



First record of humpback whale songs in Southern Chile: Analysis of seasonal and diel variation

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ABSTRACT

Male humpback whales (*Megaptera novaeangliae*) produce complex, patterned songs that are traditionally recorded on their breeding grounds. In this work, we report results from the first continuous acoustic monitoring of a humpback whale feeding ground off southern Chile, Corcovado Gulf. Using an autonomous continuously recording system anchored to the seafloor and an automatic signal detector, we used the units within a song to analyze the temporal distribution and diel patterns of humpback whales. Acoustic recordings were made at the end of the austral summer and autumn of 2012. Songs occurred over the entire 130 d monitoring period, from 1 February to 15 June 2012. The percentage of units detected increased throughout the monitored period with the highest detections in the last recorded month (June), despite recording for fewer days that month. Furthermore, songs were detected during all light regimes studied, but most frequently during darkness. This study provides further evidence that, far from being rare or sporadic, humpback whale songs occur commonly at a feeding ground in high latitudes over different light conditions and in all months, with a peak in autumn.

Key words: humpback whales, *Megaptera novaeangliae*, feeding grounds, songs, units, diel patterns, light regimes, southern Chile.

Communication is an integral part of social behavior in many taxa, such as insects, frogs, fish, birds, and cetaceans (Wiley and Richards 1982, Bailey 1991, Richardson *et al.* 1995, Zelick *et al.* 1999). Marine mammals have unique capabilities to both generate and detect sounds since they depend on sound for foraging, reproduction, communication, detection of predators, and even navigation (Richardson *et al.* 1995). Given that light diminishes in the first few meters of the water column (Wartzok and Ketten 1999) and that the propagation of sound in water allows sound waves to travel long distances (Weilgart 2007, Moore *et al.* 2012), the main way in which marine mammals relate to their environment is *via* auditory signaling. Marine mammal species produce a large variety of sounds, from whales that generate low frequency

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signals, *i.e.*, below 20 Hz, to dolphins that generate high frequency signals, *i.e.*, above 100 kHz (Richardson *et al.* 1995).

In recent years, the use of passive acoustic monitoring (PAM) has been extended for acoustic detection of the presence of cetaceans (Clark and Ellison 1989, Frankel *et al.* 1995, Charif *et al.* 2001, Oswald *et al.* 2003, Clark and Clapham 2004, Moore *et al.* 2006, Mellinger *et al.* 2007, Stimpert *et al.* 2011). PAM devices are capable of functioning over long periods of time, at day or night, in any weather condition (although their reliability and range decrease when the weather and sea state deteriorate), and in any geographical area; thus, these tools have allowed for extensive monitoring, far beyond that of visual surveys (Richardson *et al.* 1995, Au and Hastings 2008).

The song of the humpback whale (*Megaptera novaeangliae*) has been well-documented through its duration, complexity, stereotypical sound, and repetitive nature that can last for hours, initially by Payne and McVay (1971) and subsequently by many additional studies (*i.e.*, Winn and Winn 1978; Guinee *et al.* 1983; Mercado *et al.* 2003, 2005; Au *et al.* 2006; Green *et al.* 2011; Cholewiak *et al.* 2013). Multiple sounds or "units" occur in a stereotyped sequence called a phrase, phrases are repeated to make a "theme," and a series of themes, usually produced in a particular order, define a song (Payne and Payne 1985). The acoustic units within a song are highly variable in frequency, ranging between 100 and 4,000 Hz (Tyack and Clark 2000), although other studies have found units with a fundamental frequency below 30 Hz (Payne and Payne 1985) or a frequency oscillation over a bandwidth of approximately 16–65 Hz (Cerchio and Dahlheim 2001) and harmonics have been shown to extend beyond 24 kHz (Au *et al.* 2006). Songs are only sung by male humpback whales (Winn and Winn 1978) and directly or indirectly related to mating (Winn and Winn 1978, Tyack 1981, Darling and Bérubé 2001, Smith *et al.* 2008, Darling *et al.* 2012, Herman *et al.* 2013). Humpback whale songs occurring in the same year and in the same geographic area tend to contain similar elements that are repeated in a consistent order (Winn and Winn 1978, Payne *et al.* 1983, Payne and Payne 1985). Humpback whales also produce many nonsong vocalizations in both summer and winter areas, which include social and feeding calls (Silber 1986, Dunlop *et al.* 2008), but few data exist regarding their variation or behavioral significance (Herman 2016). Despite this knowledge, the behavior associated with humpback whale song is still not well understood (Clapham 2000, Herman 2016).

Seasonal and daily variation in the occurrence of vocalizations exists for a wide range of species; examples of this include the dawn call of many birds (Brown and Handford 2003) and the evening call of frogs and insects (Gerhardt and Huber 2002). There is also nocturnal vertical migration of zooplankton and fish species (Brinton 1967). Largely due to the difficulty of following cetaceans for long periods of time, the circadian rhythms of cetaceans in the wild have not been as well-documented as those of terrestrial animals. Despite this, several factors that influence circadian activity of marine species have been documented, including sleep patterns, the need for respiration, lunar tidal fluctuations, and feeding requirements (Palmer 1976). There are studies about diurnal and seasonal patterns in whale singing activity, *e.g.*, in humpback whales (Helweg and Herman 1994, Au *et al.* 2000, Cerchio *et al.* 2001) or blue whales (*Balaenoptera musculus*) and fin whales (*Balaenoptera physalus*) (Širović *et al.* 2004).

Eastern South Pacific humpback whales, also termed stock G by the International Whaling Commission, migrate along the South American coast during austral

autumn–winter toward breeding grounds off Ecuador, Colombia, Panama, and Costa Rica (Kellogg 1929, Mackintosh 1965, Flórez-González 1991, Rasmussen *et al.* 2007). Feeding grounds for this population during austral summer–autumn are: Antarctic Peninsula’s west coast (Kellogg 1929); western end of the Magellan Strait (Gibbons *et al.* 2003, Acevedo 2005); and the Corcovado Gulf (Hucke-Gaete *et al.* 2013). There is information concerning the connectivity between these feedings areas and the migration from breeding regions to these feeding grounds (Acevedo *et al.* 2006, 2013). There are no data available from the Corcovado Gulf about the variability in the temporal presence off the humpback whales or from behavior studies, as for example the singing activity. Such information is essential for determining the abundance of this particular stock, understanding the migrations routes or the behavior associated in a feeding area and to monitor the conservation status of this species. In this study, we conducted the first long-term continuous recording of humpback whale songs in the Corcovado Gulf. We focus on automatically detected acoustic units within a song with the objective to determine the temporal distribution and diel patterns of humpback whales in this feeding area. The present study evaluates the frequency of occurrence of humpback whale songs in this feeding ground with the aim of better understanding the presence and behavior of the eastern South Pacific population of humpback whales.

MATERIALS AND METHODS

Acoustic Data Collection

In this study a marine autonomous recording unit (MARU) was moored to the seafloor (200 m) near the island of Guafo North ($43^{\circ}31.889'S$, $074^{\circ}26.488'W$) in the Corcovado Gulf. The MARU was left to record ambient sounds from 30 January until the 17 June 2012 (Fig. 1).

MARU is an archival bottom-mounted acoustic recording unit designed by the Cornell University’s Laboratory of Ornithology Bioacoustics Research Program and consists of an external hydrophone attached to a glass sphere containing batteries, computer electronics, and internal memory storage (Calpuca *et al.* 2000, Clark *et al.* 2002, Clark and Clapham 2004). The hydrophone employed was the model HTI-94-SSQ, with a frequency response of -151.2 dB re $1 \mu\text{Pa}$ from 2 to 300 kHz, a sensitivity of -198 dB re: $1 \text{ V}/\mu\text{Pa}$, and a gain of 23.5 dB. We used a sampling rate of 2 kHz, resulting in a functional band width range of 0–1,000 Hz. humpback whale acoustic units within a song often include frequencies inside this range, with dominant frequencies below 500 Hz (Levenson 1969, 1972; Norris 1995). The MARU was programmed to record continuously for 24 h. The recorded data were stored on a hard drive and only accessible upon instrument recovery.

Automatic Detection/Acoustic Analyses

After the data were recovered, the sound files were analyzed using standard audio processing software (especially Audacity and functions in Matlab) and Listening to the Deep–Ocean Environment (LIDO) software. LIDO was developed by the Laboratory of Applied Bio-Acoustics at the Polytechnic University of Catalonia in Spain. LIDO has several independent algorithms that allow for noise assessment and for the detection and localization of acoustic sources. From the acoustic data flow,

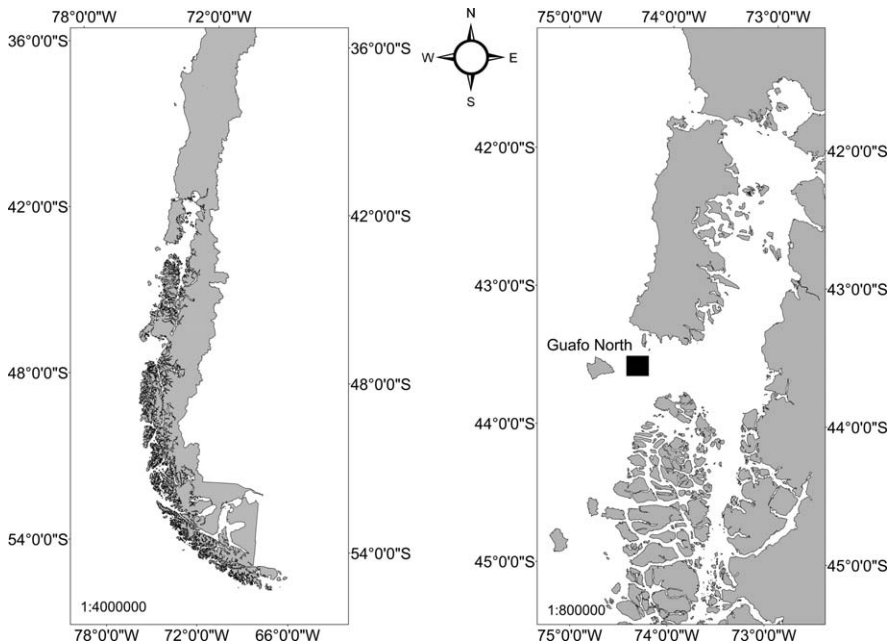


Figure 1. Study areas showing in left panel a map of Chile and in the right panel a zoom of the region and position of the Marine Autonomous Recording Unit (MARU) near Guafo North Island.

LIDO characterizes and locates detected sound events and produces spectrograms for viewing the data (André *et al.* 2011).

In total, the recordings of 130 d were analyzed after the elimination of 2 d both at the beginning and at the end of the recording; these days were removed to avoid noise contamination from the installation and the recovery of the device. We identified the presence of complete songs of humpback whales through the stored spectrograms. A detection algorithm was configured to trigger on acoustic units that exhibited characteristics unique to humpback whale song (*i.e.*, frequency-modulated signals or repetition in a rhythmic pattern) in a fundamental frequency range of 200–900 Hz. In this study, we will refer to these signals as units following the suggestions made by Cholewiak *et al.* (2013). The original 15 min sound files were broken into segments of 32 s. The length of a segment is decided such that it is long enough to include sufficient signals of a target species to allow its detection, while being short enough to have a stationary background noise pattern; these patterns are removed in denoising functions. In addition, it is preferred to use a power of two as a segment length to optimize the processing speed (especially Fourier transforms). The detection process for tonal sound under LIDO is described in detail in Zaugg *et al.* (2012). Signals can be detected in multiple, specific time, and frequency scales, allowing it to focus on the tonal vocalizations of a particular species if there are not many other conflicting sources in the recordings, as was the case here, avoiding the need for an additional classifier. The output of the detector (processing a segment) is a value between 0 and 100, based on the detected signal with the highest intensity: a single strong signal present in the segment can give a higher detector output

than multiple weak signals. The number of signals or acoustics units within a song in each segment was not quantified. The presence analysis was always performed in terms of segments, *i.e.*, the number of segments in a day that were labeled positively and with at least one humpback whale song unit. Once the detector was set up, its efficacy was evaluated using a receiver operating characteristic curve (ROC). The ROC was used to determine the threshold or the cutoff point where detector sensitivity was maximized. Furthermore, the ROC was used to determine the discriminatory ability of the detector, *i.e.*, the ability to differentiate between units of humpback whale song and false signals (Cerdeira and Cifuentes 2012). In this study, reliability and certainty were optimized to favor true positive detections (real humpback whale units within a song) and accepting a higher number of false negative detections. With these criteria, the number of true detections was likely reduced, but false detections were also minimized.

Seasonality and Diel Patterns

In order to determine the seasonal patterns of the humpback whale, first we determined the total number of segments obtained for each month. Then, we quantified the number of segments that were labeled positively, containing at least one humpback whale song unit. Following this, for each month we determined the percentage of segments with at least one unit present out of the total number of segments recorded. Finally, a chi-squared test was used to determine if the presence of segments with at least one acoustic unit differed by month (Quinn and Keough 2002).

To study the possible existence of a diel patterns in the humpback whale songs, the recordings for each day were divided into three light regimes according to previously published studies (*sensu* Mussoline *et al.* 2012), for this, the altitude of the sun was used to calculate the number of hours of daylight, darkness, dusk, and dawn that each day possessed. The number of hours in the three light regimes was calculated based on the altitude of the sun using data from SEA-MAT (<https://seamat.github.io/sea-mat/>). The day was divided into (1) light: the altitude of the sun was greater than 0° ; (2) dark: the altitude of the sun was less than -12° ; (3) twilight, including dawn and dusk: the altitude of the sun was between -12° and 0° . From this, the hours composing each regime were calculated for each month, taking into account the local time and the summer/winter time change in May. Because the different light regimes did not cover the same number of hours, the number of segments with units were averaged for each hour of every month and for each period of the day; multiple segments with units detected in the same hour were treated as replicates. In order to study the differences between the percentages of segments with at least one unit of a song in each regime for each month, chi-squared tests were performed on the frequencies of segments (Quinn and Keough 2002).

RESULTS

Song Detections

The detected signals corresponded to units typically found in humpback whale song, varying greatly in frequency between 200 and 900 Hz (Fig. 2); in some cases, the units were repeated for hours.

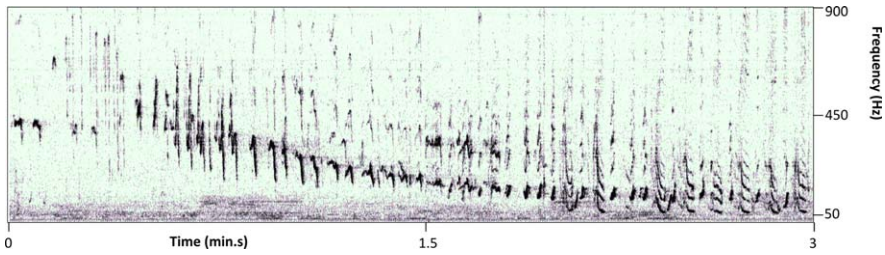


Figure 2. Spectrograms and time series of humpback whale units within in a song recorded in the southern Chile, Corcovado Gulf.

Table 1. Results of the receiver operating characteristic curve.

True positives	True negatives	False positives	False negatives	Total positives	Total negatives
525	1,949	175	251	776	2,124

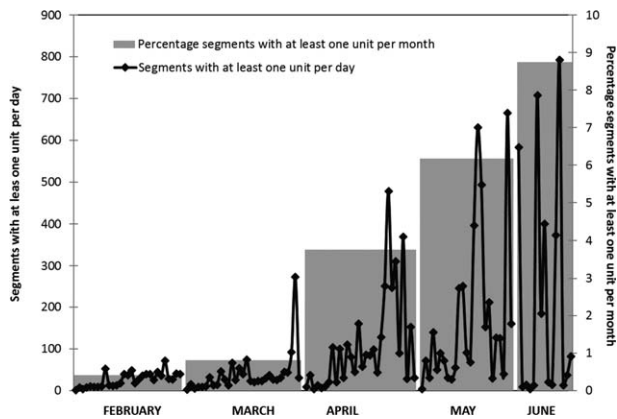


Figure 3. Percentages of segments with at least one unit from a humpback whale song in the southern Chile, Corcovado Gulf, among months studied.

Seasonality and Diel Patterns

The humpback whale detector's accuracy was 85%, *i.e.*, in 85% of the time the automatic detection was a real signal of humpback whale song. Our validations concluded a true positive rate of 0.68 and a negative positive rate of 0.08 (see Table 1 for more details). Evaluation of the percentage of segments that had at least one humpback whale acoustic unit indicated the presence of humpback whale songs for every month studied (Fig. 3).

In total, we studied 130 d divided in 332,836 segments of 32 s; 10,761 segments included acoustic units typical of a humpback whale song. Differences were found among months ($n = 10,761$, $\chi^2 = 8,547.78$, $df = 4$, $P = 0.013$): in February, we

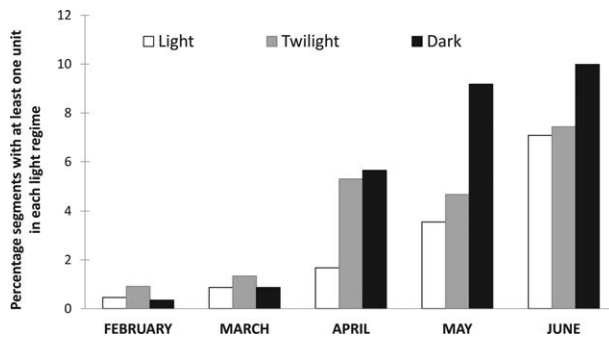


Figure 4. Percentages of segments with at least one unit of a humpback whale song in the southern Chile, Corcovado Gulf, in each light regime among the studied months.

Table 2. Summary of the two generalized lineal models used with a quasi-Poisson distribution and ANOVA test from the most explicative model.

Model	Residual df	Residual deviance	Deviance
Model 1: Vocalizations \sim month + light regime (without interaction)	3,114	36,315	7,069.6
Model 2: Vocalizations \sim month \times light regime (with interaction)	3,106	35,841	473.9
Final model: month \times light regime (with interaction)			
Factor	S.C.	F	P
Month	7,070	75.8359	$<2.2e-16^a$
Light regime	1,136	24.3698	$3.151e-11^a$
Interaction month: light regimes	474	2.5419	0.009297^b
Residuals	72,387		

^a $P < 0$.

^b $P < 0.001$.

obtained 321 segments with units from a humpback whale song, 676 in March, in 2,734 April, 3,903 in May, and in 3,127 June. The percentage of segments containing at least one acoustic unit increased throughout these months, despite June containing only 15 d of sampling.

Examination of diel patterns indicated that songs (determined by the percentage of segments with units within a song) occurred at all hours of the day (Fig. 4). There were, however, significant differences among the months and light regimes (Fig. 4, Table 2). Thus, during the end of summer (February and March), more songs were detected during twilight (0.9% and 1.3%) than in periods of light (0.5% and 0.9%) and darkness (0.3% and 0.9%) (Fig. 4). In autumn (April, May, and June) this pattern shifted, in periods of darkness more songs were detected (5.6%, 9.2%, and 10%) than during twilight (5.3%, 4.7%, and 7.4%) or in periods of light (1.7%, 3.6%, and 7.1%) (Fig. 4). Although songs occurred during all three light regimes studied, the highest number of detections occurred during periods of low light during darkness and twilight. The only exception

Table 3. Multiples comparisons between month and light regimes.

Light regime	Estimate Std.	Error	Z	Pr(> z)
Light-dark	-0.7255	0.1097	-6.613	<0.001 ^a
Twilight-dark	-0.3002	0.1638	-1.833	0.432
Twilight-light	0.4253	0.1785	2.382	0.146
Month				
February–April	-2.0172	0.2889	-6.983	<0.001 ^a
June–April	0.7711	0.1283	6.010	<0.001 ^a
March–April	-1.3723	0.2130	-6.526	<0.001 ^a
May–April	0.4958	0.1223	4.055	<0.001 ^a
June–February	2.7884	0.2874	9.701	<0.001 ^a
March–February	0.6449	0.3316	1.945	0.358
May–February	2.5131	0.2847	8.827	<0.001 ^a
March–June	-2.1435	0.2081	-10.301	<0.001 ^a
May–June	-0.2753	0.1176	-2.341	0.160
May–March	1.8682	0.2043	9.143	<0.001 ^a

^a $P < 0.001$

was February, where the number of songs was highest during periods of light (Fig. 4, Table 2).

Two generalized linear models were constructed to determine which factors (light regimes, month, and the interaction between light regimes and month) best explained the variability of the data (Quinn and Keough 2002). The results indicated that the model including the interaction between light regimes and month explained the data best (Table 2). For this reason, we examined the differences between months and light regimes and carried out a multiple comparison test (Tukey) for each factor (month and light regimes) obtained by the generalized linear model that included the interaction between light regimes and month (quasi-Poisson distribution) (Table 3). This statistical analysis indicated differences between light-dark regimes but there were no differences with twilight. There were significant differences in vocalizations between months except between February–March and May–June (Table 3).

DISCUSSION

This study presents the first results of PAM of humpback whale (*M. novaeangliae*) song in a feeding area in Chile. These observations demonstrate that, far from being rare or sporadic, humpback whale songs occurred throughout the different light regimes and during all the months of the study, with a peak in autumn. Because this study was conducted on populations that had not previously been studied acoustically, information from other populations from the Southern and Northern Hemispheres were used to correctly identify the units within in a humpback whale song. These constraints may have limited the number and type of signals that were identified. In addition, the instruments used in this study had a frequency range between 0 and 1,000 Hz and the detector was programed between 200 and 900 Hz; while this range is sufficient to detect humpback whale signals, this species can sing at higher frequencies (Payne and McVay 1971). We recommend that future studies target the entire acoustic spectrum of this species. Still, the signals most frequently

detected in this study were among the most representative units that have been described as parts of songs. Songs have been shown to occur within the frequency range studied here and not at higher frequencies (Payne and McVay 1971).

Humpback whales detected in Guafo North, in the feeding area known as the northern Chilean Patagonia, were constantly present from February to June. This temporal presence coincided with sightings in the Magellan Strait (Acevedo 2005) and Western Antarctic Peninsula (Mackintosh 1965). Humpback whales were detected in summer and with a maximum in autumn. Our results support the idea proposed by Hucke-Gaete *et al.* (2013) that a fraction of the eastern South Pacific humpback whale population is using mid-latitudes waters to feed without migrating more south. If these whales migrate farther south to feed, they would arrive late in the feeding season, making migration energetically inefficient with the short residence time that they could remain at the feeding grounds. Other studies have shown a similar strategy where whales feed in mid-latitudes waters. For example, Best (1995) and Barendse *et al.* (2010) show that some humpback whales use the mid-latitude waters off Africa to feed, and thus do not complete the traditional migration entirely to more southern waters; rather, these whales remain in the productive Benguela upwelling coastal system. Dawbin (1956) describes many humpback whale sightings off the coast of New Zealand between January and March during several consecutive years. These sightings were associated with a local concentration of food, allowing Dawbin (1956) to conclude that humpback whales may remain in such areas for relatively long periods of time without the need to migrate to Antarctic waters. The high productivity in the Chiloé marine ecoregion (Silva *et al.* 1995, 1997, 1998) would explain the permanence of humpback whales in this area at the end of summer and autumn compared to their traditional migration patterns. There are photo-identification, genomics, and satellites studies that confirmed the connection between the feeding area of the Magellan Strait with breeding areas in Colombia, Costa Rica, and Panama (Acevedo *et al.* 2007, Capella *et al.* 2008, Guzman *et al.* 2015) and between feeding areas in the Antarctic Peninsula with Ecuador, Colombia, and Panama (Stone *et al.* 1990, Caballero *et al.* 2001, Stevick *et al.* 2004, Acevedo *et al.* 2007, Guzman *et al.* 2015). These feeding areas and the Corcovado Gulf are considered independent, without migratory movements of humpback whales between these areas (Acevedo *et al.* 2013). Nevertheless, the migratory movements of humpback whales feeding in Corcovado Gulf is unknown. We recommend futures studies to identify the time of residence in this area and the migratory connections between this northern feeding area and the breeding areas.

Humpback whale songs were detected throughout the acoustic range studied; however, they mainly occurred at the high end of the detection range (500–900 Hz). Additionally, the detected segments composed patterns that were repeated for hours and were constant from February to June though the presence of songs increased as summer and autumn progressed. The detection of more segments containing at least one unit is not an exact indication of a greater presence of whales; rather it could represent more communication activity by the present whales. In this study, we found complete humpback whale songs at high latitudes of Chile, similar to what has been found in the North Atlantic (Mattila *et al.* 1987, McSweeney *et al.* 1989, Clark and Clapham 2004, Stimpert *et al.* 2012, Vu *et al.* 2012). Mattila *et al.* (1987) suggest that singing is cued by interaction of local whales with whales that have come from other feeding areas. This hypothesis, however, would not explain the results obtained here considering that movements or exchanges of animals were not described between the three feeding areas of Chile (Acevedo *et al.*

2013). Independent of whether humpbacks sing only when there are other whales near, song is far more common during the feeding season than previously thought. Similarly, there are other studies from humpback, blue, and fin whales (Croll *et al.* 2002, Moore *et al.* 2002, Clark and Gagnon 2004, Stimpert *et al.* 2012, Vu *et al.* 2012) singing during the feeding season.

Clapham (1996) suggested, from the observations of Mattila *et al.* (1987) and McSweeney *et al.* (1989), that the occurrence of male songs at high latitudes during summer, when humpback whales are not mating, could represent low-cost advertisement by males as well as a way for females to possibly evaluate males as potential mates. Similarly, songs in feeding areas have been linked to high rates of association between females and males in summer (Clapham 1996); this, in turn, could be a reproductive strategy in which males are in contact with many females during the feeding season which could then create an advantage for them during the summer breeding season. In this hypothesis, any male reproductive success gained from male singers in high latitudes would occur during the mating season at low latitudes. An alternative hypothesis is that singing during the feeding season is a way to ensure immediate mating with sexually mature females who failed to conceive during the previous breeding season, winter. Considering that humpback whales arrive at feeding areas in high latitudes in early spring, Clark and Clapham (2004) suggest that it is possible that some of the smaller fetuses were conceived in such areas; this would imply that the breeding season is not restricted to low-latitude regions. Although most sexual activity in humpback whale occurs in winter in the tropics, male intersexual competitive behavior has been observed in autumn in feeding areas (Weinrich 1995). Another hypothesis is that humpback whale song production is related to the seasonal cycle of hormones (Clark and Clapham 2004, Wright and Walsh 2010). Vu *et al.* (2012) suggest that their results of highest occurrences of songs in spring or in late autumn coincide with elevated testosterone levels in spring and autumn documented in feeding grounds. This relation is similar to hormonal control of the avian song control system (Brenowitz 1997); however, it has not been thoroughly studied in humpback whales. Our results about songs detected in autumn in the Corcovado Gulf for humpback whales supports the hypotheses that singing is used as a reproductive strategy extending mating geographically and temporally to autumn feeding, that it is an advantage for males courting females who failed to conceive in the previous season, or that it is used to generate more contacts with females to increase reproductive success in summer (as suggested by Clark and Clapham 2004, Herman *et al.* 2013). Behavioral studies are needed before more can be concluded about the purpose of these songs. Similarly, acoustic studies of the timing and routes of migration could help to explain when and what type of humpback whales are found in the studied feeding area. These studies could also help to determine how common these units are compared to units within a song in other humpback whale feeding areas.

In this study, the highest percentage of positive segments occurred during periods of low light at twilight and dark. This can be interpreted as more active acoustic performance during periods of low light. This behavior is consistent with other studies of humpback whales and other species (Au *et al.* 2000, Wiggins *et al.* 2005, Munger *et al.* 2008, Cerchio *et al.* 2010, Mussoline *et al.* 2012, Risch *et al.* 2013, Magnúsdóttir *et al.* 2014), there are few studies where the behavioral changes were not associated with light (*i.e.*, Helweg and Herman 1994). Maximum singing has been shown to be related to the daily migration in the water column of whale prey, specifically copepods and euphausiids (Wiggins *et al.* 2005). The daily migration of

krill, which aggregate at depth during the day, is believed to allow krill to avoid its visual predators such as seals, fish, and birds (Brinton 1967). Thus, humpback whales likely sing more at twilight, or dark because feeding is less efficient during those hours when the krill are dispersed in the water column migrating to or from the water's surface. That is, the whales might sing less when they are busy feeding (during the day when the krill are aggregated at depth) and sing more at night to announce resources; this would be an example of songs associated with foraging, which has been reported in other studies (Stafford *et al.* 2005, Wiggins *et al.* 2005, Magnúsdóttir *et al.* 2014). As discussed previously, if songs of male humpback whales are associated with social interactions, singing could be the pursuit of females in estrus (Baker and Herman 1984), or may reflect a switch to sexual advertisements as the primary male mating strategy at this time (Au *et al.* 2000). If more whales are singing at night, then fewer males may be engaging in direct competition for females. This further suggests that competitive group formation occurs primarily during the day, and that daylight and vision play key roles in such intrasexual interactions (Au *et al.* 2000). Then daily patterns of songs are potentially not only influenced by feeding alone but other variables should also be considered to explain the more active behavior in hours of low light. These variables could be the lack of visual cues for displaying competitive behavior (Au *et al.* 2006), or the levels of marine ambient sound or a combination of these possibilities. Whales are capable of communicating over hundreds of kilometers under favorable conditions, but the success of communication is impaired in noisy environments (Slabbekoorn *et al.* 2010). For this reason, we are currently studying the dynamics of the sound environment in this region to determine the main sources of sound and how these might affect humpback whale behavior. Additionally, intense visual observations along with skin sample or biopsy collection will be needed for a better understanding of the humpback whales' behavior during the summer and winter in this region.

These findings provide further evidence that singing is not confined to tropical waters in winter, but occurs in a feeding area in high latitudes. These results emphasize the importance of Corcovado Gulf for humpback whale conservation and the need for continued research.

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LITERATURE CITED

- Acevedo, J. 2005. Distribución, filopatría, residencia e identidad poblacional de la ballena jorobada, *Megaptera novaeangliae*, que se alimentan en las aguas del estrecho de Magallanes, Chile [Distribution, philopatry, residence and population identity of the humpback whale, *Megaptera novaeangliae*, which feeds in the waters of the Strait of Magellan]. M.Sc. thesis, Universidad de Magallanes, Punta Arenas, Chile. 119 pp.
- Acevedo, J., A. Aguayo-Lobo and L. Pastene. 2006. Filopatría de la ballena jorobada (*Megaptera novaeangliae* Borowski, 1781), al área de alimentación del estrecho de Magallanes [Philopatry of the humpback whale (*Megaptera novaeangliae* Borowski, 1781), to the

- feeding area of the Strait of Magellan]. *Revista de Biología Marina y Oceanografía* 41: 11–19.
- Acevedo, J., K. Rasmussen, F. Félix, *et al.* 2007. Migratory destinations of humpback whales from the Magellan Strait feeding ground, southeast Pacific. *Marine Mammal Science* 23:453–463.
- Acevedo, J. A., D. Haro, L. Dalla Rosa, E. Secchi, J. Plana and L. A. Pastene. 2013. Evidence of spatial structuring of eastern South Pacific humpback whale feeding grounds. *Endangered Species Research* 22:33–38.
- André, M., M. van der Schaar, S. Zaugg, L. Houegnigan, A. M. Sanchez and J. V. Castell. 2011. Listening to the Deep: Live monitoring of ocean noise and cetacean acoustic signals. *Marine Pollution Bulletin* 63:18–26.
- Au, W. W. L., and M. C. Hastings. 2008. Signal recording and data acquisition. Pages 121–175 in *Principles of marine bioacoustics: Modern acoustics and signal processing*. Springer, New York, NY.
- Au, W. W. L., J. Mobley, W. C. Burgess, M. O. Lammers and P. E. Nachtigall. 2000. Seasonal and diurnal trends of chorusing humpback whales wintering in waters off western Maui. *Marine Mammal Science* 16:530–544.
- Au, W. W. L., A. A. Pack, M. O. Lammers, L. M. Herman, M. H. Deakos and K. Andrews. 2006. Acoustic properties of humpback whale songs. *Journal of the Acoustical Society of America* 120:1103–1110.
- Bailey, W. J. 1991. *Acoustic behaviour of insects: An evolutionary perspective*. Chapman and Hall Ltd., London, U.K.
- Baker, C. S., and L. M. Herman. 1984. Aggressive behavior between humpback whales (*Megaptera novaeangliae*) wintering in Hawaiian waters. *Canadian Journal of Zoology* 62:1922–1937.
- Barendse, J., P. B. Best, M. Thornton, C. Pomilla, H. C. Rosenbaum and L. Henríquez. 2010. Migration redefined? Seasonality, movements and group composition of humpback whales *Megaptera novaeangliae* off the west coast of South Africa. *African Journal of Marine Science* 32:1–22.
- Best, P. B. 1995. A suspended migration of humpback whales *Megaptera novaeangliae* on the west coast of South Africa. *Marine Ecology Progress Series* 118:1–12.
- Brenowitz, E. A., D. Margoliash and K. W. Nordeen. 1997. An introduction to birdsong and the avian song system. *Journal of Neurobiology* 33:495–500.
- Brinton, E. 1967. Vertical migration and avoidance capability of euphausiids in the California Current. *Limnology & Oceanography* 12:451–483.
- Brown, T. J., and P. Handford. 2003. Why birds sing at dawn: The role of consistent song transmission. *Ibis* 145:120–129.
- Caballero, S., H. Hamilton, C. Jaramillo, *et al.* 2001. Genetic characterisation of the Colombian Pacific Coast humpback whale population using RAPD and mitochondrial DNA sequences. *Memoirs of the Queensland Museum* 47:459–464.
- Calpuca, T. A., K. M. Fistrup and C. W. Clark. 2000. A compact digital recording system for autonomous recording system for autonomous bioacoustics monitoring. *Journal of the Acoustical Society of America* 108:2582.
- Capella, J. J., J. Gibbons, L. Flórez-González, M. Llano, C. Valladares, V. Sabaj and Y. A. Vilina. 2008. Migratory round-trip of individually identified humpback whales at the Strait of Magellan: Clues on transit times and philopatry to destinations. *Revista Chilena Historia Natural* 81:547–560.
- Cerchio, S., and M. Dahlheim. 2001. Variation in feeding vocalizations of humpback whales *Megaptera novaeangliae* from southeast Alaska. *Bioacoustics* 11:277–295.
- Cerchio, S., J. K. Jacobsen and T. F. Norris. 2001. Temporal and geographical variation in songs of humpback whales, *Megaptera novaeangliae*: Synchronous change in Hawaiian and Mexican breeding assemblages. *Animal Behaviour* 62:313–329.
- Cerchio, S., T. Collins, S. Strindberg, C. Bennett and H. Rosenbaum. 2010. Humpback whale singing activity off northern Angola: An indication of the migratory cycle,

- breeding habitat and impact of seismic surveys on singer number in Breeding stock B1. Report to the International Whaling Commission Scientific Committee SC/62/SH12. 21 pp.
- Cerda, J., and L. Cifuentes. 2012. Uso de curvas ROC en investigación clínica: Aspectos teórico-prácticos [Use of ROC curves in clinical research: Theoretical-practical aspects]. *Revista Chilena de Infectología* 29:138–141.
- Charif, R., P. J. Clapham, W. Gagnon, P. Loveday and C. W. Clark. 2001. Acoustic detections of singing humpback whales in the waters of the British Isles. *Marine Mammal Science* 17:751–768.
- Cholewiak, D. E., R. S. Sousa-Lima and S. Cerchio. 2013. Humpback whale song hierarchical structure: Historical context and discussion of current classification issues. *Marine Mammal Science* 29:E312–E332.
- Clapham, P. J. 1996. The social and reproductive biology of humpback whales: An ecological perspective. *Mammal Review* 26:27–49.
- Clapham, P. J. 2000. The humpback whale: Seasonal feeding and breeding in a baleen whale. Pages 173–196 in J. Mann, R. C. Connor, P. Tyack and H. P. Whitehead, eds. *Cetacean societies: Field studies of dolphins and whales*. University of Chicago Press, Chicago, IL.
- Clark, C. W., and P. J. Clapham. 2004. Acoustic monitoring on a humpback whale (*Megaptera novaeangliae*) feeding ground shows continual singing into late spring. *Proceedings of the Royal Society of London Series B: Biological Sciences* 271:1051–1057.
- Clark, C. W., and W. T. Ellison. 1989. Numbers and distributions of bowhead whales, *Balaena mysticetus*, based on the 1986 acoustic study off Pt Barrow Alaska. Report of the International Whaling Commission 39:297–303.
- Clark, C. W., and G. J. Gagnon. 2004. Low-frequency vocal behaviors of baleen whales in the North Atlantic: Insights from integrated undersea surveillance system detections, locations, and tracking from 1992 to 1996. *U.S. Navy Journal of Underwater Acoustics* 52:609–640.
- Clark, C. W., J. F. Borsani and G. Notabartolo di Sciara. 2002. Vocal activity of fin whales *Balaenoptera physalus*, in the Ligurian Sea. *Marine Mammal Science* 18:286–295.
- Croll, D. A., C. W. Clark, A. Acevedo, B. Tershy, S. Flores, J. Gedamke and J. Urban. 2002. Only male fin whales sing loud songs. *Nature* 417:809.
- Darling, J. D., and M. Bérubé. 2001. Interactions of singing humpback whales with other males. *Marine Mammal Science* 17:570–584.
- Darling, J. D., M. E. Jones and C. P. Nicklin. 2012. Humpback whale (*Megaptera novaeangliae*) singers in Hawaii are attracted to playback of similar song (L). *Journal of the Acoustical Society of America* 132:2955–2958.
- Dawbin, W. H. 1956. The migrations of humpback whales which pass the New Zealand coast. *Transactions of the Royal Society of New Zealand* 84:147–196.
- Dunlop, R. A., D. H. Cato and M. J. Noad. 2008. Non-song acoustic communication in migrating humpback whales (*Megaptera novaeangliae*). *Marine Mammal Science* 24:613–629.
- Flórez-González, L. 1991. Humpback whales *Megaptera novaeangliae* in the Gorgona Island, Colombian Pacific breeding waters: Population and pod characteristics. *Memoirs of the Queensland Museum* 30:291–295.
- Frankel, A. S., C. W. Clark, L. M. Herman and C. M. Gabriele. 1995. Spatial distribution, habitat utilization, and social interactions of humpback whales, *Megaptera novaeangliae*, off Hawaii, determined using acoustic and visual techniques. *Canadian Journal of Zoology* 73:1134–1146.
- Gerhardt, H. C., and F. Huber. 2002. *Acoustic communication in insects and anurans*. University of Chicago Press, Chicago, IL.
- Gibbons, J., J. Capella and C. Valladares. 2003. Rediscovery of a humpback whale (*Megaptera novaeangliae*) feeding ground in the Straits of Magellan, Chile. *Journal of Cetacean Research and Management* 5:203–208.

- Green, S. R., E. Mercado III, A. A. Pack and L. M. Herman. 2011. Recurring patterns in the songs of humpback whales (*Megaptera novaeangliae*). *Behavioural Processes* 86:284–294.
- Guinee, L. N., K. Chu and E. M. Dorsey. 1983. Changes over time in the sings of known individual humpback whales (*Megaptera novaeangliae*). Pages 59–80 in R. S. Payne, ed. *Communication and behavior of whales*. Westview Press, Boulder, CO.
- Guzman, H. M., R. Condit, B. Pérez Ortega, J. J. Capella and P. T. Stevick. 2015. Population size and migratory connectivity of humpback whales wintering in Las Perlas Archipelago, Panama. *Marine Mammal Science* 31:90–105.
- Helweg, D. A., and L. M. Herman. 1994. Diurnal patterns of behaviour and group membership of humpback whales (*Megaptera novaeangliae*) wintering in Hawaiian waters. *Ethology* 98:298–311.
- Herman L. M. 2016. The multiple functions of male song within the humpback whale (*Megaptera novaeangliae*) mating system: Review, evaluation, and synthesis. *Biological Reviews* 92:1795–1818.
- Herman, L. M., A. A. Pack, S. Spitz, E. Y. K. Herman, K. Rose, S. Hakala and M. H. Deakos. 2013. Humpback whale song: Who sings? *Behavioral Ecology and Sociobiology* 67:1653–1663.
- Hucke-Gaete, R., D. Haro, J. P. Torres Florez, Y. Montecinos, F. Vididi, L. Bedriñana Romano and J. Ruiz. 2013. A historical feeding ground for humpback whales in the eastern South Pacific revisited: The case of northern Patagonia, Chile. *Aquatic Conservation: Marine and Freshwater Ecosystems* 23:858–867.
- Kellogg, R. 1929. What is known of the migration of some of the whalebone whales. *Smithsonian Institution Annual Report* 1928:467–494.
- Levenson, C. 1969. Behavioral, physical, and acoustic characteristics of humpback whales (*Megaptera novaeangliae*) at Argus Island. Informal Report No. 69–54. Naval Oceanographic Office, Washington, DC.
- Levenson, C. 1972. Characteristics of sounds produced by humpback whales (*Megaptera novaeangliae*). NAVOCEANO Technical Note No. 7700-6-72. Naval Oceanographic Office, Washington, DC.
- Mackintosh, N. A. 1965. The stocks of whales. Fishing News (Books) Ltd., London, U.K.
- Magnúsdóttir, E. E., M. H. Rasmussen, M. O. Lammers and J. Svavarsson. 2014. Humpback whale songs during winter in subarctic waters. *Polar Biology* 37:427–433.
- Mattila, D. K., L. N. Guinee and C. A. Mayo. 1987. Humpback whale songs on a North Atlantic feeding ground. *Journal of Mammalogy* 68:880–883.
- McSweeney, D. J., K. C. Chu, W. F. Dolphin and L. N. Guinee. 1989. North Pacific humpback whale songs: A comparison of southeast Alaskan feeding ground songs with Hawaiian wintering ground songs. *Marine Mammal Science* 52:139–148.
- Mellinger, D. K., S. L. Nieukirk, H. Matsumoto, *et al.* 2007. Seasonal occurrence of North Atlantic right whale (*Eubalaena glacialis*) vocalizations at two sites on the Scotian Shelf. *Marine Mammal Science* 23:856–867.
- Mercado, E., III, L. M. Herman and A. A. Pack. 2003. Stereotypical sound patterns in humpback whale songs: Usage and function. *Aquatic Mammals* 29:37–52.
- Mercado, E., III, L. M. Herman and A. A. Pack. 2005. Song copying by humpback whales: Themes and variations. *Animal Cognition* 8:93–102.
- Moore, S., W. A. Watkins, J. R. Davies and M. F. Dahlheim. 2002. Blue whale habitat associations in the Northwest Pacific: Analysis of remotely-sensed data using a geographic information system. *Oceanography* 15:20–25.
- Moore, S. E., K. M. Stafford, D. K. Mellinger and J. A. Hildebrand. 2006. Listening for large whales in offshore waters of Alaska. *BioScience* 56:49–55.
- Moore, S. E, R. R. Reeves, B. L. Southall, T. J. Ragen, R. S. Suydam and C. W. Clark. 2012. A new framework for assessing the effects of anthropogenic sound on marine mammals in a rapidly changing arctic. *BioScience* 62:289–295.
- Munger, L. M., S. M. Wiggins, S. E. Moore and J. A. Hildebrand. 2008. North Pacific right whale (*Eubalaena japonica*) seasonal and diel calling patterns from long-term acoustic

- recordings in the southeastern Bering Sea, 2000–2006. *Marine Mammal Science* 24: 795–814.
- Mussoline, S. E., D. Risch, L. T. Hatch, M. T. Weinrich, D. N. Wiley, M. A. Thompson and S. M. Van Parijs. 2012. Seasonal and diel variation in North Atlantic right whale up-calls: Implications for management and conservation in the northwestern Atlantic Ocean. *Endangered Species Research* 17:17–26.
- Norris, T. F. 1995. The effects of noise on the singing behavior of humpback whales (*Megaptera novaeangliae*). M.S. thesis, California State University, Los Angeles, CA. 69 pp.
- Oswald, J. N., J. Barlow and T. F. Norris. 2003. Acoustic identification of nine delphinid species in the Eastern Tropical Pacific Ocean. *Marine Mammal Science* 19:20–37.
- Palmer, J. 1976. An introduction to biological rhythms. Academic Press, New York, NY.
- Payne, R. S., and S. McVay. 1971. Songs of humpback whales. *Science* 173:585–597.
- Payne, K., and R. Payne. 1985. Large scale changes over 19 years in songs of humpback whales in Bermuda. *Zeitschrift für Tierpsychologie* 6:89–114.
- Payne, K., P. Tyack and R. Payne. 1983. Progressive changes in the songs of humpback whales (*Megaptera novaeangliae*): A detailed analysis of two seasons in Hawaii. Pages 9–57 in R. Payne, ed. *Communication and behavior of whales*. Westview Press, Boulder, CO.
- Quinn, G. P., and M. J. Keough. 2002. *Experimental design and data analysis for biologists*. Cambridge University Press, Cambridge, U.K.
- Rasmussen, K., D. M. Palacios, J. Calambokidis, *et al.* 2007. Southern Hemisphere humpback whales wintering off Central America: Insights from water temperature into the longest mammalian migration. *Biology Letters* 3:302–305.
- Richardson, W. J., C. R. J. Greene, C. I. Malme and D. H. Thomson. 1995. Measurement procedures. Pages 33–58 in *Marine mammals and noise*. Academic Press, San Diego, CA.
- Risch, D., C. W. Clark, P. J. Dugan, M. Popescu, U. Siebert and S. M. Van Parijs. 2013. Minke whale acoustic behavior and multi-year seasonal and diel vocalization patterns in Massachusetts Bay, USA. *Marine Ecology Progress Series* 489:279–295.
- Silber, G. 1986. The relationship of social vocalizations to surface behavior and aggression in the Hawaiian humpback whale (*Megaptera novaeangliae*). *Canadian Journal of Zoology* 64:2075–2080.
- Silva, N., H. A. Sievers and R. Prado. 1995. Características oceanográficas y una proposición de circulación, para algunos canales australes de Chile entre 41°20'S y 46°40'S [Oceanographic characteristics and a proposal of circulation, for some southern channels of Chile between 41°20'S and 46°40'S]. *Revista de Biología Marina Valparaíso* 30: 207–254.
- Silva, N., C. Calvete and H. A. Sievers. 1997. Características oceanográficas físicas y químicas de canales australes chilenos entre Puerto Montt y laguna San Rafael (Crucero Cimar-Fiordo 1) [Physical and chemical oceanographic characteristics of southern Chilean channels between Puerto Montt and Laguna San Rafael (Crucero Cimar-Fiordo 1)]. *Ciencia y Tecnología del Mar* 20:23–106.
- Silva, N., C. Calvete and H. A. Sievers. 1998. Masas de agua y circulación general para algunos canales australes entre Puerto Montt y laguna San Rafael (Crucero Cimar-Fiordo 1) [Bodies of water and general circulation for some austral channels between Puerto Montt and Laguna San Rafael (Crucero Cimar-Fiordo 1)]. *Ciencia y Tecnología del Mar* 21:17–48.
- Širović A., J. A. Hildebrand, S. M. Wiggins, M. A. McDonald, S. E. Moore and D. Thiele. 2004. Seasonality of blue and fin whale calls and the influence of sea ice in the Western Antarctic Peninsula. *Deep-Sea Research II* 51:2327–2344.
- Slabbekoorn, H., N. Bouton, I. van Opzeeland, A. Coers, C. ten Cate and A. N. Popper. 2010. A noisy spring: The impact of globally rising underwater sound levels on fish. *Trends in Ecology & Evolution* 25:419–427.
- Smith, J. N., A. W. Goldizen, R. A. Dunlop and M. J. Noad. 2008. Songs of male humpback whales, *Megaptera novaeangliae*, are involved in intersexual interactions. *Animal Behaviour* 76:467–477.

- Stafford, K. M., S. E. Moore and C. G. Fox. 2005. Diel variation in blue whale calls recorded in the eastern tropical Pacific. *Animal Behaviour* 69:951–958.
- Stevick, P., A. Aguayo-Lobo, J. Allen, *et al.* 2004. Migrations of individually identified humpback whales between the Antarctic Peninsula and South America. *Journal of Cetacean Research and Management* 6:109–113.
- Stimpert, A. K., W. W. L. Au, S. E. Parks, T. Hurst and D. N. Wiley. 2011. Common humpback whale (*Megaptera novaeangliae*) sound types for passive acoustic monitoring. *Journal of the Acoustical Society of America* 129:476–482.
- Stimpert, A. K., L. E. Peavey, A. S. Friedlaender and D. P. Nowacek. 2012. Humpback whale song and foraging behavior on an Antarctic feeding ground. *PLOS ONE* 7(12): e51214.
- Stone, G., L. Flórez-González and S. Katona. 1990. Whale migration record. *Nature* 346: 705.
- Tyack, P. 1981. Interactions between singing Hawaiian humpback whales and conspecifics nearby. *Behavioral Ecology and Sociobiology* 8:105–116.
- Tyack, P. L., and C. W. Clark. 2000. Hearing by whales and dolphins. Pages 156–224 in W. W. L. Au, A. N. Popper and R. R. Fay, eds. *Communication and acoustic behaviour of dolphins and whales*. Springer-Verlag, New York, NY.
- Vu, E. T., D. Risch, C. W. Clark, *et al.* 2012. Humpback whale *Megaptera novaeangliae* song occurs extensively on feeding grounds in the Northwest Atlantic Ocean. *Aquatic Biology* 14:175–183.
- Wartzok, D., and D. R. Ketten. 1999. Marine mammal sensory systems. Pages 117–175 in J. E. Reynolds II and S. A. Rommel, eds. *Biology of marine mammals*. Smithsonian Institution Press, Washington, DC.
- Weilgart, S. 2007. A brief review of known effects of noise on marine mammals. *International Journal of Comparative Psychology* 20:159–168.
- Weinrich, M. T. 1995. Humpback whale competitive groups observed on a high-latitude feeding ground. *Marine Mammal Science* 11:251–254.
- Wiggins, S. M., E. M. Oleson, M. A. McDonald and J. A. Hildebrand. 2005. Blue whale (*Balaenoptera musculus*) diel call patterns offshore of Southern California. *Aquatic Mammals* 31:161–168.
- Wiley, R. H., and D. G. Richards. 1982. Adaptations for acoustic communication in birds: Sound transmission and signal detection. *Acoustic Communication in Birds* 1: 131–181.
- Winn, H. E., and L. K. Winn. 1978. The song of the humpback whale *Megaptera novaeangliae* in the West Indies. *Marine Biology* 47:97–114.
- Wright, A. J., and L. A. Walsh. 2010. Mind the gap: Why neurological plasticity may explain seasonal interruption in humpback whale song. *Journal of the Marine Biological Association of the United Kingdom* 90:1489–1491.
- Zaugg, S, M. van der Schaar, L. Houégnyan and M. André. 2012. A framework for the automated real-time detection of short tonal sounds from ocean observatories. *Applied Acoustics* 73:281–290.
- Zelick, R., D. A. Mann and A. M. Popper. 1999. Acoustic communication in fishes and frogs. Pages 363–411 in R. R. Fay, ed. *Comparative hearing: Fish and amphibians*. Springer, New York, NY.

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