



Temporal segregation of the Australian and Antarctic blue whale call types (*Balaenoptera musculus* spp.)

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We examined recordings from a 15-month (May 2009–July 2010) continuous acoustic data set collected from a bottom-mounted passive acoustic recorder at a sample frequency of 6 kHz off Portland, Victoria, Australia (38°33′01″S, 141°15′13″E) off southern Australia. Analysis revealed that calls from both subspecies were recorded at this site, and general additive modeling revealed that the number of calls varied significantly across seasons. Antarctic blue whales were detected more frequently from July to October 2009 and June to July 2010, corresponding to the suspected breeding season, while Australian blue whales were recorded more frequently from March to June 2010, coinciding with the feeding season. In both subspecies, the number of calls varied with time of day; Antarctic blue whale calls were more prevalent in the night to early morning, while Australian blue whale calls were detected more often from midday to early evening. Using passive acoustic monitoring, we show that each subspecies adopts different seasonal and daily call patterns which may be related to the ecological strategies of these subspecies. This study demonstrates the importance of passive acoustics in enabling us to understand and monitor subtle differences in the behavior and ecology of cryptic sympatric marine mammals.

Key words: Australia, *Balaenoptera musculus breviceauda*, *Balaenoptera musculus intermedia*, calls, cryptic sympatric marine mammals, diel, ecology, seasonal, vocalizations

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Cryptic species are closely related animals that are morphologically similar but genetically variable (Mayr 1977; for additional information, see Bickford et al. 2007). The diagnostic characteristics separating cryptic species may be based on nonvisual traits (Kingston et al. 2001; Bickford et al. 2007) such as acoustic signaling rather than traditional morphological traits. The niche or role that a species plays in its environment may differ between cryptic species, differences that may go undetected using morphological techniques. However, passive acoustic monitoring, a technique that relies purely on the animals' vocalizations, provides an alternative method for separating them.

Morphologically similar but acoustically divergent species are widespread. In the tropical forest of southeast Asia, 2 species of tree shrews, *Tupaia glis* and *T. belangeri*, are

morphologically similar but display acoustic divergence in the loud chatter call (Esser et al. 2008). Similarly in Malaysia, a population of bicolored leaf-nosed bats (*Hipposideros bicolor*) that are hard to distinguish morphologically but are genetically distinct can be separated on the basis of 2 different vocal types. These bats have different echolocation call frequencies, and it has been suggested that the acoustic divergence in these species is a consequence of social selection for a clear communication channel (Kingston et al. 2001). Cryptic species are also well documented in the marine environment (Lee 2000; Haig et al. 2013) and the Antarctic (*Balaenoptera musculus intermedia*) and Australian blue whale (*B. m. breviceauda*) subspecies of the Southern Hemisphere are good examples of marine cryptic species living in sympatry. Visual observations of blue whales

in the southeastern Indian Ocean, near the Bonney Upwelling off South Australia, have been thought to be Australian blue whales (Gill et al. 2011), while genetic and acoustic information have shown that both Antarctic and Australian blue whales are present in the region (Attard et al. 2012). The 2 subspecies are difficult to visually discriminate in the wild based on morphology (Donovan 1984) but can be separated by their distinct vocalizations (Ljungblad et al. 1998; McCauley et al. 2000).

The use of calls may vary both seasonally and throughout the day, variation that might be used to indicate the social context in which calls are made. Vocalizations can also be modified by ecological factors such as changes in the environment (Van Opzeeland et al. 2010). Tundra-nesting shorebirds on the Colville River Delta and Yukon-Kuskokwim Delta in northern and western Alaska, respectively, show seasonal variation in calling behavior in which the number of calling individuals decreased throughout the season (Nebel and McCaffrey 2003). The study also found site-specific changes where calling behavior was affected by the weather at each site, particularly wind, which was associated with changes in display behavior (Nebel and McCaffrey 2003). In addition, Van Parijs et al. (2004) showed that ice cover fluctuations affected the vocalization patterns of “territorial” and “roaming” male bearded seals differently. Roaming males were not heard in years with increased ice cover, while territorial males were present during all ice conditions.

Here, we use recordings from a 15-month Integrated Marine Observing System (IMOS) hydroacoustic data set collected offshore Portland, Victoria, in the southeastern Indian Ocean. By analyzing the vocalizations of whales, we examine the differences in the acoustic behavior of both the Antarctic and Australian blue whales. We propose that by studying the seasonal and diel acoustic behavior of blue whales, one may be able to discriminate and understand the behavior unique to these 2 cryptic subspecies and elucidate the ecological and breeding strategy for blue whales in the study area.

There are many different call types recorded worldwide for blue whales (McDonald et al. 2006). In Australia, there are 2 predominately recorded blue whale calls: the Antarctic and Australian blue whales. The Antarctic blue whale calls vary in their appearance, and they are reported to occur as a 3-part,

2-part, and/or single-part call (Rankin et al. 2005). In the current study, the single-part call from Antarctic blue whales was predominately detected (Fig. 1). This call is suspected to be produced by male whales only and it is uncertain whether females also produce this call (Oleson et al. 2007). The Australian blue whales recorded in the study area (Fig. 2) are similar to those recorded in Western Australia and have been referred to as the “Australia call type” (Gavrilov et al. 2011).

MATERIALS AND METHODS

Data collection.—Data used in the study were collected from May 2009 to July 2010 from the IMOS sea noise loggers, located in Portland (38°33'2"S, 141°15'14"E), Victoria, southeast Indian Ocean (Fig. 3). The Bonney Upwelling occurs off the coast of Portland and flows west past Robe in South Australia and is known to attract blue whales (Butler et al. 2002). The IMOS acoustic recording system is composed of 4 independent sea noise loggers, with 3 located on the seafloor in an approximate equilateral triangle of 5-km sides with the 4th logger placed at the center. The recordings were taken from a fixed acoustic sensor, which is approximately 23 km from shore and at a depth of approximately 168 m during 2 separate deployments, with no recordings made in January 2010 due to strong currents impeding the exchange of acoustic recorders during this period. The data set was composed of 500-s recordings, each starting 900 s (15 min) after the previous one. The sampling frequency was 6 kHz and the upper limit of the frequency band at -3 dB is 2.8 kHz.

Call detection.—To detect Antarctic blue whale calls, we used the energy ratio detector, which extracts energy in the frequency bands 25–26.5 and 14–16 Hz in the software package Ishmael version 2.3.1 (Mellinger 2001) to detect the 1st tonal part (~ 26 Hz) of this call (Ishmael detector configuration files used in the study are available upon request). The energy ratio significantly reduced false detection caused by broadband low-frequency signals. The detected signal had to be 2.5–15-s in duration. This call is repeated approximately every 65 s (McDonald et al. 2006).

The detection process for Australian blue whales involved using the spectrogram correlation detector in Ishmael to detect the 2nd part of the Australian blue whale call. More specifically,

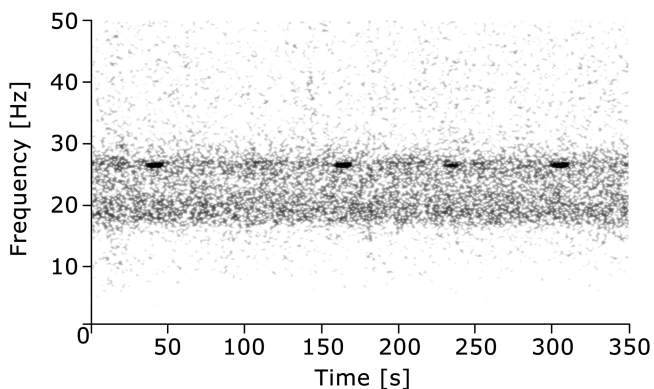


Fig. 1.—Spectrogram of Antarctic blue whale calls at approximately 26 Hz; spectrogram parameters: 1,024-point Fast Fourier Transform and 1,024-point Hann window with 95% overlap.

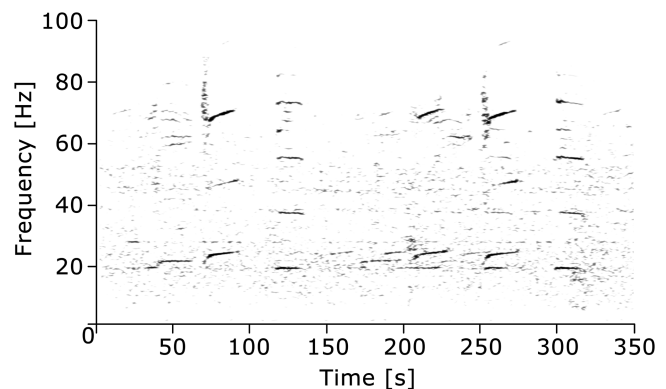


Fig. 2.—Spectrogram of Australian blue whale calls; spectrogram parameters: 1,024-point Fast Fourier Transform and 1,024-point Hann window with 95% overlap.

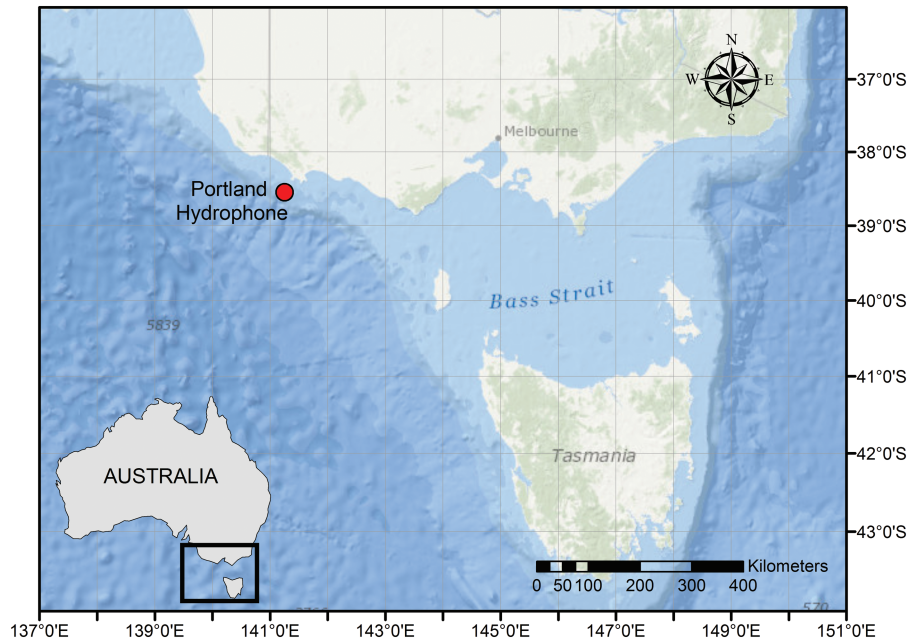


Fig. 3.—Location of Integrated Marine Observing System hydroacoustic array off the coast of Portland, Victoria, Australia.

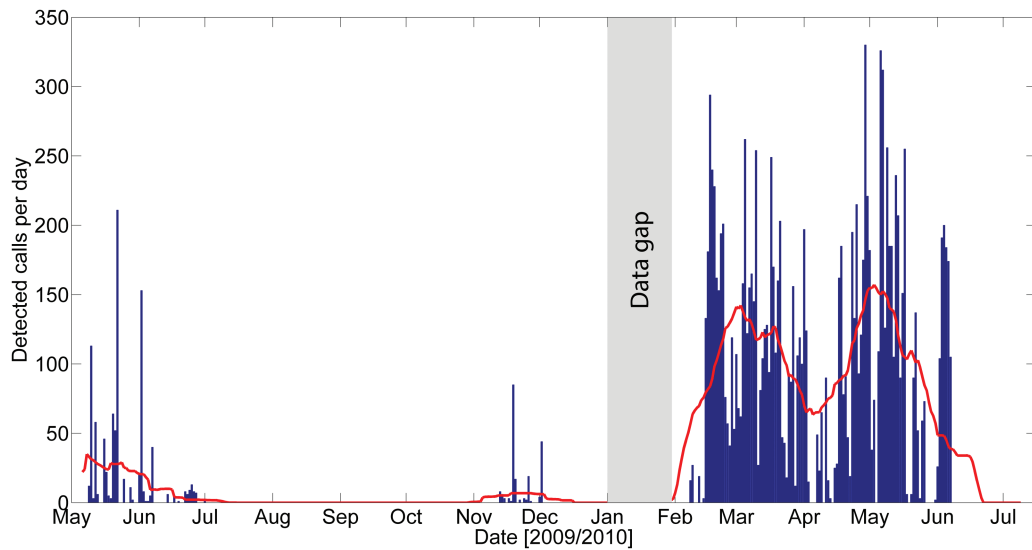


Fig. 4.—Call detections of Australian blue whale calls in the southeastern Indian Ocean (May 2009–July 2010; $n = 13,989$). The line indicates a 7-day moving average.

we aimed for the harmonic with the highest energy at around 70 Hz. We cross-correlated the spectrogram with a template of 15-s duration characterized by a frequency up-sweep from 66 to 71 Hz and a kernel bandwidth of 1.5 Hz. This call is repeated approximately every 180 s (McDonald et al. 2006).

Both Antarctic and Australian blue whale call detections were manually verified by an experienced analyst. Spot checking was also performed to ensure that no major calling periods were missed.

Acoustic behavior.—To analyze the seasonal calling patterns of behavior for both species, we examined the daily call detections and presented them over the duration of the study period (May 2009–July 2010; Figs. 4 and 5). We also examined the diel calling patterns throughout the study period and present

the call detections during the peak periods. For Australian blue whales, calls were examined hourly for the period March–May 2010 (Fig. 6) and from August to October 2009 for Antarctic blue whales (Fig. 7).

Statistics.—To allow for the assessment of whale call counts changing over the time of day as well as over the 15 months of the study period, a generalized additive model (GAM) was used. Inclusion of splines in the model allowed a nonlinear association between (log-) mean counts and month as well as time of day to be modeled, with separate nonlinear terms for both species (Antarctic whale or Australian whale). The form of the model was as follows:

$$\log_e \mu = \text{constant} + \text{species} + s^{(\text{Sp})}(\text{Month}) + s^{(\text{Sp})}(\text{Time})$$

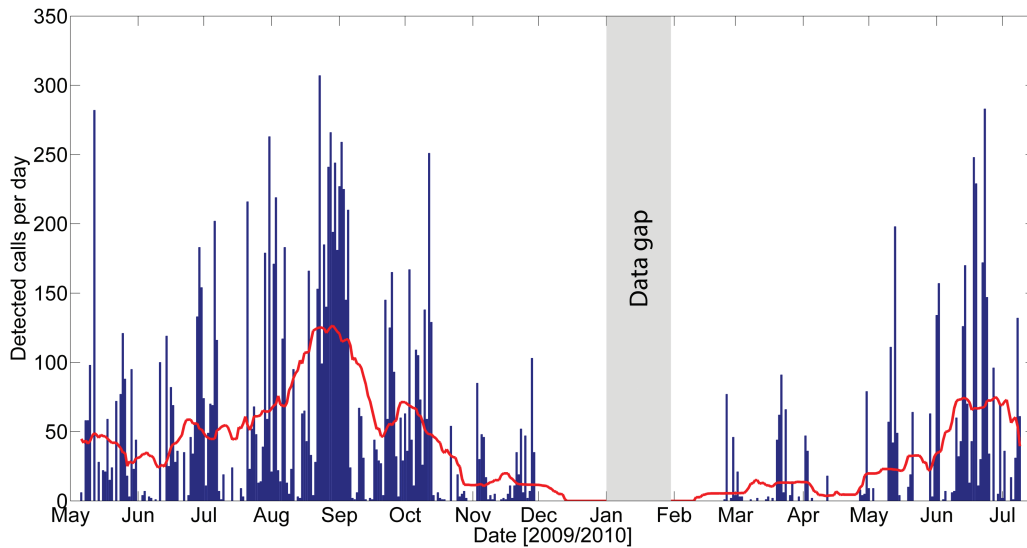


Fig. 5.—Call detections of Antarctic blue whale calls in the southeastern Indian Ocean (May 2009–July 2010; $n = 15,064$). The line indicates a 7-day moving average.

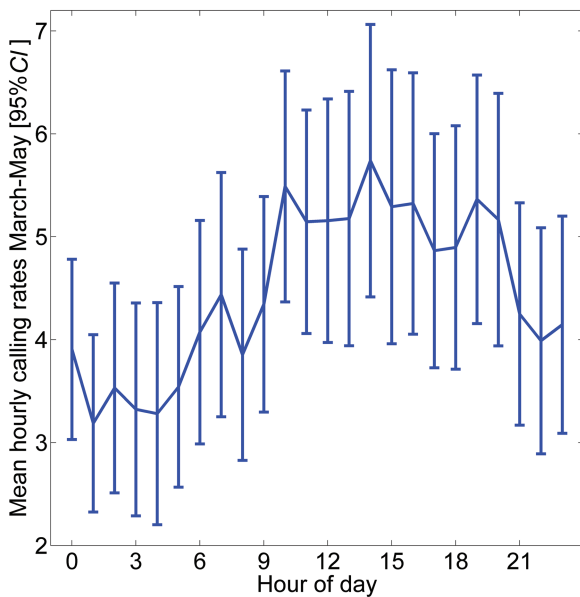


Fig. 6.—Diel patterns in calling behavior for Australian blue whales in the southeastern Indian Ocean (given for peak periods of calling: March–May 2010). The error bars indicate the standard error of the mean (SD/\sqrt{n}).

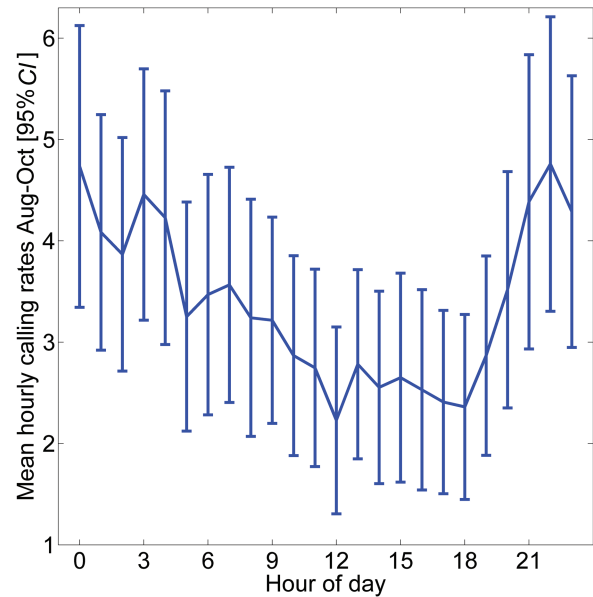


Fig. 7.—Diel patterns in calling behavior of Antarctic blue whales in the southeast Indian Ocean (given for peak periods of calling: August–October 2009). The error bars indicate the standard error of the mean (SD/\sqrt{n}).

where μ is the mean number of calls per hour, species is the effect of Antarctic whale versus Australian whale, $s^{(Sp)}(\text{Month})$ is the spline function of month for the particular species, and $s^{(Sp)}(\text{Time})$ is the spline function of time of day for the particular species.

To allow for the number of calls being a count variable, and highly skewed, a quasi-Poisson model was specified, allowing for overdispersion. Note that specifications of the terms $s^{(Sp)}(\text{Month})$ and $s^{(Sp)}(\text{Time})$ effectively is an interaction between Species and the smooth functions of Month and Time. Significance of the interactions was assessed by fitting reduced models involving single spline functions for Month and Time, i.e., $s(\text{Month})$ and $s(\text{Time})$, and then comparing models using

deviance difference tests. The GAM was fitted using the “gam” function, which is contained in the “mcgvm” package in R. To ensure that time was fitted as a periodic function (24-h period), a cyclic penalized cubic regression spline smooth form was specified.

RESULTS

A total of 29,053 blue whale calls were detected over the 15-month period (i.e., after false positives were removed). Of these detections, 52% (15,064 of 29,053 calls) were attributed to Antarctic blue whales and 48% (13,989 of 29,053 calls) were attributed to Australian blue whales. The false detection rate for

Antarctic blue whales calls was 14.6% and for Australian blue whales 36.6%.

Seasonal patterns.—There was a significant interaction between Species and Month ($P < 0.0001$) indicating separate seasonal patterns for the 2 subspecies. Australian blue whales were detected more often from March to June 2010 (Fig. 4), while Antarctic blue whales were detected more frequently from July to October 2009 with a peak in September 2009, and in the following year, peaks were recorded in June and July 2010 (Fig. 5). Figure 8 illustrates the nature of this interaction. There were also more Australian blue whale calls detected in May 2010 compared to the same time period in the previous year (May 2009; Fig. 4).

Diel calling patterns.—There was a significant interaction between Species and Time ($P < 0.0001$). During peak calling periods, more Australian blue whale calls were detected from midday to early evening (Fig. 6), while Antarctic blue whale calls tended to be detected more through the night to early morning than in the day (Fig. 7). Both the Antarctic and Australian blue whales had calling behavior that varied throughout the day and Fig. 9 demonstrates the features of this interaction.

DISCUSSION

Visual observations of blue whales near the Bonney Upwelling in the southeastern Indian Ocean have long been thought to be Australian blue whales (Gill et al. 2011), while recent genetic and acoustic studies have shown that both the Antarctic and Australian blue whales are present in the region (Attard et al. 2012; current study). Analyzing the calls detected for the 2 subspecies of blue whales suggested 2 distinct ecological strategies employed by both subspecies at this site: feeding for Australian blue whales and breeding or as a corridor to the breeding site for

Antarctic blue whales. The use of passive acoustic monitoring enabled us to examine both subspecies based on their respective calling behavior. The results illustrate the calling patterns employed by both Australian and Antarctic blue whales within the study period.

Seasonal pattern.—Antarctic blue whale calls were detected more often during July–October 2009 and June–July 2010, which coincides with the literature that suggests that whales move to warmer waters in winter to breed (Small 1971). While Australian blue whale calls were detected more often during March to June 2010, which matches the feeding period for blue whales in this region. According to visual observations, blue whales feed in the Bonney upwelling during November–May (Gill et al. 2011).

Studies recording the calls of Antarctic blue whales from the Western Antarctic Peninsula compliment the calling behavior of Antarctic blue whales in the current study. Antarctic blue whale calls recorded in the Western Antarctic Peninsula (Širović et al. 2004) were lowest during June–September and in December. In the current study, Antarctic blue whales from the southeastern Indian Ocean (current study) show calling rates peak in the Austral winter/early spring (July–October). This is in direct contrast with the calling rates in the Antarctic suggesting that Antarctic blue whales are potentially in their northward migration in the southeastern Indian Ocean during the austral winter where they are suspected to head north to warmer waters to breed.

There were no acoustic detections recorded in December for Antarctic blue whales (there were no data from January) and February–April numbers of calls detected were low and this corresponds well with the literature (Branch et al. 2007; Samaran et al. 2013). This is particularly noteworthy as the austral summer is when Antarctic blue whales are presumed

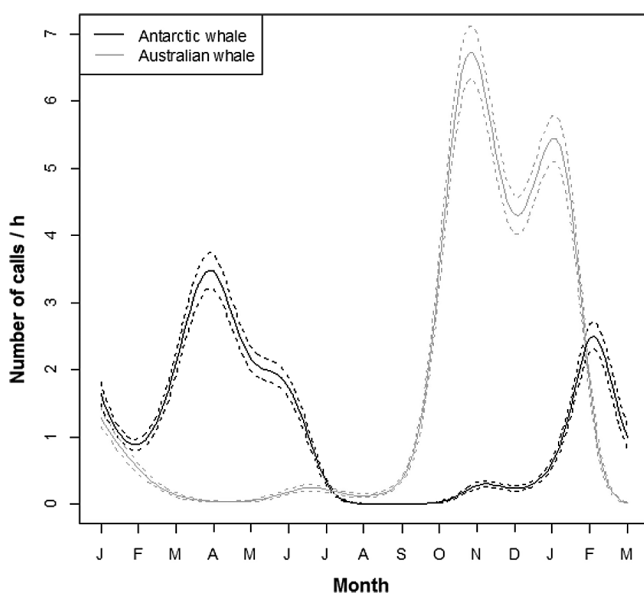


Fig. 8.—Generalized additive models comparing Antarctic and Australian blue whales over the season (May 2009–July 2010). Note that these represent model-based means, with standard errors of these means shown as the dashed lines.

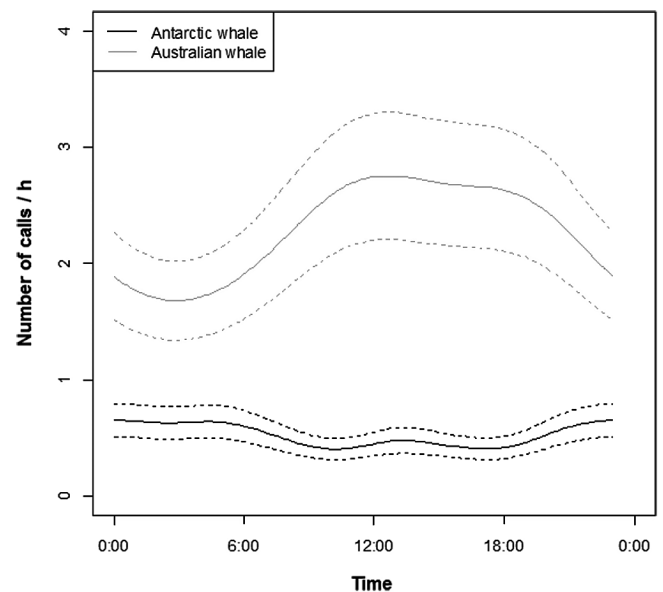


Fig. 9.—Generalized additive models comparing Antarctic and Australian blue whales throughout the day (May 2009–July 2010). Note that these represent model-based means, with standard errors of these means shown as dashed lines.

to have returned to the Antarctic waters to forage (Attard et al. 2012).

The absence of calls in December, outside the suspected breeding season, indicates that either the animals have left the region for this short period, or alternatively they are present but are not calling, or that calls were not detected due to the distance of whales from the hydrophone. The calls detected for Antarctic blue whales suggest that whales are moving in and out of the area or alternating calling and noncalling periods. Calls were absent from the area around the buoy for days to weeks at a time, depending on the time of year. Outside the breeding season, when few Antarctic blue whale calls were recorded, animals were not heard for weeks at a time. This may or may not have reflected the absence of whales as calls are likely to be heard only out to a limited distance from the buoy. The presumed detection range based on the literature is less than 200 km (Širović et al. 2007). If an animal had moved from this region, it would no longer be detectable to the buoy. It is proposed, due to the low numbers of calls detected in February–April, that a small proportion of the Antarctic blue whale population do not migrate south to the Antarctic feeding grounds; instead some whales remain in the region and potentially feed on krill (*Nyctiphanes australis*) in Australian waters or there is asynchrony in the arrival of whales. Alternate foraging and migratory behavior is discussed for the north Atlantic fin and blue whales (see Silva et al. 2013 for a discussion).

The number of Australian blue whale calls peaked from March to June coinciding with the feeding season for whales and the time when krill are usually at their highest densities in the region at the Bonney Upwelling (Butler et al. 2002). This area is a highly productive upwelling of nutrient-rich cool water and is one of only 12 known feeding grounds for the Australian blue whale (Butler et al. 2002). The whales consume the krill both as they swarm at the sea surface and also by deep dives (Gill et al. 2011). It would appear that for the majority of the Australian blue whales in the region, this area is important for feeding, as the number of calls decreased at the commencement of the breeding season, in June, suggesting that most Australian blue whales migrate out of the area to breed.

The migratory paths of Australian blue whales which are found in Indonesia to western and southern Australia (McDonald et al. 2006) are not clearly understood. These whales are reported to migrate along the Western Australian coast, to the upwelling areas along the south Australian coast and south possibly as far as, or potentially further than, the Antarctic convergence zone (Gedamke et al. 2007) and were recorded in this study. There is also evidence to suggest a migratory link between Australia and Indonesia around the northwest coast of Australia (McDonald et al. 2006; Double et al. 2014). Australian blue whales have been reported from Perth Canyon, Western Australia, during November to May (McCauley et al. 2004). In June, there is a drop in the numbers of animals recorded, and presumably whales are moving northward out of the area, possibly to breed, and then are suspected to move southward in November (McCauley et al. 2004; Double et al. 2014). This trend is also seen in our study, where Australian blue whales show a decrease in calling in

July for presumably the same reason as they move northward to breed.

Diel calling patterns.—Australian blue whales were more vociferously active from midday to early evening and we suppose that this calling pattern is related to the availability of *N. australis*, the dominant krill species, where whales may sing when prey are less available or call at opposite times to feeding. Previous studies on krill off eastern Australia have suggested that *N. australis* descends to the bottom during the day and at night migrates to the surface (Blackburn 1980). However, current evidence on vertical migration of *N. australis* in the region of the Bonney Upwelling is unclear. Studies of *N. australis* off New Zealand support vertical migration of krill (Bartle 1976); however, there is also evidence of this species not migrating (Young et al. 1993). At this stage, we can only speculate that daytime calling behavior in Australian blue whales may be related to the behavior and presence of krill. Other studies on blue whales show calling to be negatively correlated with blue whale feeding (Oleson et al. 2007; Širović and Hildebrand 2011), where calling is produced at the opposite times to feeding.

In Antarctic blue whales, this pattern of calling may be related to its breeding behavior as we assume it may be in the region for breeding purposes and generally not in the region to feed. However, at this stage, the diel calling behavior of Antarctic blue whales is unclear and further investigations are warranted to understand its diel calling pattern.

Interannual variations.—General observations from the available multiyear data indicate that calling activity varied considerably between May 2009 and May 2010 although year was not considered as an effect due to the lack of data (i.e., only 3 months where data were available from both years). This interannual difference in calls recorded may indicate that there were different numbers of Australian blue whales present between years, perhaps due to fluctuations in the seasonal occurrence of krill (Young et al. 1993) or other oceanic changes. Another explanation is that the same numbers of Australian blue whales were present but were calling less in 2010 for unknown reasons. This interannual change in the numbers of calls reported for blue whales has been described in other areas (Samaran et al. 2013) and these significant variations in calling behavior should be explored further to understand the driving factors affecting the changes in the interannual calling behavior of blue whales.

Using passive acoustic monitoring, we describe 2 subspecies of blue whales in this region, and each subspecies exhibits different seasonal and diel patterns. These patterns may reflect differing ecological strategies and/or habitat uses by each subspecies. This study demonstrates the importance of using passive acoustics in allowing us to understand and monitor differences in the behavior and ecology of cryptic sympatric and endangered marine mammals.

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