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Humpback Whales in the Western Indian Ocean

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Editorial Note

Humpback whales are well known especially for their very long migration routes and also because of the songs that males emit during the breeding season. In 1971, in their famous article published in the journal 'Science', Payne and McVay describe these songs as "a series of surprisingly beautiful sounds"! Since 1971, more acoustic data have been collected and more knowledge generated; we now know that the song 'leitmotiv' is different from one geographic area to another, and from one year to the next. We also now know how they produce these sounds from their respiratory system.

In the last two decades, different techniques have been deployed to observe humpback whales in all the oceans. Not only have passive acoustic monitoring techniques been used, but also visual observations, electronic devices, and genetics. The objectives of these studies have been to better understand whale activities, behaviors, and also the underwater environment in which they live, and the potential effects of anthropogenic activities on their societies. This has involved many different research teams, with their own skills, methods and programmes. Results have been published in the scientific literature and presented at different international conferences.

However, three things have recently become apparent: Firstly, the study of humpback whales is a wide subject requiring people with complementary skills. It was apparent that it was necessary to bring these people together to discuss this species of whale for several reasons: a) because it would highlight the major results obtained thus far; b) because it would be interesting to share experiences (especially on the data and methods used, but also on common challenges); c) to co-design future projects and identify priorities; and d) because it would provide an opportunity to start new collaborations.

Secondly, before 2015, no international scientific conference or workshop existed with regular annual sessions especially dedicated to this species of Mysticeti whales. In order to address this, we initiated the creation of the Humpback Whale World Congress (HWWC, http://www.hwwc.mg/). The first session was held in Madagascar in 2015 and the second in La Réunion Island in 2017. Our idea was to bring together researchers and technicians from universities, research institutes, government organizations, and industry, dealing with all aspects of the biology, ethology, genetics, ecology, acoustics, signal processing, pattern recognition, mathematics, and computer sciences applied to the study of the humpback whales and their environment, and the potential effects of anthropogenic activities on the species. The goal of the HWWC is to provide a forum for exchange of new results obtained from the latest advances in instrumentation and methods.

Thirdly, during the BaoBaB project I led from 2012 to 2014, it became apparent that the extensive movement of humpback whales, even during the breeding season (with more than 100 km being covered per day), resulted in the same individuals being observed from the east coast of Africa to the Mascarene Islands. Because of this remarkable characteristic of this baleen whale species, it was obvious that we needed to encourage collaboration at a regional level, and we envisaged a consortium of people who work collaboratively on the Southwestern Indian Ocean humpback whale population.

During the international HWWC we were very pleased by the quality of the work shared by different teams, and the strong motivation to exchange information and work together. For this reason, we requested some colleagues to describe their projects in full papers, to put them together, and publish this unique special issue.

I would like to thank all the authors and co-authors, all the persons who contributed to this special issue, and more strongly the Cetamada Team who currently does such amazing work on these humpback whales!

Enjoy reading!

Olivier ADAM
Professor
Institut d'Alembert
Sorbonne University, Paris, France

Acoustic ecology of humpback whales in Brazilian waters investigated with basic and sophisticated passive acoustic technologies over 17 years

Renata S. Sousa-Lima[1,2,3,9,*], Márcia H. Engel[3], Victor Sábato[4], Bianca R. Lima[5], Thiago S. M. Queiróz[4], Marcos R. M. Brito[1], Deborah P. Fernandes[1,2], Cristiane A. C. Martins[3,6], Paula S. Hatum[1,2], Thamires Casagrande[1,2], Laura K. Honda[1,2], M. Isabel C. Goncalves[1,7], Júlio E. Baumgarten[7], Artur Andriolo[8,9], Milton C. Ribeiro[10], Christopher W. Clark[11]

[1] Laboratório de Bioacústica, Departamento de Fisiologia e Comportamento, Centro de Biociências, Universidade Federal do Rio Grande do Norte, Natal, RN, Brasil

[2] Programa de Pós-Graduação em Psicobiologia, Centro de Biociências, Universidade Federal do Rio Grande do Norte, Natal, RN, Brasil

[3] Projeto Baleia Jubarte, Instituto Baleia Jubarte, Caravelas, BA, Brasil

[4] Laboratório de Mastozoologia, Departamento de Zoologia, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Belo Horizonte, MG, Brasil

[5] Instituto de Ciências Biológicas e da Saúde, Pontifícia Universidade Católica de Minas Gerais, Belo Horizonte, MG, Brasil

[6] Tryphon Océans, Tadoussac, QC, Canada

[7] Laboratório de Ecologia Aplicada à Conservação, Universidade Estadual de Santa Cruz, Ilhéus, BA, Brasil

[8] Laboratorio de Ecologia Comportamental e Bioacústica, Universidade Federal de Juiz de Fora, Juiz de Fora, MG, Brasil

[9] Instituto Aqualie, Juiz de Fora, MG, Brasil

[10] Universidade Estadual Paulista (UNESP), Rio Claro, SP, Brasil

[11] Bioacoustics Research Program, Cornell Lab of Ornithology, Cornell University, Ithaca, NY, U.S.A.

* Corresponding author: sousalima.renata@gmail.com

Abstract

Whales are difficult to study. These large marine mammals cannot be maintained in captivity so they have to be studied in nature, and observing their underwater behavior becomes a challenge. The extensive distribution, large size, and aquatic life style of these leviathans constrain efforts to observe and understand the scale of what is being studied. Researchers have dealt with this challenge with wit, determination and creativity. Large whales are known for using long distance acoustic communication to coordinate social interactions such as mate attraction and group feeding, as well as a means for orientation and navigation. Therefore, sound is relied on to help "see" beyond the surface. Marine mammalogists were the first to modify existing technology from ocean bottom sensors to develop novel ways to listen underwater, taking advantage of the fact that these animals rely mostly on sound to survive and reproduce. In effect, biologists eavesdrop on the underwater lives of marine mammals by listening. Researchers listen to humpback whales using different passive acoustic technologies that span a variety of spatial and temporal scales. In this paper, studies conducted in Brazilian waters are reviewed, primarily in the Abrolhos Bank region, where basic and advanced technologies have been used to understand the acoustic ecology of this large marine mammal species. Male humpback whale culture, their social dynamics revealed by spatial and temporal vocal activity patterns, and their interaction with the encroaching noise generated by humans, are reviewed.

Keywords: male display, communication, *Megaptera novaeangliae*, song, passive acoustics.

Introduction

"Technology advances rapidly. Nonetheless our listening technology remains limited to study large whales. The future will continue to bring us tools that will enable humans to pick up whale sounds far away in ocean refugia. We can only hope that whales will still exist and not be made of the fabric of legends, as they once were...monsters and mermaids....". (Sousa-Lima, 2007).

Who are we listening to? The humpback whale.

The humpback whale (*Megaptera novaeangliae*) is a baleen whale (Fig. 1) that has a cosmopolitan distribution, inhabiting all oceans of the world. Similar to other large whales, the humpback has a distinct temporal geographical distribution, undertaking long migrations annually that can exceed 8000 km one-way (Horton *et al.*, 2011), between their feeding and breeding grounds. In the Southern hemisphere during summer months, they feed at high latitudes off South Georgia and the Sandwich Islands in Antarctica (Zerbini *et al.*, 2006, 2011; Stevick *et al.*, 2006; Engel and Martin, 2009). During winter, they migrate to tropical waters, where they mate, give birth and nurse the young, and occasionally feed along the South Atlantic coast (Dawbin, 1966; Danilewicz *et al.*, 2009; Alves *et al.*, 2009). Migrations are structured by age, sex and reproductive status. Lactating females leave the feeding grounds first, followed by immature whales, mature males and females, and pregnant females leaving last. On the return migration, newly pregnant females are the first to return to the feeding grounds (Dawbin, 1966, 1997). Individual humpback whales show variable levels of site fidelity even within the same population (Weddekin *et al.*, 2010; Baracho-Neto *et al.*, 2012) and some return to the same area between migrations (Clapham *et al.*, 1993; Baracho-Neto *et al.*, 2012).

During summer while feeding, social organization of humpback whales is often limited to small, unstable groups, mostly pairs (Whitehead, 1983). Groups with calves are often composed only of calf and mother (Clapham *et al.*, 1993). When in the breeding grounds, interactions are often composed of small groups with brief associations. Nevertheless, frequent agonistic behavior between several males happen (Mattila *et al.*, 1994). Singletons, dyads and trios are common during this period, where dyads and trios are frequently seen with different associates (Mobley and Herman, 1985). Females with calf are often accompanied by a male, betting on the possibility of mating, in the event of the female entering postpartum estrus (Tyack, 1981). Larger groups, with surface activity and aggression between members, have been named competitive or active groups, where males actively compete for access to a mature female (Tyack and Whitehead, 1983; Clapham *et al.*, 1992).

The Western South Atlantic Ocean (WSA) humpback whale population that winters off Brazil is distributed from Rio de Janeiro to Rio Grande do Norte (24° to

Figure 1. Humpback whales, *Megaptera novaeangliae*, photographed by Renata Sousa-Lima on the Abrolhos Bank, Brazil.

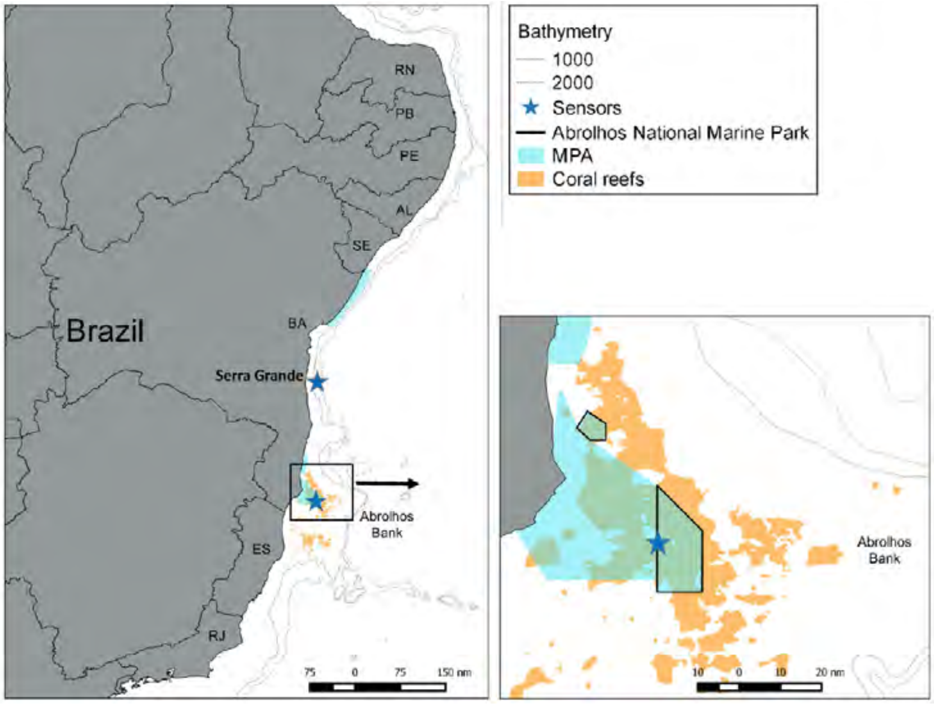

Figure 2. Map of the coastal Brazilian states where humpback whales are known to occur and limits of the Abrolhos National Marine Park within the Abrolhos Bank.

5° S) (Andriolo *et al*., 2006; Wedekin *et al*., 2010) and re-occupying areas along the coast (Rossi-Santos *et al*., 2008; Gonçalves *et al*., 2018). The WSA population has been estimated to be close to 20,000 (Bortolotto *et al.,* 2016; Pavanato *et al*., 2017) indicating a population size of around 60% of its estimated pre-modern whaling abundance and may recover to its pre-exploitation size sooner than previously thought (Bortolotto *et al.,* 2016).

Where are we listening for humpback whales?

Since the year 2000 systematic passive acoustic monitoring efforts have focused on the Abrolhos Bank (AB). AB is located off the east coast of Brazil between 16°40'and 19°30'S with a mean depth of 30 m, covering an area of approximately 30,000 km² (Fainstein and Summerhayes, 1982). Five small islands comprise the Abrolhos archipelago in the northeastern part of the AB. The Abrolhos Marine National Park was created on 6th April 1983 (Decree 88.218) and is located in the northeast portion of the AB. It includes the Abrolhos archipelago and two reefs: Abrolhos and Timbebas, a total area of 913 km² (IBAMA/FUNATURA, 1991).

Individual whales tend to have longer residence times on the AB when compared to other areas north of the bank (Wedekin *et al*., 2010; Baracho-Neto *et al*., 2012), which corroborates previous evidence that suggests that the AB is the main area of concentration for humpback whales wintering in Brazilian waters (Siciliano, 1997; Martins *et al*., 2001; Andriolo *et al*., 2006). Approximately 80% of all individuals that visit the coast of Brazil are in this region, while the remaining 20% are distributed along the northeastern coast (Andriolo *et al*., 2006). AB is especially important for nursing females, which represent 50% of social groups in the area contrasting with only 17 % of female with calf groups registered on the northern coast of Bahia (NCB) (Rossi-Santos *et al*., 2008). These data justified the concentration of our acoustic monitoring efforts in the AB region.

How are we listening for humpback whales?

During the quiet age of sail, under conditions of exceptional calm and proximity, whalers were occasionally able to hear the sounds of whales transmitted faintly through a wooden hull (Aldrich, 1889). Then, seamen could hear the sounds of humpback whales, but to explore the intricacies of this vocal behavior was still out of reach. Detailed qualitative description of a species' behavior, such as their sound repertoire, is important. Nevertheless, the questions that drive the advancement of knowledge about a species' communication system are often answered by quantitative analyses of the variation on some specific trait. Metrics of this variation should provide objective evidence for determining the occurrence of the evolutionary mechanisms hypothesized by researchers (Sousa-Lima, 2007).

As Tchernichovski *et al*. (2004) point out, the invention of the spectrogram at Bell Laboratories in the late 1950's was invaluable for the quantitative investigation of animal vocal behavior. Animal sounds started to be further inspected quantitatively as analytical tools became handy and sound acquisition hardware became available for recording underwater sounds. Nowadays we employ basic and advanced technologies to explore the acoustic ecology of large whales such as humpbacks.

Dipping hydrophones

Listening to marine mammals underwater today is only possible due to the early findings of Pierre Curie, who together with his elder brother Jacques, in 1880, observed that an electric potential was produced when mechanical pressure was exerted on a quartz crystal (Curie and Curie; 1880a, b). Hydrophones are built based on this observation. In this study ,different combinations of recording equipment were used that allow the recording of sounds within the frequency ranges know for humpback whales: Sony DAT D8 or Marantz PMD670 solid state recorders (frequency response up to 20 kHz) connected to hydrophones HTI 90 series (frequency response up to 30 kHz).

Singers were silently approached to within approximately 100m to obtain high quality recordings, and depth measurements at the site of the singing whale were col-

Figure 3. Basic passive acoustic methods, showing dipping hydrophone deployed from a boat or a zodiac at the Abrolhos Bank, Brazil.

lected using a small zodiac or boat (a trawler, a sailboat with or without outboard engine, or a fiberglass center engine fishing boat). The approach aboard the zodiac was carried out using an umbrella as an improvised sail, or a paddle to get as close as possible without disturbing the whale. Silent boat approaches were done by navigating upwind from the singer and then cutting the boat engine and drifting downwind toward the focal whale with the engine off. When a silent approach was not feasible, we attempted recordings from the research boat by cutting the engine off, and drifting towards the focal animal. The song and behavior observed above the water of the focal singer (breathing, swimming, exposure of body parts) were simultaneously recorded and the exact time that a behavior occurred was registered on the recordings (second voice channel) or on a data sheet (Fig. 3).

Array of autonomous recording systems

During the late 1960's, a change of spatial scale occurred in marine geophysical research when studies on earthquakes became focused in smaller areas of the seafloor. This shift required higher accuracy and resolution of measurements made using geophysical instruments, which then led to the development of 'autonomous instruments' to monitor and record earthquakes underwater. Incidentally, these fixed autonomous instruments are also capable of recording low frequency sounds of baleen whales. McDonald *et al.* (1995) were the first to use Ocean Bottom Seismometer (OBS) or Hydrophone (OBH) data to study blue and fin whale calls. OBSs and OBHs were too expensive for most researchers so, during the 1990's, several laboratories started to develop their own autonomous recorders to lower costs and to collect bio-acoustic data from marine mammals. More recently, advances in low-power electronics, high-data capacity data-storage, computer processing technology, and power supply units have enabled the proliferation of autonomous recording systems capable of monitoring the acoustic behavior of many species of marine mammals as well as environmental sounds (Sousa-Lima *et al.*, 2013). Ongoing continuous improvements in data-storage and battery technologies are making data collection possible for much longer periods of time and at higher data-sampling rates.

The first deployment of autonomous bottom mounted acoustic sensors in South America was in 2003. Sounds of humpback whales were listened for on the ocean floor off the Abrolhos archipelago and the local acoustic habitat (Fig. 4). A variable percentage of the park area was acoustically monitored using an array of MARUs ("Marine Autonomous Recording Units" developed by the Bioacoustics Research Program of the Cornell Laboratory of Ornithology - BRP) between the years 2003 and 2005. These devices includes a microprocessor, hard disks for data storage, acoustic communications circuitry, and batteries, all sealed in a glass sphere and protected by a plastic harness (Fig. 4). An external hydrophone was connected to the unit through a waterproof connector.

Figure 4. Array of marine autonomous recording units (MARUs) synchronized on land and tested before deployment. Photograph of a MARU showing the internal electronics and external hydrophone.

Each MARU carries an onboard clock that is synchronized before and after deployment in order to time signals received from global positioning system (GPS) satellites with a precision of ± 10 µsec. This makes it possible to perform sound source localization and tracking of signals recorded by an array of MARUs. The arrays consisted of 4-5 MARUs deployed northwest and south of the Abrolhos archipelago where Martins (2004) calculated the density of whales to be similar. The MARUs were programmed to record continuously at a sampling rate of 2,000 Hz during 26 days to 4 months, depending on the logistics to redeploy after a change in batteries. At the conclusion of the field season, a boat equipped with an acoustic transponder unit communicated with the deployed MARUs and commanded each one to separate from its anchor using a unique acoustic release signal. The MARUs floated to the surface where they were retrieved.

What are we listening to?

Humpback whales of all ages and both sexes display a variety of aerial behaviors: breaching, lobtailing, flippering and tail breaching, which are thought to be used as a means of communication (Whitehead, 1985). Furthermore, both males and females can produce sounds used for communication (Zoidis *et al*., 2008), but only males are known for producing long and patterned sequences of sounds, called songs (Payne and McVay, 1971). Song is heard mainly on the breeding grounds and are thought to function to mediate mating (see the seminal song evolution review by Herman, 2016).

The song

As early as 1951, mysterious sounds were recorded in the ocean by the U. S. Navy and described by Schreiber (1952). The mystery sounds were believed to be from humpback whales, but were only attributed to the species a decade later (Schevill and Watkins, 1962; Schevill, 1964; Watkins, 1967). Payne and McVay (1971), inspired by bird literature and armed with acoustic spectrographic analyses tools, first described the basic patterned hierarchical structure of humpback whale sounds recorded during the late winter and early spring off Bermuda.

Payne and McVay (1971) noted that "one of the characteristics of bird song is that they are fixed patterns of sounds that are repeated" and, having observed fixed patterns in the sounds of humpback whales, subsequently adopted the term "song" to describe it. These authors relied on Broughton's (1963) categories of the term "song" to choose the best definition for the observed pattern in humpback whale sounds: "… a series of notes, generally of more than one type, uttered in succession and so related as to form a recognizable sequence or pattern in time".

After justifying their choice to call the humpback whale sounds "song", Payne and McVay (1971) provided a terminology for the various hierarchical levels they observed. Starting from the smallest element, when listening to a sound at lower speeds, subunit is defined as a single element in a series of short pulses comprising a sound. A unit, or note, is defined as a continuous sound to the human ear if played in normal speed. Thus, some units are composed from subunits. Units are arranged in phrases, which are generally composed of combinations of similar units. Similar phrases are repeated to form themes, which are "unbroken" sequences or repetitions of phrases. The song is defined as the combination of several distinct themes. The highest hierarchical level is the song session, which consists of a series of songs with silent intervals of less than a minute. Songs recorded from a boat by Payne and McVay (1971) lasted between 7 and 30 minutes but continuous singing activity may last much longer. The duration of individual male humpback whales' singing bouts recorded with the MARU array during the current study (N =136) varied between 30 to 1,230 minutes (20.5 hours, similar to the 22 hours of singing recorded by Winn and Winn (1978)).

The role of the long and complex song of male humpback whales was initially described as having a fixed stereotyped pattern within a population, but subsequent studies have shown that the song changes during one or more breeding seasons within a single population and this may be regarded as cultural transmission (Noad *et al*., 2000). The structural variability of the humpback whales' song in AB has been studied by the authors since the year 2000, describing the variations found on the level of phrases to identify lineages of themes along the different years as suggested by Cholewiak *et al*. (2012).

The identification of theme lineages was only possible after determining where the song of the humpback whale started. Considering the long duration of song sessions, manual browsing of 26 continuous days of acoustic recordings from MARUs was done to find instances where song was heard abruptly preceded by silence (Lima and Sousa-Lima, 2012). Data from dipping hydrophones were also browsed to determine

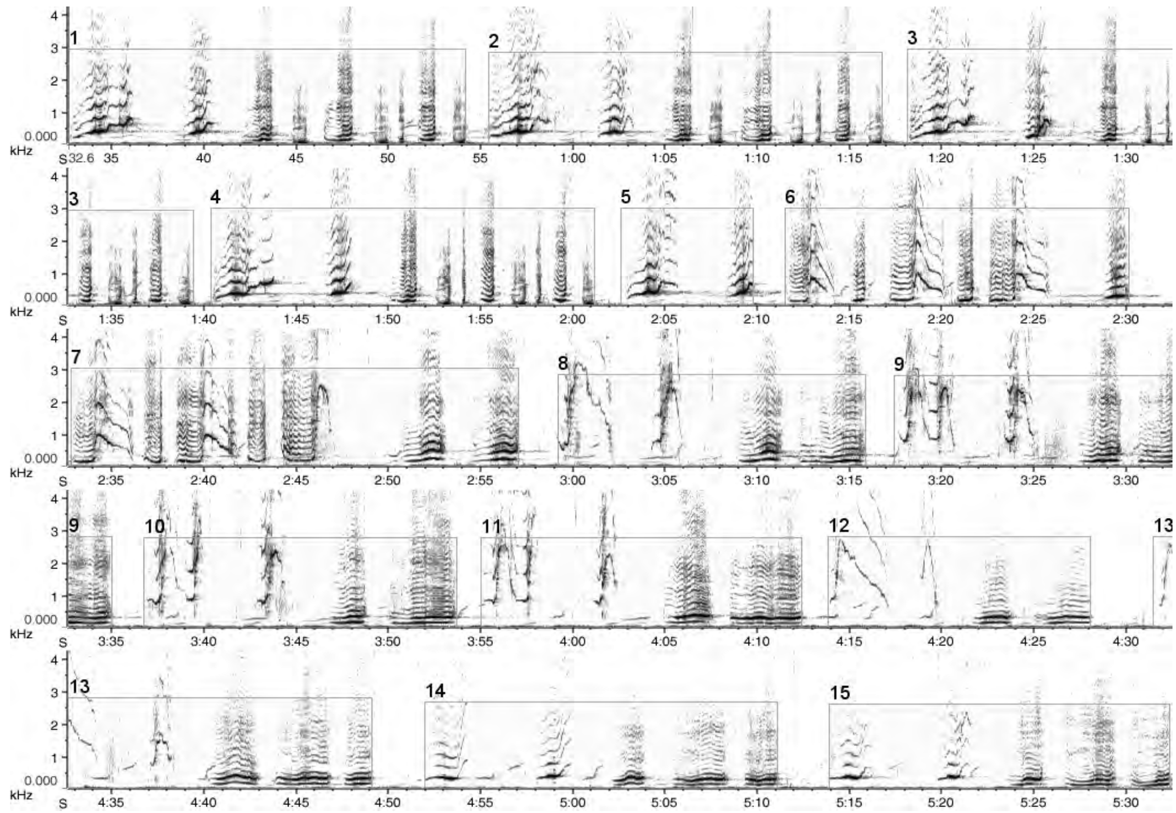

Figure 5. Spectrogram of part of a Brazilian humpback song recorded with a dipping hydrophone connected to a portable recorder from a boat.

the contribution of each phrase type within each song cycle, allowing statistical testing if the initial themes found in the MARU data were indeed preferred as the first theme to be sung by males, or if they appeared as the initial theme by chance alone.

Merging information from two different datasets acquired by deploying basic, simple recording equipment and advanced autonomous technologies allowed this very difficult question to be answered: Yes, males that sing in AB do have a preference to start a song session with a specific theme which has been defined as theme 1 for all subsequent AB song analyses.

Listening to song to understand humpback whale culture

Even though there have been many debates about the definition of culture and many difficulties in quantifying cultural transmission in non-humans species (Laland and Janik, 2006), studies of humpback whale song provide compelling evidence for cultural transmission in the learning of vocal patterns in these large animals.

Knowing that different humpback whale populations, living in different ocean basins, normally have distinct song patterns that change through time within their own population, Noad *et al.* (2000) reported a radical song change in the population inhabiting the Australian east coast. In a period of approximately two years, the song they used to sing was completely replaced by a new song. Brought by a small group of singers coming from the Australian west coast, the group rapidly incorporated the new patterns in their own song, which was completely modified after two years. In Mexico and Hawaii, two breeding grounds 4800 km apart, synchronous changes in songs have been documented (Cerchio *et al.*, 2001), with many variables in song pattern changing in a similar manner. The same was observed between songs recorded more than 5500 km apart, from AB and Gabon (Darling and Sousa-Lima, 2005). Songs from the Brazilian humpback whale population in Abrolhos were strikingly similar to songs from the African population recorded in Cape Lopez, sharing five themes in their songs, with very similar units and phrases. Song patterns had more in common between sites than songs from the same population in different years. It was speculated that these song similarities could be indicative of cultural transmission or according to an innate template.

Long term monitoring of humpback whale songs from Bermuda (Payne and Payne, 1985) and Tonga

(Eriksen *et al*., 2005) showed that through the years, songs contained unique twists every year, as well as material from the previous year's song, and also that the speed of this change could vary, sometimes changing drastically in a span of two years, while at other times changing at a slower pace over a larger timespan. Nonetheless, change was always directional, indicating learning instead of drifting.

Changes over a much larger geographical scale were only detected in a comparative study conducted by Garland *et al*. (2011). They were able to document, in an 11-year period, a fast paced and repeating horizontal cultural transmission in six populations in the western and central South Pacific Ocean. The song types clearly changed and were spread from the western populations to the eastern populations. New types of songs identified in one population would spread to another population further east between consecutive breeding seasons. This rapid transmission, combined with a high level of site fidelity of the studied populations, was a strong indicator of cultural transmission.

Research in AB has focused on identifying changes between years at the phrase level within the same population. Twenty-one themes were registered in AB between 2000 and 2005, and lineages were built for the themes in which it was possible to define a standard phrase (as suggested by Cholewiak *et al*., 2012). Changes were observed in the spectral structure of the units, introduction of new units, removal of units and also variation in the general sentence structure intra- and inter-individually (Brito and Sousa-Lima, 2014; Hatum, 2015).

Using simple dipping hydrophones connected to portable recorders in AB, distinct forms of male phrase variation were found: changes in unit spectral structure, insertion of new units, unit removal and also variations in the general structure of phrases, both intra and inter-individually. The identification of song lineages between years has allowed for a better understanding of cultural changes, as shown in the lineage for theme 1 recorded in Abrolhos in 2003 (Fig. 6). In the first year, the theme was composed of one phrase of 4 units (A3-B3-B3-B3), and it was maintained in the following year. Nonetheless, in 2005, only the first unit remained the same, and the following units underwent spectral changes (from B3 to B5) and repetitions of a new unit appeared for the first time (b5).

Understanding the variations found in the evolution of songs in humpback whales is of fundamental importance to allow for a better understanding of song learning and cultural transmission within and between populations. Ongoing development of metrics capable of pointing out how and where in the song the changes are happening will allow for more accurate assertions of patterns being transmitted and learned by interacting individuals.

Humpback culture can be investigated at varying spatial and temporal scales using very basic passive acoustic technologies. The challenge is to think of creative ways to ask questions about this behavioral trait that will inspire collaborative efforts throughout the oceans.

Listening to understand the social dynamics of singing

Real time monitoring of humpback whale vocal activity in AB has been carried out using basic equipment deployed from boats. Surveys dedicated to investigating the AB underwater acoustic ecology focused on humpbacks have been carried out since 2000 (Sousa-Lima *et al*., 2002). A total of 201 humpback whale groups and 493 individuals were sighted and 103 of these were vocally active groups and 98 were vocally inactive. Of the vocally active groups (N = 103), 72% did not include calves (N = 74) and 28% did (N = 29). The remaining groups were vocally inactive (N = 98) and 43% of these did not include calves (N = 42) and 57% did (N = 56).

Figure 7 shows that each group category had a different level of vocal activity. Mother and calf (MoCa) groups showed the smallest occurrence of vocal activity. However, in groups with calves and the presence of principal and secondary escorts, the percentage of vocal activity was higher. Solitary individuals presented the highest percentage of vocal activity in AB.

What do male humpback whales do when they are singing?

Due to the hierarchical structure and long duration of their songs, male humpback whales are an excellent model for applying passive acoustic source localization to track their movement. This was possible with the use of a set of synchronized acoustic sensors (MARUs). By comparing differences on time-of-arrival of the same acoustic signal on each sensor, it was possible to estimate with precision the location of each singer in short time intervals, which allowed their trajectories to be traced at a fine scale. This made it possible to visualize how and where singing humpback males moved, what were the characteristics of their trajectories, if they had preferred

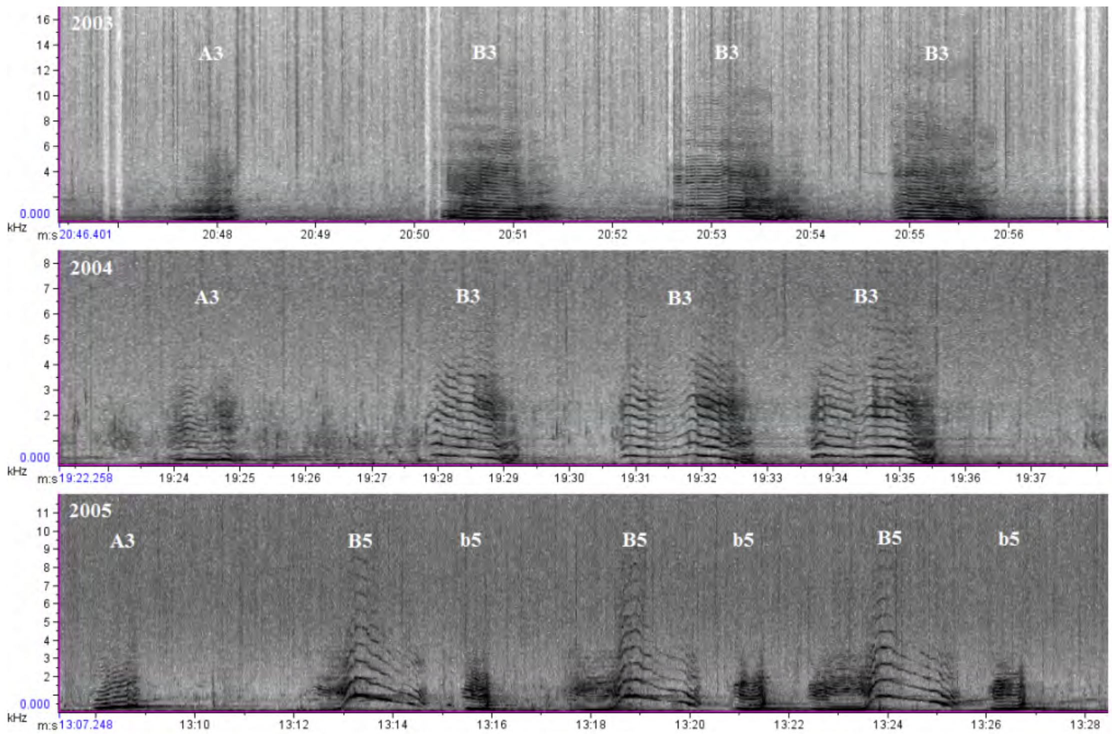

Figure 6. Spectrograms containing phrases of the Theme 1 lineage for the years 2003, 2004 and 2005. Capital letters indicate the position of the unit in the phrase, numbers indicate the year they first appeared, lower case letters indicate a new type of unit not present in the years before.

locations, if they interacted among themselves, and even to make inferences about their behavior.

Male singers were acoustically followed for up to 5 hours with individuals traveling up to 16 km at speeds of up to 30 km/h. These animals live in areas of transcontinental proportions; therefore, movement parameters must present different values when migration paths and trajectories are compared inside reproductive and feeding areas. Typically, the movement speed is higher and the trajectory is less tortuous when the animals are migrating (Kennedy *et al.*, 2014; Mate *et al.*, 1998; Zerbini *et al.*, 2011).

Around the Abrolhos archipelago males spent 47% of the time moving, while during the other 53% they practically stayed at the same spot. The average movement speed in Abrolhos was 2.3 km/h, but the highest speed ever recorded for this species, 30.05 km/h, was registered within the trajectories. Mean speed of singing males in Australia is 2.5 km/h (Noad and Cato, 2007), and silent males travelled faster (4 km/h).

While singing in Abrolhos, males showed a bias towards persisting in the same direction – a directionality index of 0.58, in a range where 0 is a highly tortuous trajectory and a straight trajectory is represented by a value of 1. This means that, although most of the time they were stationary, when singers moved they tended to have a set direction of movement rather

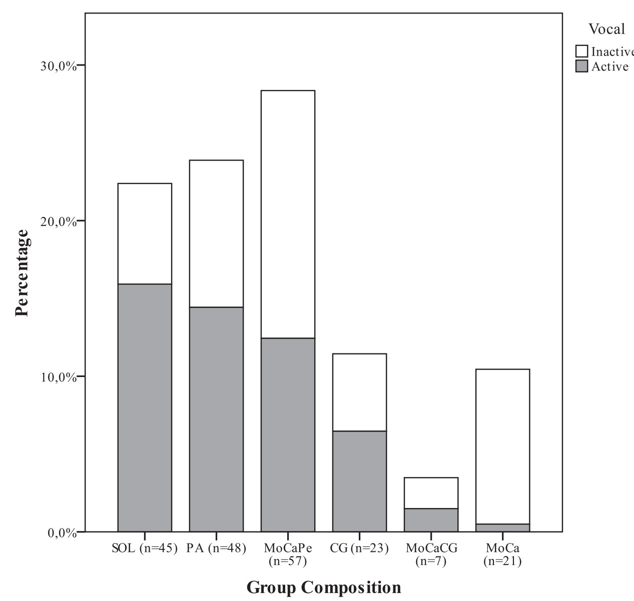

Figure 7. Distribution of the percentage of sighted humpback whale groups that were vocal, or not, during acoustic monitoring dedicated boat surveys in AB in two consecutive years (2004 and 2005). MoCa: mother and calf; MoCaPe: mother and calf with principal escort; MoCaCG: competitive group with a mother-calf pair; SOL: individual; PA: pair; CG: competitive group.

than moving at random, which suggests an interaction between singers and a conspecific (as observed by Darling *et al*., 2006) or in response to a localized stimulus.

Even at the start of the reproductive season, singing activity at AB was high. In a 391 h recording at the beginning of the reproductive season in 2005, more than 90% of the hours showed singing activity of at least two males simultaneously. This fact highlights the importance of acoustic interactions between singers, independently of their movement. Visualization of male tracks using advanced technologies as applied here is a strong tool to understand the function of the humpback whale song.

Darling *et al*. (2006), recording focal males from a small boat, were capable of detecting 167 interactions among singing males over a timespan of around 6 years. Similar inferences were reached during the present study using data from a few days but with a much larger spatial coverage provided by the detection range of the MARU array. However, complementary real time visual information was not available in the present study about silent interacting animals as potential sources of stimuli to elicit singer responses.

Figure 8 shows trajectories of two males recorded simultaneously by the methods used in the present study as compared with the interaction schematics published by Darling *et al*. (2006). It is possible to see that the information of localization resulting from acoustic tracking is more detailed, so that the inferences about male-male interactions may be explored in a finer scale than using traditional visual observations while recording from a boat. Nonetheless, acoustic tracking methods coupled with simultaneous information from sightings, such as individual identification, age and behavior interactions of other nearby individuals (as realized by Darling *et al*., 2006) can lead to a higher level of understanding. The application of more advanced technologies of acoustic tracking of singing males may greatly enhance the potential of continuous and intensive observation of these animals and open avenues for a deeper comprehension of ecological and behavioral aspects of the species.

Listening to understand the spatial distribution of vocal activity

The spatial model that best predicted vocal activity in AB included "Calf Presence", "Distance to Reefs" and "Depth". The model predicted that vocally active groups were less likely to have calves, were farther away from coral reefs and found in shallower waters. When a calf was present in the group, it was unlikely that there would be a singing male present. Even though mothers and calves produce vocalizations (Simão and Moreira, 2005; Zoidis *et al*., 2008; Videsen *et al*., 2017), they have not yet been documented singing.

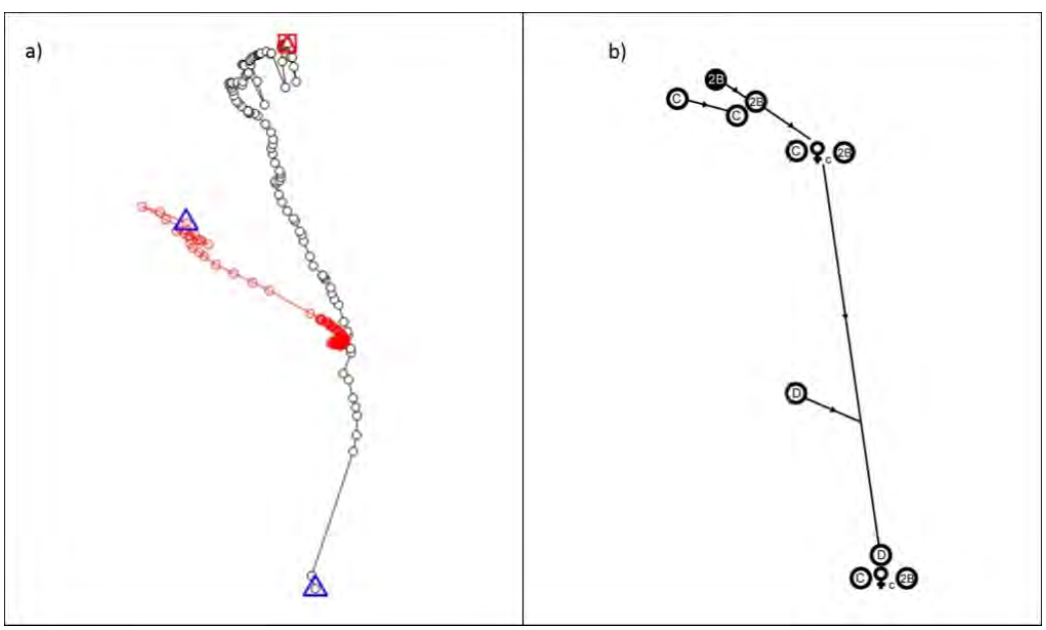

Figure 8. (a) Original trajectories inferred using PAM. Red and black dots represent different singers, and blue and red marks show the starting and final locations of each singer; (b) Trajectory schemes simplified from Darling *et al.* (2006). Each code composed of a letter (or a letter and a number) represents one different individual.

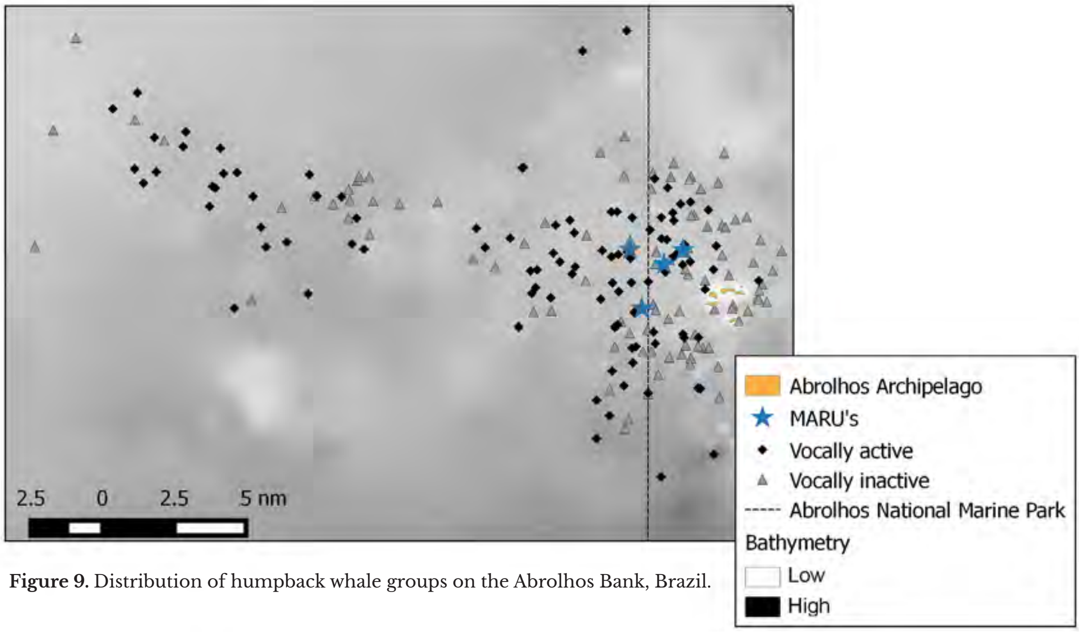

Figure 9. Distribution of humpback whale groups on the Abrolhos Bank, Brazil.

Mother and calf pairs are most likely found in shallow waters (Martins *et al*., 2001; Félix and Botero-Acosta, 2011) and the presence of calves not only has an effect on singing, but also on distribution of humpback whales. Shallow waters are ideal for mothers to care for their calves, but the small water column is not adequate for courting males (Smultea, 1994; Ersts and Rosenbaum, 2003). Mothers might prefer shallow waters possibly to avoid harassment by males, disruption of nursing, and injury or separation from calves (Smultea, 1994; Elwen and Best, 2004). Félix and Botero-Acosta (2011) suggest that different groups may show discrete reproductive strategies when responding to social and environmental conditions. Even though females mate *post partum*, they are not the ideal partner for courting males (Smultea, 1994). Locations in which receptive females congregate may determine the main singing areas (Frankel *et al*., 1995).

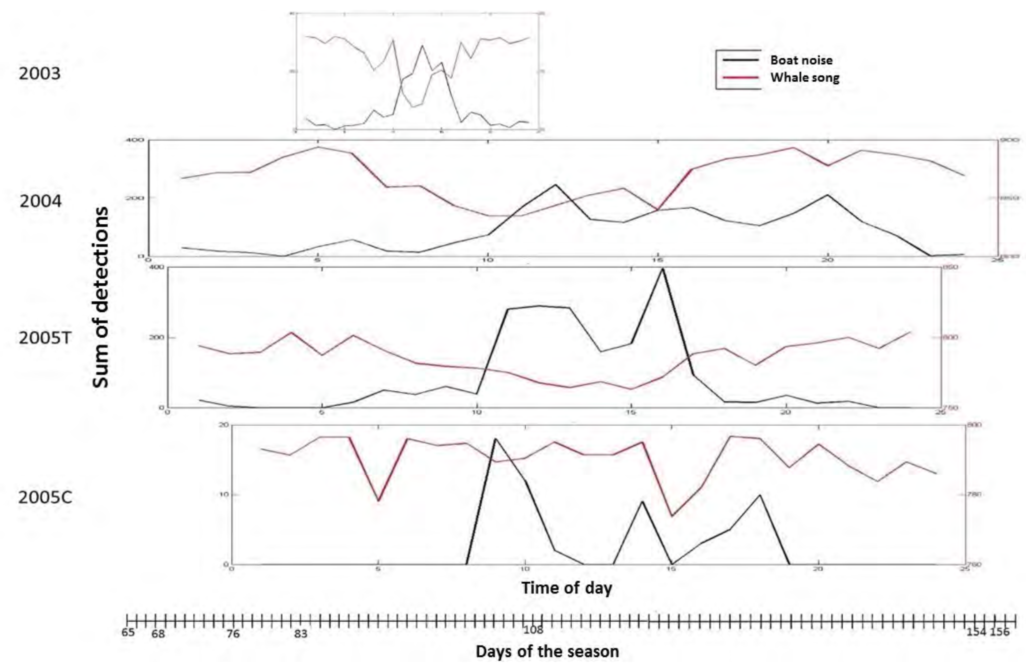

Figure 10. Number of 2-minute segments with detections of singing activity around the Abrolhos archipelago, Brazil in the years 2003, 2004 and 2005 (in two different areas) recorded with arrays of marine acoustic recorder units (MARUs) plotted in 24 hour panels. The width of the panel corresponds to the period during the winter season that the recordings were made.

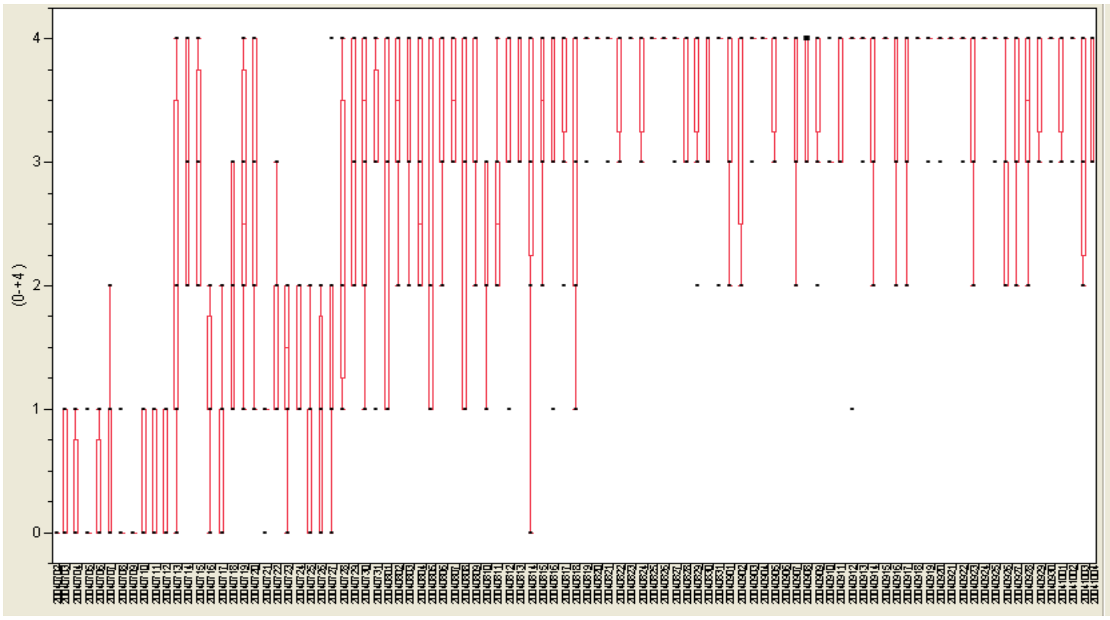

Figure 11. Number of humpback whale singers (0 to 4 or more) counted in 2004 off the Abrolhos archipelago showing an increase in singing activity as the season progresses.

Listening to identify the temporal patterns of male humpback singing behavior

Much investigation has taken place on the occurrence of a temporal pattern in vocal activity of humpback whale males, and how endogenous and exogenous factors would act on its expression. Sousa-Lima and Clark (2008) and Casagrande (2016) investigated the existence of a daily variation pattern in which there is high vocal activity during the night until early morning, showing a decrease in the afternoon (Fig. 10). This decrease in vocal activity by humpback whales during the day may be a behavioral response to an external stimulus that creates a temporal reorganization in song performance. However, the pattern of less vocal activity during the day loses its intensity throughout the months, being more evident at the beginning rather than the end of the reproductive season.

Other observations show that even though the number of individual animals on AB reaches its highest density between the months of August and September, and decreases until November (Martins *et al.*, 2001; Morete *et al.*, 2008), singing activity of humpback males increases as the season progresses (Queiróz, 2010; Cerchio *et al.*, 2014) (Fig. 11).

Humpback whales remained in AB for up to 71 days (Wedekin *et al.*, 2010), and during this period and throughout the season, males were observed producing songs and in physical combat with other males over access to females, in addition to the energetic cost of the journey towards the reproductive area (Dawbin, 1966; Craig and Herman, 1997). Spending energy on physical combat at the end of their period in the breeding area may pose higher costs and resulting survival risks, making them use a less costly strategy at this time; that of singing.

Listening to the interaction between singing male humpback whales and noise

While listening for humpback whales, other environmental sounds present in the area were also recorded. The Abrolhos archipelago is an important tourist destination in Brazil, and boats take tourists to diving spots as well as to watch whales. Tracks of tourism boats obtained with GPSs in the area during the winter of 2005 are shown in Figure 12.

The ocean is certainly not a silent environment. Biological sounds, waves, tides, earthquakes and wind play important roles in the acoustic ecology of the seas. This constant background noise has modulated the communication systems of several aquatic species and organized their acoustic niches accordingly. Only with the advent of the Industrial Revolution did human activities begin to contribute energy to the acoustic seascape of the oceans. Examples of anthropogenic noise in AB include shipping and recreational boat traffic, which generate low-frequency noises that overlap in time and in frequency with many marine mammal sounds, and these noises often affect the

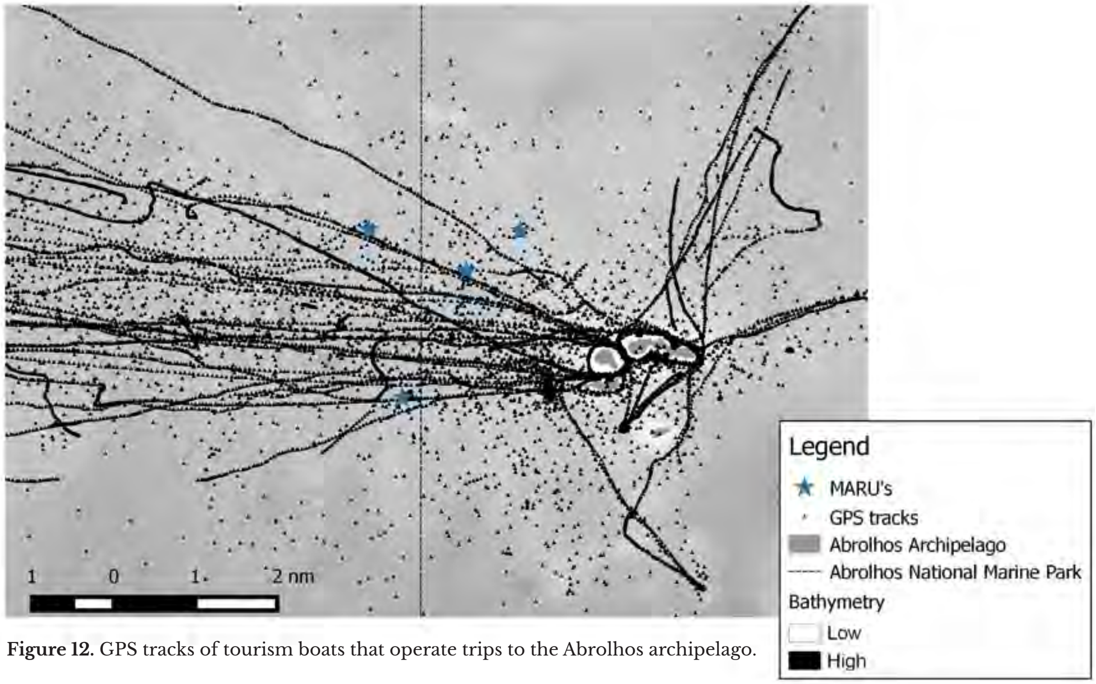

Figure 12. GPS tracks of tourism boats that operate trips to the Abrolhos archipelago.

animals negatively (Richardson *et al.*, 1995). Shipping is the greatest source of man-made low-frequency noise in the ocean (Richardson *et al.*, 1995; McDonald *et al.*, 2006). Vessels create noise through their engines, bearing changes, vibrations of the hull, and propeller cavitation (Urick, 1983; Richardson *et al.*, 1995). Documented short-term displacement of marine mammals exposed to these noise events (reviewed in Richardson *et al.*, 1995) includes disruption of important activities that may result in loss of food or mating opportunities for the animals involved. Further, a sustained increase in vessel noise can result in avoidance of the affected area temporarily or even permanently, as suggested by Bryant *et al.* (1984) for gray whales.

Advanced technology now provides the unique opportunity to follow the movements of these animals by sequential localization of their sounds, as shown above, as well as a tool to investigate the effects of noise-producing anthropogenic activities on their movements and behavior. A major new contribution of passive acoustic tracking technology is that it enables simultaneous follows of multiple "focal" singers. This greatly increases the efficiency of assessing the effects of boats by locating and discriminating multiple vocally active animals and their relative distance to an approaching boat (Sousa-Lima and Clark, 2009). Song cessation (Fig. 13) and displacement were detected by Sousa-Lima and Clark (2009). Masking is another important issue and in AB, MARU recordings show the same individual song can be masked at different levels depending on the relative distance between boat and singing male (Fig. 14).

Listening to humpback whales beyond the Abrolhos bank

With the increasing number of humpback whales off the Brazilian coast (Bortolotto *et al.*, 2016; Pavanato *et al.*, 2017), the population is re-occupying areas used before being affected by the whaling period (Rossi-Santos *et al.*, 2008; Andriolo *et al.*, 2010). Few studies have been carried out in coastal areas other than the Abrolhos bank (Baracho-Neto *et al.*, 2012; Lunardi *et al.*, 2008; Gonçalves *et al.*, 2018).

Passive acoustic monitoring was conducted approximately 400 km north of Abrolhos Bank in Serra Grande (Bahia, Brazil) from July to October of 2014 and 2015 (Gonçalves, 2017). Oceanpods, autonomous underwater sound recorders developed by LADIN from São Paulo University (Sánchez-Gendriz and Padovese, 2016), were deployed at depths of 16 to 22 m, up to 3 km away from the coast of Serra Grande to listen for humpback whales. Vocal and non-vocal activity was recorded, including song and percussive sounds produced by the whale body's impact with the surface of the water through breaching, flipper and tail slapping.

A preliminary description of song lineages from the Serra Grande region identified eight themes, including static, shifting, and non-patterned theme types

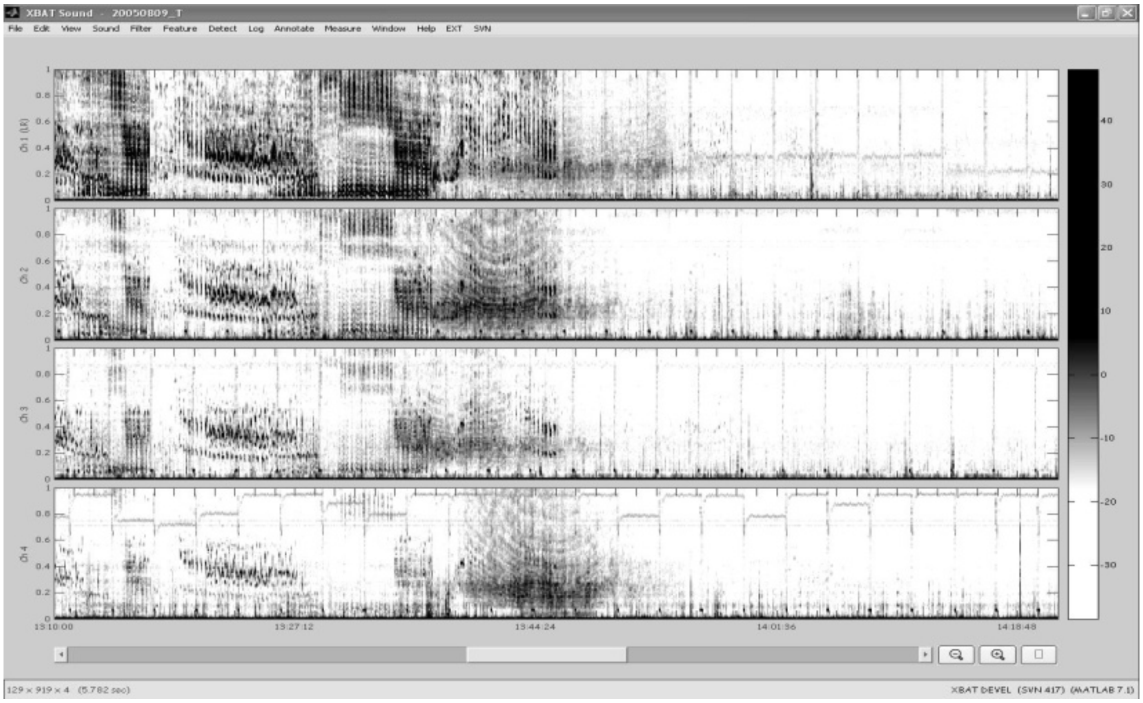

Figure 13. Spectrogram of four channels representing four synchronized MARUs showing the first third of the duration of a humpback whale song session, followed by a boat noise, and then showing cessation of song in the Abrolhos archipelago.

(Payne *et al.*, 1983). New units appeared, existing units were modified, and themes were subtracted and added over a two year period. The Levenshtein distance similarity index between Serra Grande songs from the years 2014 and 2015 was 50%.

Males also use areas north of Abrolhos during the breeding season to display vocally. These lower density areas could be essential for males that cannot successfully compete directly with other males, and theoretically contain less mates, but also contain less

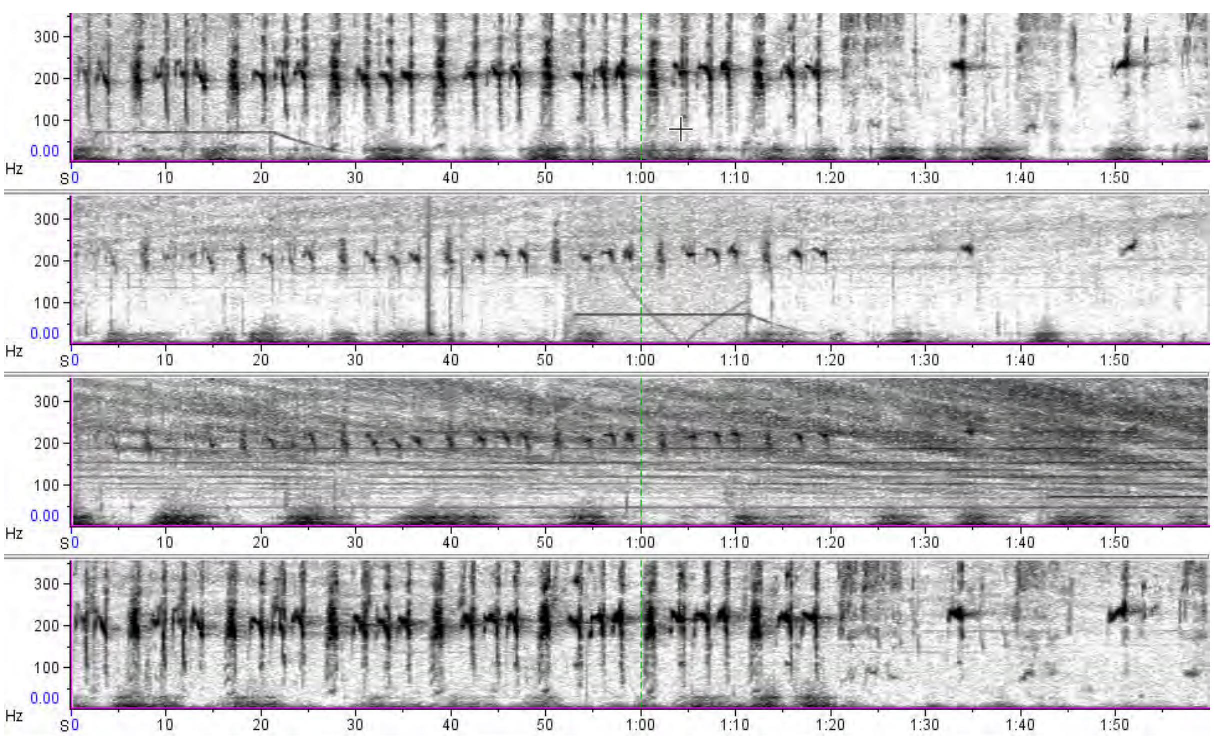

Figure 14. Spectrogram of four channels representing four synchronized MARUs showing a humpback whale song session in the Abrolhos archipelago, masked in the 3rd channel by a boat noise.

competitors (Clapham, 2000). Employing basic and advanced tools to investigate how singing activity is distributed along the entire distribution of humpback whales off Brazil is a unique opportunity to further explore this complex behavior at a larger scale, more appropriate for the humpback whale.

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