



Temporal separation of blue whale call types on a southern California feeding ground

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Northeast Pacific blue whales, *Balaenoptera musculus*, migrate annually between productive summer feeding grounds off North America and tropical winter breeding grounds off Central America. These migratory movements have been confirmed through acoustic monitoring of the long-duration, low-frequency sounds produced by males (type B calls). However, other calls in the species' repertoire might prove a better proxy for the migratory and foraging behaviour of the population as a whole. To explore the seasonal and daily calling behaviour of this population, we evaluated the occurrence of three blue whale call types (song B, singular B and D) recorded between 2000 and 2004 at Cortez and Tanner Banks, a summer feeding area offshore of southern California. We recorded a significant temporal separation among the type B and D calls, both seasonally and daily, suggesting preferred use of certain call types during different behavioural states. A consistent seasonal pattern was evident, with D calling from April to November and song and singular B calling from June to January. In addition, D calls were heard primarily from dawn through to dusk, in contrast to the crepuscular pattern of song, suggesting that the production of D calls is related to feeding behaviour, which occurs primarily during the day on aggregated krill at depth. An increase in the length of the overall calling season was also observed from 2000 to 2004 and may be related to increased prey availability in the Southern California Bight relative to more southerly feeding areas.

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Seasonal and daily patterns of call production are common for several vocal taxa. Bird song production is often highest during the summer breeding season and is confined to this period for some species (Kroodsmá & Miller 1982). Some fish (Fine et al. 1977; Bass et al. 1999), anurans and insects (Gerhardt & Huber 2002) sing to attract mates during specific breeding periods. Furthermore, the dawn chorus in bird song (Staicer et al. 1996), the dusk and/or dawn peaks in anuran and insect sound production (Gerhardt & Huber 2002), and the night-time choruses of fish (Breder 1968) have been well documented. Most research on these temporal patterns has focused on the association of specific behaviours such as mate attraction, territory guarding or food locating with specific call output. While the vocal repertoires of

some mysticete species have been well studied, the relative occurrence of different call types has rarely been examined. Humpback whales, *Megaptera novaeangliae*, are known to sing primarily during the winter breeding season and during migration (Mattila et al. 1987; Clapham & Matilla 1990; Clark & Clapham 2004). However, the occurrence of song relative to other call types, such as feeding calls (e.g. Cerchio & Dahlheim 2001) and social sounds (Edds-Walton 1997), has not been compared seasonally or daily. Unlike some other baleen whale species, blue whales, *Balaenoptera musculus*, are known to sing year-round (Stafford et al. 2001). While other call types have been reported for this species (Thompson et al. 1996; McDonald et al. 2001), the seasonal occurrence of these calls has not been studied and may provide insight into the behavioural ecology and energetics of calling in this species.

Blue whales in the eastern North Pacific are known to produce at least four sound types. Type A and B calls

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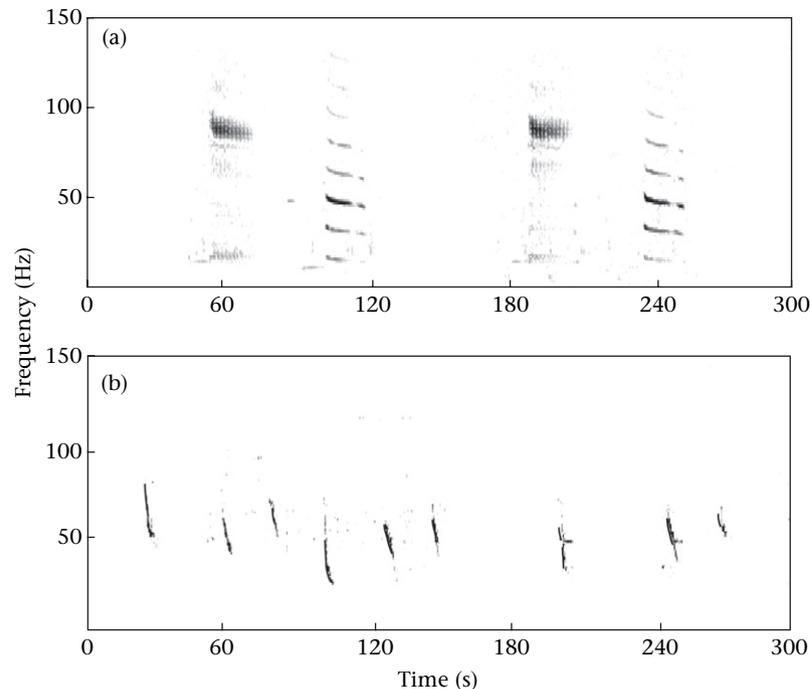


Figure 1. Northeast Pacific blue whale call types used in this study. (a) Blue whale pulsed A and tonal B calls organized into a song pattern. These calls may also occur infrequently (singular A-B calls), with frequency and call duration characteristics similar to those represented here. (b) Blue whale downswamped D calls show large variability in frequency content and sweep rate.

(Thompson et al. 1996) are long (~20 s), low-frequency (16 Hz), harmonically rich sounds, which can occur together in an alternating series of A and B calls (Rivers 1997; McDonald et al. 2001), termed song (McDonald et al. 2006) (Fig. 1a), or as individual, singular calls (Oleson et al. 2007a). Most acoustic descriptions of blue whale distribution and seasonality are based on A and B calls, although their distinction as song or singular calls is overlooked. Song A and B calls are produced by males (Oleson et al. 2007a) and may be involved in reproduction, although the year-round occurrence of this call (Stafford et al. 2001) may indicate a wider function for this call type. Singular A and B calls have been recorded from males in pairs and in groups engaged in a variety of behaviours including travelling and feeding (Oleson et al. 2007a). Although the sex bias in the call type may also suggest a reproductive purpose, its occurrence in a wide variety of contexts so far prevents assignment of specific function. A third call type, known as the D call, was originally described by Thompson et al. (1996) as a down-sweeping (90–25 Hz), short duration (1–4 s) call (Fig. 1b). Type D calls are heard from both sexes and occur among feeding blue whales and in short sequences from individual whales (Oleson et al. 2007a), potentially suggesting a role in attracting others to feeding grounds or maintaining group cohesion during feeding. Highly variable amplitude-modulated (AM) and frequency-modulated (FM) calls (Thode et al. 2000; Oleson et al. 2007a) also have been recorded, although their behavioural significance is unknown.

Eastern North Pacific blue whales migrate annually between productive summer feeding areas extending

from California to the Gulf of Alaska and tropical winter breeding areas near Mexico (Calambokidis et al. 1990; Reilly & Thayer 1990) and Costa Rica (Mate et al. 1999). This annual migration, identified through photo-identification and satellite tracking of individual blue whales, is supported by acoustic recordings of this population's characteristic low-frequency type A and B calls throughout the migratory range (Stafford et al. 2001; Burtenshaw et al. 2004). In feeding areas off the coast of California, the seasonal abundance of blue whales has been described from ship and aerial surveys, indicating that the density of blue whales is an order of magnitude higher in the summer and autumn (0.0049 animals/km²; Carretta et al. 2000; Calambokidis & Barlow 2004) than in the winter and spring (0.00045 animals/km²; Forney & Barlow 1998; Carretta et al. 2000). Concurrently, the greatest amount of calling occurs off southern and central coasts of California in the summer and autumn (Burtenshaw et al. 2004).

To date, acoustic monitoring for blue whales has been used primarily to understand large-scale patterns of population distribution. Using calls to evaluate whale behaviour, habitat and population size has been difficult because of a lack of understanding of calling behaviour. Most previous work on the distribution of calling blue whales has focused on the presence and geographical distribution of type A and B calls, without attention to the occurrence of other calls in the species' repertoire. It has not been previously examined whether the commonly reported type A and B calls are a robust indicator of the overall presence and distribution of this population, or if use of additional call types could provide

a more complete assessment of the population in some regions or seasons. The association of some calls with feeding and others with reproduction suggests that each call type has a different pattern of occurrence depending on the availability of prey, the local population density and the time of year.

While several studies have described the occurrence of type A and B calls over broad spatial and temporal scales (e.g. Watkins et al. 2000; Stafford et al. 2001; Burtenshaw et al. 2004), little attention has been paid to the seasonal variability of each of the blue whale call types. To evaluate the temporal variation in blue whale calling, we collected continuous acoustic data at Cortez and Tanner Banks in the Southern California Bight from August 2000 to February 2004. Our purpose was to determine how the timing of blue whale calls varies annually, seasonally and daily, and to evaluate how these relationships depend on animal behaviour and environmental conditions.

METHODS

Acoustic Data Collection

Continuous acoustic data were recorded at Cortez and Tanner Banks (Fig. 2) using autonomous seafloor-mounted hydrophone recorders from 20 August 2000 to 20 February 2004, except for the period during 5 February–15 April 2002. Cortez and Tanner Banks are approximately 180 km west of San Diego, California, in the southwestern portion of the Southern California Bight and rise to within 100 m of the sea surface. Several species of cetacean, including blue whales, feed near the banks.

Data were recorded at several sites around Cortez and Tanner Banks from 2000 through 2004; however, to reduce ambiguities due to local sound propagation differences between sites, this analysis includes only data from site 1, located on the northeast end of Tanner Bank, for all years except 2002, when site 2, located between the banks, was monitored. These sites were chosen because they represent the only sites with full seasonal coverage for each year. The detection range of blue whale calls at these two sites was not measured. However, owing to differences in the bathymetric landscape surrounding these sites, the detection ranges may be quite different. We expected site 2 to have a smaller detection range than site 1 because of constraints on sound propagation due to the local shallow bathymetry, potentially introducing variability into our results if certain call types were detected at a greater range than other call types. For this reason, seasonal differences in calling were tested only within sites.

The primary instruments used for this study were Acoustic Recording Packages (ARPs) (Wiggins 2003). ARPs are autonomous seafloor-mounted acoustic recorders. Their data-logging systems include a 16-bit A/D converter, 36 GB of storage capacity, a hydrophone tethered 10 m above the seafloor, a release system, ballast weights, and flotation. Data were collected with a sample rate of either 500 or 1000 samples/s, with a low-end roll-off of 5 Hz, resulting in an effective bandwidth between 5 and 250 Hz or 5 and 500 Hz, respectively. The lesser bandwidth completely samples the known blue whale calling repertoire. The maximum recording duration at a 500-Hz sampling rate was 400 days, although

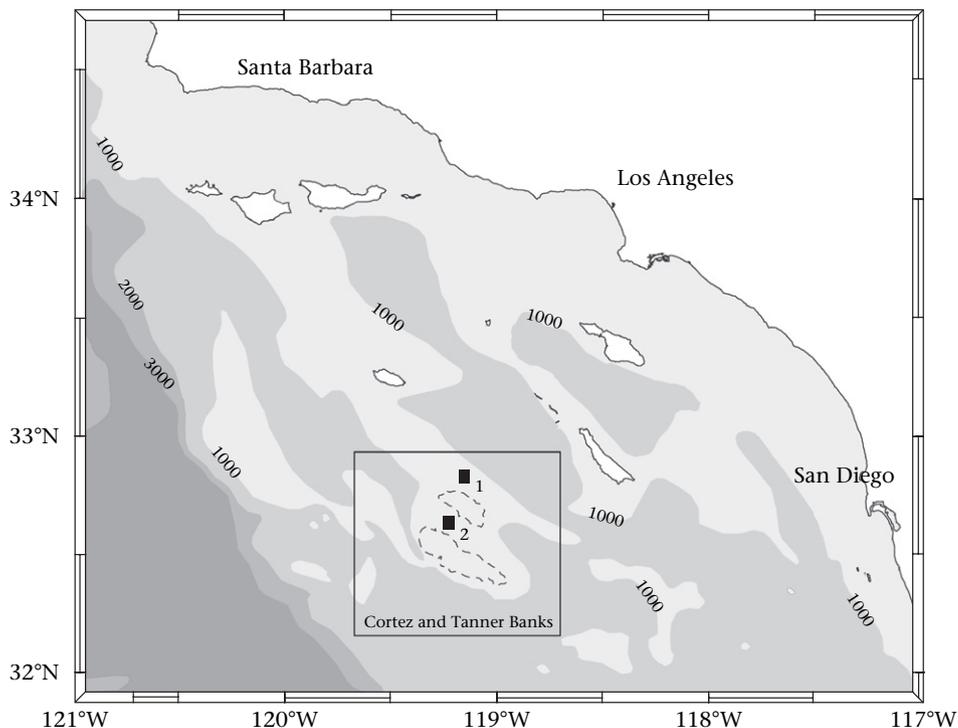


Figure 2. Southern California Bight bathymetry (in metres) showing Cortez and Tanner Banks study site. Acoustic data collected at site 1, located at the northeast corner of Tanner Bank (location: 32°41.3'N, 119°01.9'W; depth: 305 m), was analysed for all years except 2002. Acoustic data collected at site 2, located between the banks (location: 32°35.8'N, 119°08.8'W; depth: 215 m), was analysed for 2002.

recorders were generally serviced with new batteries and data disks every 2–6 months.

During two periods, from June to July 2002, and November 2003 to February 2004, Ocean Bottom Seismometers (OBSs) equipped with hydrophones were used while the ARPs were removed from the area. Although OBSs were designed for monitoring seismic sounds, they also record the low-frequency sounds of blue whales (McDonald et al. 1995). Bottom-mounted OBSs are similar to ARPs; the primary difference between these systems is the reduced maximum sampling rate (128 Hz) of the OBSs, resulting in an effective bandwidth of 1–60 Hz (Sauter et al. 1990). This bandwidth encompasses the third harmonic of the blue whale B call used for automatic detection (described below). Although the upper portion of the D-call frequency sweep is often above 60 Hz, the lower portion of the downsweep is within the frequency range of the OBS recording system.

Call Detection

B calls

Acoustic data were examined for the presence of blue whale B calls using the spectrogram correlation function within the software program Ishmael (Mellinger 2002). Ishmael's spectrogram correlation detects calls by cross-correlating a synthetic time–frequency kernel representing a whale call with the acoustic power spectral data (Mellinger & Clark 1997) and dictating cross-correlations above a user-specified threshold. Detected segments are saved to computer disk for later analysis. Spectrogram correlation was found to be the best detection method for the blue whale B call type relative to the other automatic detection functions provided in Ishmael, resulting in the fewest false detections (incorrect classification) and the fewest missed detections, compared to a manually scanned data set.

The B call detection kernel used in the spectrogram correlation consisted of a series of four connected frequency downswept segments for a total duration of 10 s. We chose the third harmonic of the blue whale B call for detection because its signal-to-noise ratio (SNR) is typically better than at the fundamental frequency and other harmonics. For the year 2000, the first three segments were each 1.5 s long and consisted of downsweeps with start frequencies of 52.5 Hz, 51 Hz and 49.2 Hz. The fourth segment continued from the end frequency of the third segment, sweeping from 48.8 to 48.4 Hz for 5.5 s. Annual shifts in the frequency content of the blue whale B call (Hildebrand et al. 2001) were accommodated by annually adjusting the kernel downward by 0.5 Hz at each segment endpoint. Spectrogram equalization was used to reduce the effect of time-varying ambient noise on call detection rate. Spectrogram equalization is a form of automatic gain control, which subtracts the time averaged spectral level in each frequency bin from the spectrogram, resulting in more consistent background noise levels through time. This type of signal conditioning is particularly useful for detecting nearly tonal calls, such as the blue whale B call, during periods of high shipping noise. The A call was not

chosen for detection because its pulsed character is not well suited for this type of detection scheme and it generally has a lower SNR relative to B calls.

Spectrogram correlation parameters, including the threshold and the duration that the detection function must exceed the threshold, were iteratively adjusted until the rate of false detections was less than 3%. The false detection rate was verified through manual examination of approximately 1000 detections per month. A trade-off exists between the number of false detections and the number of missed calls, such that a 3% false detection rate produces a missed call rate of approximately 20%. The missed call rate was computed by comparing the number of calls picked manually to the number of calls automatically detected. This was repeated for eight randomly selected days, with one day selected for each of the months during June–January, and 2 days for each year of data collection. Because the missed call rate exceeds the false detection rate, the number of B calls detected is an underestimate of the total number of calls present. However, the percentage of calls missed was consistent hourly and daily, such that there was no impact on diel or seasonal analyses of call rate based on this detection method. The high missed call rate is partly due to variation in signal characteristics among whales and to variable ambient noise character over the duration of the call.

Following automatic detection, blue whale B calls were sorted into song and singular call categories based on intercall intervals. For the purposes of this paper, song is defined as a sequence of stereotypical calls or phrases occurring in a repeated pattern, as described for blue whales by McDonald et al. (2006). Conversely, singular calls are those occurring irregularly, without a recognizable pattern. Song intervals were computed from calls recorded on eight randomly chosen days by manually picking all B calls occurring as part of a regular sequence and calculating the interval between successive calls. Two consistent intervals were identified for song B calls, with mean \pm SD call intervals of 48 ± 3 s for consecutive B calls (BBB) and 128 ± 6 s for B calls with an interspersed A call (BAB). These intervals were then used to automatically sort B call detections into song and singular categories based on the following process. The interval between each detected call and all successive calls within 200 s was computed. When two calls were found occurring within an interval defined for song, both calls were classified as song. This method allowed for the detection and classification of overlapping songs due to the presence of more than one singing whale. Blue whale calls occurring at intervals other than those defined above were classified as singular calls.

D calls

Blue whale D calls are highly variable in sweep rate and frequency content, making it difficult to design a time–frequency kernel that can reliably detect this call automatically while excluding similar down-sweeping sounds. Instead, we manually picked D calls from one randomly chosen day per week throughout the monitoring period using software written in MatLab (Mathworks, Natick,

MA, U.S.A.), allowing for quick examination of the data and providing capabilities for logging the time of each call. Downswep calls were chosen based on their similarity to published reports of this call type (Thompson et al. 1996; McDonald et al. 2001; Oleson et al. 2007a), with a duration of 1–4 s and a frequency sweep of at least 30 Hz within the range of 120–30 Hz.

To ensure that day-to-day variation in call rate did not invalidate our call-picking method, we compared average daily call rate, computed from all calls occurring with a week, to the call rate from a single day in that week. This process was repeated for eight separate weeks, with one week chosen from each month during April–November and 2 weeks chosen from each of the 4 years of data collection. The average call rate from each week was not significantly different from a single day in that week (paired *t* test: $t_7 = 0.357$, $P = 0.731$). Because the call rate from the single, randomly chosen day was a valid representation of the surrounding week, we estimated the total season duration for D calls by multiplying the number of randomly chosen days containing calls by seven.

Calling Patterns

The relative seasonal distribution of each call type was evaluated by testing for significant differences in the season duration (using variance as a test statistic) and season timing (using the midpoint as a test statistic). For this analysis, each call was indicated by the Julian day on which it occurred, and tests were performed within each year. Only B song and singular calls detected on the randomly chosen days used for D call picking were used in these analyses to avoid bias associated with sampling more B calling days. The equality of seasonal variances was tested using a modified Levene's test based on the distribution median (Brown & Forsythe 1974). The timing or midpoint of distributions was tested using the Kruskal–Wallis test for differences of location (Sokal & Rohlf 1981). All statistical analyses used a yearly start date of 1 March to account for continuation of the blue whale calling season into the next calendar year.

Annual and daily changes in call rate were evaluated using the mean-adjusted daily or hourly call rate. Annual variation in call rate was tested by comparing the mean-adjusted call rate for each day among years. Hourly variation in call rate was tested by comparing the mean-adjusted number of calls occurring in each hour for each day containing at least one call. Both annual and daily changes were tested using a nonparametric analysis of variance, the Kruskal–Wallis test (Sokal & Rohlf 1981). This test was chosen because of the heterogeneity of variances among sampled units.

RESULTS

Seasonal Variation

Song calls were the most common blue whale call type, with an average of 27 582 calls occurring per year. The average annual call detection rates for the other

blue whale call types were 12 872 for single B calls and 16 573 for D calls. There was no significant annual change in the daily call rate for any blue whale call type (Kruskal–Wallis test: D calls: $H_{39} = 1.76$, $P = 0.416$; B song: $H_{202} = 3.42$, $P = 0.181$; B singular: $H_{254} = 0.3$, $P = 0.862$), although there were slightly fewer D and song B calls in 2002 than in other years (Fig. 3). This difference may be attributed to the use of a different monitoring location in that year or may be due to changes in the number of calling whales near Cortez and Tanner Banks in 2002.

Seasonal separation in the occurrence of B and D calls was apparent (Fig. 4, Table 1), with D calls detected from April to November and B calls detected from June to January. The seasonal difference in timing between the call types was significant in all years (Table 2), although the magnitude of the seasonal separation between D calls and song and singular B calls fluctuated annually (Table 1). This annual fluctuation was most apparent in 2001 when D calls were nearly 40% more frequent than B calls in July, and in 2003, when D calls were detected several weeks earlier than in the previous two seasons. Although D calls always occurred earlier than either B call type, the relative midpoint timing of song versus singular B calls also fluctuated annually.

Significant differences in the variance of the seasonal distribution were also observed between all call types within each year (Table 2), except for the comparison between D and singular B calls in 2002, which was marginally nonsignificant. Differences in variance may indicate differences in season duration or in the shape of the seasonal distribution of calls. The significant difference in variance between D calls and song and singular B calls may be attributed to both season duration and seasonal distribution of calls (Table 1, Fig. 3), while differences between song and singular B calls were due to relatively high levels of singular B calling at the beginning and end of the calling seasons (Fig. 3). Season duration also increased annually for each call type (Table 1).

Daily Variation

The production of blue whale call types also varied within the day, with significant hourly changes in the occurrence of D calls and song B calls (Kruskal–Wallis: D calls: $H_{23} = 47.8$, $P = 0.002$; song B: $H_{23} = 169.2$, $P < 0.001$). Blue whale D and song B calls showed similar patterns of occurrence from dusk to dawn; however, during the day, D calls were the most common and B song calls were the least common call types detected (Fig. 5). Although the diel occurrence of singular B calls was marginally nonsignificant (Kruskal–Wallis test: $H_{23} = 64.94$, $P = 0.0527$), slight increases in calling were apparent near dawn and dusk (Fig. 5).

DISCUSSION

We observed significant seasonal and daily separation in the occurrence of blue whale B and D calls during the

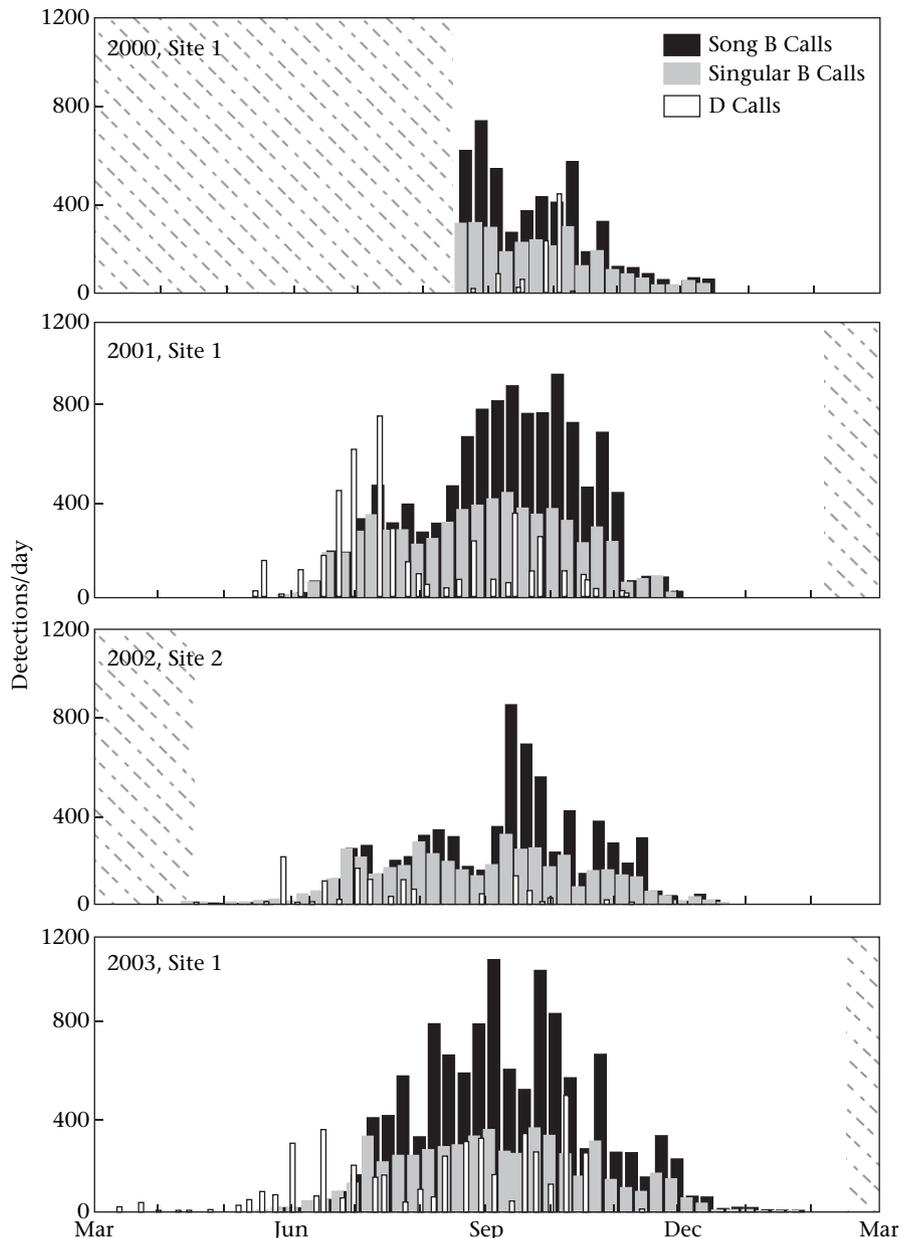


Figure 3. Blue whale call detections (song B, singular B, and D), shown as daily detections in 1-week bins from 20 August 2000 to 20 February 2004. Grey hatching indicates no data were available. Month labels indicate the first day of the month. Type D calls were picked on one randomly chosen day per week and are shown according to the day on which they were picked.

summer and autumn feeding season at Cortez and Tanner Banks in the Southern California Bight. Blue whale D calls were heard predominantly during dawn and day from April to November, while B song and singular calls were heard from June to January, with peaks in song at dusk and dawn. The detection of D calls in the spring and summer and B calls in the summer and autumn was consistent between years. Our results indicate that blue whales arrive on southern California feeding grounds earlier and depart later than has been previously recognized from visual surveys in this region.

The timing and character of calling is correlated with social, feeding and reproductive ecology in several mammal species (Busnell 1963; Morton 1977), including some

mysticetes (Edds-Walton 1997). The observed seasonal and daily separation between B and D calls and the increasing length of the blue whale calling season at this feeding ground is probably governed by the functional significance of each call type. The timing of blue whale migration into the Southern California Bight probably also depends on these behavioural and environmental factors, including feeding and breeding success during the winter and spring and oceanographic productivity and prey availability in the Southern California Bight and other parts of the feeding range. Finally, the temporal separation of call types may have implications for the use of calls in the study of blue whale habitat and population abundance.

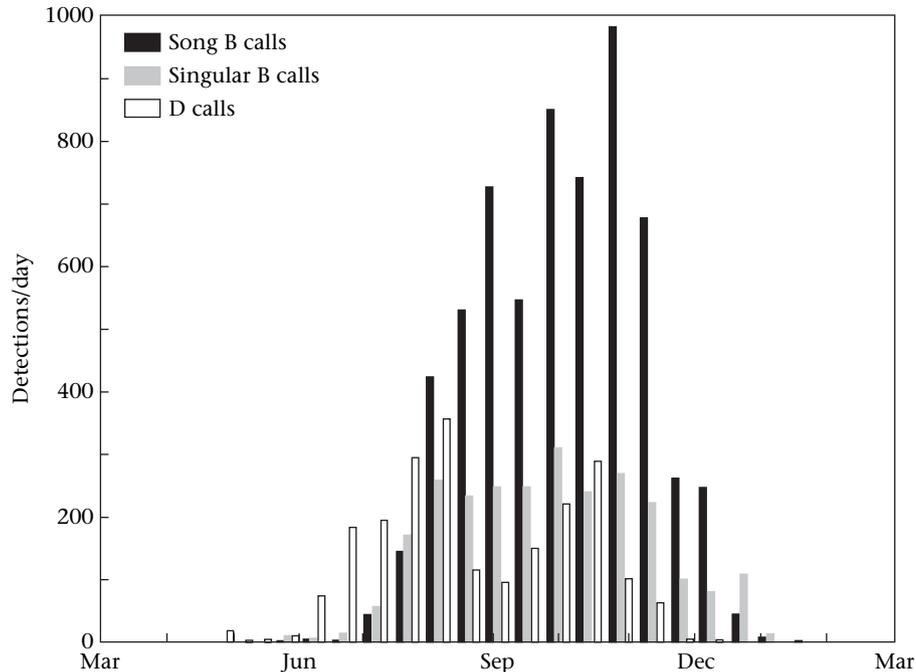


Figure 4. Four-year average seasonality of blue whale calling rates (detections per day) at Cortez and Tanner Banks shown in 2-week bins.

Calling Behaviour

Although the specific functions of blue whale vocalizations remain unknown, general patterns of behaviour in association with specific calls have been observed that help to explain the seasonal and daily separation in blue whale call occurrence that we report here. Behavioural observations of individual calling blue whales using suction-cup tags and visual-acoustic tracking indicate an apparent separation in foraging versus singing activities (Oleson et al. 2007a). In that study, all calls were observed at shallow depths (< 50 m), with D calls being produced between deep foraging dives by pairs and by groups of animals of both sexes. Similarly, singular B calls also were occasionally heard between foraging dives. In contrast, song was not heard from feeding animals, but rather from solitary travelling males. It is likely that the character and context of song make feeding and singing incompatible. Deep foraging dives are theoretically prohibitive to the production of high-intensity, low-frequency, long-duration B calls owing due to insufficient available air

volume at depth (Aroyan et al. 2000). This physical constraint would force the separation of foraging at depth from the production of long sequences of A and B calls that make up blue whale song. It is unknown whether these same physical constraints govern the production of D calls; however, their shorter duration should theoretically require a smaller air volume. In this case, the production of D calls at shallow depth may be related to their function rather than to physical requirement.

Production of song exclusively by male blue whales suggests a reproductive function (Bradbury & Vehrencamp 1998) similar to song production by male humpback (Darling 1983) and fin, *Balaenoptera physalus* (Croll et al. 2002) whales. However, production of song on summer feeding grounds raises the question of whether there may be other, nonreproductive functions of song. Clark & Ellison (2004) suggested that blue whale song components that reflect off of bathymetric features may provide navigational clues to migrating whales and they provided anecdotal evidence of this from a whale travelling past

Table 1. Season length and Julian day midpoint for each blue whale call type detected by year

Call type	2001–2002		2002–2003		2003–2004	
	Season length (days)	Midpoint (Julian day)	Season length (days)	Midpoint (Julian day)	Season length (days)	Midpoint (Julian day)
All calls	231	221	266	253	308	236
Song B	202	249	242	283	256	263
Singular B	200	274	238	260	255	262
D	30 (210)	202	29 (203)	200	36 (252)	208

Year is defined as 1 March–28 February to allow for extension of the blue whale calling season into the next calendar year. Data from 2000 were excluded because they did not represent an entire blue whale season. Season length for D calls is shown as the number of randomly chosen days containing calls and the extrapolated number of days likely to include calls (in parentheses).

Table 2. Outcome of statistical tests of equality of seasonal timing and duration among blue whale call types for each full season of acoustic listening effort

Year	Call type comparison	N	Test of seasonal timing*		Test of season duration†	
			H	P	W	P
2001–2002	D vs B song	2967, 6406	158.7	<0.0001	134.3	<0.0001
	D vs B singular	2967, 2612	63.9	<0.0001	10.5	0.0012
	B song vs B singular	6406, 2612	160.5	<0.0001	50.2	<0.0001
2002–2003	D vs B song	1029, 1621	1837.9	<0.0001	199.1	<0.0001
	D vs B singular	1029, 554	1063	<0.0001	113.5	<0.0001
	B song vs B singular	1621, 554	19.7	<0.0001	222.3	<0.0001
2003–2004	D vs B song	3021, 1425	2874	<0.0001	261.6	<0.0001
	D vs B singular	3021, 2359	269.6	<0.0001	3.8	0.0502
	B song vs B singular	1425, 2359	2612.7	<0.0001	120.1	<0.0001

Year is defined as 1 March–28 February to allow for extension of the blue whale calling season into the next calendar year. *N* = number of calls of each type used in the analysis.

**H*₀: call types have the same seasonal midpoint (Kruskal–Wallis test for location).

†*H*₀: seasonal distributions of call types have the same variance (modified Levene's test for equality of variances).

Bermuda. Similarly, it may be possible for blue whales to locate prey by listening for the reflections of their repeated calls off of large krill swarms. However, Berchok (2004) estimated the target strength of an euphausiid patch incident with an infrasonic blue whale call to be far below that required for detection, indicating that it is unlikely that prey detection is possible with blue whale song. Although we cannot absolutely discount the use of song in echo-sensing, production of song by a single sex and with highly consistent call characteristics argue against this hypothesis. Rather, we suggest that the increased occurrence of song into the autumn on the feeding grounds does indicate that song is primarily reproductive in function. Some parallels may be drawn from humpback whales, whose song may be heard during the spring and autumn on feeding grounds and during migration (Clapham & Matilla 1990; Norris et al. 1999; Clark & Clapham 2004), as well as in winter on low-latitude breeding grounds (Payne & McVay 1971). Humpback whales show high rates of male–female pairing during the feeding season, such that singing on the feeding grounds may serve to promote pair bonding for the coming breeding season or to advertise to oestrous females that did not breed the previous winter (Clapham 1996). High rates of male–female pairing during the feeding season also have been observed in blue whales (Sears 2002), suggesting that singing during the feeding season may serve a similar role in blue whales. However, in contrast to blue whales, singing by humpbacks is rare during the height of the feeding season. Therefore, year-round singing by blue whales may indicate a more complex reproductive system for this species, or a nonbreeding function for this call type. It is possible that male blue whales may use song in an attempt to mate during the feeding season; however, blue whale calving in the summer or autumn has not been reported, suggesting that out-of-season mating is rare. Alternatively, we may speculate that the blue whale mating system is not based solely on short-term mate attraction within the breeding season, but may also include long-term assessment and association prior to mating.

Although song production by blue whales on the feeding grounds is common, its absence in the spring when blue whales are present and producing D calls is intriguing. Blue whales are thought to feed on the breeding grounds (Reilly & Thayer 1990; Palacios 1999), and therefore should not have been entirely resource limited upon arrival on the southern California feeding grounds. This would suggest that, if adequate food resources had been obtained by male blue whales on breeding grounds, then no preference should be given to foraging versus singing activities. However, if feeding and singing are incompatible, recently reproductive males may not have obtained as much food during the breeding season because they spent their time singing to attract a mate or ward off potential competitors. The delay in song production on the southern California feeding grounds may be indicative of the time necessary for male blue whales to obtain adequate food resources following relatively sparse feeding on the southern breeding grounds. A gradual increase in singing during the summer may then signal that some males have consumed enough prey and are sufficiently sated to allocate more time to singing. If this hypothesis is correct, it would predict that years with scarce food resources on feeding grounds would be characterized by an overall reduction in song because males must dedicate more time to locating prey patches. A reduction in calling in southern California and an increase in calling at northern feeding areas, where prey are more abundant, was observed during the 1997–1998 El Niño (Burtenshaw et al. 2004) and thus supports this hypothesis.

In contrast to the reproductive, male-only bias associated with singing, intermittent, swept D calls may be more akin to the swept-up calls of right whales, *Eubalaena australis*, and downswept-call counter calls of fin whales. Frequency sweeps can provide clues for binaural localization and may be more detectable above the background noise than are narrowband constant tones (Wiley & Richards 1978), supporting use of swept calls for locating conspecifics. Right whale up-calls, produced by single

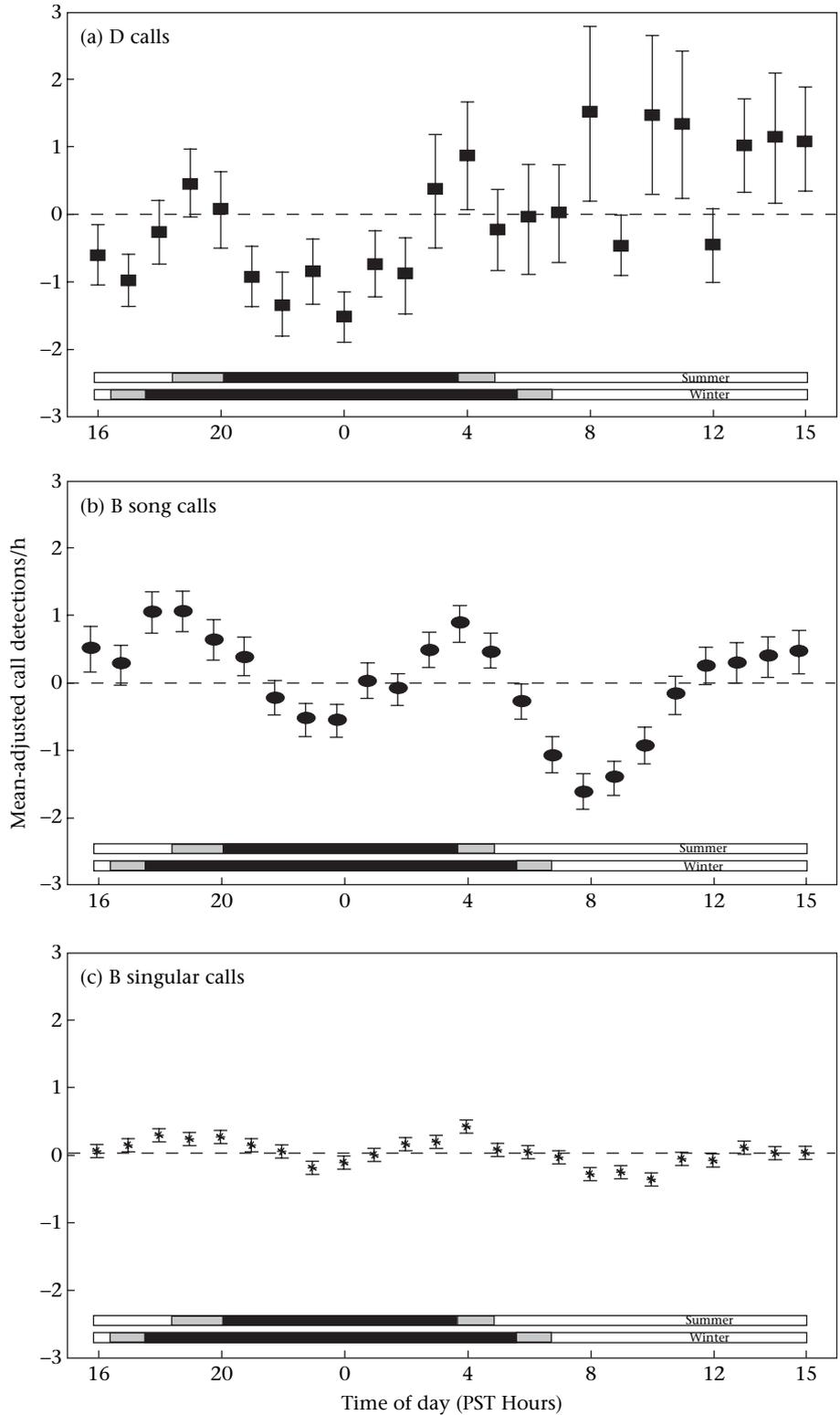


Figure 5. Mean-adjusted hourly detections of (a) D calls, (b) B song and (c) B singular calls over the entire study period. The grey-scale bars represent the summer and winter solstice periods of day (white), dusk (grey) and night (black). PST: Pacific Standard Time.

whales and joining pairs, cease when the pair is united, suggesting that the purpose of the call is to locate a conspecific (Clark 1982). Similarly, fin whales producing intermittent downswept calls have been approached by other fin whales from distances of up to 10 km (Watkins

1981), and coordinated calling has been observed within widely dispersed groups of travelling fin whales (McDonald et al. 1995), suggesting that calls are produced to maintain group cohesion. Although specific call–response interactions have not been documented for blue whale D

calls, the production of this call among dispersed groups of whales and between pairs (McDonald et al. 2001; Oleson et al. 2007a) suggests a similar role.

Alternatively, the association between feeding and D calling by blue whales may suggest that this call type facilitates feeding. The feeding cries of humpback whales are produced immediately before vertical lunging through prey by the humpback group (D'Vincent et al. 1985; Cerchio & Dahlheim 2001) and are coincident with bubble-net production (Thompson et al. 1986). The temporal link between engulfment of prey and call production suggests that these calls are directly related to obtaining food, either to herd prey or to coordinate the feeding group activity (Cerchio & Dahlheim 2001). In contrast to the feeding screams of humpbacks, D calls are heard during shallow excursions between deep foraging dives and they do not immediately precede feeding events (Oleson et al. 2007a). In addition, a Crittercam video of feeding blue whales showed no cooperative feeding among pairs or groups (J. Calambokidis, personal communication), suggesting that calls, or other cues, are not used to cooperatively herd prey or coordinate underwater activity during feeding. However, D calls may be used during competitive or agonistic interactions, to attract other whales to the feeding area, or to maintain contact with other individuals between feeding dives. Large variability in the spectral characteristics of D calls (Thompson et al. 1996; Thode et al. 2000; McDonald et al. 2001; Oleson et al. 2007a) may indicate individual- or context-specific variants of this call type, suggesting that D calls may serve more than one purpose during the feeding season.

Although it is unlikely that D calls directly facilitate prey capture, the association of these calls with feeding behaviour does predict that seasonal and daily fluctuations in the occurrence of this call may be related to the availability of prey. Although the local density of blue whales in the spring has not been studied, it is likely that blue whales gradually migrate into a feeding area, with local densities increasing from late spring into summer. As the whales migrate into the Southern California Bight to feed, they may be attracted to specific regions of locally high prey density by the D calls of feeding conspecifics. This attraction may be intended by the calling whale if the presence of other whales facilitates prey capture or promotes social bonds, or it may be an unintended consequence of communication among local whales. Competition for food resources would argue against intentional attraction of other blue whales to food patches; however, we cannot discount intentional attraction because so little is known of blue whale social behaviour. Without further study of the behavioural response to D calling we cannot determine whether blue whales are actively attracting others to food resources through production of D calls, if D calls are intended for communication with nearby conspecifics, or if both local and long-range communication are taking place.

Foraging behaviour may also explain the observed separation in the production of D and B calls throughout the day. The patterns of D and B calling shown here indicate that blue whales change their calling behaviour over a 24-h period, producing D calls during the day and B

calls at night. Our results also indicate that the hourly fluctuations in B calling may be attributed primarily to song calling. Diel patterns of blue whale B calling have been described previously in the Southern California Bight (Thompson 1965; Wiggins et al. 2005) and in the eastern tropical Pacific (Stafford et al. 2005). Both Wiggins et al. (2005) and Stafford et al. (2005) suggested that elevated levels of B calling from dusk through to dawn were related to the diel migration behaviour of the blue whale's euphausiid prey. Stafford et al. (2005) further argued that night-time calling may be intended to advertise the location of food resources, as has been suggested for fin whales (Croll et al. 2002). Although B call production at night near daytime food resources might indicate advertisement of prey, the travelling behaviour observed from singing whales away from prey patches (Oleson et al. 2007a) does not support this conclusion. Instead, we suggest that D calls may be a more robust indicator of the availability of food resources than are B calls because of their production by feeding whales.

Migratory Behaviour

Previous studies using long-term acoustic monitoring of the blue whale B call have supported the seasonal migration of blue whales between the eastern tropical Pacific and feeding grounds extending from southern California to the Gulf of Alaska (Stafford et al. 2001; Stafford 2003; Burtenshaw et al. 2004). In some regions, including the eastern tropical Pacific, blue whales can be heard year-round, with a winter and spring increase in call detection (Stafford et al. 1999). As the whales migrate along the west coasts of Central and North America, fewer calls are detected in one region and more calls are detected in another. The seasonal occurrence of D calls has not been studied previously, and our results suggest that monitoring of both B and D call types is required to accurately assess the seasonal distribution of blue whales in foraging regions.

The results of our acoustic monitoring effort in the Southern California Bight indicate that blue whales are present on the southern California feeding grounds for much more of the year than is suggested by visual surveys in this region. Visual surveys for cetaceans are generally not conducted often enough to detect weekly changes in abundance, although they typically report few to no blue whales in winter and spring (November–April; Forney & Barlow 1998; Carretta et al. 2000). We are aware of only two studies that used visual methods to evaluate the year-round occurrence of blue whales in the Southern California Bight. During monthly aerial surveys near San Clemente and San Nicolas Islands, the first sightings of blue whales occurred in May and the last occurred in November (J. Carretta, unpublished data). Similarly, bi-monthly ship surveys throughout the Southern California Bight documented blue whales from June to November (Oleson et al. 2007b). Our acoustic results extend the known seasonal presence of blue whales in the Southern California Bight by 1–2 months at the beginning and end of the feeding season, indicating the presence of

blue whales from April to January each year. Blue whales are absent from this feeding ground for as few as 10 weeks per year.

The observed increase in the number of days in which blue whale calls were recorded from 2001 to 2003 (Table 1) suggests that the specific timing of migration can fluctuate and may be linked to prey availability throughout the species' range. In 1999, the climatology of the California Current changed, with stronger-than-normal local upwelling bringing relatively cool, pigment-rich waters, yielding higher zooplankton biomass than had been observed since 1991 (Venrick et al. 2003). Blue whales are also known to feed off of the Baja California Peninsula in the spring (Rice 1974); however, zooplankton concentrations off Baja have been anomalously low since 2001 (Venrick et al. 2003). A lack of food resources off of Baja may have forced the early migration of blue whales north into the Southern California Bight where prey was abundant. Blue whale movement and distribution in the California Current is well correlated with the location of euphausiid aggregations (Schoenherr 1991; Fiedler et al. 1998), suggesting that long-term monitoring of the relative abundance of blue whales off Baja Peninsula and along the California coast may reveal changes in migratory behaviour that are tied to prey availability. Changes in blue whale distribution have been observed during anomalous warm conditions, including a general northward shift in the abundance of singing blue whales during the 1997–1998 El Niño (Burtenshaw et al. 2004), in addition to higher-than-normal densities of blue whales in local productive areas during the same period (Benson et al. 2002).

We have suggested that the seasonal separation of D and B calling may be related to energy requirements, such that male blue whales may delay singing until adequate food has been obtained. Alternatively, the early season absence of B calls at Cortez and Tanner Banks may be related to differences in the migratory timing or geographical distribution of whales of different sexes or age classes. Temporal segregation of whales by sex, age and reproductive status has been shown for several migratory baleen whale species. During the northward and southward migration, grey whale, *Eschrichtius robustus*, females migrate earlier than males, and mature whales migrate before juveniles (Rice & Wolman 1971). Humpback whales in the southern hemisphere are segregated in their migration by sex, age and reproductive condition; pregnant and resting females are the first to arrive and the last to leave productive Antarctic waters, followed by immature whales, mature males and lactating females (Dawbin 1997). The limited availability of food resources in breeding areas of grey and humpback whales probably affects different age, sex and reproductive classes of these whales at different times, resulting in a temporally segregated migration. Antarctic whaling data suggest an early arrival of pregnant blue and fin whales on the Southern Ocean feeding grounds (Mackintosh 1965), in addition to a delayed arrival of juvenile whales (Lockyer 1978). However, the location of and thus prey availability at blue whale feeding grounds in Antarctica is unknown, and therefore, it is difficult to evaluate the cause of the segregated migration of blue whales into Antarctic waters.

In contrast to humpback and grey whales, eastern North Pacific blue whales are not thought to fast during the winter breeding season (Reilly & Thayer 1990; Palacios 1999), suggesting that individuals with high nutritional requirements, such as lactating females, would have a reduced need to migrate to high-latitude waters ahead of the rest of the population. However, the seasonal separation of D versus B calls could represent the delayed arrival and departure of reproductive males on southern California feeding grounds. This interpretation is complicated by the production of D calls by both sexes (Oleson et al. 2007b), suggesting that the lack of song does not necessarily infer a lack of male presence. Additional study on the migratory timing and reproductive condition of individual blue whales and on the geographical distribution of song versus D calls, including the association of these call types with age, sex and reproductive condition, is necessary before this hypothesis can be rigorously tested.

Using Calls to Monitor Abundance and Habitat

The type A and B calls have been traditionally used to monitor blue whale seasonal movements in the eastern North Pacific. Our results indicate that blue whales are present in the spring, based on the occurrence of D calls, when they would have been considered absent based on B call detection alone. Conversely, monitoring D calls alone would indicate that blue whales leave the Southern California Bight in November, 2 months before the final detections of B calls in the region. This seasonal difference indicates that both call types must be monitored to completely describe the presence of calling blue whales in this region. Alternatively, this finding also suggests that monitoring for a specific call type may provide a means to determine the distribution and movements of certain segments of the population. In particular, examination of the relative occurrence of blue whale call types on breeding and other feeding grounds may help us to evaluate the extent of feeding during the winter breeding season and the movement of reproductive males throughout the migratory range.

The utility of call detection for abundance estimation has been debated among whale researchers for several years (i.e. Mellinger & Barlow 2003). Much of this debate has focused on how call occurrence may be evaluated within a robust statistical framework when individual call rates, variation in call rate, and the environmental and behavioural context of calling are unknown. Because of its inherently consistent call rate, blue whale song has been considered for use in estimates of abundance. However, recent observations of singular A and B calls with similar spectral characteristics to song could complicate the use of song calls for abundance estimation. This would be particularly true if the ratio of song to singular calls changed throughout the day or throughout the season. Separation of B calls into song and single categories as part of this study has shown that relatively fewer song calls occur in the beginning and end of the season and

that the seasonal timing of song versus singular calls may vary annually. Because whales producing single B calls make fewer calls per unit time than singing whales, the high proportion of single calls at the edges of the calling season suggest more whales are calling during those periods than would be accounted for if all calls were assumed to be part of song. Future studies attempting to use A or B calls to assess whale abundance will require separation of calls into song and singular categories and must address the variation in call rate between these call types.

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