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Changes in bottlenose dolphin whistle parameters related to vessel presence, surface behaviour and group composition

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Cetacean watching from tour boats has increased in recent years and has been promoted as an ethically viable alternative to cetacean viewing in captive facilities or directed take. However, short- and long-term impacts of this industry on the behaviour and energetic expenditure of cetaceans have been documented. Although multiple studies have investigated the acoustic response of dolphins to marine tourism, there are several covariates that could also explain some of these results and should be considered simultaneously. Here, we investigated whether common bottlenose dolphins, *Tursiops truncatus*, inhabiting Walvis Bay, Namibia vary their whistle parameters in relation to boat presence, surface behaviour and/or group composition. We detected an upward shift of up to 1.99 kHz in several whistle frequency parameters when dolphins were in the presence of one or more tour boats and the research vessel. No changes were demonstrated in the frequency range, number of inflection points or duration of whistles. A similar, although less pronounced difference was observed in response to engine noise generated by the research vessel when idling, suggesting that noise alone plays an important role in driving this shift in whistle frequency. Additionally, a strong effect of surface behaviour was observed, with the greatest difference in whistle parameters detected between resting and other behavioural states that are associated with higher degrees of emotional arousal. Group composition also contributed to the variation observed, with the impact of boats dependent on whether calves were present or not. Overall these results demonstrate high natural variation in the frequency parameters of whistles utilized by dolphins over varying behavioural states and group composition. Anthropogenic impact in the form of marine tour boats can influence the vocalization parameters of dolphins and such changes could have a long-term impact if they reduce the communication range of whistles or increase energy expenditure.

Wildlife tourism involving cetacean (whale, dolphin and porpoise) watching has experienced rapid growth since the 1990s (Hoyt, 2001; O'Connor, Campbell, Cortez, & Knowles, 2009). Globally, boat-based cetacean watching generates an estimated 2.2 billion US dollars annually (IWC, 2014). Revenue can provide a valuable subsidy to fishing communities and in some cases wild cetacean viewing has replaced direct hunting of whales and dolphins (Amir & Jiddawi, 2001; Berggren et al., 2007). Compared with captive facilities, responsible boat-based cetacean watching has been promoted as an ethically acceptable option for observing dolphins, providing a valuable forum for environmental education and promotion of conservation efforts (IFAW, 1997). However, a considerable body of work has shown that boats and boat-based cetacean watching can have multiple negative impacts on the behaviour of the focal individual, population or species (Parsons, 2012). Short-term impacts associated with boat interactions include group directional changes (Steckenreuter, Möller, & Harcourt, 2012; Stensland & Berggren, 2007), changes in group dispersion (Arcangeli & Crosti, 2009; Steckenreuter et al., 2012), heightened breathing synchrony (Hastie, Wilson, Tufft, & Thompson, 2003), increased dive times (Lusseau, 2003b) and changes in vocalizations (Buckstaff, 2004; Scarpaci, Bigger,

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Corkeron, & Nugegoda, 2000). Such changes can have longer lasting impacts resulting in seasonal (Rako et al., 2013) or long-term (Bejder et al., 2006) displacement and increased energy expenditure (Williams, Lusseau, & Hammond, 2006).

Relative to observable changes in surface behaviour, the impacts of boats on the acoustic behaviour of cetaceans has received less attention. Changes in the production or parameters of vocalizations may be related to elevated levels of anthropogenic noise associated with vessel engines (Jensen et al., 2009; Parks, Johnson, Nowacek, & Tyack, 2011; Pirotta et al., 2012), the physical presence of boats (Pirotta, Merchant, Thompson, Barton, & Lusseau, 2015), boat type (La Manna, Manghi, Pavan, Lo Mascolo, & Sarà, 2013) or vessel behaviour during encounters, and the interplay between these factors can be difficult to disentangle (see Ellison, Southall, Clarke, & Frankel, 2011).

As cetaceans are highly acoustically oriented and rely on acoustic signals throughout their daily lives, they are particularly sensitive to elevated noise levels. Sound generated through outboard engines, which are typically used by small-scale cetacean watching boats, can be loud (149–152 dB re 1 μPa root mean square at 1 m) and broadband, extending between 0.2 and 40 kHz and result in significant reduction of communication range (Jensen et al., 2009). Although excessive noise can cause hearing damage, and even strandings in cetaceans (Weilgart, 2007), the more relevant impacts of boat noise generated through marine tourism activities are likely to be the masking of calls (Jensen et al., 2009) or biological cues (Clark et al., 2009), behavioural changes (Williams et al., 2006) or displacement (Rako et al., 2013), and stress (Rolland et al., 2012). Animals can adjust their acoustic signalling behaviour to respond to increases in noise in several different ways, which are not necessarily mutually exclusive. These are summarized by Radford, Kerridge, and Simpson (2014) as (1) avoidance of noise, by moving away from the noise source or adjusting the timing of acoustic signals to coincide with low noise periods, (2) adjustment of acoustic signal temporal parameters, such as increasing call duration or rate, (3) amplitude shifts, such as the 'Lombard effect' whereby animals produce higher amplitude acoustic signals in noise (Lombard, 1911), (4) frequency shifts in acoustic signals or the relative amplitude of signal components and (5) shifting emphasis to an alternative signal modality, for example by increasing the use of visual or chemical signals. Cetaceans are known to respond to boat noise sources in the first four ways (Ansmann, Goold, Evans, Simmonds, & Keith, 2007; Foote, Osborne, & Hoelzel, 2004; Holt, Noren, Veirs, Emmons, & Veirs, 2009; Parks, Clark, & Tyack, 2007; Parks et al., 2011; Rako et al., 2013) and may also increase their use of visual cues in elevated noise conditions (point 5 above, see Dunlop, Cato, & Noad, 2010).

In bottlenose dolphins (*Tursiops* spp.) long-range communication relies on whistles, defined as narrow-band, frequency-modulated signals, ranging between 0.8 and 28.5 kHz in frequency (May-Collado & Wartzok, 2008; Schultz & Corkeron, 1994). In favourable conditions, these signals can propagate over tens of kilometres (Janik, 2000). Whistle production is usually higher during socializing contexts (Jones & Sayigh, 2002; Quick & Janik, 2008) and when animals experience stress (Esch, Sayigh, Blum, & Wells, 2009). Each bottlenose dolphin uses an individually distinctive signature whistle which is acquired through vocal production learning in the first year of life (Caldwell & Caldwell, 1979; Janik & Slater, 1997). Around 50% of all whistles recorded from free-ranging bottlenose dolphins are signature whistles (Cook, Sayigh, Blum, & Wells, 2004) which are used to convey identity information (Janik, Sayigh, & Wells, 2006), facilitate group contact (Janik & Slater, 1998; Quick & Janik, 2012) and address conspecifics (King & Janik, 2013). The function of other, nonsignature whistles in the dolphin's repertoire is less well understood. Nonsignature whistles may include shared whistle types (King & Janik, 2015), copies of conspecifics' signature whistles (King, Sayigh, Wells, Fellner, & Janik, 2013; Tyack, 1986; Watwood, Owen, Tyack, & Wells, 2005) and nonstereotyped whistles produced by calves (Caldwell & Caldwell, 1979).

Although several studies have investigated the likely impact of boat presence on dolphin communication signals including whistles (Buckstaff, 2004; May-Collado & Quiñones-Lebrón, 2014; Scarpaci et al., 2000), few have controlled for other key covariates that may influence whistle parameters such as behavioural context (Lemon, Lynch, Cato, & Harcourt, 2006; May-Collado & Quiñones-Lebrón, 2014; Scarpaci et al., 2000). Furthermore, although variation in acoustic parameters can relate to behavioural state (Azevedo et al., 2010; May-Collado, 2013) and may be useful in predicting surface behaviour (Henderson, Hildebrand, & Smith, 2011; Henderson, Hildebrand, Smith, & Falcone, 2012; Hernandez, Solangi, & Kuczaj, 2010) the available information poorly explains the causative factors of this variability. Esch, Sayigh, Blum, et al.'s (2009) study is the notable exception in detailing the influence of stress on whistle parameters and production rates. This contrasts with a wealth of comparative behavioural literature detailing consistent patterns in vocal parameters associated with varying levels of emotional arousal. In reviewing the available mammalian literature, Briefer (2012) highlighted strong evidence that heightened emotional arousal is associated with an increase in fundamental frequency (F0), F0 range, energy distribution and peak frequency, as well as increases in amplitude and vocalization rate. Vocalization or element duration may also increase with arousal, although this pattern is less consistent across species (Briefer, 2012).

Here we investigated variation in the acoustic parameters of whistle vocalizations of bottlenose dolphins in relation to key covariates: tour boat presence, surface behaviour and group composition. We also investigated the influence of engine noise generated by the research vessel as a possible source of disturbance. The study population in Walvis Bay, Namibia is the only inshore population of common bottlenose dolphins, *Tursiops truncatus*, inhabiting the southern African coastline (Best, 2007). This population is small, numbering around 100 individuals (Elwen, Snyman, & Leeney, 2011), and is the focus of an intensive boat-based cetacean-watching industry involving approximately 23 motorized boats and generating an annual income of around 2.5 million US dollars per annum (Leeney, 2014). Quantifying the influence of tour boats on dolphins is necessary for effective management of cetacean populations in Namibian coastal waters. Previous research in the area by Indurkhya (2012) has shown a change in group surface behaviour during tour boat presence with dolphins decreasing their time spent resting and increasing time spent travelling and socializing. The duration of behavioural bout length (measured as the average length of time dolphins are continuously engaged in one of a predetermined number of key behavioural states, as defined below) also decreases when tour boats are present, indicating agitation during tour boat presence (Indurkhya, 2012). The frequency of engine noise produced by these tour boats has the potential to overlap the frequency of whistles produced by bottlenose dolphins in Walvis Bay (Gridley, Nastasi, Kriesell, & Elwen, 2015). Short-term changes in the acoustic behaviour of this population relative to tour boat presence could indicate a human impact which should be properly managed to mitigate any potential long-term, negative effects on this small population of dolphins.

METHODS

Data were collected during five field seasons between 2009 and 2014 (see Table 1) in Walvis Bay (22°57′S, 14°30′E), central Namibia.