservation-, and management-related questions. The differences in detection probability among relatively close

hydrophones highlighted above (< 5.5 km maximum separation between any two sites) suggest that these issues of capture heterogeneity might act at different scales for methods using SWT identification versus photographic MR studies, where investigators may be able to move within detection range. However, acoustic methods potentially have an advantage in that arrays of hydrophones can be deployed and managed over a much larger area than typically can be studied from small boats using photographic methods.

The correlation between the number of SWTs detected in an encounter and the time taken within the encounter to detect all SWTs present was weak and likely influenced by the clear outlier encounter that occurred on 23–24 April, which was retained in the correlation analysis and will have strengthened the relationship. In over 80% of acoustic encounters with SWTs present, all SWTs were captured within 30 min of cumulative recording time (50% sampling rate over 1 h), indicating that when this threshold is met, the number of SWTs (and therefore individuals) present has little effect on the time taken to

detect them all. Coupled with the lack of relationship between total encounter duration and number of SWT detected, this suggests that in the majority of encounters when the dolphins were whistling, we were able to capture all SWTs present. Capturing SWTs will likely be influenced by behavior. The results suggest the dolphins use the Aphrodite Beach site for activities such as socializing, in which signature whistles are more likely to occur in a short amount of time (Cook et al. 2004). If a hydrophone were placed in an area predominantly used for traveling (a behavior associated with lower SWT production—Cook et al. 2004) not all individuals may produce their SWTs whilst in range. It therefore is important to understand how the study population use a site. The threshold of time taken to detect all SWTs present in an encounter also could differ among study populations—with some populations being more or less vocally active.

In addition to heterogeneity resulting from differential space use and behavioral context, capture heterogeneity also may occur if vocal production differs with age or sex class or among individuals (Caldwell et al. 1990; Sayigh et al. 1990, 1995), and this potentially could affect the probability of capture. In general, the more a signal repeats, the more likely it is to be detected. It is possible that some individuals are motivated to repeat their SWT more often and therefore are detected more frequently. However, the range in number of SWT repeats in an encounter both within and between individuals (Fig. 5) suggests that repetition per se does not increase recapture rates. On 49 occasions, SWTs were identified only from a single repetition in a single encounter (Fig. 5). The repetition rates of SWTs per encounter varied among encounters (Fig. 5), indicating that individual dolphins are not consistently more or less vocal than others. These differences in detectability are similar to those that occur in photographic MR studies, and may be due to individual behavioral differences during the encounter.

The SWT catalog used in this study has been developed over 8 years from a combination of focal follows of groups (Kriesell et al. 2014) and long-term passive acoustic monitoring (this study). The majority of SWT we identified (75%) could be matched to this catalog, with 13 new SWTs identified over the 6-month study period. The accumulation of SWT recaptures indicated a closed population that informed our choice of MR model. However, one outlying encounter caused a peak in number of SWTs detected in April (deployment four; Fig. 2). The sporadic occurrence of large groups or aggregations of animals has been detected during photo-identification studies in Walvis Bay, and is not unusual for this population (Kriesell et al. 2014) but all animals are part of the population and are seen on a regular basis with only a slow accumulation of new individuals (Elwen et al. 2019). Over the 6-month deployment at Aphrodite Beach, 53 SWTs were identified and a MR abundance estimate of 58 individuals (95% *CI* = 54–68) was calculated using the SWT data. This falls within the seasonal estimates of the size of the population, which ranges between 54 and 76 (lowest to highest, N_{Total} values—Elwen et al. 2019). However, this is below the maximum number of 76 individuals identified photographically in any season (Elwen et al. 2019)

and at the lower end of the photographic MR confidence intervals. This suggests that despite considerable effort during 2016, we did not acoustically detect the SWT of several animals in the population and extrapolation for undetected animals may be warranted. Unidentifiable animals are a common problem in photographic MR studies that rely on accumulation of marks to the dorsal fin for identification. Animals with unmarked dorsal fins typically are young (Wilson et al. 1999) and their proportion in a population is estimated at an encounter or season level; final MR estimates of population abundance calculated from identifiable animals are then further extrapolated upwards by the proportion of unmarked individuals (Urian et al. 2014). The accurate calculation of the proportion of marked animals in a population can have significant effects on final study results, so is a very important consideration (Cheney et al. 2013). Although it is expected that all animals within a population have a signature whistle (Sayigh et al. 2007), it is possible that some do not produce their whistle or do so rarely (Caldwell et al. 1990), with signature whistle production related to motivation and maturation effects as well as behavioral context (Cook et al. 2004; Esch et al. 2009; Janik et al. 2013). By following the SIGID criteria and only using SWTs with an SNR of 2 or 3, we may have missed individuals whose whistles did not meet this quality threshold, as well as those not whistling. Further study combining visual photo-identification and acoustics will be required to ground-truth any extrapolation and the necessity and degree may vary between populations.

Data processing in this study was conducted manually using visual inspection of LTSAs to ensure that all whistles were identified. However, this approach is not effective for much larger data sets than the one used here. Acoustic data generally are amenable to automated methods, and this field is growing rapidly. Automated classification algorithms working on spectrogram images have been used to recognize successfully calls of crickets, frogs, and whales (Mellinger and Clark 2000; Brandes et al. 2006) and freely available software, such as ISHMAEL (Mellinger 2002) and PAMGuard (Gillespie et al. 2008), are able to automatically detect different call types (e.g., echolocation, whistles). Future studies should look at expanding automation of methods past detecting the focal call type, allowing the calls to then be matched to a catalog of individual call types as well as detecting new uncataloged individual call types.

We have provided evidence that individually distinctive calls can be used to monitor wild animal populations, and that MR methods can be applied successfully to call data. We have highlighted areas were biases may occur and MR assumptions violated, as well as potential ways of overcoming these obstacles. The ability to match SWTs to photographic identification data and use the two methods simultaneously could provide a dynamic and efficient monitoring tool for use in the wild. This methodology also could be extended over a larger area by incorporating a spatial element into a spatially explicit capture–recapture framework (Marques et al. 2013) to monitor wild animal populations that cover large, inaccessible areas in a cost- and labor-effective way.

Literature Cited

Best, P. B. 2007. Whales and dolphins of the southern African subregion. Cambridge University Press. Cambridge, United Kingdom.

Blumstein, D. T., et al. 2011. Acoustic monitoring in terrestrial environments using microphone arrays: applications, technological considerations and prospectus. Journal of Applied Ecology 48:758–767.

Borchers, D., G. Distiller, R. Foster, B. Harmsen, and L. Milazzo. 2014. Continuous-time spatially explicit capture-recapture models, with an application to a jaguar camera-trap survey. Methods in Ecology and Evolution 5:656–665.

Borchers, D. L., and M. G. Efford. 2008. Spatially explicit maximum likelihood methods for capture-recapture studies. Biometrics 64:377–385.

Boughman, J., and C. Moss. 2003. Social sounds: vocal learning and development of mammal and bird calls. Pp. 138–224 in Acoustic communication (A. Simmons, A. Popper, and R. Fay, eds.). Springer-Verlag. New York.

Brandes, T. S., P. Naskrecki, and H. K. Figueroa. 2006. Using image processing to detect and classify narrow-band cricket and frog calls. The Journal of the Acoustical Society of America 120:2950–2957.

Burton, A. C., et al. 2015. Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. Journal of Applied Ecology 52:675–685.

Caldwell, M. C., and D. K. Caldwell. 1979. The whistle of the Atlantic bottlenosed dolphin (*Tursiops truncatus*)-ontogeny. Pp. 369–401 in Behavior of marine animals: current perspectives in research (H. Winn and B. Olla, eds.). 3rd ed. Springer. New York.

Caldwell, M. C., D. K. Caldwell, and P. L. Tyack. 1990. Review of the signature-whistle hypothesis for the Atlantic bottlenose dolphin. Pp. 199–234 in The bottlenose dolphin (S. Leatherwood and R. Reeves, eds.). Elsevier. London, United Kingdom.

Center for Conservation Bioacoustics. 2014. Raven Pro: interactive sound analysis software. Ver. 1.5. The Cornell Laboratory of Ornithology. Ithaca, New York.

Cheney, B., et al. 2013. Integrating multiple data sources to assess the distribution and abundance of bottlenose dolphins *Tursiops truncatus* in Scottish waters. Mammal Review 43:71–88.

Clark, C. W., and P. J. Clapham. 2004. Acoustic monitoring on a humpback whale (*Megaptera novaeangliae*) feeding ground shows continual singing into late Spring. Proceedings of the Royal Society of London, B. Biological Sciences 271:1051–1057.

Conn, P. B., A. M. Gorgone, A. R. Jugovich, B. L. Byrd, and L. J. Hansen. 2011. Accounting for transients when estimating abundance of bottlenose dolphins in Choctawhatchee Bay, Florida. Journal of Wildlife Management 75:569–579.

Cooch, E., and White, G. 2010. Program MARK: a gentle introduction. 16th ed. http://www.phidot.org/software/mark/docs/book/. Accessed 8 Novmber 2016.

Cook, M. L., L. S. Sayigh, J. E. Blum, and R. S. Wells. 2004. Signature-whistle production in undisturbed free-ranging bottlenose dolphins (*Tursiops truncatus*). Proceedings of the Royal Society of London, B. Biological Sciences 271:1043–1049.

dos Santos, M. E., S. Louro, M. Couchinho, and C. Brito. 2005. Whistles of bottlenose dolphins (*Tursiops truncatus*) in the Sado Estuary, Portugal: characteristics, production rates, and long-term contour stability. Aquatic Mammals 31:453–462.

Dudgeon, C. L., K. H. Pollock, J. M. Braccini, J. M. Semmens, and A. Barnett. 2015. Integrating acoustic telemetry into mark-recapture models to improve the precision of apparent survival and abundance estimates. Oecologia 178:761–772.

Efford, M. G., D. K. Dawson, and D. L. Borchers. 2009. Population density estimated from locations of individuals on a passive detector array. Ecology 90:2676–2682.

Elwen, S. H., R. H. Leeney, and T. Gridley. 2019. Abundance estimates of an isolated population of common bottlenose dolphins (*Tursiops truncatus*) in Walvis Bay, Namibia, 2008–2012. African Journal of Marine Science 41:1–10.

Esch, H. C., L. S. Sayigh, and R. S. Wells. 2009. Quantifying parameters of bottlenose dolphin signature whistles. Marine Mammal Science 25:976–986.

Gillespie, D., et al. 2008. PAMGUARD: semiautomated, open source software for real-time acoustic detection and localisation of cetaceans. Pp. 54–62 in Proceedings of the Institute of Acoustics 30, no. 5, 14–15 October 2008, Southampton, United Kingdom.

Gowans, S. 2019. Grouping behaviors of dolphins and other toothed whales. Pp. 3–24 in Ethology and behavioral ecology of odontocetes (B. Würsig, ed.). Springer Nature. Cham, Switzerland.

Hammond, P. S. 1986. Estimating the size of naturally marked whale populations using capture-recapture techniques. Reports of the International Whaling Commission 8:253–282.

Hanson, M. T., and R. H. Defran. 1993. The behaviour and feeding ecology of the Pacific bottlenose dolphin, *Tursiops truncatus*. Aquatic Mammals 19:127–142.

Hastie, G. D., B. Wilson, L. J. Wilson, K. M. Parsons, and P. M. Thompson. 2004. Functional mechanisms underlying cetacean distribution patterns: hotspots for bottlenose dolphins are linked to foraging. Marine Biology 144:397–403.

Huggins, R. M. 1989. On the statistical analysis of capture experiments. Biometrika 76:133–140.

James, B. S., M. N. Bester, G. S. Penry, E. Gennari, and S. H. Elwen. 2015. Abundance and degree of residency of humpback dolphins *Sousa plumbea* in Mossel Bay, South Africa. African Journal of Marine Science 37:383–394.

JANIK, V. M. 1999. Pitfalls in the categorization of behaviour: a comparison of dolphin whistle classification methods. Animal Behaviour 57:133–143.

JANIK, V. M. 2000. Whistle matching in wild bottlenose dolphins (*Tursiops truncatus*). Science 289:1355–1357.

JANIK, V. M., S. L. KING, L. S. SAYIGH, AND R. S. WELLS. 2013. Identifying signature whistles from recordings of groups of unrestrained bottlenose dolphins (*Tursiops truncatus*). Marine Mammal Science 29:109–122.

JANIK, V. M., AND L. S. SAYIGH. 2013. Communication in bottlenose dolphins: 50 years of signature whistle research. Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology 199:479–489.

JANIK, V. M., AND P. J. B. SLATER. 1998. Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls. Animal Behaviour 56:829–838.

KING, S. L., E. GUARINO, L. KEATON, L. ERB, AND K. JAAKKOLA. 2016. Maternal signature whistle use aids mother-calf reunions in a bottlenose dolphin, *Tursiops truncatus*. Behavioural Processes 126:64–70.

KING, S. L., L. S. SAYIGH, R. S. WELLS, W. FELLNER, AND V. M. JANIK. 2013. Vocal copying of individually distinctive signature whistles in bottlenose dolphins. Proceedings of the Royal Society of London, B. Biological Sciences 280:20130053.

KRIESELL, H. J., S. H. ELWEN, A. NASTASI, AND T. GRIDLEY. 2014. Identification and characteristics of signature whistles in wild bottlenose dolphins (*Tursiops truncatus*) from Namibia. PLoS ONE 9:e106317.

LAAKE, J., AND E. REXSTAD. 2008. RMark - an alternative approach to building linear models in MARK. Pp. C4–C101 in Program MARK: a gentle introduction (E. Cooch and G. White, eds.). 9th ed. http://www.phidot.org/software/mark/docs/book/. Accessed 8 November 2016.

LUKACS, P. 2016. Closed population capture-recapture models. Program MARK, a gentle introduction (E. Cooch and G. White, eds.). 16th ed. http://www.phidot.org/software/mark/docs/book. Accessed 8 November 2016.

MANLY, B. F. J., S. C. AMSTRUP, AND T. L. MCDONALD. 2006. Capture-recapture methods in practice. Pp. 266–274 in Handbook of capture-recapture analysis (S. C. Amstrup, T. L. McDonald, and B. F. J. Manly, eds.). Princeton University Press. Princeton, New Jersey.

MANN, J. 1999. Behavioral sampling methods for cetaceans: a review and critique. Marine Mammal Science 15:102–122.

MARQUES, T. A., ET AL. 2013. Estimating animal population density using passive acoustics. Biological Reviews of the Cambridge Philosophical Society 88:287–309.

MARTIN, S. W., ET AL. 2013. Estimating minke whale (*Balaenoptera acutorostrata*) boing sound density using passive acoustic sensors. Marine Mammal Science 29:142–158.

MATHSWORKS. 2012. Matlab. Ver. 8.0 (R2012b). The MathsWorks. Inc. Natick, Massachusetts.

MELLINGER, D. K. 2002. ISHMAEL: integrated system for holistic multi-channel acoustic exploration and localization. NOAA Technical Memorandum OAR PMEL-120. Newport, Oregon.

MELLINGER, D. K., AND C. W. CLARK. 2000. Recognizing transient low-frequency whale sounds by spectrogram correlation. The Journal of the Acoustical Society of America 107:3518–3529.

NICHOLSON, K., L. BEJDER, S. J. ALLEN, M. KRTZEN, AND K. H. POLLOCK. 2012. Abundance, survival and temporary emigration of bottlenose dolphins (*Tursiops* sp.) off Useless Loop in the western gulf of Shark Bay, Western Australia. Marine and Freshwater Research 63:1059–1068.

NORRIS, K. S., AND T. P. DOHL. 1980. Behavior of the Hawaiian spinner dolphin, *Stenella longirostris*. Fishery Bulletin 77:821–849.

PARRA, G. J., P. J. CORKERON, AND H. MARSH. 2006. Population sizes, site fidelity and residence patterns of Australian snubfin and Indo-Pacific humpback dolphins: implications for conservation. Biological Conservation 129:167–180.

POPPER, A. N. 1980. Sound emission and detection by delphinids. Pp. 1–52 in Cetacean behavior: mechanisms and functions (L. M. Herman, ed.). Wiley. New York.

QUICK, N. J., AND V. M. JANIK. 2012. Bottlenose dolphins exchange signature whistles when meeting at sea. Proceedings of the Royal Society of London, B: Biological Sciences 279:2539–2545.

SAYIGH, L. S., H. C. ESCH, R. S. WELLS, AND V. M. JANIK. 2007. Facts about signature whistles of bottlenose dolphins, *Tursiops truncatus*. Animal Behaviour 74:1631–1642.

SAYIGH, L. S., P. L. TYACK, R. S. WELLS, M. D. SCOTT, AND A. B. IRVINE. 1995. Sex difference in signature whistle production of free-ranging bottlenose dolphins, *Tursiops truncatus*. Behavioral Ecology and Sociobiology 36:171–177.

SAYIGH, L., P. TYACK, R. WELLS, AND M. SCOTT. 1990. Signature whistles of free-ranging bottlenose dolphins *Tursiops truncatus*: stability and mother-offspring comparisons. Behavioral Ecology and Sociobiology 26:247–260.

SCRIPPS WHALE ACOUSTIC LABORATORY. 2016. Triton. Ver. 1.93. Scripps Institution of Oceanography. La Jolla, California.

SEBER, G. A. F. 1982. The estimation of animal abundance. Macmillan. New York.

SIMON, M., H. NUUTTILA, M. M. REYES-ZAMUDIO, F. UGARTE, U. VERFUB, AND P. G. H. EVANS. 2010. Passive acoustic monitoring of bottlenose dolphin and harbour porpoise, in Cardigan Bay, Wales, with implications for habitat use and partitioning. Journal of the Marine Biological Association of the United Kingdom 90:1539–1545.

SMITH, H. C., K. POLLOCK, K. WAPLES, S. BRADLEY, AND L. BEJDER. 2013. Use of the robust design to estimate seasonal abundance and demographic parameters of a coastal bottlenose dolphin (*Tursiops aduncus*) population. PLoS ONE 8:e76574.

SMOLKER, R. A., J. MANN, AND B. B. SMUTS. 1993. Use of signature whistles during separations and reunions by wild bottlenose dolphin mothers and infants. Behavioral Ecology and Sociobiology 33:393–402.

STEVENSON, B. C., D. L. BORCHERS, R. ALTWEGG, R. J. SWIFT, D. M. GILLESPIE, AND G. J. MEASEY. 2015. A general framework for animal density estimation from acoustic detections across a fixed microphone array. Methods in Ecology and Evolution 6:38–48.

TERRY, A. M., T. M. PEAKE, AND P. K. MCGREGOR. 2005. The role of vocal individuality in conservation. Frontiers in Zoology 2:10.

THOMISCH, K., ET AL. 2019. Temporal patterns in the acoustic presence of baleen whale species in a presumed breeding area off Namibia. Marine Ecology Progress Series 620:201–214.

THOMPSON, W., G. WHITE, AND C. GOWAN. 1998. Monitoring vertebrate populations. Academic Press. London, United Kingdom.

URIAN, K., ET AL. 2014. Recommendations for photo-identification methods used in capture-recapture models with cetaceans. Marine Mammal Science 31:1–33.

WEARN, O. R., J. M. ROWCLIFFE, C. CARBONE, H. BERNARD, AND R. M. EWERS. 2013. Assessing the status of wild felids in a highly-disturbed commercial forest reserve in Borneo and the implications for camera trap survey design. PLoS ONE 8:e77598.

WHITE, G. C., AND K. P. BURNHAM. 1999. Program mark: survival estimation from populations of marked animals. Bird Study 46:S120–S139.

WHITEHEAD, H. 1997. Analysing animal social structure. Animal Behaviour 53:1053–1067.

WILSON, B., P. HAMMOND, AND P. THOMPSON. 1999. Estimating size and assessing trends in a coastal bottlenose dolphin population. Ecological Applications 9:288–300.