



NOTE

Visual and passive acoustic observations of blue whale trios from two distinct populations

Elena Schall^{1,2}  | Lucia Di Iorio³  | Catherine Berchok⁴ |
Diego Filún^{1,2} | Luis Bedriñana-Romano^{1,6} | Susannah J. Buchan^{7,8,9} |
Ilse Van Opzeeland^{2,10} | Richard Sears⁵ | Rodrigo Hucke-Gaete^{1,6}

¹NGO Centro Ballena Azul, Universidad Austral de Chile, Valdivia, Chile

²Physical Oceanography of the Polar Seas, Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, Germany

³Chorus Research Institute, Grenoble Institute of Engineering, Grenoble, France

⁴Marine Mammal Laboratory, Alaska Fisheries Science Center/NOAA, Seattle, Washington

⁵Mingan Island Cetacean Study, Saint-Lambert, Canada

⁶Instituto de Ciencias Marinas y Limnológicas, Universidad Austral de Chile, Valdivia, Chile

⁷Center for Oceanographic Research COPAS Sur-Austral, University of Concepción, Concepción, Chile

⁸Centro de Estudios Avanzados en Zonas Áridas (CEAZA), Coquimbo, Chile

⁹Woods Hole Oceanographic Institution, Biology Department, Woods Hole, Massachusetts

¹⁰Helmholtz Institute for Functional Marine Biodiversity, Carl von Ossietzky University Oldenburg, Oldenburg, Germany

Correspondence

Elena Schall, Alfred Wegener Institute for Polar and Marine Research, Klufmannstraße 3d, 27570 Bremerhaven, Germany.
Email: elena.schall@awi.de

Blue whale populations from both hemispheres are thought to undertake annual migrations between high latitude feeding grounds and low latitude breeding grounds (Mackintosh, 1966). For individuals of some populations these predetermined movements to and from wintering areas where calving occurs have been confirmed through photo-identification, satellite-tracking, and passive acoustic monitoring (Burtenshaw et al., 2004; Mate, Lagerquist, & Calambokidis, 1999; Sears & Perrin, 2002; Stafford, Nieukirk, & Fox, 1999a). However, for many blue whale populations no clear migratory behavior has been reported and locations of respective breeding grounds remain unclear (e.g., Hucke-Gaete, Osman, Moreno, Findlay, & Ljungblad, 2004; Samaran et al., 2013; Stafford, Chapp, Bohnenstiel, & Tolstoy, 2011; Thomisch et al., 2016). On feeding grounds in the Gulf of St. Lawrence and along the coast of California, blue whales have been observed to form female-male pairs during summer, which can remain stable up to over several weeks, with the number of pairs increasing towards the end of summer (Sears & Perrin, 2002; Calambokidis, unpublished data;¹ RS, unpublished data). These pairs are sometimes joined by a second male, forming a blue whale trio, which often is observed to engage in surface active behaviors lasting several minutes

Richard Sears and Rodrigo Hucke-Gaete contributed equally to this study.

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(Sears & Perrin, 2002; RS, unpublished data). The formation of blue whale trios is probably related to reproductive competition between male escorts and female choice (RS, unpublished data). Blue whale males produce population-specific songs likely functioning as reproductive advertisement (Edds-Walton, 1997; Oleson et al. 2007a; Stafford, Fox, & Clark, 1998). Several studies have reported song year-round in low-, mid-, and high-latitude waters, frequently with high song production rates during summer on the feeding grounds (e.g., Barlow et al., 2018; Buchan, Stafford, & Huckle-Gaete, 2015; Samaran, Adam, & Guinett, 2010; Širović et al., 2004; Stafford, Niekirk, & Fox, 1999b; Thomisch et al., 2016). Therefore, breeding activities in blue whales may be more opportunistic, i.e., not restricted to the breeding season or to a specific habitat.

Besides songs, blue whales also emit nonsong vocalizations that differ significantly from the repeated pattern of vocalizations present in songs and that show similarities among the different blue whale populations (Ljungblad, Stafford, Shimada, & Matsuoka, 1997; McDonald, Calambokidis, Teranishi, & Hildebrand, 2001; Mellinger & Clark, 2003; Rankin, Ljungblad, Clark, & Kato, 2005; Thompson, Findley, Vidal, & Cummings, 1996). One specific type of nonsong vocalization has been found in the repertoire of almost all blue whale populations. This vocalization is a variable downsweep, which in the literature has been referred to as: "D-call" (McDonald et al., 2001), "S-call" (Thompson et al., 1996), "contact call" (McDonald et al., 2001), "downsweep" (Berchok, Bradley, & Gabrielson, 2006; Rankin et al., 2005), "FM downsweep" (Ljungblad et al., 1997), and "arch sound" (Mellinger & Clark, 2003). This type of call (hereinafter referred to as D-Call) is common to both sexes (Oleson et al., 2007a), can often be observed as call-counter-call events within a group of two or more blue whales (McDonald et al., 2001; Oleson et al., 2007a), and is produced in various social contexts. Oleson et al. (2007a), for example, found a correlation between the D-Calls and group feeding behavior, relating these sounds to shallow dives occurring during breaks from feeding. Shabangu et al. (2019) found a correlation of D-Call presence and higher chlorophyll-a concentrations. D-Calls are also known to be produced during encounters of different group compositions, including mother-calf interactions (Lewis et al., 2018; Oleson et al., 2007a; CB & LDI, unpublished data). Lewis et al. (2018) reported the production of D-Calls from tagged female and male blue whales, with D-Calls being produced mainly during surface behaviors. The communicative function of D-Calls and the interpretation of their presence in remote sensing data, however, remain widely unresolved, due to the different behavioral contexts in which D-Calls have been recorded.

Here, we report three encounters with blue whale trios from two different populations in a putative reproductive context on their respective feeding grounds. During these three events, data from concurrent passive acoustic and visual observations were collected. Joint visual-acoustic data are essential for understanding the communicative function and behavioral context of vocalizations (e.g., Lewis et al., 2018; Oleson et al., 2007a). By comparing blue whale acoustic and surface behavior during three independent blue whale encounters, we explored the similarities in display behavior, focusing on vocalization characteristics and potential functionality. Such behavioral information on blue whale reproductive behavior is extremely rare (De Vos, Brownell, Tershy, & Croll, 2016), but crucial to better understand the reproductive strategies of this species and thereby potentially boost the effectiveness of management decisions for conservation purposes.

Acoustic recordings of blue whales were made on 15 April 2015 between Chiloe Island and the Chilean continent (41°87.46'S, 73°23.11'W; encounter ID: SP), in the St. Lawrence Estuary on 19 September 2001 (48°39.16'N, 68°57.06'W; encounter ID: NA1) and on 4 September 2004 (48°30.45'N, 69°06.30'W; encounter ID: NA2) (Figure 1, Table 1). The encounters were further documented by annotating GPS position of the observer, GPS time, and visual observations of surface behavior and by taking photos and videos for photo identification and visual documentation of surface behaviors. Visual and acoustic observations were synchronized to GPS time. Further, in the case of the two North Atlantic encounters, the sex of photo-identified individuals was determined by analyzing skin biopsies using standard genetic techniques (Palsbøll, Vader, Bakke, & El-Gewely, 1992).

The recordings from the different recording systems were adjusted in sampling frequency (SF) by decimating the SP (original SF: 96 kHz) and NA1 (original SF: 44.1 kHz) recordings to match the SF of NA2 of 1,000 Hz. Limitations in signal-to-noise ratios of some of the recorded D-Calls did not allow reliable measurements of durations using the

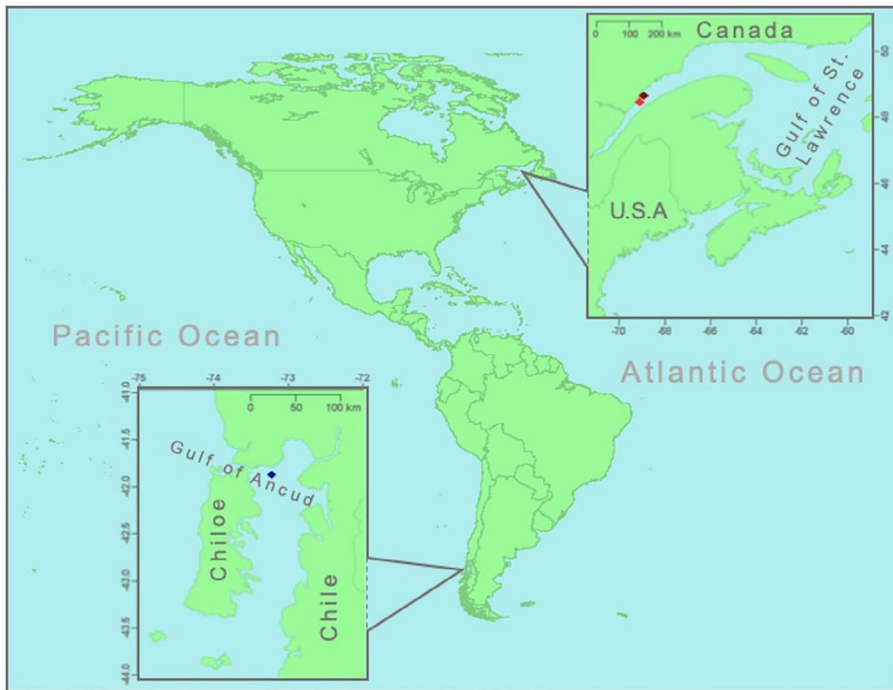


FIGURE 1 Recording locations at the two study sites: in the Gulf of Ancud marked with a blue diamond (SP) and in the Gulf of St. Lawrence marked with a light and a dark red diamond (NA2 and NA1, respectively).

TABLE 1 Acoustic recordings systems used during the three different encounters. HS for hydrophone sensitivity, LFR for linear frequency range, AG for amplification gain, BF for bandpass filter.

Encounter	Hydrophone	Amplification	Digitalization
SP	Reson TC-4034 omni-directional hydrophone (HS: -218 dB re 1 Vrms/ μ Pa, LFR: 1 Hz– 250 kHz)	Reson VP2000 amplifier (AG: 20 dB, BF: 10 – $1,000$ Hz)	National Instrument USB-6343 data acquisition card (SF: 96 kHz)
NA1	Geospace Corporation MP-18 (200') hydrophone (HS: -133 dB re 1 V/ μ Pa, LFR: 8 – $1,000$ Hz)	Custom-made submerged and boat-side amplifiers (AG: 57 dB, BF: 4.25 – 840 Hz)	Sony PCM recorder (SF: 44.1 kHz)
NA2	Autonomous bottom-moored recording unit (MARU; HS: -164 dB re 1 V/ μ Pa, LFR: 2 Hz– 30 kHz, SF: 1 kHz; Cornell University, Bioacoustics Research Program, Ithaca, NY)		

waveform. Therefore, two different spectrogram settings were used to measure temporal and spectral characteristics separately. First, all recorded vocalizations were visualized in Raven Pro 1.5 (Bioacoustics Research Program, 2014), implementing the following spectrogram settings: Hann window, 80% overlap, and a window and DFT size of 1024 samples, resulting in a frequency resolution of 0.977 Hz. The spectral characteristics of D-Calls were captured by measuring maximum frequency, minimum frequency, bandwidth, and peak frequency using the built-in Raven Pro functions (Charif, Strickman, Waack, 2010). For the temporal measurements (D-Call durations), all recordings were further decimated to 250 Hz, and visualized in a Hann window, with a window and DFT size of 64 samples, and 0% overlap, resulting in a time resolution of 256 ms.

Encounter SP started on 15 April 2015 at approximately 10:50 a.m. local time, when two blue whales (larger individual BM4, smaller adult individual BM5) were joined by a third individual (BM6). Immediately, at least two of the three whales started to exhibit vigorous surface displays, including active chasing, body collisions, water splashing,

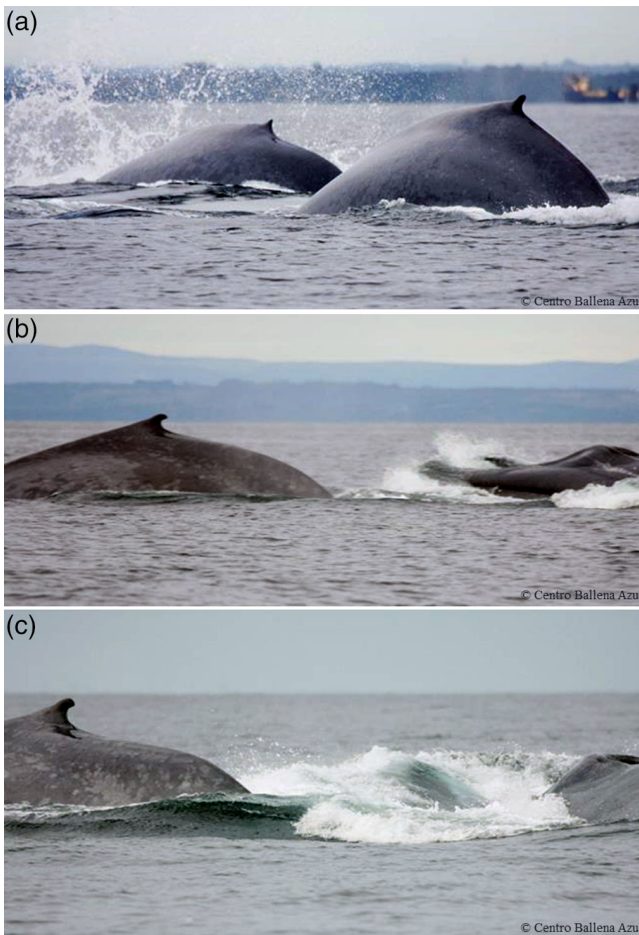


FIGURE 2 Sample photos of the behavior observed on 15 April 2015 in the Gulf of Ancud. (a) Left individual BM5, right individual BM6. (b, c) The larger individual BM4 is on the left and one of the other two individuals (BM5 or BM6) is following (right side of picture).

and partial breaching, which lasted approximately 10 min (Figure 2). Concurrent with the observation of these behaviors, a sequence of 13 D-Calls were recorded. After the trio split into the initial pair and the single individual, at approximately 11:00 a.m., one more very faint D-Call was recorded. In total 14 observed D-Calls occurred in a continuous period of 24 min (Figure S1). Two overlapping calls in the fourth minute of the recordings (Figure S1) indicated that at least two individual blue whales were vocalizing.

Encounter NA1 started on 19 September 2001 at approximately 10:30 a.m. local time, when a blue whale pair, identified as a leading female (B207) and a flanking male (B081) were joined by a third whale, which was male (B378). At the moment the trio formed, the three whales began courasing (fast swimming), and intense blows, sharp turns and rolls, chin breaching, and bubbling were observed. The female continued in the leading position with both males flanking her for approximately 9 min. The intruding male then split from the previously formed pair and both groups dispersed. Within 3 s after trio formation and 8 s before the trio split, 31 D-Calls were recorded. They were interspersed by other harsh vocalizations sounding like “blurps,” “grunts,” and “bubbling” (Figure 3). No song-related vocalizations were detected directly before, during, or directly after the interaction. On at least one occasion, two D-Calls overlapped in time of occurrence (i.e., during minute seven; Figure 3), indicating that at least two of the three animals were vocalizing.

Encounter NA2 started on 4 September 2004 at approximately 9:30 a.m. local time, when again a blue whale pair consisting of a leading female (B205) and a flanking male (B378) was observed to be followed by another male blue whale (B185). At the moment of trio formation, all three whales started courasing behavior with large portions of

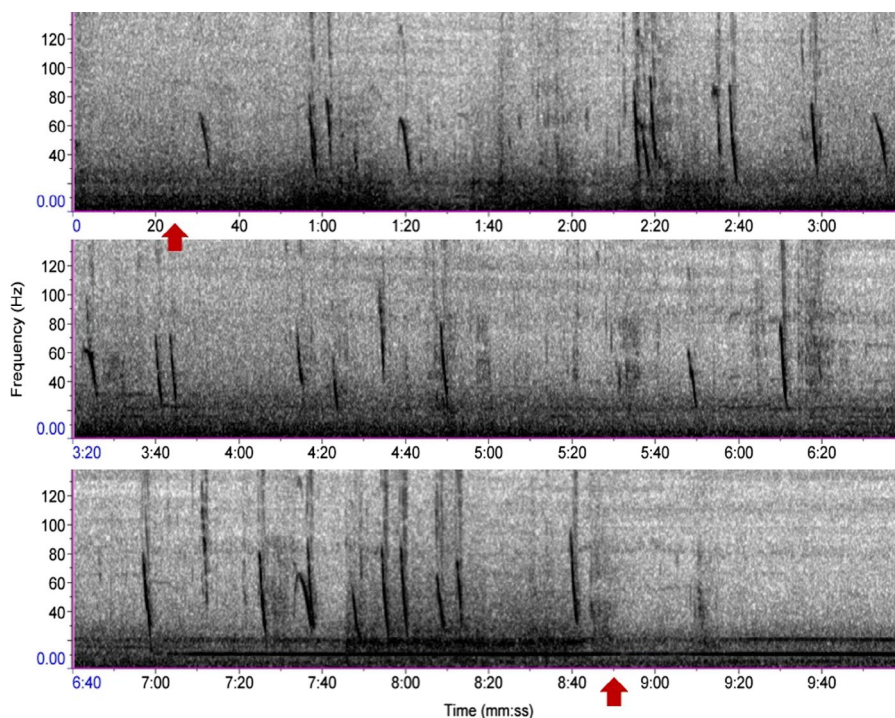


FIGURE 3 Spectrogram of blue whale calls recorded during the NA1 encounter on 19 September 2001 in the Gulf of St. Lawrence. Trio formation and separation are marked with red arrows.

the body exposed, intense blows, bubbling, and surfacing. The two males following the leading female interacted aggressively towards each other including slapping of different body parts (i.e., chin, fluke) and one male breached and hit the other male while falling. This behavior lasted approximately 11 min, during which time 12 D-Calls accompanied by broadband pulses and other harsh vocalizations were recorded (Figure S2). The intruding male then moved away and the tracks of the initial pair and the intruder diverted. Until approximately 10 min before trio formation a single blue whale was singing. No song was detected during the interaction, but singing recommenced approximately 8 min after the trio split. It is unknown whether the singer was one of the males from the trio. Song structure showed small changes after the interaction as compared to before. The song recorded before the interaction was composed of all four possible song units (“A,” “B,” “A-B,” and “9 Hz”; Mellinger & Clark, 2003). The song recorded after the interaction did not contain any A-B units.²

The D-Calls from encounter SP were low frequency downsweeps with a minimum duration of one second and a maximum duration of 5.6 s (Table 2A). The lower frequency limit was 28.3 Hz and the upper frequency limit was 95.3 Hz. Mean vocalization bandwidth was 48 ± 7.8 Hz. Peak frequencies ranged between 32.2 and 71.3 Hz with a mean of 50.6 ± 11.7 Hz. Coefficients of variation between 0.1 and 0.5 of all temporal and spectral characteristics showed the variability of D-Calls within a single encounter. This variability was most pronounced with duration, bandwidth, and peak frequency (Table 2A).

The D-Calls from the North Atlantic encounters were very similar to those from the southeastern Pacific (Table 2B). These vocalizations were also low frequency downsweeps, in this case with a wider frequency range of 19.3 (minimum frequency) to 113 Hz (maximum frequency) compared to the southeastern Pacific D-Calls. Compared to the southeastern Pacific, calls from the northwestern Atlantic, on average, also were shorter in duration and reached lower frequencies (mean values of 1.8 ± 0.7 s and 27.2 ± 6.9 Hz). The coefficients of variation demonstrated an elevated variability in duration, bandwidth, and peak frequency, and lower frequency limit for the D-Calls of the

TABLE 2 Summary statistics for the acoustic features of D-Calls. Descriptive statistics are given for the duration, minimum frequency (F_{\min}), maximum frequency (F_{\max}), bandwidth (BW), and peak frequency (F_{peak}). Summary of D-Calls from A: encounter SP; B: combined encounters NA1 and NA2.

	Statistic value	Duration (s)	Fmin (Hz)	Fmax (Hz)	BW (Hz)	Fpeak (Hz)
A SP (n = 13)	Minimum	1.0	28.3	70.3	36.1	32.2
	Maximum	5.6	44.3	95.3	64.6	71.3
	Mean	2.4	35.5	83.5	48.0	50.6
	SD	1.3	5.2	7.8	7.3	11.7
	CV	0.5	0.1	0.1	0.2	0.2
B NA (n = 43)	Minimum	0.6	19.3	57.0	32.2	22.5
	Maximum	4.1	50.7	113.0	69.6	87.9
	Mean	1.8	27.2	79.3	52.0	46.7
	SD	0.7	6.9	12.9	11.0	12.3
	CV	0.4	0.3	0.2	0.2	0.3

two encounters from the North Atlantic (both independent and combined; see Table 2B for combined representation and Table S1 for separate representation).

Independently, in three different years and over a time span of more than a decade, similar visual observations of surface-active blue whale trios that exhibited a specific acoustic behavior was described for two geographically distant blue whale populations. The observed blue whale behavior, in all three cases, likely represented a competitive behavior linked to reproduction, as described by Sears and Perrin (2002). Escorting behavior (a male accompanying a female) is known to occur in many animal taxa, e.g., humpback whales (*Megaptera novaeangliae*) and African elephants (*Loxodonta africana*), as well as in various bird and primate species; Alberts, Altmann, & Wilson, 1996; Baker & Herman, 1984; Birkhead, 1979; Birkhead, Johnson, & Nettleship 1985; Clapham, Palsbøll, Mattila, & Vasquez, 1992; Poole, 1989; Tyack & Whitehead, 1982). Escorting allows a male to defend a female, limiting access of other males to the female and thereby increasing the likelihood of siring potential offspring. Rival males may challenge the escorting male to take his place, which is likely to have been the case in the three blue whale trio encounters described in this study. In the Gulf of St. Lawrence, it is often observed that when a blue whale pair is joined by a third whale—usually a male—the trio starts coursing, racing high out of the water involving vigorous surface displays causing explosive splashes and bow waves (Sears & Perrin, 2002; see also De Vos et al., 2016 for a record from the Indian Ocean). This behavior can either end with the intruding male leaving the pair or the primary escort being replaced by the intruding male. The latter displacement of the primary escort has been very rarely observed and most often the initial female–male pairing is maintained (RS, unpublished data). In all three observed cases reported here, the intruding individual (male, in the two cases where sex was known) did not displace the primary escort. Although actual mating was not observed during the three encounters described here, the observations are in line with early whaling data (Lockyer, 1984; Mackintosh & Wheeler, 1929), which state that conceptions are not seasonally or regionally restricted.

One type of vocalization, the D-Call, was consistently recorded during all three escort events reported here. The use of D-Calls in blue whales has been described for several populations and behavioral contexts (e.g., Berchok et al., 2006; Ljungblad et al., 1997; Mellinger & Clark, 2003; Rankin et al., 2005; Thompson et al., 1996). Many studies reporting this vocalization have interpreted its function as social rather than reproductive (McDonald et al., 2001; Oleson et al., 2007a; Oleson, Wiggins, & Hildebrand, 2007b). This study is the first description of D-Calls produced in a reproductive context. Within this reproductive context, D-Calls could have different functions. The production of D-Calls during reproductive competition could be restricted to males, which would suggest that D-Calls in this

context might function as an agonistic male mating display, as it has been documented for different vocalizations in songbirds as well as right whales (Kunc, Amrhein, & Naguib, 2006; Parks, Hamilton, Kraus, & Tyack, 2005). For two of the three encounters, we obtained evidence that at least two individuals were vocalizing, as calls were occasionally overlapping in time. Overlapping calls can function as a sign of aggressive competition, as it has been shown for song overlapping in different bird species (Hyman, 2003; Kunc et al., 2006). However, the proportion of overlapping calls was relatively low (14.3% and 6.5% for the southeastern Pacific and northwestern Atlantic, respectively). Additionally, since female blue whales also produce D-Calls, they could be using these calls to actively signal their receptivity or to participate in agonistic displays. Females of other marine mammal species (e.g., right whales and pinnipeds; Clark, 1983, Parks & Tyack, 2005; Rogers, Cato, & Bryden, 1996), have been known to use calls in association with reproductive or agonistic behaviors.

The observed temporal and spectral properties of the D-Calls from the three described encounters were within the range of D-Call characteristics documented for these and other populations of blue whales recorded in varying behavioral contexts (McDonald et al., 2001; Oleson et al., 2007a; Thompson et al., 1996). This is indicative of a common functionality for D-Calls in different (interpopulational) behavioral contexts, rather than being characteristic for a specific behavior or population. A similar hypothesis has, for example, also been proposed for a specific humpback whale vocalization (the “whup” of the North Pacific population), which can be found both as a part of songs as well as during social interactions (Wild & Gabriele, 2014). A review from Clay, Smith, and Blumstein (2012) notes that often functionally specific vocalizations, as for example food or alarm calls in birds and mammals, are used in various behavioral contexts, in which they mostly can be interpreted to serve social recruitment.

It is possible that D-Calls, in the context of escorting behavior, may be used to maintain pair cohesion, i.e., within the initial female-male pair during surface active behavior. In two of the three presented cases (NA1 and NA2), D-Call production started immediately when the second male intruded, and stopped instantly when the intruder left. In the third case (SP) 93% of D-Calls were recorded while the two escorting individuals were trying to keep up with the leading whale, the remaining 7% were produced after the trio split. This indicates that D-Calls could be produced in two cases: during a higher risk of separation compared to pair-only situations, as in the case of the initial female-male pair trying to maintain contact in the presence of the intruder, or when the chance of pair-formation for the intruder is higher compared to in a lone individual situation, as in the case of the intruding male trying to establish contact with the female. This is in line with the “contacting behavior” described for right whales, *Eubalaena* spp., (Clark, 1982) where individuals (male and females, including calves) producing upcalls are often subsequently joined by another up-calling whale, whereupon calling stops as soon as the two individuals pair up. Blue whales likely produce D-Calls in situations when two or more individuals try to establish or maintain contact independent from the specific behavioral context, as for example events of reproductive competition.

It seems likely that D-Call call rates play a role in encoding information for specific behavioral contexts, as has been described for various other mammal and bird species (see Clay et al., 2012 for a review). Oleson et al. (2007a) for example reported 4 ± 3.7 D-Calls per hour during feeding activities, whereas call rates between 1 and 3.5 calls per minute (extrapolated, 60–210 per hour) were observed during the three encounters reported here. This pattern of nonsong vocal behavior might be specific to reproductive competition events in blue whales and deserves further investigation.

The existence of comprehensive information on timing and locality of breeding activities in blue whales is a crucial prerequisite for effective conservation measures. Whereas traditional visual observation methods often are restricted to specific seasons, autonomous monitoring techniques provide a versatile tool to monitor baleen whales year-round (e.g., Stafford, Mellinger, Moore, & Fox, 2007). The occurrence of D-Calls in series, occurring at a comparatively high call rate, provides potentially important baseline information for future autonomous PAM to investigate blue whale behavior, habitat use and density. Should further investigation show that high D-Call call rates are

typical for blue whale courtship behavior, then these could function as acoustic markers for remote sensing to contribute to the identification of areas where reproductive activities occur.

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ORCID

Elena Schall  <https://orcid.org/0000-0002-7740-5466>

Lucia Di Iorio  <https://orcid.org/0000-0002-3354-830X>

ENDNOTES

¹ John Calambokidis, 2181/2 West 4th Avenue, Olympia, WA 98501, June 2019.

² The "A-B" unit is a joined vocalization, comprised of an "A" and "B" unit with no interunit separation.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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