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Humpback Whales in the Western Indian Ocean

Guest Editor Olivier Adam

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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

Do the new-born calves of humpback whales (*Megaptera novaeangliae*) have a preference to position themselves at the side of their mother?

Anjara Saloma[1,3,5,*], Schédir Marchesseau[4,5], Isabelle Charrier[1], Aristide Andrianarimisa[3], Emmanuel Antogiorgi[6], Olivier Adam[1,2]

[1] Institute of Neurosciences Paris Saclay, France, NeuroPSI-CNRS, bat. 446, University of Paris Sud Orsay, 91400 Orsay, France

[2] Institut d'Alembert, *équipe* Lutheries Acoustique Musicale (LAM), CNRS UMR 7190, Université UPMC, Paris, France

[3] Zoology and Animal Biodiversity, University of Antananarivo, 101 Antananarivo, Madagascar

[4] Facultad de Veterinaria, Universidad CEU Cardenal Herrera, Moncada, España

[5] Cetamada association, Barachois Sainte Marie Island (515), Madagascar

[6] Duocean, Port de Saint Gilles, Rue Général de Gaulle, 97434, Ile de La Réunion

* Corresponding author:
anjarasalomavola@gmail.com

Abstract

Spatial proximity to mothers is a key factor in offspring survival in group-living mammals. In humpback whales (*Megaptera novaeangliae*), an extreme migrating species, new-born calves stay close to their mothers. This proximity can be modified by the presence of other congeners or other species. The spatial relationship between mother and calf can therefore vary with social contexts. The position of the calf relative to its mother was investigated in different social contexts: alone, with one or several escorts; and in the presence of free divers. The positions of the calves in the 3D space surrounding their mothers were recorded using video footage of mother-calf pairs in 3 breeding sites located in the Indian and Pacific oceans, with the space methodically divided into ten positions. Calves mainly preferred positions above their mother, either on the right or the left; a strategy allowing the calf to be in an optimal position to breathe and to benefit from the hydrodynamic aspiration flow of its mother. A position below the mother was significantly related to resting behaviour, involving physical contacts with the mother and thus reinforcing their social bond. Finally, calves in the presence of free divers neither approached nor moved away from them, suggesting limited direct impact on their behaviour.

Keywords: humpback whale, calf, laterality, behaviour, preferred position.

Introduction

For large marine mammals that bear a single offspring every two to three years, calf survival is critical for the perpetuation of the species, and this depends on the mother's ability to both feed and protect the new-born, as well as on the calf's abilities to stay close enough to the mother for protection and care. Only females provide care to the young with no paternal care after conception recorded (Barlow and Clapham, 1997). Humpback whales are born in sub-tropical areas where they spend their first months surrounded by males displaying aggressive behaviour, which occur within "competitive groups" composed of multiple males competing for proximity to a female, with or without calf (Baker and Herman, 1984; Tyack, 1981; Tyack and Whitehead, 1982). Mother-calf pairs must deal with the presence of other individuals surrounding them, calves must be able to follow their mother, and their schedules vary according to the number of males associated with the group (Cartwright and Sullivan, 2009a).

Spatial relationship and behaviour between mother-calf pairs in mysticetes present three distinctive phases that have also been observed in the southern right whale, *Eubalaena australis* (Taber and Thomas, 1982). The youngest calves spend most of their time travelling and breathing while maintaining proximity to their mothers. This spatial relationship becomes more distant as calves get older and allocate most of their time to playing and circling at the surface, while mothers stay a few meters underneath (Cartwright and Sullivan, 2009b; Zoidis, 2014). During movement, the young reduce their proximity to the mother and synchronize their movements and breathing, especially for long journeys such as on migration routes (Zoidis, 2014). As they grow, calves acquire new skills but still remain energetically-dependent on their mother (Cartwright and Sullivan, 2009b; Zoidis, 2014).

Depending on the social and maternal context, different sensory modalities are used to maintain such spatial proximity between mothers and new-borns, and the initiative can come either from mothers or calves. In a wide variety of vertebrates including odontocetes, the right-hemisphere of the brain, which is dedicated to social interactions, obtains information from the left eye, resulting in a right-side social lateralization pattern being observed in mother and infant positioning (Damerose and Vauclair, 2002; Manning and Chamberlain, 1990). In belugas, continuous visual contact is more important in mother-calf interactions than tactile contacts, and these are initiated by calves (Karenina *et al.*, 2010). In wild belugas, calves present a highly significant right-side swimming position preference with their mothers (Hill *et al.*, 2017; Karenina *et al.*, 2010; Yeater *et al.*, 2014). Much like in belugas, dolphin mother-calf pairs maintain right-side visual contact and the mothers seem to be partially responsible for maintaining proximity to their calves (Lyamin *et al.*, 2007). The same right-side infant position preference has been observed in wild orcas (Karenina *et al.*, 2013). All these examples of cetaceans include only odontocetes species, but nothing is known for mysticetes.

In the present study, we quantify the prevalent spatial positions chosen by humpback whale calves

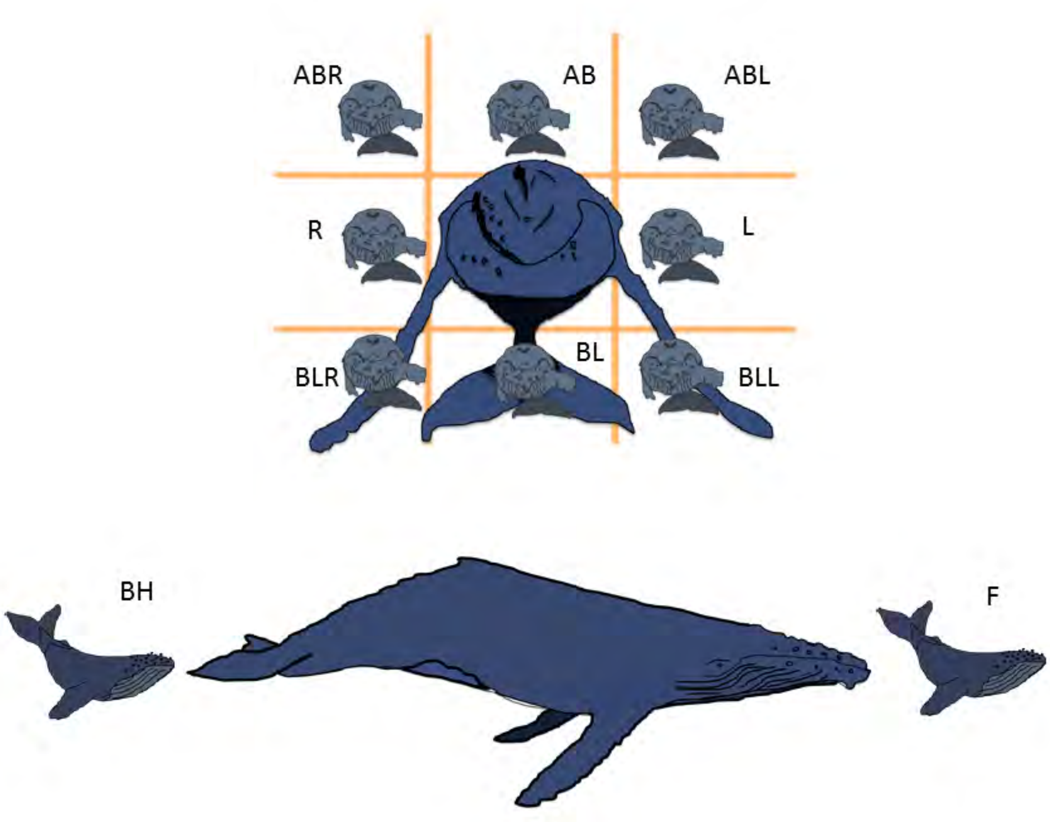

Figure 1. Schematic presentation of calf position (AB - above, ABR - above right, ABL - above left, R - right, L - left, BL - below, BLR - below right, BLL - below left, BH - behind, F - in front)

(a mysticetes species) around their mother, considering static and travelling behaviours, and their behaviour in the presence of free divers.

Methods

Video recordings

Opportunistic video data were obtained from different sources: 186 videos from snorkelers (using a GOPRO Hero 3 cameras); 2 videos from a drone (DJI Phantom 3 model); and 26 videos from immerged GOPRO Hero 4 cameras using a one-meter rigid pole from a boat or kayak. Videos were obtained from different geographic areas in the Indian Ocean (149 videos from Reunion Island, France, and 64 from Sainte Marie Island, Madagascar) and in the Pacific Ocean (1 video from Polynesia). From these 214 video files, a total of 91 mother-calf pairs were scored, representing a total observation time of 4 hours and 56 minutes. The mean duration of video files was 00:01:28 ± 00:00:06. The sex of the calves was identified when possible, and resulted in a sample of 20 female calves, 9 male calves, and 62 sex-undetermined calves.

Determination of calf position

For consistent interpretation of the results, only spatial positions initiated by calves were considered in the analysis, performed in two different ways. First, at a group level, all 91 mother-calf pairs were considered and the duration of each calf's position around the mother was noted, and average values for each position and for each calf was obtained. Secondly, all video files (214 videos) were considered without focussing on individual mother-calf pairs, and the average duration for each position of the calves was obtained. The position of calves was defined by using 8 grid positions around the mother, in addition to the position "in front (F)" and "behind (BH)" the mother. These were: above (AB); above right (ABR); above left (ABL); right (R); left (L); below (BL); below right (BLR); and below left (BLL) (Fig. 1). To compare the duration of each position among the 10 possible positions of the calf around its mother, Wilcoxon tests were used, and the p-values were correlated for multiple comparisons using Bonferroni correction. To detect any possible effect of side preference by the calves, the positions AR, R, and BR were pooled

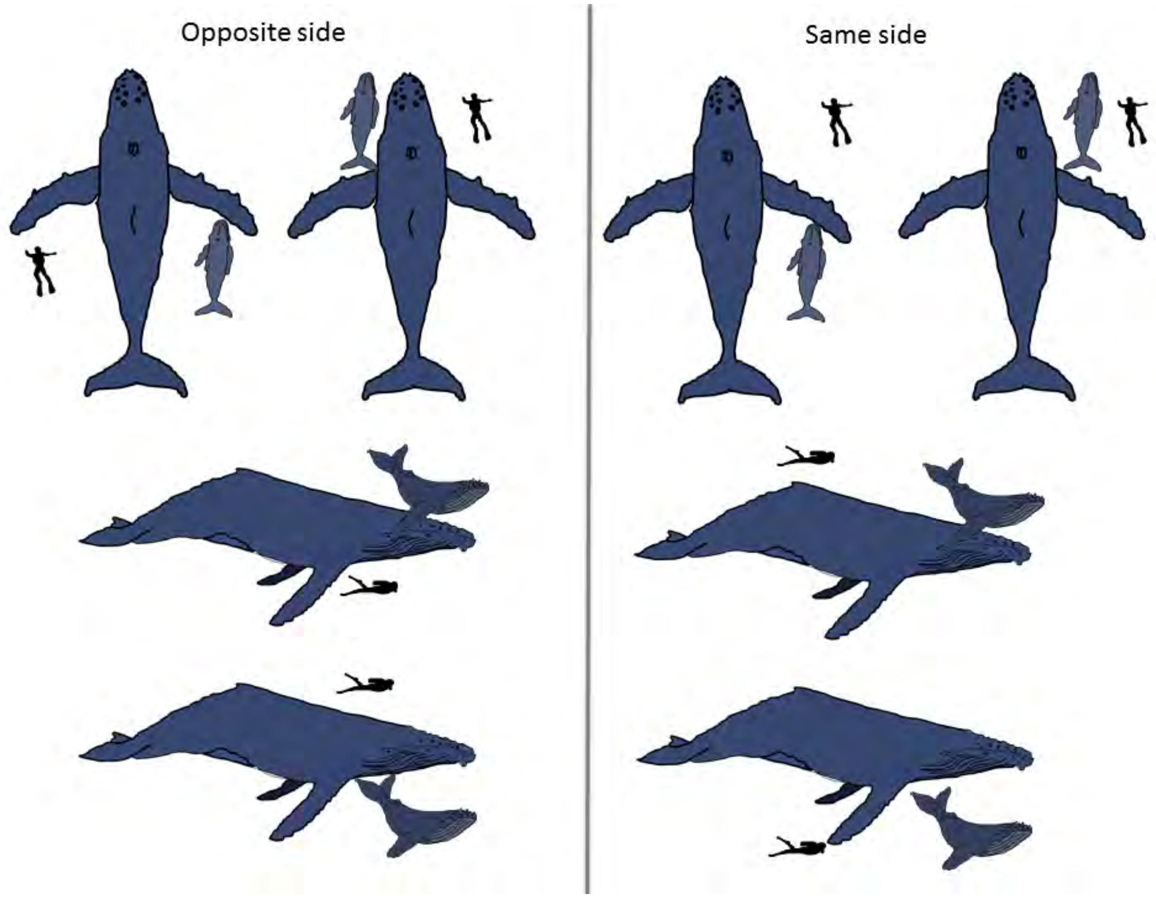

Figure 2. A schematic representation of free diver position in relation to calf position.

as "Right side", and AL, L, and BL as "Left side". Chi-squared tests were then carried out to compare the distribution of positions. Comparison between male and female calves could not be investigated due to the low number of sex-identified calves and an unbalanced number (9 males versus 20 females). Finally, to ensure that the position of the free divers' underwater video recording did not influence the calf's choices, the impact of the free divers' position on the calf's position was also assessed. The lateral position of calves compared to the free divers' positions were observed and categorized as "opposite" side, "same" side, or "others" when calves and divers were not in a lateral position (Fig. 2). In this analysis, only the position initiated by the calf itself was considered. Moreover, as the free divers did not behave in the same manner on each occasion when interacting with the calf, their behaviour was divided into two categories: "interaction behaviour", when the free divers aimed at interacting with the calf (e.g. proximity, or an attempt of physical contact); and "neutral", when free divers kept their distance from the calf.

Results

Calf position

Analysis of all groups pooled together

The analysis performed on 91 mother-calf pairs showed that the positions that accumulated the longest durations were "Above Right" (ABR=01:16:48) and "Above Left" (ABL=01:21:52). Wilcoxon tests performed for each category showed that the durations for "Above" positions were significantly different from all others (Table 1). However, there was no significant difference between "Above Right" and "Above Left" positions (test χ^2, ddl=1, χ^2=0.16, p=0.68) (Fig. 3).

Positions "Above" (AB= 00:37:22) and "Below" (BL= 00:49:50) were the second most important positions chosen by calves. No significance difference between these 2 categories was found (test χ^2, ddl=1, χ^2=1.74, p=0.18).

Right and left positions showed similar average durations and there was no significant difference between the two (test χ^2, ddl=1, χ^2=3.39, p=0.06) (Fig. 4).

Analysis at the group level

At a group level, 91 different pairs were considered. When a given group presented on several videos, an average of the position duration was calculated (Table 2). Considering the mean per group of the position durations, the main calf position choices around the mother were "Above left" (00:47:30) and "Above right" (00:44:27), followed by "Below" (00:30:36) and "Above" positions (00:18:41).

However, as for the summation of all groups, the main position durations "Above left" vs. "Above right" were not significantly different. This was also true for the second choices "Below" vs. "Above" (respectively, test χ^2, ddl=1, χ^2=0.10, p=0.75 and test χ^2, ddl=1, χ^2=2.93, p=0.08). Similarly, when pooling all right positions together, as well as all left positions, no significant difference was found in their durations (test χ^2, ddl=1, χ^2=1.32, p=0.24) (Fig. 5).

Table 1. Comparison of sum durations for each of the 10 calf positions around the mother. P values were assessed using pairwise Wilcoxon tests and a Bonferroni correction for multiple comparisons was applied.

	AB	ABR	ABL	R	L	BL	BLR	BLL	F	BH
AB										
ABR	**4.75E-06**									
ABL	**6.48E-05**	1.65E+01								
R	**1.27E-02**	< 9.90E-15	< 9.90E-15							
L	5.24E+00	**4.23E-11**	**1.68E-09**	1.16E+00						
BL	1.46E+01	**4.59E-04**	**4.03E-03**	**2.04E-04**	4.01E-01					
BLR	**3.00E-02**	**9.90E-15**	**1.09E-13**	4.18E+01	1.97E+00	**6.61E-04**				
BLL	2.99E-01	**1.60E-13**	**< 9.90E-15**	1.47E+01	1.04E+01	**1.08E-02**	1.85E+01			
F	**3.00E-02**	**3.30E-13**	**1.22E-11**	1.75E+01	9.98E+00	**7.61E-03**	2.37E+01	4.25E+01		
BH	**2.02E-06**	**< 9.90E-15**	**< 9.90E-15**	3.05E-01	**4.43E-04**	**1.30E-08**	2.89E-01	**3.12E-02**	**5.41E-02**	

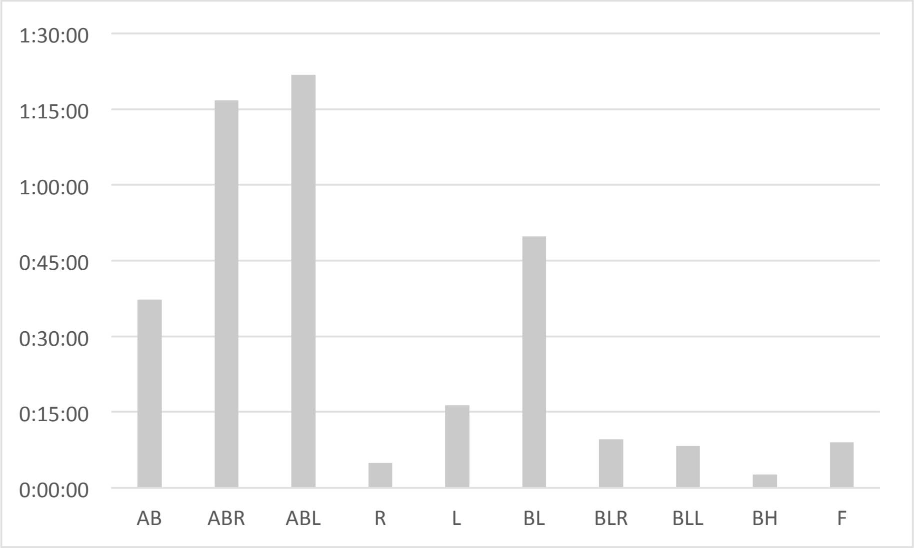

Figure 3. Sum durations for each of the 10 positions for all groups (AB - above, ABR - above right, ABL - above left, R - right, L - left, BL - below, BLR - below right, BLL - below left, BH - behind, F - in front).

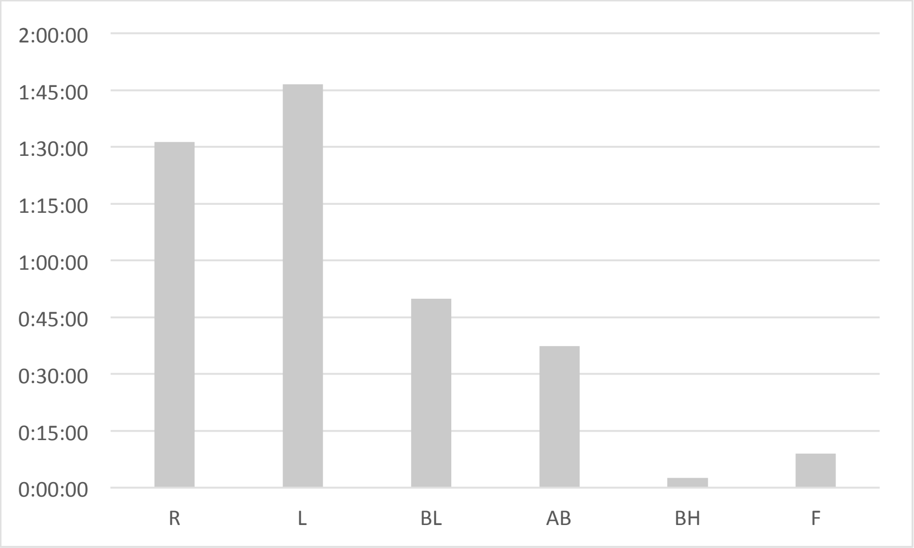

Figure 4. Sum durations for the 6 main positions: pooled right positions (R), pooled left (L), below (BL), Above (AB), behind (BH) and in front (F) for all groups together.

Impact of diver position on calf positioning

Results show that the position of free divers did not influence the position of the calf. The position durations where calves and free divers were on the same side of the mother ("Same Side" = 01:13:07) and those where the mother was between them ("Opposite Side" = 00:55:17) did not show any significant difference (test χ^2, ddl=1, χ^2=2.50, p=0.11). Calf-diver configurations that placed them on the same axis ("Same Side" and "Opposite Side") were significantly less frequent than all the other configurations (test χ^2, ddl=2, χ^2=74.72, p=5.93E-17). No effect of the position of the free diver on the calf positioning around the mother was found. Indeed, whatever the behaviour of the free diver, either attempting to interact with the calf or keeping a distance from the calf, no significant differences between the position durations between "Same side" and "Opposite Side" were found (test χ^2, ddl=1, χ^2=0,00053, p=0,98 and test χ^2, ddl=1, χ^2=3.43, p=0.06, for interaction or neutral behaviour, respectively) (Fig. 4). Regarding the behaviour of free divers towards the calves, most attempted to interact with the calf (test χ^2, ddl=1, χ^2=101.57, p=6.87E-24).

Discussion

This study investigated initiative and preferential position of young calves (i.e. less than 3-month old) around the mother during surface activities. Only two

Table 2. Comparison of mean durations for each of the 10 calf positions around the mother. P values were assessed using Wilcoxon tests and a Bonferroni correction for multiple comparisons.

	AB	**ABR**	**ABL**	**R**	**L**	**BL**	**BLR**	**BLL**	**F**	**BH**
AB										
ABR	**3.92E-06**									
ABL	**2.78E-04**	1.39E+01								
R	**4.22E-03**	**< 9.90E-15**	**< 9.90E-15**							
L	4.14E+00	**6.05E-11**	**1.43E-08**	9.06E-01						
BL	1.22E+01	**1.53E-03**	**3.16E-02**	**6.56E-05**	2.76E-01					
BLR	**1.66E-02**	**< 9.90E-15**	**4.62E-13**	4.18E+01	1.66E+00	**3.31E-04**				
BLL	1.65E-01	**2.36E-13**	**4.09E-11**	1.68E+01	8.22E+00	**4.83E-03**	2.23E+01			
F	3.28E-01	**4.77E-12**	**5.18E-10**	1.48E+01	1.17E+01	**7.70E-03**	2.07E+01	4.06E+01		
BH	**1.10E-06**	**< 9.90E-15**	**< 9.90E-15**	3.17E-01	**4.73E-04**	**6.74E-09**	2.84E-01	**5.51E-02**	**4.90E-02**	

calves were new-borns with one being 2-hours old. Mother-calf dyad position is critical when the calf is young, as proximity must be maintained during travelling, surfacing and diving activities. In other cetacean species such as bottlenose dolphins, it has been demonstrated that some calf positions provide locomotor advantages (Noren and Edwards, 2011). In this study, the prevailing positions of calves were "Above Right" and "Above Left" during static and travelling behaviour. Being above the mother near the rostrum allowed the mother-calf pair to keep visual contact during static behaviour. While travelling, these positions could be explained as a strategy used to benefit from aspiration flow or "drafting effect of swimming" (Chatard and Wilson 2003) produced by the movement of the mother, which creates a pressure wave around her while diving or travelling. This drafting effect is beneficial to the calves only if they stay close to their mother. Back-riding by calves has been reported recently in blue, fin and grey whales, and this supports the hypothesis of adaptive benefits of locomotion energy savings for calves (Smultea *et al.*, 2017). For humpback whales that have a large and mobile lek mating system (Clapham 1996), females accompanied by their calves are exposed to breeding males. Association with groups of multiple males

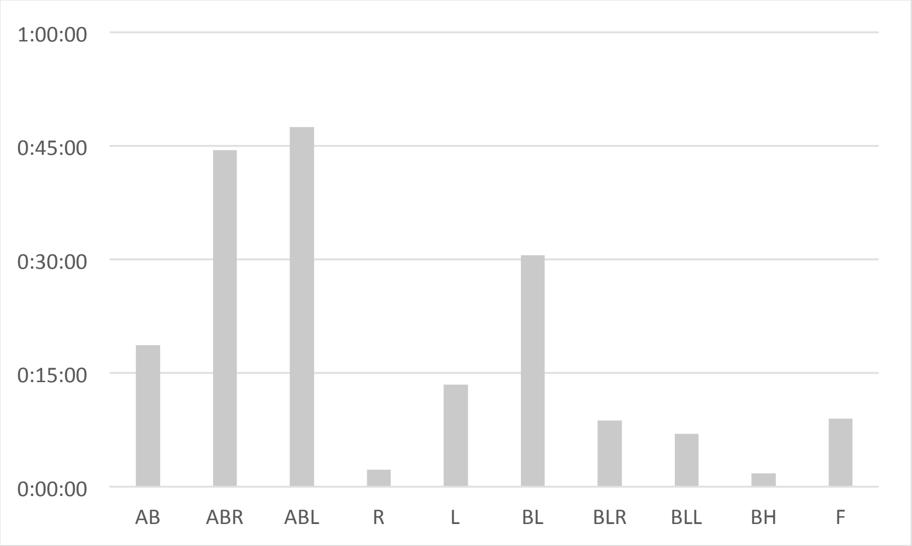

Figure 5. Average durations per observed group for the 10 studied positions (AB - above, ABR - above right, ABL - above left, R - right, L - left, BL - below, BLR - below right, BLL - below left, BH - behind, F - in front).

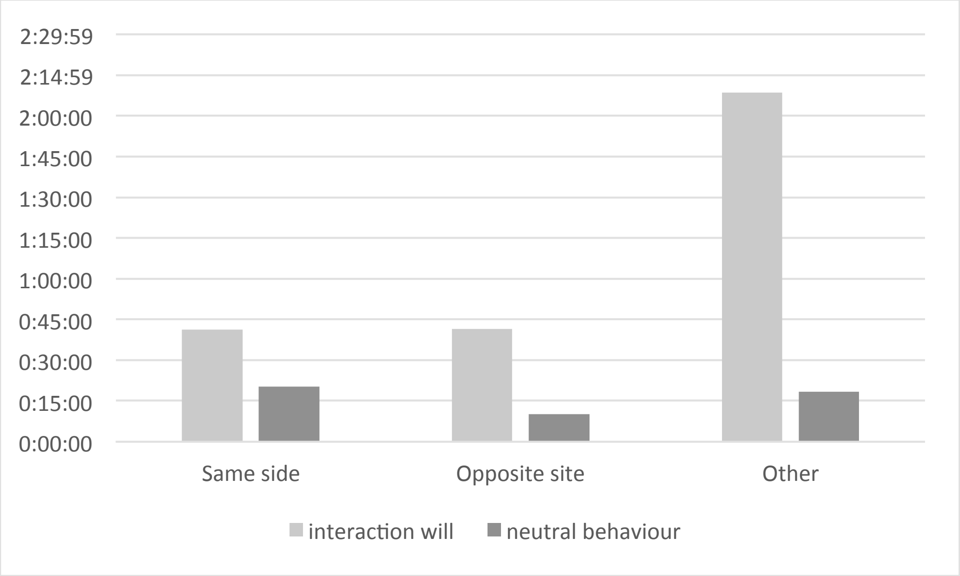

Figure 6. Position durations of the diver-calf dyad in 2 different free diver contexts (i.e. the free diver willing to interact with the calf - "interaction will", or the free diver keeping distant from the calf - "neutral behaviour").

encourages mother-calf travelling behaviour and thus energy expenditure (Cartwright and Sullivan, 2009a).In the case of a very large lek such as the population in the breeding area off Madagascar (Cerchio *et al.*, 2016), humpback whales travel long distances during the breeding season and females accompanied by their young calves can travel up to 100 km in 24 hours (Dulau *et al.*, 2017; Trudelle *et al.*, 2016). Keeping a position above and close to the mother allows calves to move securely, controlling their space orientation and reducing energetic expenditure, while having the same swimming performance as their mother.

The second most common position observed is "below" the mother (below the rostrum and flipper) that corresponds mostly to resting behaviour of calves, or occasionally below the caudal peduncle (when nursing), although there was no nursing behaviour observed in the present study. Humpback whales are well known for their ability to maintain neutral buoyancy in a head-down position during resting and singing behaviours (Adam *et al.*, 2013). Controlling their buoyancy is one of the skills that calves must acquire early on in life. Staying below the mother provides a secure place to rest and pause when the buoyancy of the calf is not yet well controlled, and this position also allows the pair to maintain physical contact.

In contrast to what has been described in the literature for odontocetes species, calf lateralization with regard to their position around the mother appears to be absent in humpback whales. Even though lateralization has been observed in humpback whales for some active surface behaviours such as flippering (Clapham *et al.*, 1995), and potentially for nursing (Zoidis and Lomac-MacNair, 2017), these results should be considered with caution as further work with a larger sample size is required. Further investigations are needed to explore laterality in humpback whale mother-calf interactions.

The assessment of simultaneous calf and free diver positions revealed no significant impact on calf positioning. The presence of free divers did not seem to have an attraction or repulsion effect on the calf. However, it is possible that other non-behavioural impacts such as physiological stress could result from these interactions (e.g. an increase in heart rate, or increased stress hormone levels such as cortisol) (Martin and Réale, 2008; Ropert-Coudert *et al.*, 2009). Furthermore, it has been shown that during interaction with divers, the mother often moves closer to her calf when the calf produces a series of grunts, considered to be an alarm signal (Zoidis *et al.*, 2008). In the present study, only one scream (a mid-frequency harmonic sound) was heard while free divers were very close to the calf. The behaviour of the mother after this call could not be assessed, as the mother was not in the visual field of the camera. This was the only such alarm call encountered in the sample from the present study, suggesting that in general, free divers do not have a direct impact on the behaviour of humpback whale calves.

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Distribution and biological characteristics of Humpback whales in the Northwest region of the Indian Ocean according to data from the Soviet whaling fleet

Yuriy A. Mikhalev

Institute of Marine Biology,
National Academy of Sciences
of Ukraine
yuriy.a.mikhalev@gmail.com

Abstract

The distribution and biological condition of humpback whales (*Megaptera novaeangliae* Borowski, 1781) caught during the 1960s by Soviet whaling flotillas in the relatively poorly studied Northwest region of the Indian Ocean, from the Asian coast to 40°S, and from the east coast of Africa to 80°E, were analyzed. Two distinct clusters were identified: South of Madagascar (Southern region); and off the coast of the Arabian Peninsula (Northern region). The humpbacks of the Southern region do not differ significantly from humpbacks from the higher latitudes of the Southern Ocean, and the humpbacks of the Northern region are similar to the humpbacks of the Northern Hemisphere, not only geographically, but also in their biological characteristics.

Keywords: Humpbacks, northwest region, Indian Ocean, distribution, sizes, nutrition, embryos, reproduction, biological condition.

Introduction

Soviet Antarctic whaling began after the Second World War when a former German whaling base (Wikinger) and several whalers were transferred to the Soviet Union as reparations. After repair and restoration in Liverpool (Great Britain) the fleet of vessels was named “Slava”. The fleet’s first season was in 1946, and the first whale was captured in January 1947. Another whaling vessel, “Yuri Dolgoruky”, was converted from the German passenger liner “Hamburg” in 1960. Two domestic whaling vessels, “Soviet Ukraine” (1959), and “Soviet Russia” (1961), were built at the Nikolaev shipbuilding plant.

Between 1947 and 1972 (the years when whaling of large species of baleen whales was abandoned) Soviet Antarctic whalers caught 38,832 humpbacks, but only 1,555 whales (a quota assigned to the Soviet Union) were reported to the IWC. Actual extraction exceeded the allocated quota by 25 times, and at the same time the requirements related to the size and biological condition of whales were violated (Yablokov, 1994; Zemsky *et al.*, 1994, 1995, 1996; Yablokov & Zemsky, 1995, 2000; Yablokov *et al.*, 1998a, 1998b; Mikhalev, 2008).

It is known that in these years, and much earlier, the poaching of whales was conducted by the fleets of other countries. The main damage to the global whale population was caused long before the Soviet whaling (Golovlev, 2000). Strangely enough, even when the International Convention for the Regulation of Whaling was signed and adopted in 1946 and the Rules for whaling were designated, control of whaling was not implemented.

In 1961, by order of the Minister of Fisheries of the USSR, a state inspection was introduced for Soviet whaling flotillas. This act had a certain political significance, but in fact it covered-up the poaching even more. Not until 1972, when only the whaling flotillas of Japan and the Soviet Union remained in the Southern Ocean targeting small Minke whales (*Balaenoptera*

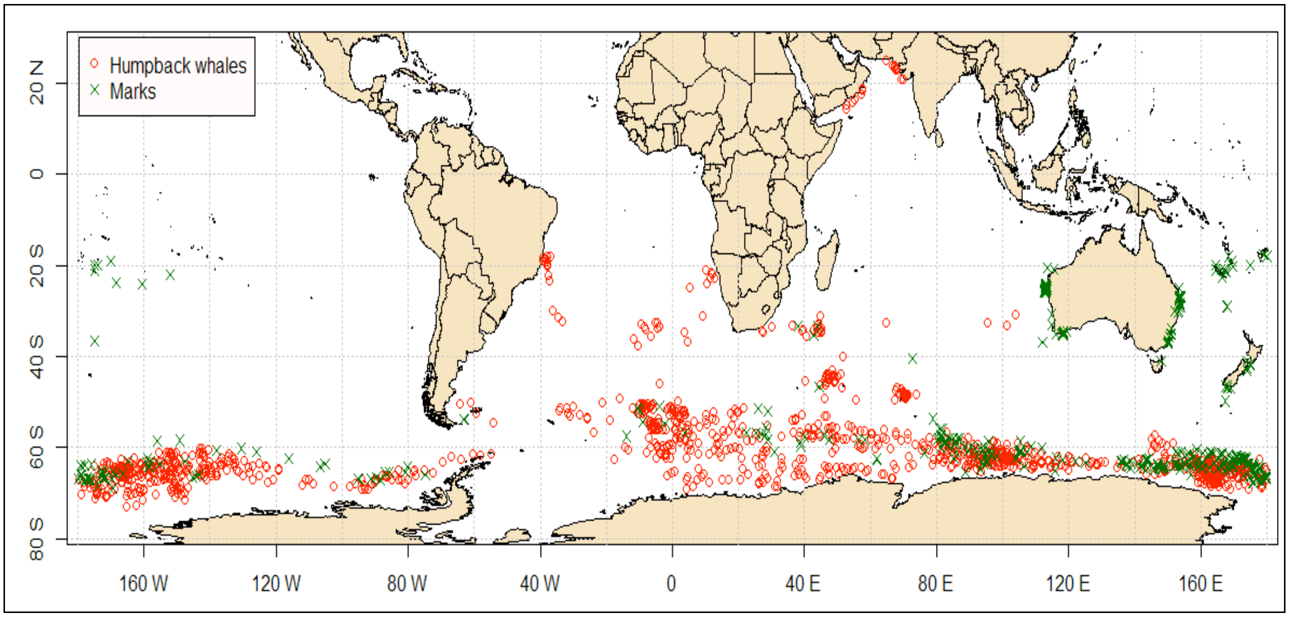

Figure 1. Distribution of humpbacks in the Southern Ocean and adjacent waters as per Soviet whaling data.

acutorostrata), were so-called "observers" introduced. However, because Japanese representatives began to appear on Soviet vessels, and Soviet ones on Japanese vessels, this could hardly be considered effective international observer programme. Poachers quickly learned to work together, and poaching and falsification of data continued.

Fortunately, scientific groups constantly worked on the Soviet vessels, and kept independent records of the whales surveyed by them. At the end of each season, the scientific groups submitted reports to the relevant institutions. Most of the whale watching logs kept by research workers on the flagships "Slava" and "Soviet Ukraine" have been accessed, and together with season reports from other flotillas, have allowed a more accurate picture of the actual distribution and biological status of the whales of the Southern Ocean and adjacent waters to become apparent.

At the session of the Scientific Committee of the International Whaling Commission (Puerto Vayarta, Mexico, 1994), Russian scientists reported on large-scale poaching of whales by Soviet flotillas and made public the actual data on whaling activities. The Russians believed that other countries would also divulge this information, but this never happened, and Russia remains the only country to have done so. The Russian data is therefore the only absolutely reliable information available in terms of species composition, volume of whaling, size, distribution and biological status of whales.

In this study it was possible to obtain objective results on the distribution and migration of humpback whales (*Megaptera novaeangliae* Borowski, 1781) based on the exact coordinates of the locations where 9,418 whales were caught, as well as the tagging of 3,944 whales (Fig. 1). As a result of tagging it became known that for feeding these whales migrate from the waters of Brazil to the west of the Bellingshausen Sea; the West African herds migrates to the vicinity, and to the south of, Gough Island; the West Australian herds migrate to the Commonwealth Sea; the East Australian herds migrate to Balleny Island, to the Commonwealth and Ross Seas; and the New Caledonian herds feed in the region of the Balleny Islands to the Bellingshausen Sea. In May, whales were observed in the Cook Strait and near the southern tip of Africa (Tomilin, 1957, 1980; Dawbin, 1964, 1966; Rice & Scheffer, 1968; Yablokov *et al.*, 1972; Ivashin, 1973, 1990; Mikhalev & Tormosov, 1997; Mikhalev, 2000, 2008).

In warm waters in breeding areas active migration of humpbacks is observed in April, but some whales remain in cold high latitudes for winter. In the low latitudes, breeding zones are noted off the coast of Brazil and the southwestern coast of Africa, south of Madagascar, off the southwestern coast of Australia, off the coast of Tasmania and New Zealand, and in subantarctic waters in the vicinity of Bouvet, Crozet and Kerguelen islands. The breeding areas of humpbacks in high latitudes of the Southern Ocean are in the Bellingshausen Sea, an area east of the Commonwealth Sea, and the waters east of Balleny Island.

The present study focuses on humpbacks in the relatively poorly studied Northwest region of the Indian Ocean, north of 40°S. This is the area for which reliable data exists on humpback whaling even while the Soviet Union was violating IWC rules. Other countries were whaling in these waters long before the signing of the 1946 Convention. Humpback whaling in this region was conducted in the Mozambique Strait, in the Seychelles, and in the coastal waters of Madagascar (Townsend, 1935; Angot, 1951; Rorvik, 1980; Keller *et al.*, 1982; Kasuya & Wada, 1991; Leatherwood & Donovan, 1991; Findlay *et al.*, 1994). According to the International Whaling Statistics, for the whaling season of 1909/10 to 1946/47, to the south of Madagascar, as well as the southeast coast of Africa, 12,759 humpbacks were caught. Strangely, on the maps of Townsend (1935), compiled from distribution data from ship's logs of American whalers of the 19th century, the humpback population in this region was concentrated only in the Mozambique Channel and on the eastern and west coast of Madagascar, and not to the south and north of Madagascar, as well as in the open waters of the region under investigation. This was despite the fact that at that time, American whalers were hunting throughout the Northwest region of the Indian Ocean, right up to the shores of the Arabian Peninsula. These maps even show sperm whales as being encountered off the coast of the Arabian Peninsula.

Material and Methods

In this paper, the humpbacks of the Northwest region of the Indian Ocean are discussed. The analysis covers the area from the east coast of Africa to 80°E and from the northern coast of the Arabian Sea to 40°S. The analysis included data from the examination of humpbacks by members of scientific groups on the Soviet whaling fleet of vessels "Slava" (1963-1966), "Soviet Ukraine" (1964-1967) and "Yuri Dolgoruky" (1962-1965). Determination of the species composition of whales and their measurements were conducted according to the "Unified methodology for studying cetaceans" (Yablokov *et al.,* 1972). The database of these data is included in the computer programme "Kit", created by the son of the author, Vladimir Mikhalev. The programme uses algorithms of graphical methods, construction of maps, the construction of histograms of dimensional series, and algorithms for processing digital material by biometric statistical methods (e.g. Plokhinsky, 1961, 1978; Rokitsky, 1961, 1964; Urbakht, 1964).

Results

"Yuri Dolgoruky" was the first of the Soviet fleet of vessels to begin whaling of humpbacks in the Northwest region of the Indian Ocean. They caught only one humpback whale each month to the south of Madagascar from November to January during the 1962/63 season. In November 1964, seven humpbacks were caught in the same area by this flotilla, and at the end of the voyage in May 1965 another humpback was caught. The flotilla "Soviet Ukraine" and "Slava" caught humpbacks in the Northwest region of the Indian Ocean, voyaging from Odessa to the Southern Ocean for whaling, not as usual through the Strait of Gibraltar, but through the Suez Canal, the Red Sea and the Bab-el-Mandeb Strait. They returned home by the same route. It is possible that information received from the Kuwaitis on whaling in the Persian Gulf drew the attention of Soviet whalers to this region, and, consequently, to adjoining waters.

The flotilla "Slava" caught 6 humpbacks; 3 in November and 3 in December during the voyage of 1964/65 to the area under investigation. The flotilla "Soviet Ukraine" operated with much greater success in the Northwest region. In November 1965, it caught one humpback, and on the next voyage in November 1966, 238 humpbacks. In November 1967, this flotilla

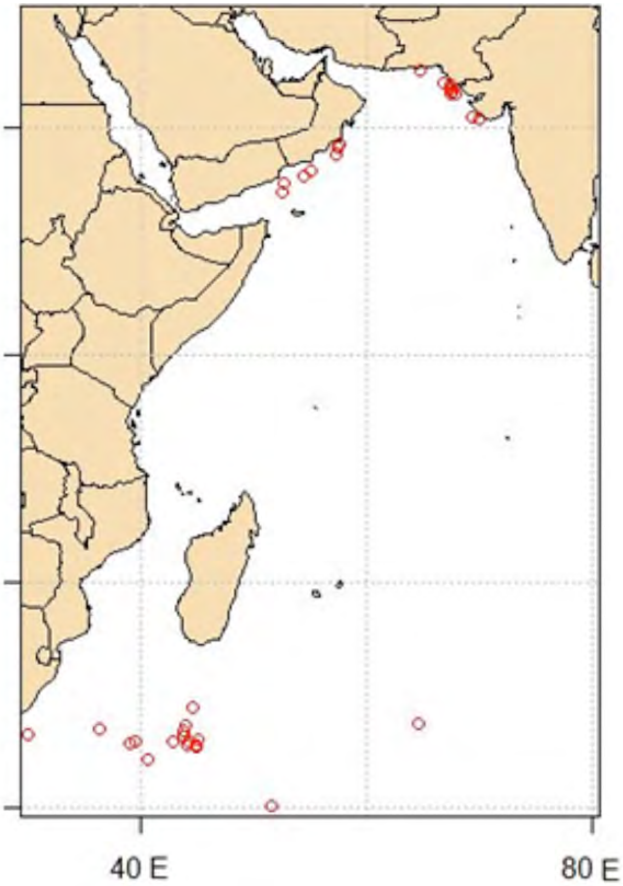

Figure 2. Distribution of humpbacks caught by Soviet fleets in the northwestern area of the Indian Ocean.

caught 41 humpbacks, and in December another 42 humpbacks (Mikhalev, 1997, 2000a, 2000b, 2008). So humpbacks were caught in November to December in the Northwest region, and only one whale was taken in January and May. When analyzing the distribution of humpbacks in this region, the presence of two areas that are fairly remote from each other is clearly visible; the southern region (south of Madagascar) and the northern region (the northern part of the Arabian Sea) (Fig. 2).

Dimensions and biological condition of humpbacks

In total, Soviet flotillas caught 318 humpbacks in the Northwest region of the Indian Ocean, of which 182 (57.2%) were males and 136 (42.8%) were females. The length distribution of humpback whales in dimensional classes is illustrated by the histogram in Fig. 3. In females, the length varied from 6.7 m to 15.5 m, with an average length of 13.3 m. The males ranged from 6.9 m to 14.9 m, with an average length of 12.9 m. The histogram is not symmetrical and shows visually that "small-sized" individuals (less than 11 m), including suckers, were banned from whaling to a considerable extent. In this case, the average size of animals is better characterized not by mean lengths, but by modal values of dimensional series. For females, the modal value is 13.75 m, and for males, 13.25 m, showing that, as is typical for humpbacks, females are on average half a meter larger than males. The average size of humpbacks without separation by sex was 13.04 m, with a modal value of 13.25 m (Table 1).

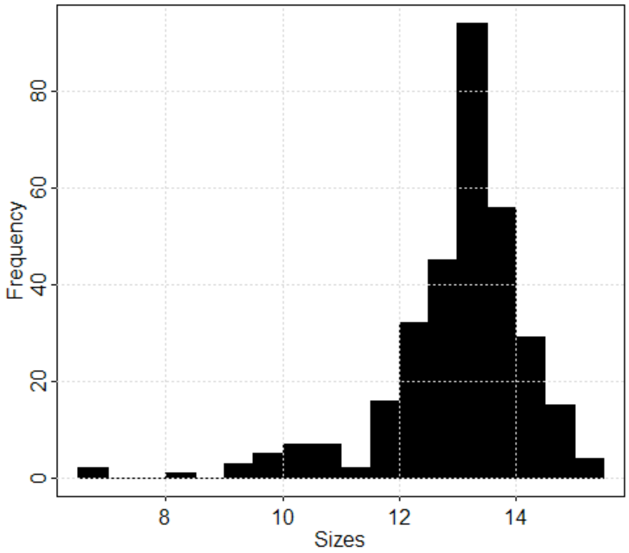

Figure 3. Histogram of humpback whale sizes for the northwestern area of the Indian Ocean (n=318).

Characteristics of humpbacks in the Southern region

The humpbacks in the Southern region accounted for a small part (76 individuals, or 23.9%), of all humpbacks caught in the Northwest region. They were mainly concentrated in the 30 latitudes, south of Madagascar (Fig. 2). There were twice as many males (53 or 69.7%) than females (23 or 30.3%). Dimensions of

Table 1. The size of the humpbacks of the Northwest region of the Indian Ocean according to the data of Soviet whaling flotillas.

Regions	**Number and size of adults**		
	Both sexes, ♂♀	Males, ♂	Females, ♀
All regions	N=318 Average=13.04m Min=6.7m Max=15.5m Modal=13.25m	N=182 Average=12.9m Min=6.9m Max=14.9m Modal=13.25m	N=136 Average=13.3m Min=6.7m Max=15.5m Modal=13.75m
South region	N=76 Average=13.0m Min=6.7m Max=15.5m Modal=13.25m	N=53 Average=13.0m Min=6.9m Max=14.5m Modal=13.25m	N=23 Average=13.1m Min=6.7m Max=15.5m Modal=13.25m and 14.75m
North region	N=242 Average=13.0m Min=9.1m Max=15.2m Modal=13.25m	N=129 Average=12.8m Min=9.5m Max=14.9m Modal=13.25m	N=113 Average=13.3m Min=9.1m Max=15.2m Modal=13.75m

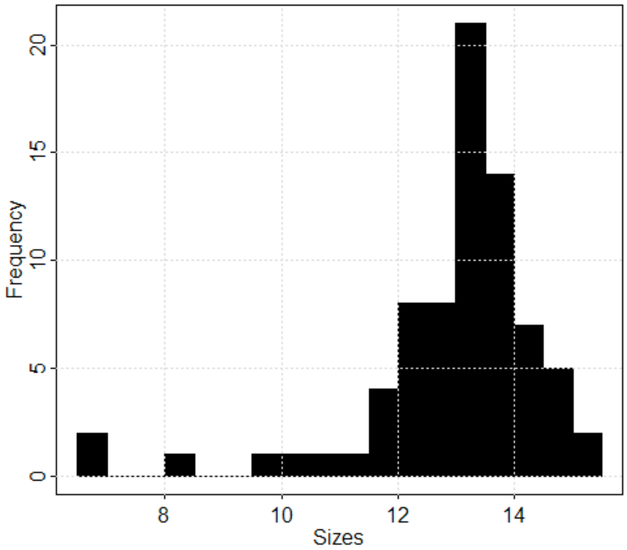

Figure 4. Histogram of humpback whale sizes for the southern area (n=76).

humpbacks of the region are given in Table 1 these are illustrated in the histogram in Fig. 4. The length of the males varied from 6.9 m to 14.5 m with an average of 13.0 m. The modal class was 13.25 m. The average size of females was slightly larger than that of males and was 13.1 m. The females also had more scatter length with a minimum of 6.7 m, and maximum of 15.5 m. There were two modal classes, 13.25 m and 14.75 m, which was most likely determined by a small sample of only 23 individuals. However, it is also possible that a part of the female population migrates to the breeding zones. The small number of pregnant females (3) at the early stages of pregnancy could support this conclusion. The aggregation of whales in the Northwest was geographically distant from other known more southern aggregations near the islands of Prince Edward, Crozet and Kerguelen, and did not differ in their biological indices from these (Mikhalev, 2008).

Characteristics of humpbacks in the Northern region.

The region is located in the northern part of the Arabian Sea, which occupies a special position in the World Ocean. Being in the Northern Hemisphere (its northern border runs through 30°N), the sea is also quite isolated from its main waters and, on the contrary, is closely connected with the waters of the Southern Hemisphere. The presence of humpbacks in the region was first reported by Gervais (1888), who described a dried humpback on the coast of Basra Bay in the Persian Gulf. The population of humpbacks in this area was not affected by whaling until the 1960s, and for these reasons is of special interest.

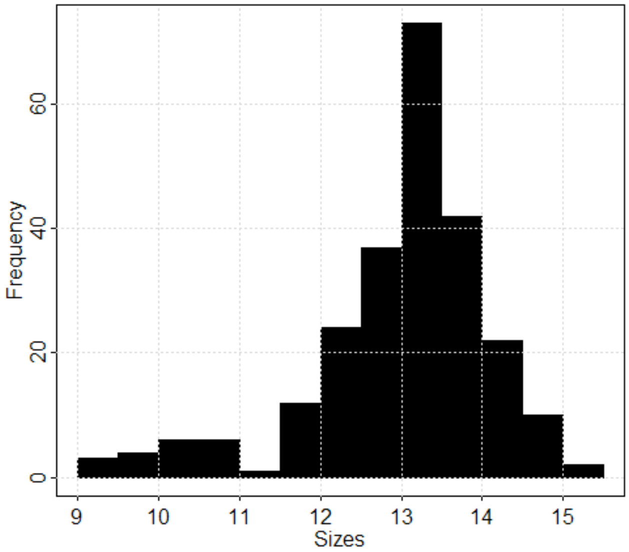

Figure 5. Histogram of humpback sizes for the northern area (n=242).

Aggregations of humpbacks were found by whalers off the Oman coast near the Kuria-Muria and Masira Islands, off the coast of Pakistan, and also on the Kathiavar Peninsula (India). Whalers learned about the humpbacks of this peninsula from the former whaling captain Alexei Solyanik, from the ship "Van Gogh", who was fishing shrimp here. Most of the humpbacks (242 whales, 76.1%) from the investigated region were caught here. Their length distribution according to the classes of the variational series is shown in Fig. 5. The minimum length of humpbacks in the area was 9.1 m and the maximum length was 15.2 m. The average size of the animals was 13.0 m, with a modal value was 13.25 m. From the 242 humpbacks, 129 (53.3 %) were males, and 113 (46.7%) females. The size of the males varied from 9.5 m to 14.9 m, with a modal value of 13.25 m, and an average length of 12.78 m. Most often males were from 12.1 m to 14.0 m (84.1 %). The average size of females was 13.31 m. Their sizes ranged from 9.1 m to 15.2 m, with a modal value of 13.75 m. More often females were from 13.1 m to 14.5 m (71.0%) (Table 1).

Biological analysis showed that the sexual maturity of both male and female humpbacks of the Northern region occurs when they reach a length of 11.5 m. Among the females, immature individuals made up 12.4% of the sample. Pregnant females made up 45.9% of the number of sexually mature individuals, while 51.8% were male, and 3.1% were nursing females. A low percentage of nursing females in the area is also confirmed by observations from a scout ship which reported that in this area only one female with a suckling was observed.

Table 2. The size of embryos found in female humpbacks in the northwestern region of the Indian Ocean.

Regions	**Number and size of embryos**		
	Both sexes, ♂♀	Males, ♂	Females, ♀
All regions	N=41(2-esd*) Average=215cm Min=1 Max=375 Modal=195	N=13 Average=195cm Min=10 Max=375 Modal=165	N=26 Average=242cm Min=140 Max=353 Modal=255
South region	N=3 (2-esd*) Average=4cm Min=1 Max=10 Modal=15	N=1 Average=10cm Min=10 Max=10 Modal=10	– – – – –
North region	N=38 Average=232cm Min=64 Max=375 Modal=195	N=12 Average=211cm Min=64 MAx=375 Modal=165	N=26 Average=242cm Min=140 Max=353 Modal=255

* esd – early stage of embryo development

41 embryos were found in pregnant females, but only 38 embryos could be measured (Table 2). A 14.6 m female had twins; a female of 190 cm in length, and a male of 210 cm in length.

Discussion

Clearly, the data show that there were two fairly distant clusters of humpbacks in the region; Southern and Northern. Despite this, the average length of humpbacks in the whole region and in the separate parts of the Southern and Northern regions was around 13.0 m. It is important to note that this length is higher than the average length according to pelagic whaling data in the middle and high latitudes of the Southern Ocean. According to the International Whaling Statistics for the period from 1933 to 1945 (13,375 individuals), the average length of humpbacks in the Southern Ocean was 12.47 m (Tomilin, 1957). Consequently, the state of humpbacks in the Northwest Indian Ocean region was better by the 1960s. A relatively small percentage of immature individuals (9%-10%) also testifies to their relatively prosperous condition.

It should be noted, however, that the maximum size of the humpbacks in the Northwest Indian Ocean was 14.9 m for males, and 15.5 m for females. According to the literature, (Tomilin, 1957; Rising, 1928) in the 1920s-30s, lengths of 17.38 m and even 18.0 m were common. Of course, in those years the sample was much higher than the present study with 12,375 humpbacks caught. However, there is some doubt about these early measurements, and it cannot be ruled out that these whales were not measured in a straight line (as is the case with the "Unified Method"), but by the body contour.

Another picture is seen in the analysis and comparison of the biological state of of whales in the two regions. Of the 23 females in the Southern region, only three animals were pregnant. The embryos found in females on November 21, 1967, were of small size; 1 cm in the female of 14.0 m, 2 cm in the female of 14.4 m, and 10 cm (male embryo) in the 14.8m female. On average, the embryos were about 4 cm in length. Such embryo sizes generally correspond to the season of mating of southern humpbacks (Mikhalev, 2008). For the humpbacks of the Northern region (the northern part of the Arabian Sea), immature individuals made up 12.4% of the 113 females. From the number of sexually mature individuals, 45.9% were pregnant, 51.8% immature, and 3.1% nursing. A close, almost equal proportion, of the percentage of pregnant and mammary females indicates a high reproductive ability of humpbacks of this population with average females giving birth every two years (one year pregnancy, one year feeding and rest).

In pregnant females, sex was determined for 38 of the embryos found. 12 (31.6%) of them turned out to be

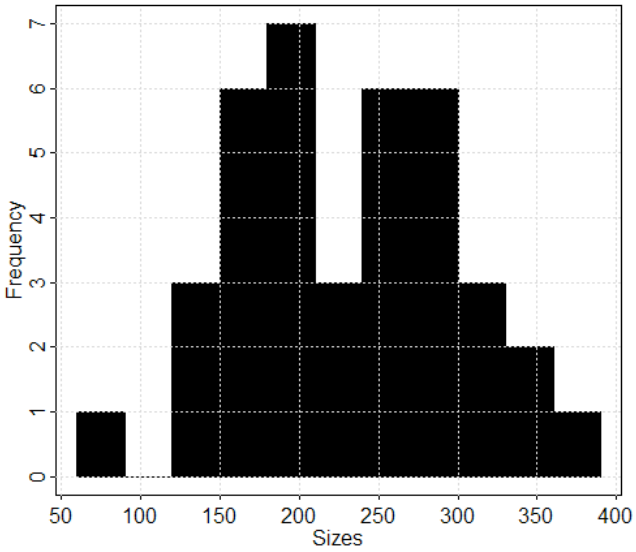

Figure 6. Histogram of humpback embryo sizes for the northern area (n=38).

males, and 26 (68.4%) female. This sex ratio is most likely influenced by a small sample. In the Southern region only 13% of the mature females where pregnant, and the embryos were small and at a relatively early stage of development. In the Northern region almost half of the mature females were pregnant (45.9%) and embryos were large. Their average length was 232 cm. The length of the measured embryos (with the exception of one of 64 cm long, which differed from the next largest embryo by 76 cm) ranged from 140 cm to 375 cm. When ranked, the difference in the length of two neighboring embryos did not exceed 20-22 cm. Such parity in embryo length is usually inherent in isolated, non-mixed herds of whales. However, the small sample (38 embryos) does not allow one to make such a conclusion with confidence, especially since two modal classes were apparent in the series of embryo length distributions (Fig. 6).

Judging by the size, and according to the methodology developed by the author for determining the age of embryos of whales (Mikhalev, 1970, 1975, 1984, 2007, 2008), the mating season for humpbacks in the Northern region lasts about three and a half months, from January to May, with a peak in the first half of March. This seems quite realistic, since the largest embryos at the beginning of November already had a length of 340-375 cm. In this case, the calving season for the humpbacks of this region begins in December, and its peak falls at the beginning of February. So the season of reproduction of humpbacks in the Northern region (the northern part of the Arabian Sea, which is in the Northern Hemisphere) coincided with those of humpbacks in other parts of the Northern Hemisphere, rather than the Southern hemisphere, as

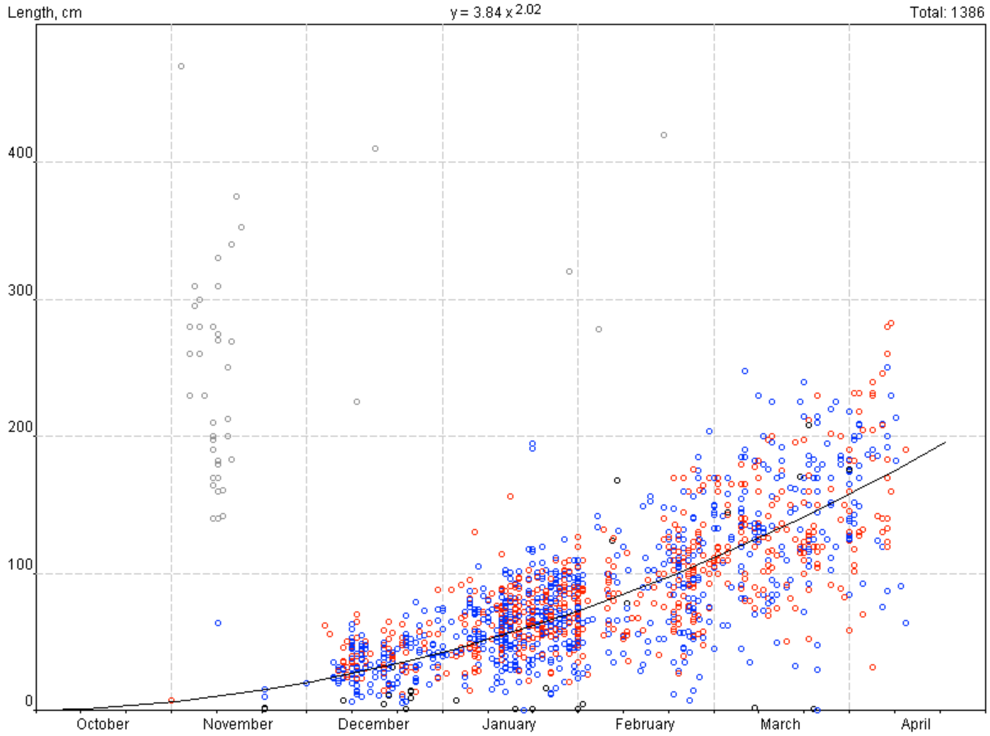

Figure 7. Humpback embryo sizes in the Arabian Sea (left-upper grey dots) and in the Southern Ocean (right-lower dots with curve formula: $l=3.84t^{2.02}$). Blue dots – males, red dots – females. Grey dots are excluded, when the curve is calculated.

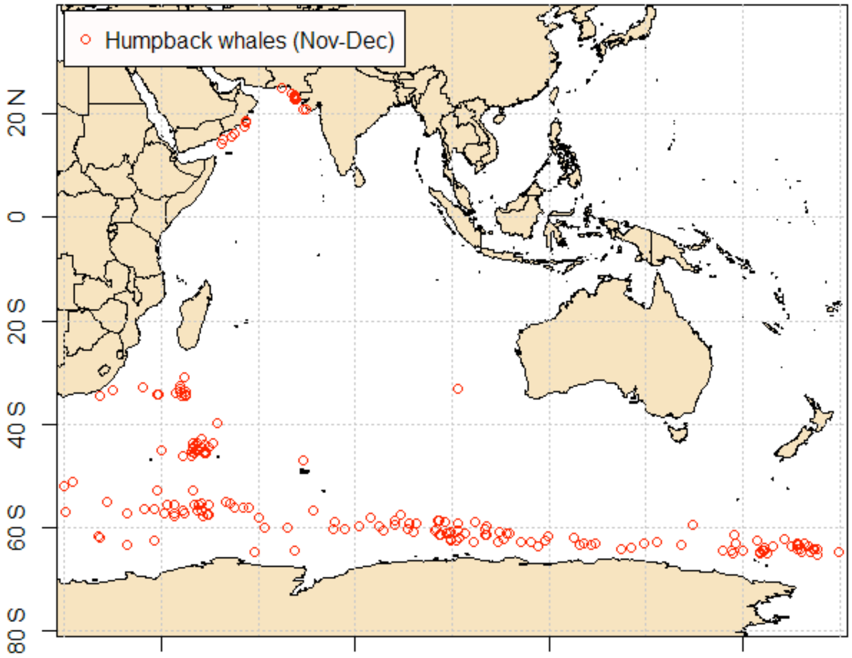

Figure 8. Distribution of humpbacks in November-December.

indicated by the location of embryo lengths by months of the year (Fig. 7). It should be noted that all other concentrations of humpbacks in the Indian Ocean in November-December are located to the south of the thirty-fifth latitude (Fig. 8).

According to the color of the ventral side of the body of humpbacks, Omura (1935), Matthews (1937), and Matsuura (1940), identified three main types; black-belly, variegated, and white-belly. According to the data by Ivashin (1958) from the Southern Ocean, the humpbacks of the South African herd are most likely to be included in the Southern region studied in the current study, and are dominated (80%) by "black-bellied" humpbacks. In the Northern region, of the 65 humpbacks examined, 46.2% were black bellied, 26.2% were variegated, and 27.6% white-bellied. That is, as in the Southern Ocean, the black-bellied humpbacks prevailed, but their percentage was much lower.

The damage to the surface of the body by the barnacle crustaceans *Coronula* sp. was noticeably different from the southern humpbacks. The damage was minor and the *Coronula* sp. were smaller. There were much fewer "white scars" on their body from the bites of small pelagic sharks than for Antarctic humpbacks (Shevchenko, 1970, 1971, 1975, 1977). Many of the humpbacks in the Northern region had a damaged liver. Out of 38 animals examined, liver pathology was registered in 68.5% of cases. There was connective tissue damage of the peripheral parts of the liver with the appearance of cone-like growths up to 20 cm in diameter. The bile ducts were filled with a thick, muddy-gray mass. The pattern of pathological changes resembled liver damage caused by parasitizing trematodes, however, it was not possible to isolate these worms from the affected areas.

The stomachs were examined for 190 humpbacks. The degree of fullness was as follows: "Full" - 10%; "Half" - 40.5%; "Little" - 34.2% and "Empty" - 15.3%. While the food of the humpbacks of the Southern region was mainly *Euphausia*, those in the Northern region also fed on bony fish including *Corangidae, Scomber* sp., *Sardinella* sp., with one whale found to have about a ton of *Sardinella* in its stomach. The degree of fullness of stomachs and the species composition of the contents indicated a good food base in the region, and confirmed the findings of other studies on the distribution and magnitude of plankton biomass in the surface waters of the Indian Ocean (Bogorov & Vinogradov, 1961).

Information on the migration of humpbacks to the Arabian Sea and back to the south is not yet available. Tomilin (1957) assumed possible migration of an "insignificant part" of the South African humpback population through the Mozambique Channel and further along the coast to the Arabian Sea. However, it is important to note here that whaling ships of the flotilla

"Slava" and "Soviet Russia" did not notice humpbacks in the area between 10° and 20°S both in October-December and in April-May. Humpbacks were also not noted in the area of Mozambique, Madagascar, Mauritius and north of 15-20°S from August to October by other researchers (Angot, 1951; Rorvik, 1980; Findlay *et al.*, 1994). Humpbacks were also not registered in the Seychelles area during aerial observations during the period April-July (Keller *et al.* 1982). There was not a single humpback observed in May and July on the expedition of 1993 that crossed the Indian Ocean from Australia to Africa (Eyre, 1995). This hypothesis of Tomilin (1957) is difficult to accept because of the already mentioned differences in the humpbacks of the Northern region from humpbacks in the Southern region, particularly in the size of the embryos. It is noted that there is no information about the penetration of northern humpbacks into the Arabian Sea, through the waters of Indonesia from the North Pacific, and it is therefore apparent that the humpbacks of the Northern region of the Northwest area of the Indian Ocean make up a discrete population. It is possible that Gervais (1988) was right in suggesting that the Persian Gulf humpbacks belong to a stand-alone species, *Megaptera indica*. Unfortunately, sufficient standardised whale measurements and age determination data are not available from the region under investigation to confirm this. Further comprehensive research is necessary to resolve the systematics of the humpbacks in the Northern region of the Arabian Sea.

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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.

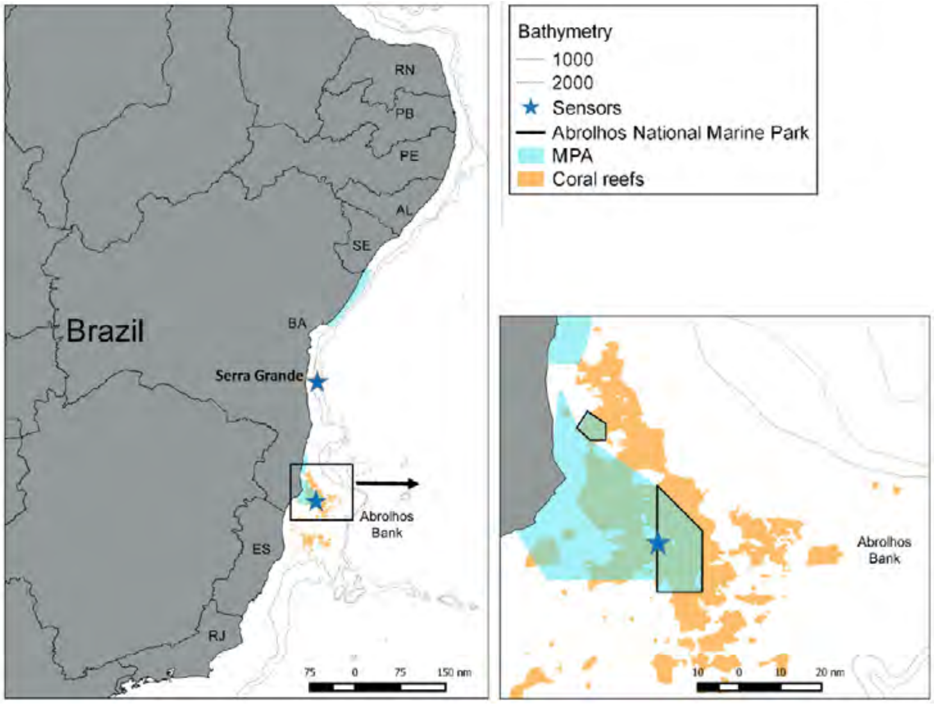

Figure 2. Map of the coastal Brazilian states where humpback whales are known to occur and limits of the Abrolhos National Marine Park within the Abrolhos Bank.

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 km^2 (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 km^2 (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

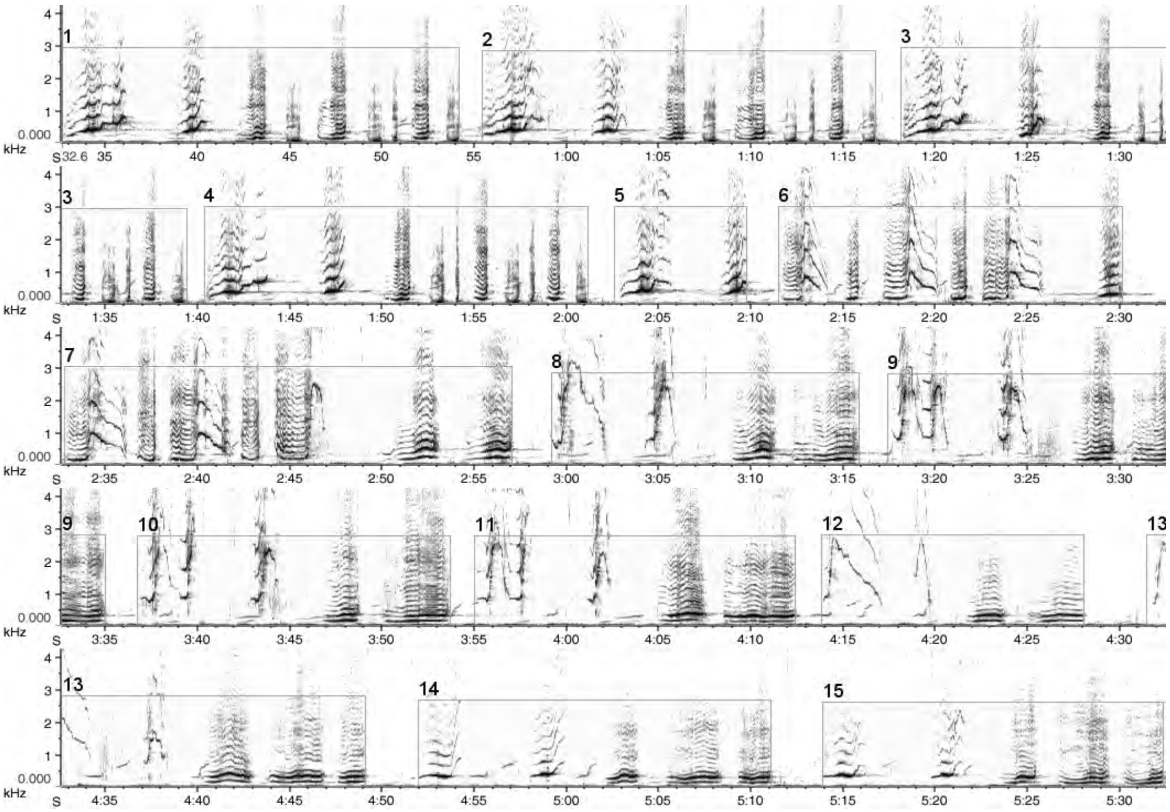

Figure 5. Spectrogram of part of a Brazilian humpback song recorded with a dipping hydrophone connected to a portable recorder from a boat.

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

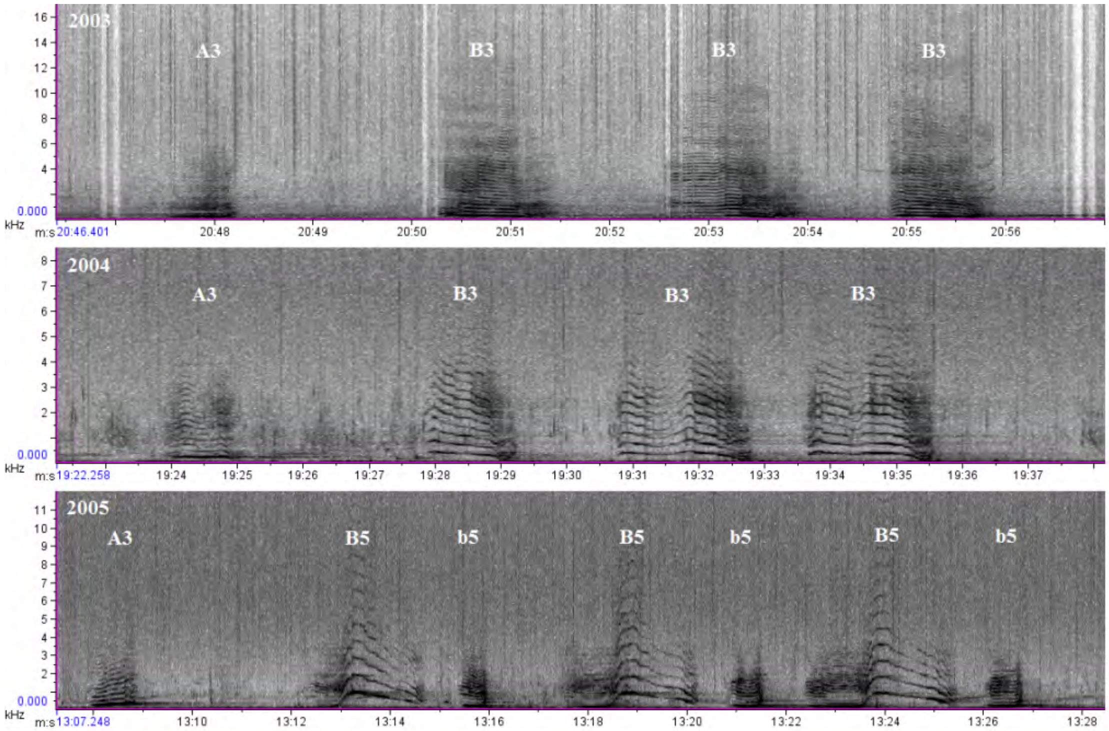

Figure 6. Spectrograms containing phrases of the Theme 1 lineage for the years 2003, 2004 and 2005. Capital letters indicate the position of the unit in the phrase, numbers indicate the year they first appeared, lower case letters indicate a new type of unit not present in the years before.

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

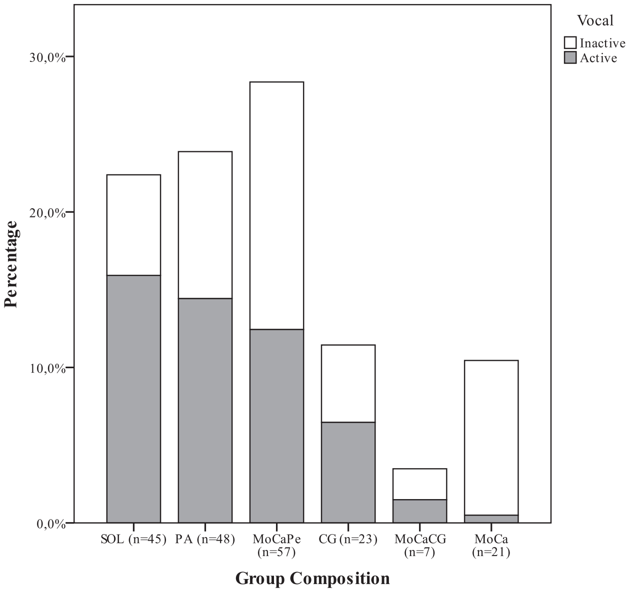

Figure 7. Distribution of the percentage of sighted humpback whale groups that were vocal, or not, during acoustic monitoring dedicated boat surveys in AB in two consecutive years (2004 and 2005). MoCa: mother and calf; MoCaPe: mother and calf with principal escort; MoCaCG: competitive group with a mother-calf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

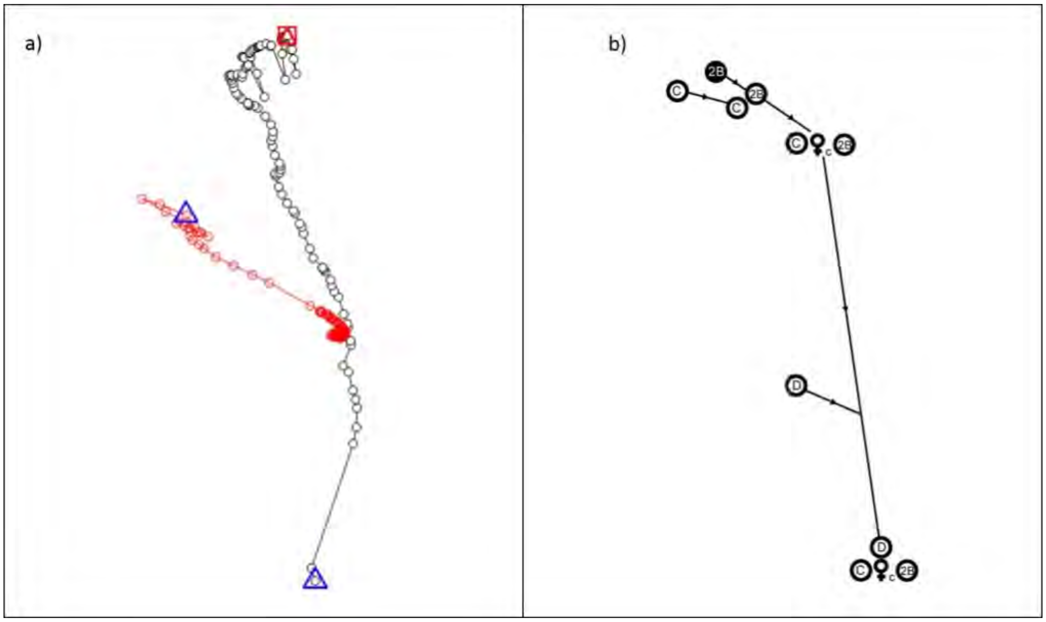

Figure 8. (a) Original trajectories inferred using PAM. Red and black dots represent different singers, and blue and red marks show the starting and final locations of each singer; (b) Trajectory schemes simplified from Darling *et al.* (2006). Each code composed of a letter (or a letter and a number)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

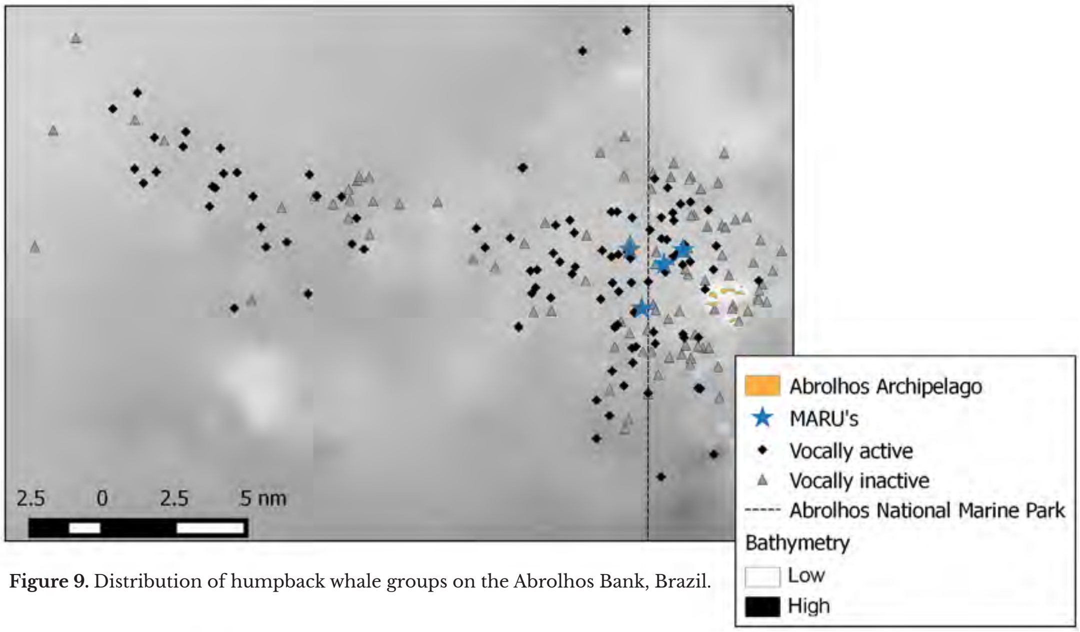

Figure 9. Distribution of humpback whale groups on the Abrolhos Bank, Brazil.

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).

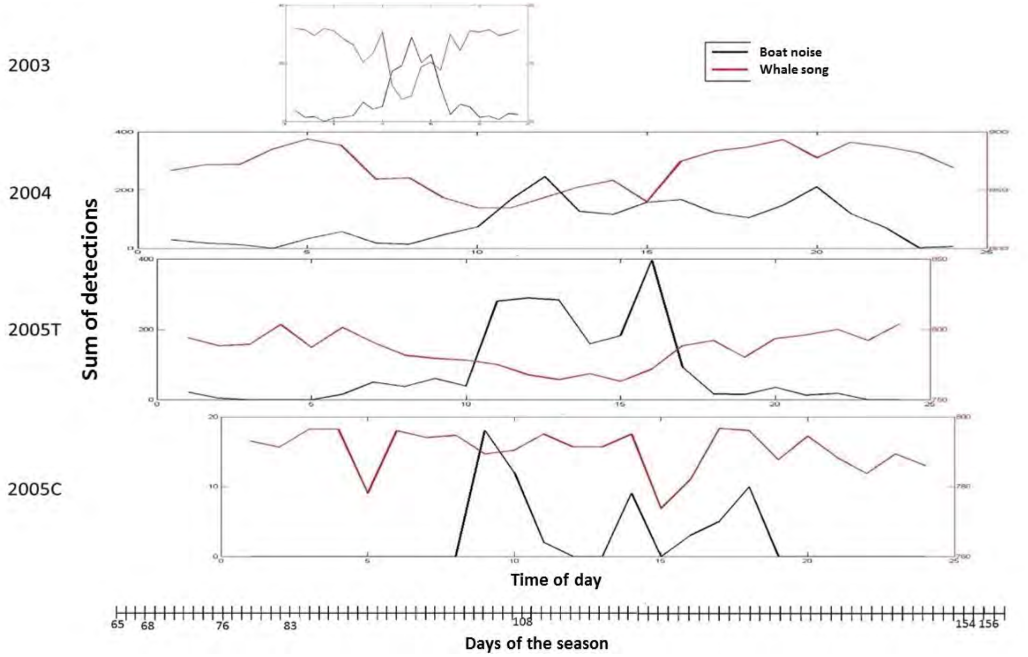

Figure 10. Number of 2-minute segments with detections of singing activity around the Abrolhos archipelago, Brazil in the years 2003, 2004 and 2005 (in two different areas) recorded with arrays of marine acoustic recorder units (MARUs) plotted in 24 hour panels. The width of the panel corresponds to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

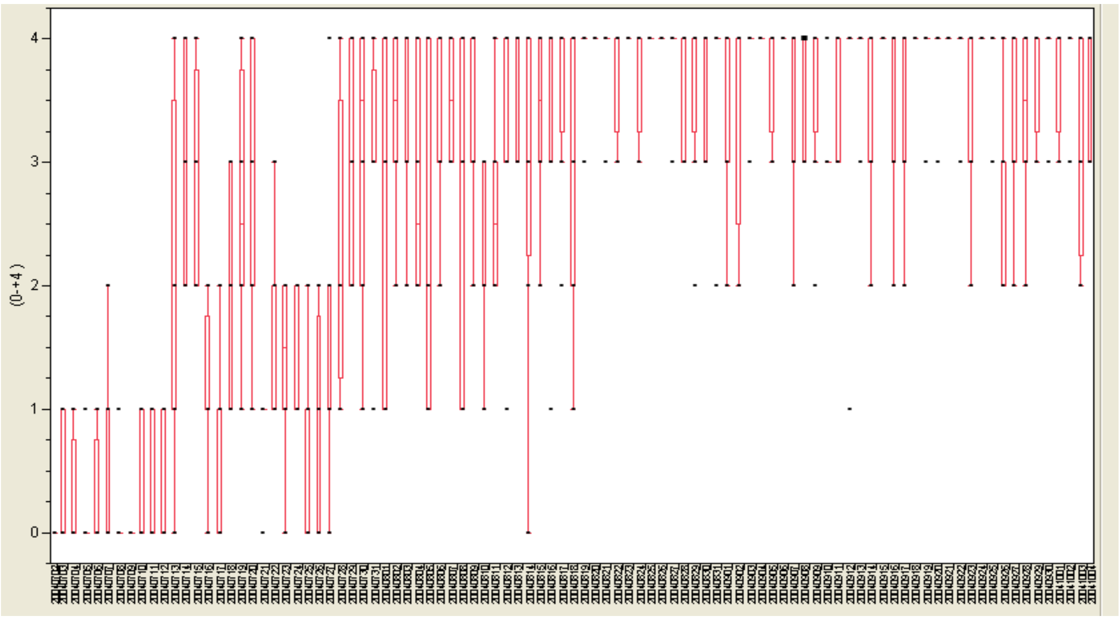

Figure 11. Number of humpback whale singers (0 to 4 or more) counted in 2004 off the Abrolhos archipelago showing an increase in singing activity as the season progresses.

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

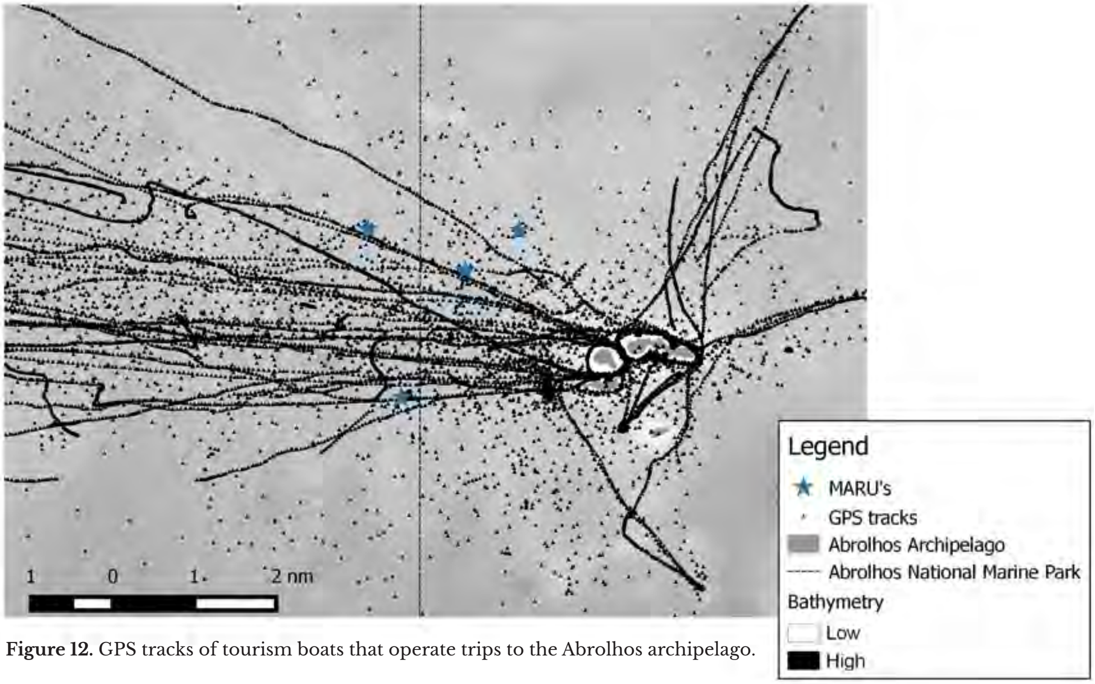

Figure 12. GPS tracks of tourism boats that operate trips to the Abrolhos archipelago.

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

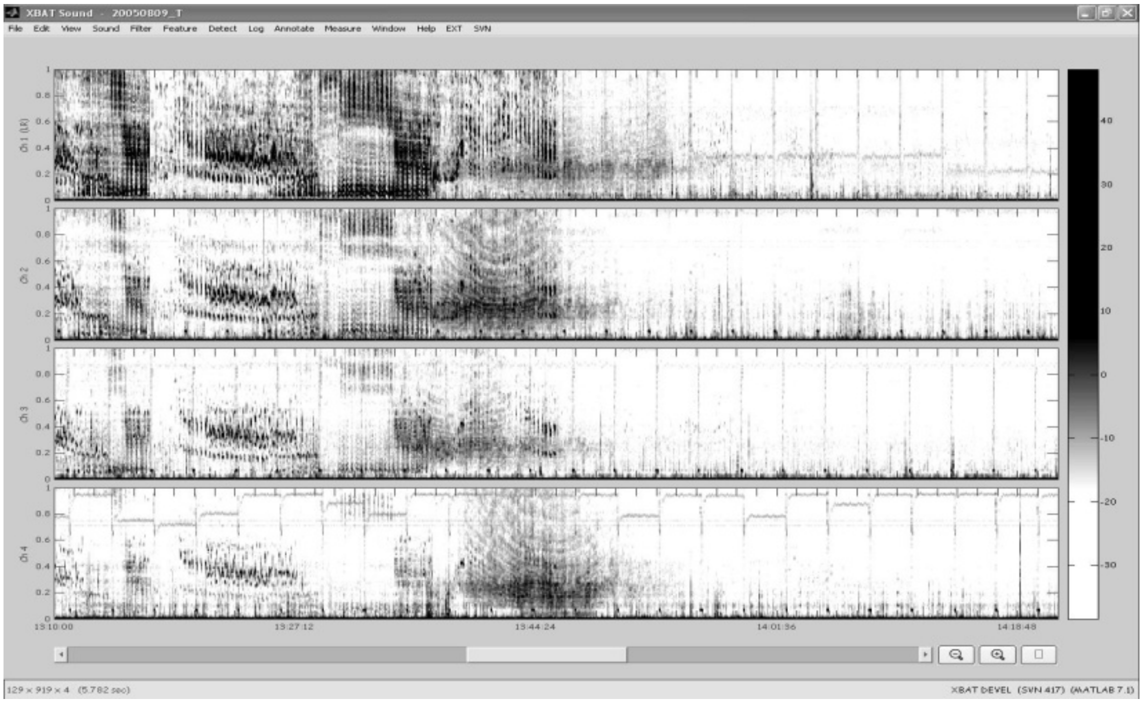

Figure 13. Spectrogram of four channels representing four synchronized MARUs showing the first third of the duration of a humpback whale song session, followed by a boat noise, and then showing cessation of song in the Abrolhos archipelago.

(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

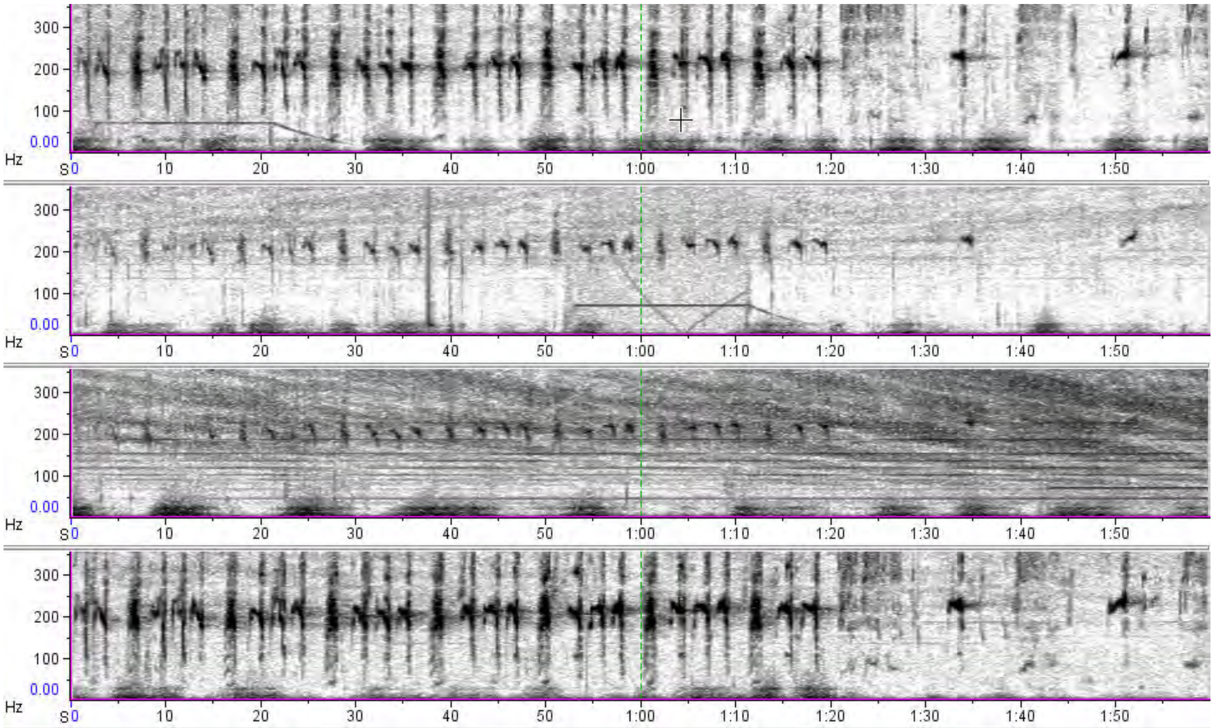

Figure 14. Spectrogram of four channels representing four synchronized MARUs showing a humpback whale song session in the Abrolhos archipelago, masked in the 3rd channel by a boat noise.

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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Recurrent acoustic patterns produced by a singing humpback whale (*Megaptera novaeangliae*)

Eduardo Mercado III

Department of Psychology;
Evolution, Ecology, & Behavior Program
University at Buffalo, SUNY, Buffalo, NY 14260,
USA
emiii@buffalo.edu

Abstract

Humpback whales (*Megaptera novaeangliae*) often sing continuously for multiple hours. Little is known about how individual singers vary the acoustic features of their songs within such prolonged song sessions. Here, a case study analysis of a seven-hour singing bout was performed to clarify the consistency with which global acoustic features can be produced by an individual singer. Analyses of 44 consecutive songs within a multi-hour sample revealed that: (1) songs of similar duration may be repeated for at least an hour; (2) frequency content and sequencing can be produced stably for several hours; and (3) multiple, narrow-band tonal streams, possibly song-generated, may co-occur within a song session. These analyses of intra-individual variations in acoustic features within a song session revealed the precision with which a singer can control acoustic fields, raising new questions about the predictability of acoustic variations in songs across different contexts and environmental conditions. The finding of spectral stability over hour-long periods further supports a potentially important functional role for song-generated reverberation and provides a baseline for future quantitative comparisons of song acoustics within and across individual singers.

Keywords: acoustics, mysticete, propagation, reverberation, song.

Introduction

One of the most unique qualities of humpback whales (*Megaptera novaeaengliae*) is their vocal prowess and perseverance. Humpback whales produce patterned sound sequences ("songs") at all times of day and night (Au *et al.*, 2000; Sousa-Lima and Clark, 2008), throughout most of the year (Clark and Clapham, 2004; Watkins *et al.*, 2000), and in a wide range of behavioral and environmental contexts (Darling and Berube, 2001; Stimpert *et al.*, 2012; Tyack, 1981). The sequential structure of songs varies across populations and years (Garland *et al.*, 2011; Payne and Payne, 1985; Payne *et al.*, 1983; Winn *et al.*, 1981), as do several acoustic features of songs (Cato, 1991; Mercado *et al.*, 2005; Payne and Payne, 1985). Variations across consecutive songs produced by individuals also occur (Chu, 1988; Perazio *et al.*, 2017), but most of the acoustic features that a singer might vary while singing (e.g., distribution of peak frequencies or unit durations) have yet to be analyzed in any detail. Characterizing intra-individual variations in song production is critical to assessing when and why humpback whales sometimes sing non-stop for many hours, as well as for determining how consistently and precisely humpback whales control sound production during such prolonged singing bouts.

Many hypotheses of humpback whale song function assume that listening whales are able to judge the location and relative sexual fitness of singers at kilometer distances (Frankel *et al.*, 1995; Helweg *et al.*, 1992; Parsons *et al.*, 2008). However, song features can become distorted as they travel long distances (Mercado and Frazer, 1999; Mercado *et al.*, 2007), in ways that could confound assessment of singer quality or position by listening whales. Even at shorter distances, song qualities depend on a specific whale's singing skills. Large intra-individual variations in song production might thus further complicate cross-singer comparisons. For instance, if song duration indicates a singer's fitness (Chu, 1988), then large within-session variations in song duration would make comparing the capabilities of different singers based on song duration difficult. Conversely, highly consistent song production might provide listeners with honest indicators of a singer's vocal control capacities and overall fitness (Cazau *et al.*, 2016). It is not a given, however, that the most effective humpback whale singers will be those that produce the most consistent songs. Singers with the ability to flexibly adapt acoustic features of their songs to account for variations in environmental and social factors might be more successful than singers that do not adequately account for such factors. Because current functional hypotheses for humpback whale songs only weakly predict how singers should vary song elements over time, descriptions of singing by individual whales are important for identifying the kinds of information that their songs may provide.

Surprisingly little is known about the factors that determine when and how humpback whales sing. Humpback whales of most ages sing (Herman *et al.*, 2013). There are indications that the probability of singing may vary with time-of-day and/or stage of the lunar cycle (Au *et al.*, 2000; Seger *et al.*, 2016; Sousa-Lima and Clark, 2008). Some individuals have been observed singing continuously for 10+ hours (Payne *et al.*, 1983; Winn and Winn, 1978), but it is unclear how prevalent such long-lasting song sessions are. Most past studies of singing humpback whales have focused exclusively on singers recorded opportunistically during the day. It is also not yet known what proportion of each day/week/month individuals spend singing, or how this distribution varies over time and across individuals. Humpback whales are known to produce songs more often at certain times of the year (particularly during the breeding season), but this could be either because more whales are singing at such times, or because a fixed number of whales increase the amount of time they spend singing. Analyses of prolonged song sessions, especially those occurring at night, can potentially provide new clues about the factors that determine how long any given humpback whale is likely to persist in singing.

Singing humpback whales can stably repeat rhythmic patterns of sound for periods of at least 40 minutes (Schneider and Mercado, 2018; Thompson, 1981). Individual singers vary the rate and rhythm of songs, suggesting flexible control of production mechanisms (Schneider and Mercado, 2018). Initial analyses of spectral energy patterns within song sessions suggest that the timing and order of spectral content may be consistent across whales (Mercado, 2016), despite changes in the absolute frequencies of units (Green *et al.*, 2011). Specifically, humpback whale singers often gradually shift from mid-range (300-500 Hz) to lower frequency content (<200 Hz) while singing (Mercado, 2016; Mercado and Handel, 2012; Mercado *et al.*, 2010). The acoustic properties of units (Au *et al.*, 2006; Mercado *et al.*, 2005), and sequences of units (Payne and McVay, 1971; Winn and Winn, 1978) have been extensively described, whereas interspersed silences between units have received little attention. Inter-unit intervals sometimes contain discrete echoes from units (Winn and Winn, 1978), as well as song-generated reverberation (Mercado, 2016). Reverberation can appear as narrow-band "tails" that may persist until a similarly reverberant unit is repeated, resulting in continuous bands of reverberant energy that collectively last several minutes across a sequence of repeated units. How often such reverberation occurs within song sessions is unknown. Because such reverberation is singer-generated (in combination with the environment), intra-individual variations in song production can also drive variations in reverberation. Exploring relationships between the stability of song repetitions and their reverberant consequences can provide new clues as to whether singing humpback whales are actively modulating reverberation.

The objective of the current study was to describe acoustic features produced by a distant humpback whale singing for several hours during the night, focusing particularly on the consistency with which temporal and spectral properties were repeated. Characterizing singer behavior in this way can potentially lay the groundwork for detailed assessments of prolonged singing bouts across individual whales and can facilitate the development and testing of hypotheses regarding why humpback whales sing continuously for such long periods.

Materials and methods

An existing archival database of continuous recordings collected off the coast of California between September 1, 2001 and November 14, 2001 was used in the current study (available at http://abdus.sfsu.edu/pioneer/scanpeg.html). These recordings were originally collected from the Pioneer Seamount Underwater Observatory, which was setup by NOAA, the Pacific Marine Environmental Laboratory (PMEL), and San Francisco State University; they have previously been used in analyses of blue whale (*Balaenoptera musculus*) songs (Hoffman *et al.*, 2010). The sample of sounds in these recordings is unbiased in that the position of the recording array was not selected to record humpback whales and was not moved or adjusted based on any detections of singing humpback whales.

A vertical array of hydrophones was anchored ~1000 m below the surface, near the peak of Pioneer Seamount. Recorded signals were transmitted to the shore via a communications cable and digitized at a sampling rate of 1000 Hz. Consequently, the frequency range of the recording is limited to signals below 500 Hz and does not span the full range of frequencies produced by singing humpback whales, which is ~20-8000 Hz (Mercado *et al.*, 2005; Payne and Payne, 1985), with some harmonics reaching 20 kHz (Au *et al.*, 2006). Recordings from one channel of the vertical array was made available within the online database. Archival sound files were stored in MP3 format and sped up by a factor of 10; three-minute long, unaltered samples from each 15 minutes of recording were also available in the database.

Spectrograms of recordings were visually scanned to identify segments that contained features consistent with singing humpback whales (e.g. repetitive production of sounds with energy between 100-500 Hz). The presence of singing humpback whales was then verified through aural analyses. The goal of this subjective approach was to identify extended periods when one or more singers were vocalizing. From this sample of singing bouts, one song session was selected for detailed acoustic analyses based on its duration and visual clarity in spectrograms (which was a function of ambient noise levels and the presence of other singers or overlapping anthropogenic noise sources).

The selected song session was manually divided into spectrographic segments that depicted similar visual patterns to provide an estimate of the duration of song-like cycles within the session. Spectral peaks were measured from a single three-minute sample taken from each hour of recording based on signal strength. Peaks were identified by creating a spectrum for each sample (FFT size = 22979, 75% overlap, giving .5 Hz resolution) using Raven Pro 1.5, Beta version. Continuous bands of narrowly focused spectral energy consistent with song-generated reverberation were also acoustically analyzed to determine their duration and focal frequencies. The spectral properties of these bands were subsequently compared with the peak frequencies within song cycles.

This methodological approach differs from those typically applied in past analyses of humpback whale songs (reviewed by Cholewiak *et al.*, 2013) in that no attempt was made to identify phrases or themes within song sessions, and no comparisons were made between songs produced by different whales. The approach corresponds more closely to a case study in that it focuses on describing the singing behavior of an individual whale. Rather than identifying behavior that is representative of any particular group of singing humpback whales, the goal of the current case study was to establish what it is possible for a singing humpback whale to do over an extended period.

Results

Humpback whale singing was visually detectable in recordings from 65 of the 75 days evaluated. Of those 65 days, individual singers were clearly visible on 16 days; in some recordings, noise levels made it difficult to determine whether singers were present. A single continuous song session recorded on October 28th and 29th was selected for analysis. This song session lasted at least eight hours. The exact duration of continuous singing could not be determined, because it is possible that the individual was singing before he became detectable on the recording array, and because later songs in the session possibly overlapped with the songs of another singer. The segment of the recording analyzed began at 9:15 PM and continued until 3:30 AM (Fig. 1).

Temporal structure

The analyzed singing bout was segmented into 44 visually comparable cycles. Most spectrographic cycles likely correspond to "songs," defined as one progression through a predictable sequence of sound patterns ("themes"). However, it is impossible to determine this from analyses of a single session from an individual singer (Cholewiak *et al.*, 2013). The starting and ending times for each cycle were selected by identifying where the sound energy was the strongest and using this to determine start and end points (see horizontal white bar in Fig. 1). This approach to segmenting a song session is similar to that used by Fristrup *et al.* (2003), where the least energetic points in recordings (typically associated with surfacing) were used to measure song duration within a series of songs. Fig. 2 summarizes the sequence of cycle durations, rounded to the nearest minute. The median and mode cycle duration were both 9 min. The median and mode difference in duration across successive cycles was 1 min.

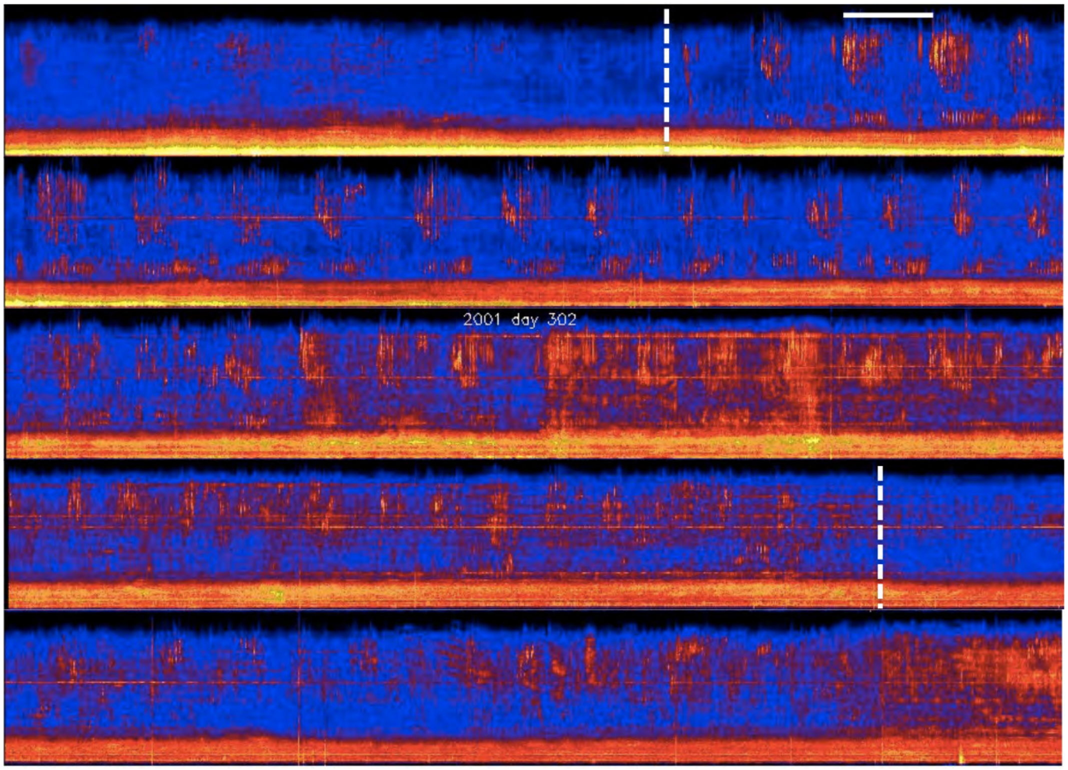

Figure 1. Spectrogram of analyzed song cycles. Each row encompasses two hours. The frequency range (vertical axis) for each row is 0-500 Hz. Vertical dashed lines indicate the section of recorded singing that was analyzed. The horizontal white bar in the top row indicates the duration of one song cycle (9 min). Tonal bands (horizontal red lines) that are correlated with the most energetic frequencies generated by the singer began to emerge after the first hour of singing.

Spectral properties

The first 24 song cycles within the analyzed singing bout showed a consistently alternating spectro-temporal pattern within each cycle in which energy was first concentrated in two bands (100-150 Hz and 200-400 Hz), before shifting primarily into the lower band (Fig. 1 and 3). Within the first half of this alternating pattern, minimum frequencies within each of the two bands gradually decreased (Fig. 3). Later cycles (25-44) showed less clear alternation, with energy primarily focused in the upper band. This difference in the observed spectral patterns of later cycles may have resulted either from changes produced by the singer, changes in the position of the singer relative to the hydrophone that led to greater signal attenuation, or changes in the recording system. Consistencies in spectral patterning over time, however, likely reflect stereotypy in sound production and/or diving patterns of the singer.

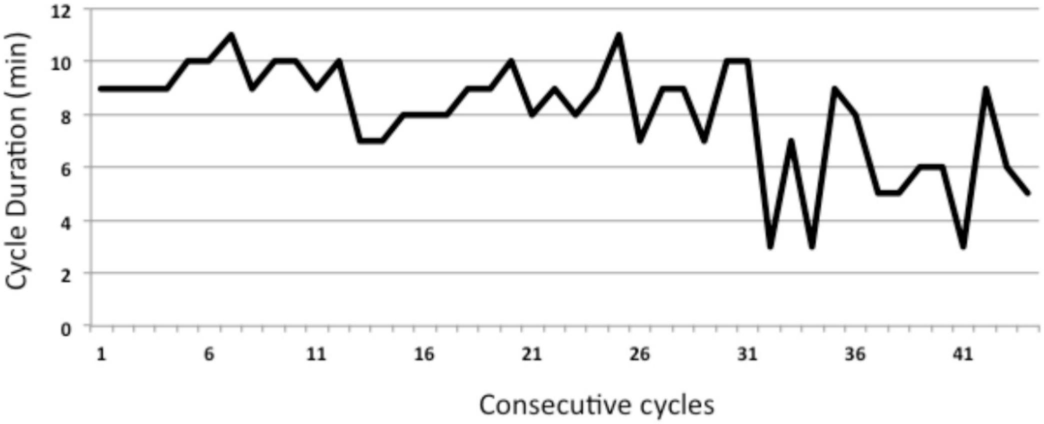

Figure 2. Durations of acoustic cycles measured from spectrograms show that most consecutive cycles change in duration by one minute or less. Shorter duration (3 min) cycles later in the sequence are likely to correspond to repeats of cycle segments rather than shorter duration songs.

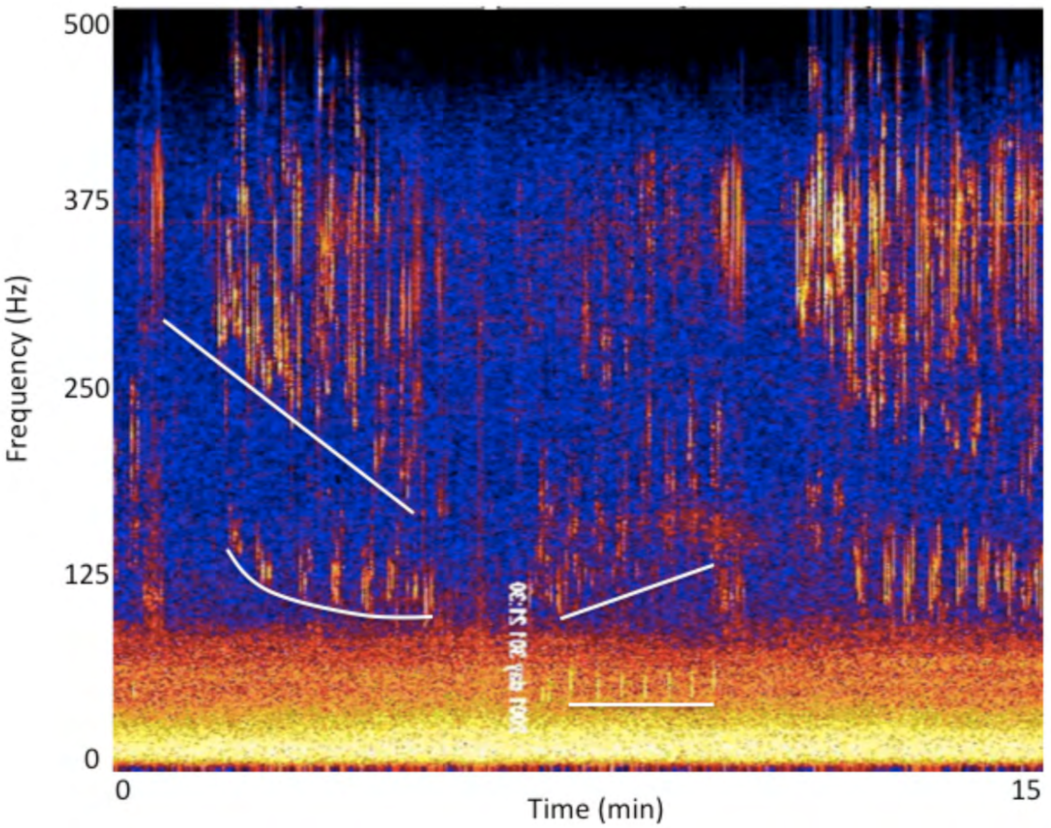

Figure 3. Spectrogram of a song cycle. White lines highlight gradual changes in the frequency content of sounds within a cycle produced by the singer. The singer repeated this general pattern of frequency modulation consistently for multiple hours.

Analyses of peak frequencies from three-minute samples within each hour of the song session showed exceptionally high consistency of frequency usage throughout the session (Fig. 4). Broad peaks were consistently found in three bands: 100-180 Hz; 200-420 Hz; and 400-500 Hz. The peak frequency of the lowest band was between 123-128 Hz for five of the seven hours analyzed. The peak in the highest band ranged between 423-433 Hz for the three hours that a peak was evident. The most energetic frequencies were consistently in the mid-range band for six of the seven hours analyzed. The specific frequencies with maximal energy were more variable over time in the mid-range band than in other bands, ranging from 252-351 Hz. In all three bands, additional narrow peaks were evident, with energy slightly less than was present at the maximum peak frequency; these secondary peaks were most prominent in the mid-range band, which showed 2-6 narrowband peaks (ranging from 208-380 Hz) in addition to the maximal peak for each sample.

Reverberant features

Individual sounds within three-minute samples showed evidence of generating both discrete echoes and reverberant tails (Fig. 5). However, not all sounds generated echoes and even fewer had reverberant tails. Reverberant tails could last significantly longer than the duration of the sound that generated them (Fig. 5), but none lasted longer than a few seconds.

Multiple, persistent narrow bands of energy appeared as the song session progressed, none of which were evident prior to the beginning of the analyzed singing bout (Fig. 1). The first band appeared after five song cycles, was centered at 295 Hz, and was continuously present for about two hours. A second band appeared in the third hour of the bout, focused at 271 Hz, which lasted over four hours. Two more tonal bands emerged in the subsequent hour, centered at 123 and 405 Hz. Finally, a fifth band emerged, five hours into the song session, focused at 305 Hz. Because these narrow tonal bands appeared to be correlated with the frequencies being used by the singing whale and were similar in certain respects to long-duration, reverberant bands sometimes produced by singing whales (Mercado, 2016), the focal frequencies of these bands were compared to the peak frequencies within song cycles (Fig. 4). The lowest tonal band exactly matched the lower peak frequency produced by the singer, and the highest tonal band was about 30 Hz less than the

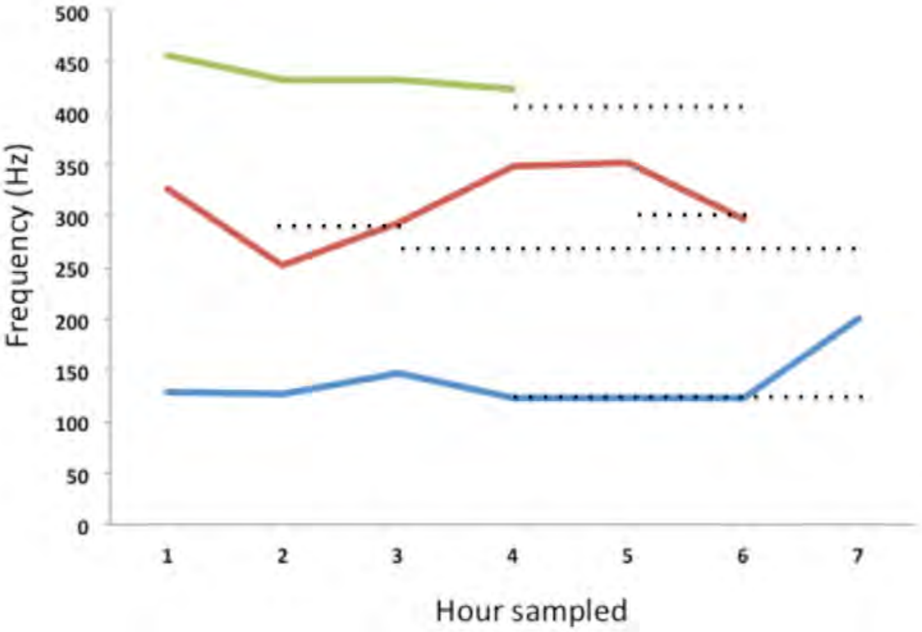

Figure 4. Peak frequencies measured from three-minute samples within each hour of the analyzed segment. Three broad spectral peaks were present for the earliest song cycles in the sample. Later cycles showed fewer peaks. Colored lines show changes in frequencies with peak energy across the song session. Dotted lines show the focal frequencies and the lengths of these lines correspond to the durations of tonal bands present during singing. The focal frequencies of extended tonal bands were correlated with the peak frequencies being used by the singer, but time-lagged relative to song production. The bands persisted during periods when the singer did not appear to be generating units with spectral energy focused at the frequencies within the bands (see Fig. 1).

highest peak frequencies produced by the singer. The mid-range tonal bands were within the range of peak frequencies produced by the singer but did not match the peak frequencies of sampled song segments as closely as in the lower and higher bands. The transitions between tonal band focal frequencies did, however, follow the pattern of changes observed in mid-range peak frequencies produced by the singer.

Discussion

The singing episode described here conforms with several global properties noted in earlier descriptions of songs recorded on several different breeding grounds, including the durations of song cycles (Fristrup *et al.*, 2003), and the distribution of spectral content within songs (Mercado, 2016), providing preliminary evidence that songs produced at night are acoustically comparable to those produced during the day (see also Seger *et al.*, 2016). Songs recorded at a distance, and at a time when the singer was likely migrating, retain acoustic features evident in close recordings collected from breeding groups. Additionally, this case study of a singing humpback whale established that singers may consistently repeat the timing and frequency content of consecutive songs for several hours, and confirmed earlier reports that singers may consistently alternate between two main frequency bands (Mercado *et al.*, 2010). These replications of earlier observations increase confidence that the focal song session analyzed in this study is not an outlier in terms of its acoustic properties, and thus that it can provide a reasonable baseline for evaluating variability in prolonged song sessions.

Temporal and Spectral Dynamics

Fristrup *et al.* (2003) reported that the duration of songs (measured as the interval between inferred surfacing events) for whales singing off the coast of Hawaii averaged 13.8 min, with an average difference in successive songs of 2.5 minutes. Song durations reported by Fristrup *et al.* (2003) closely match earlier measures of singer dive times (MN = 13 min, Chu, 1988). Thompson (1981) measured the duration of 219 songs (defined as a complete cycle through subjectively identified themes) from multiple populations and found that most of them were between 6-12 min long (see also Payne *et al.*, 1983, who reported a range of 6-17 min). Cycle durations measured in the current study ranged between 3-11 min. If the shorter duration cycles are interpreted as corresponding to repeated theme transitions (Darling and Sousa-Lima, 2005), this would give a range of within-session song cycle duration of between 6-12 min.

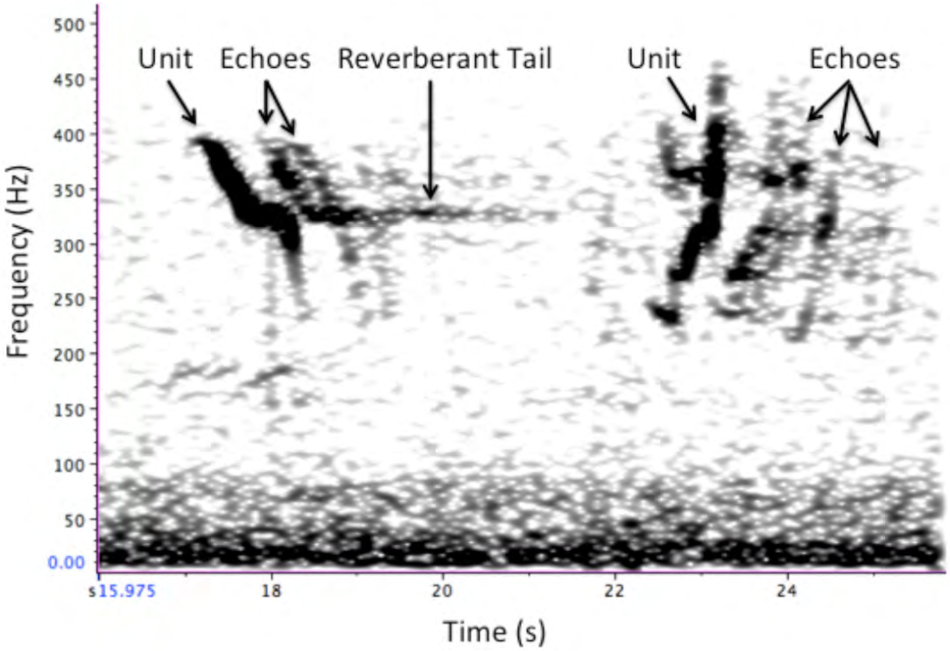

Figure 5. Spectrogram of individual sounds (units) produced by the singer within the song session showing evidence of both discrete echoes and reverberant tails.

The longest song series analyzed by Fristrup *et al.* (2003) consisted of 13 consecutive songs, compared with 44 consecutive song cycles analyzed in the current study. Fristrup *et al.* (2003) noted significant differences in song duration across individual singers but did not report on how any individual singer varied song duration. Thompson (1981) analyzed 132 consecutive song pairs and found that nine showed less than a 1% change in duration. One percent of a 10 min song is a six second difference, less than the duration of a typical song phrase. Finding nine pairs of consecutive songs that differed by such a small interval provides strong evidence that singers do sometimes repeat songs quite precisely (see also Schneider and Mercado, 2018). Frumhoff (1983) found that songs were less variable in duration than their constituent themes, leading him to suggest that song duration may be more constrained than the specific sequences (theme durations) produced within songs. Chu (1988) also noted that there was more variation in dive times between singers than within the dives of any particular singer. The current analysis found that most consecutive cycles (64%) differed in duration by a minute or less. The observed trajectory of cycle durations suggests that the singer gradually shifted to shorter duration cycles over time. Measures of song duration trajectories within song sessions may be more informative than measures of variance in duration across songs of multiple singers, if singers are gradually adjusting or maintaining song/dive durations. For instance, systematic changes in song duration trajectories may correlate with changes in diving patterns (Chu and Harcourt, 1986) and/or activity levels and the swimming behavior of a singer.

Past quantitative analyses of sequential frequency content within songs suggest that singing humpback whales often progressively switch between producing sounds with energy focused at higher frequencies to producing sounds with energy concentrated at lower frequencies (Mercado, 2016; Mercado and Handel, 2012; Mercado *et al.*, 2010). This pattern was previously found in songs from Hawaii, Puerto Rico, Madagascar, Columbia, and Brazil. The current analysis of consecutive cycles showed consistent repetition of a "hi-lo" frequency pattern for many of the cycles analyzed. Mercado and Handel (2012) previously suggested that this pattern might be a side-effect of gas exchange occurring while a singer is submerged, in combination with periodic changes in a singer's depth associated with surfacing. Alternatively, this pattern may reflect a stereotyped progression through song elements that in some way contributes to song functionality. For instance, song sounds with different frequency content will generate different patterns of constructive and destructive interference (Mercado and Frazer, 1999; Mercado *et al.*, 2007), such that a singer gradually sweeping through a broad range of frequencies may more fully ensonify the kinds of shallow water habitats frequented by singing humpback whales.

Despite cyclical shifts in the frequency content of the songs analyzed here, the frequencies with peak energy stayed remarkably stable across many song repetitions. Maximal energy was reliably found in a band between 200-400 Hz, consistent with past analyses of sound production (Mercado *et al.*, 2010), and with earlier work suggesting that frequencies in this band often propagate optimally within humpback whale habitats (Mercado and Frazer, 1999). The peak frequencies within song cycles identified in the current study also correspond closely to those of "drone units", which are individual sounds within songs that recur at regular intervals and that are prone to generating reverberant tails (Mercado, 2016). The lower frequency spectral peaks within song cycles were particularly consistent, varying by 3 Hz or less over multiple hours. High-energy, mid-range peak frequencies varied more over time than both higher and lower peak frequencies, suggesting that singers may more flexibly modulate the frequency content of sounds within this range.

Persistent Tonal Bands

There was little evidence of individual sounds generating persistent reverberant tails within the analyzed song session. The reverberant tails that were identified generally lasted less than three seconds. Initial analyses of song-induced reverberation similarly found that only some recordings show individual sounds generating persistent narrowband reverberation (Mercado, 2016). Multiple discrete echoes followed many recorded sounds, establishing that the recording system was sufficiently sensitive to detect narrowband reverberant tails if they had been present.

A surprising finding of the current analysis was the presence of long-duration bands of narrowly focused acoustic energy coinciding with song production. These bands did not appear until well after singing was evident and appeared to be correlated with the frequency content of songs. It is impossible to discount the possibility that these tonal bands are some type of recording artifact. But, it is unclear what the mechanism of such an artifact might be, especially given how the focal frequencies remain stable despite changes in the spectral content of overlapping songs, as well as changes in their received levels. The fact that the tonal bands emerge and then dissipate over hour-long periods, and are focused at various frequencies, suggests that they probably are not caused by any direct interaction between the recording system and the signals being recorded. Visual inspections of other recordings from the database revealed that tonal bands were not always coincident with song production, suggesting that they may be either some form of intermittent background signal or may result from some type of environmental resonance phenomenon. However, given the close correspondence of the focal frequencies within these bands to those being produced by the singer, it seems that either the singer may be selecting frequencies that in some way correspond to these bands (prior to the occurrence of the bands), or that song production (either by the recorded singer or by choruses of distant singers) is in some way driving the emergence of the bands. The acoustic similarity of these tonal bands to previously identified streams of continuous song-generated reverberation is particularly intriguing, but could be coincidental.

Many more observations may be needed to identify the nature and origins of these tonal bands and their relationship (if any) to singing by humpback whales. The existence of persistent, song-generated, narrowband reverberation escaped the attention of bioacousticians for many years, and it was only after the discovery of similar reverberant bands in bird songs (Mercado *et al.*, 2017), that long-lasting reverberant tails were sought for and found in recordings of humpback whale songs. Further evidence that song-generated reverberation might play an important role in humpback whale songs came from the finding that consecutive units within songs were often spectrally interleaved, such that successive units minimally masked ongoing reverberation (Mercado, 2016). Might it be possible that regular repetition of phrases in some way contributes to the persistence of acoustic energy at particular frequencies above-and-beyond the boosts that are already delivered by the regularly timed production of reverberating drone units? If so, what might be the necessary conditions for such a phenomenon to occur? The current analysis cannot adequately address such questions, but at a minimum suggests that this issue is worth considering more closely in future analyses of humpback whale songs.

Limitations and Future Directions

The current case study serves to highlight aspects of singing that previously have received little attention, and thus may act as a catalyst for future hypothesis development and scientific research. By design, this study cannot address issues related to typical singer behavior, the functional role of songs, or the factors that determine when and how humpback whales produce songs. The recorded signal analyzed in this study differs from those encountered by humpback whales in that it only includes frequencies below 500 Hz and was recorded at a depth of ~1000 m. The positions and movements of the singer relative to the recording hydrophone are unknown, but it is almost certain that the singer was at least a kilometer away from the recording array. In the ideal case study, a recording device would have been placed on the singer for multiple days and the singer would have been surrounded by a large array of hydrophones positioned at depths similar to those inhabited by humpback whales at a variety of distances from the singer. Such a recording configuration would make it possible to more fully evaluate how the acoustic properties of received sounds relate to produced sounds, and to more precisely measure the consistency of singing by an individual singer.

Neither surfacing events nor thematic structure could be reliably identified in the current study, although there were regular, short-duration "gaps" within song cycles that may correspond with the signal attenuation that often occurs when a singer surfaces (Fristrup *et al.*, 2003). Consequently, it is difficult to assess whether the measures of cycle duration used in the current study are directly comparable to past measurements of song duration. The sample analyzed here does not constitute a complete song session, because there were traces of song elements evident both before and after the analyzed segment (Fig. 1). Winn and Winn (1978) mention a 22-hour recording of continuous singing, which probably also was not a complete song session. They suggested that song sessions might extend for several months. More recent studies suggest that, instead, humpback whales most likely switch between singing and other activities (Herman, 2016). The maximum durations of continuous song production, the typical duration of song sessions, and the proportion of time humpback whales spend singing each day are all unknown. Recordings of individuals collected continuously at the source over periods of weeks or months will be needed to more fully assess the consistency and precision of song production by individuals over time.

Long-term acoustic recordings collected from the bodies of singing humpback whales (Sousa-Lima *et al.*, 2003; Stimpert *et al.*, 2012; Stimpert *et al.*, 2007) can provide more detailed information about intra-individual variations in song production. But, these need to be combined with long-range recordings to gain a complete picture of the acoustic fields that singers generate. Additionally, long-term analyses of song variations produced by singers in different geographic and social contexts may reveal different dynamics from those produced by a lone singer. More detailed measurements of temporal structure within song sessions may also prove useful in characterizing intra- and inter-individual differences in song production. Understanding what individual singers normally do can potentially provide behavioral insights that would not be revealed by traditional analyses of prototypical structural qualities of songs, or by analyses of how songs vary within and across populations.

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Medium-term stereophonic recording of humpback whales in Sainte Marie channel, Madagascar: daily variation in whale density

Yann Doh[1,*], Olivier Adam[2], Gilles Nolibé[3]

[1] Association GUALIBA
Routhiers, Rue Dumesnil,
97130 Capesterre Belle Eau,
Guadeloupe,
France

[2] Bioacoustics Team, Centre de
Neurosciences Paris Sud (CNPS),
CNRS UMR 8195, University of
Paris Sud, 91405 Orsay,
France

[3] CeSigma - Signals & Systems,
1576 Chemin de la planquette,
83130 La Garde,
France

* Corresponding author:
yanndoh.m2@gmail.com

Abstract

Humpback whales (*Megaptera novaeangliae*) are well known to be particularly active acoustically. In 2007 the research team started to investigate humpback whales in the breeding area in the Sainte Marie channel (Madagascar). An array of 2 synchronous hydrophones was deployed in 2012 as part of a feasibility study for the deployment of a permanent acoustic array in the channel for the research programme, BAOBAB. Eight continuous sets (mean duration: 27 h 15 min) were recorded between 3 August and 11 September. Stereophonic recording allows the discrimination of acoustic sources that are not spatially overlapping, as the bearing to the emitting whale can be estimated from the Time Difference Of Arrival between the sensors. Based on cross-correlation functions analyses, this paper proposes an assessment of the number of emitting whales in a given underwater soundscape, and changes in their numbers over the covered time period. The first results showed that this value changed between 0 and 10 singers over the survey period of more than a month, and a peak in density was observed in the third week of August. Daily trends indicated highest density at night and lowest density just before nightfall. The study attempts to link acoustic activity and spatial occupation to reveal interactions between the detected emitting whales.

Keywords: Humpback, Acoustics, Stereophonic, Density, Madagascar.

Introduction

Although 80 different cetacean species are known, knowledge about these animals is still disparate and marine mammal research remains of high interest, with multidisciplinary approaches being used to study classification, ecology, behaviour, acoustics and conservation. Many species were hunted over the past century and their stocks decreased drastically. Although some populations recovered, some species remain listed as endangered or vulnerable on the IUCN red list of threatened animals (IUCN, 1996). At the end of the 1990's interest began to develop about the effects of anthropogenic activities on marine mammals (Perry, 1998), including the impacts of activities on- and off-shore, fishing zone activities, emission of anthropogenic sounds, and chemical pollution. Considering past and new threats, it is of primary importance to evaluate the state of cetacean populations and introduce effective protection measures. In this context, abundance and population dynamics are key parameters that must be assessed and updated. The objective should be to estimate the number of individuals of one population in a defined area, and how this changes over time.

Simmonds and Eliott (2009) suggested that global changes could be estimated from observations of cetaceans, and also that the effects of these changes on cetaceans should be measured. Two main areas of study were proposed: 1) for migratory cetaceans, observations should focus on the short-term variation of periods spent in breeding and feeding areas; and 2) for resident cetaceans, observations should focus on the 3 primary activities of feeding, reproduction, and resting.

Observations of cetaceans can be made by using 4 different methods: visual observations; the use of electronic sensors; genetics; and passive acoustics. All of these methods have benefits and drawbacks (Swartz, 2001; Gandilhon, 2010). They can be used as complementary methods depending on the goals of the study. The usual density and abundance estimation methods applied to terrestrial and marine species have consisted of extrapolating observations made in a limited area, to the whole area of interest. Distance sampling is a statistical approach initially used for visual observation (Buckland, 2001). Marine mammal case studies allow an interesting observation method to be used, as they are very active acoustically. Visual methods have contributed to the bioacoustics field by: 1) associating visual observations and acoustic monitoring; and 2) adapting the previous estimators used to acoustic detections (Marques, 2013). Past studies have provided useful results for both odontocetes (Lewis, 2007; Marques, 2009; Küsel, 2011) and mysticetes (McDonald, 1999; Mellinger, 2007; Marques, 2010).

The humpback whale, *Megaptera novaeangliae*, is one of the most studied cetacean species, for many reasons, including because male individuals emit songs during the breeding season (Payne 1971), and because they come close to the shore during this season, facilitating approach and observation. The roles of these songs have been much studied and multiple hypotheses have been proposed, including male/female interactions (Winn, 1978; Herman, 1980; Tyack, 1981; Medrano, 1994; Adam, 2013) and/or territorial behaviour (Darling, 2001; Cholewiak, 2008). Some songs have been recorded on migration routes and are thought to be used to guide other individuals (Clapham, 1990). Humpback whale populations are present in all the oceans, migrating to high latitude areas during the spring-summer months for feeding, and to low latitude areas during the autumn-winter months for breeding. However, knowledge on humpbacks is disparate and some areas are poorly studied due to access difficulties or security concerns, as is the case for some breeding sites in the southwestern Indian Ocean. Most past studies have chosen to conduct counts of individuals using passive acoustics localization, Frankel et al. (1995) used an array of 3 hydrophones off Hawaii to detect calls and the position of whales was estimated by intersection of hyperbolic bearing lines. Improvements to these acoustic techniques have been made by the use of adequate underwater sound propagation models taking into account non constant wave speed (Tiemann, 2004). In the southern Caribbean Sea, Swartz *et al*. (2001; 2003) used Directional Frequency Analysis and Recording (DIFAR) to estimate the location of calling whales. This method uses the difference in phase and magnitude between acoustic vector sensors and an omnidirectional hydrophone. Later, various software able to process DIFAR data were designed. The major limitation though, is the availability of this expensive material and software, and the inability to work "in real time". Recently, an open-source software (PAMguard) has been developed to overcome these aspects (Miller, 2016).

In 2012, based on the previously mentioned multi-disciplinary approach, the BAOBAB (Balises et Acoustique pour l'Observation des Baleines A Bosse) project was initiated in the Sainte Marie channel of Madagascar. Despite this area being considered a major humpback whale site, there was no scientific study on estimating animal density or seasonal fluctuation. Evaluating the density of whales in this defined area in a quantitative manner is useful to establish conservation approaches, actions and rules. The project followed on from the work carried out in the region since 2007 by members of the team in collaboration with Cetamada, a Malagasy NGO dedicated to the protection of cetaceans in this austral winter breeding area for humpback whales. The first step, between 2007 and 2011, was to evaluate methods based on signal processing and pattern recognition algorithms of real songs instantaneously recorded with one hydrophone deployed from a motor-boat (Pace, 2010; Doh, 2013; Doh, 2014). The second step was to design an original array dedicated to provide continuous recordings from the Sainte Marie channel. The aim of collecting and analysing acoustic data in the medium or long term was to produce assessments on whale distribution and changes over time. Moreover, a large amount of data ensured validity, and could reveal seasonal aspects. During the austral winter of 2012, a first version of the device made up of only 2 hydrophones was deployed for testing and adjustment, and it provided the first dataset.

The width of the channel between the Madagascar mainland and the island of Sainte Marie is about 30 km. The study area was at the southern end of the channel, which is characterized by low bathymetry (<60 m) and coral reefs along the coast, and is an important concentration area for humpback whales. As acoustics need sound production, it was necessary to answer the question as to whether the number of emitting humpback whales could be estimated from the stereophonic data. In order to answer this question, it was necessary to consider aspects such as multiple emitting animals, time/frequency overlapping of the sound emissions, variations in Sound Pressure Level (SPL), spatial overlapping of the animals, and anthropogenic and environmental noises.

The soundscape of the large diversity of humpback sound production seems to be dominated by persistent "songs". Humpback whale songs are based on successive patterned sound units (a sound unit is an emitted sound between two silences). Some of these sound units are repetitively organized in successive sequences, phrases and themes (Payne, 1971). Pace *et al.* (2009) defined the concept of sub-units as the elementary basis for forming sound units by combination. Males share these sound units in the same area at the same period of time (Payne, 1983; Helweg, 1990; Cerchio, 2001). This means that these emitted sounds can be used to differentiate one population from another in different areas, and to discern a specific year. Basic features of these sound units are low fundamental frequency (<100Hz), powerful sound (165-175dB re 1μPa at 1m), and a short time duration (< 5sec), with or without harmonics (Au, 2006). These sound units could roughly be classified into two types; tonal and pulsed (Cazau, 2013). Nevertheless, variations in the intrinsic features of these sound units are significant even for the same individual and, of course, from one individual to another. Therefore, automatic detection and classification of sound units is still a challenge, especially in areas where more than one singer is present, because they produce songs simultaneously.

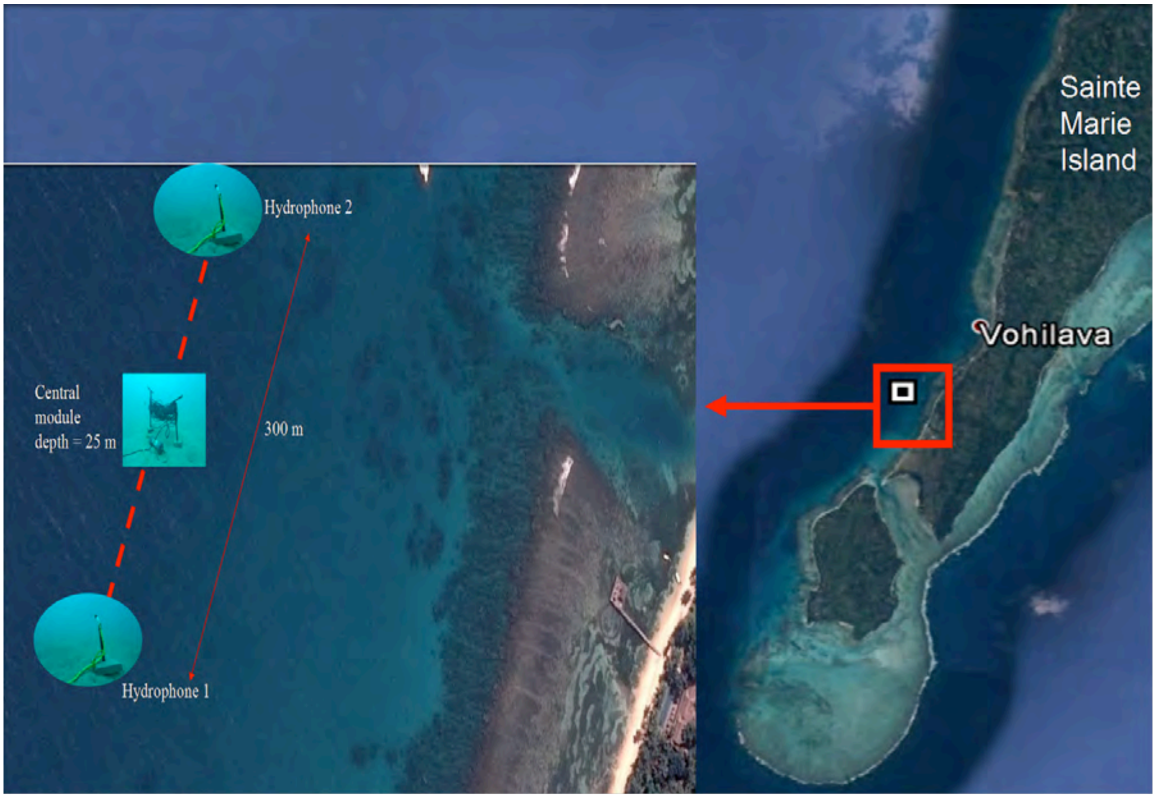

Figure 1. Location of the prototype array in front of the former CETAMADA Research Center (Vohilava), south of Sainte Marie Island.

Despite the fact that precise trajectography or positioning could not be performed from this prototype device, the current study had the objective to exploit the data by taking advantage of stereophony. This paper aims to present the methods developed and the first results about the number of emitting humpback whales in the Sainte Marie channel based on the extraction of acoustic indicators.

Method and materials

Preliminary and new designs

From 2007 to 2011, humpback whale singers were recorded during the breeding seasons off Sainte Marie Island on the northeast coast of Madagascar, using a single hydrophone (ColmarItalia GP0280) digitized by a Tascam HD-P2 recorder. This approach was appropriate to provide recordings from isolated singers, but required a boat to search for singers at sea. This is always a challenge because when males sing, they spend very little time at the sea surface (Adam, 2013), so they are very difficult to observe. The major limitations of this approach are: 1) it provides short-term recordings (30 min recording), thus collecting a large amount of data requires much time and energy; 2) as the singer is acoustically isolated, songs are studied out of interaction context of other singers; and 3) the state of the sea can be rough during the austral winter which does not allow the boat engines to be turned off for recordings.

The BAOBAB project was launched in 2012 and started off with a general test of the feasibility of hydrophone array deployment in the channel (Doh, 2014). It took 2 h on 3 August to deploy the prototype version of the array (Fig. 1) designed and provided by CeSigma Signals & Systems. It was made up of 2 omni-directional hydrophones spaced by 300 m and linked to an immersed autonomous central device supplying energy and allowing the stereophonic data acquisition at a 44.1 kHz sample rate. The whole device was located at 500 m from the shore outside the coral reef, and anchored at 25 m depth. It was necessary to regularly change the battery (every 2 or 3 days) and recover the data with scuba from a surface boat.

Dependent on weather conditions and logistic factors, 8 recording sessions of continuous recordings (duration between 22 and 42 h) were conducted from 3 August to 11 September. This period corresponds to the second half of the breeding season. The diagram in Fig. 2 gives basic information on the sampling method and includes the date, recording duration, and hour of starting. The variation in session duration is explained by fluctuations in the battery charging process which was dependant on erratic local power supply. The longest duration (42 h) occurred after the replacement of a new battery. In total, 218 h of stereophonic data were recorded.

Methods

Given the configuration of the device (only 2 hydrophones), obtaining the precise location of sound sources is not possible. However, counting the acoustic sources is possible if they can be discriminated. This method is based on the hypothesis that different emitting whales have a high probability of obtaining a distinctive position in space, allowing a distinctive bearing to the recording hydrophone(s) to be obtained. Geometric relationships involving the Time Difference Of Arrival (TDOA) between hydrophones, and the angle of arrival, are included in a set of geometric solutions formed by a hyperbola branch (Gebbie, 2015; Medwin, 2005). Thus, analysis of the TDOAs allows the extrapolation of the bearing of the acoustic source.

The signal received at the hydrophone (*i*) is a time-translated version of the signal at the source, and is represented as:

$$x_i(t) = x(t - t_i) + N_i(t),$$

Where t_i is the time of arrival at the hydrophone, and *i* and N is a noise factor (external and numerical). The geometric and frequency attenuation is not formalized in this equation. Therefore, $\tau_{ij} = t_j - t_i$, and is considered to be the TDOA between hydrophones *i* and *j*. In this study, the value of the time delay has been estimated by an analysis of the normalized correlation function R_{ij}. Computing of this function is

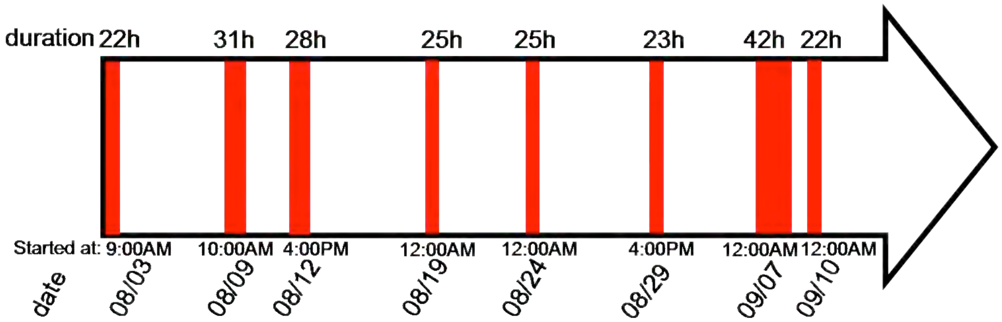

Figure 2. Acoustic temporal cover and duration, and starting hour of each recording session (date/month/day).

based on the spectrum correlation for reasons of time computing efficiency, as follows:

$$R_{ij} = \frac{1}{\sqrt{E_i E_j}} TF^{-1}\left\{TF\left\{x_i(t)\right\} \times TF\left\{x_j(t)\right\}^*\right\},$$

Where E_i and E_j are the respective received energies on hydrophones *i* and *j*. The peak of R_{ij} appears at the value corresponding to the TDOA between both channels. Thus, the TDOA t_{ij} is expressed by:

$$\tau_{ij} = Arg \max\left\{R_{ij}\right\}.$$

Several peaks can be found in the framework of multiple acoustic sources. Although the sources are emitted simultaneously with possible frequency overlap, the cross-correlation gives a multimodal representation discriminating each source by its specific TDOA. The number of peaks is directly linked to the number of acoustic sources. As one source cannot emit from different positions at the same time, this approach is consistent if the whales are not spatially overlapping. The major limitation of this method is the case of animals emitting close together, or when physically in contact. Depending on the ability of the array to discriminate respective bearings, one peak may be produced, leading to poor estimation of the true number of sources.

Tool box dedicated to data processing

A customized tool box was developed (using Matlab) in order to analyze 218 hours of data, processing each recording file (10 min duration) as described in Fig. 3. The toolbox includes: Step 1 - cross correlation functions between both channels are computed over a 73 ms sliding window. Each channel spectrum is computed by standard Fast Fourier Transform (FFT). The choice of the window duration is a compromise between a reasonable time of computing and the time needed for resolution in order to discriminate sources and time-overlapping sound emissions. The output is a matrix [time x time delay] describing the different TDOAs as a function of the running time. The spacing between both hydrophones determines the maximum time delay which is 200 ms given the current dimensions. This stage is the most time consuming as it requires about 10 min to process a 10 min recording. Step 2- the cross correlation matrix is preconditioned by a binarization of its magnitude. Either 1 if the value is over an arbitrary energy threshold criterion, or 0. This operation allows only the most powerful sources to be taken into account, to make the next manipulation easier and to also fix the acoustic volume of reference for further source number estimation. Step 3 - a one dimensional reduction is conducted on the binary matrix by an average along the time duration of the file. This contains the different time delays appearing over

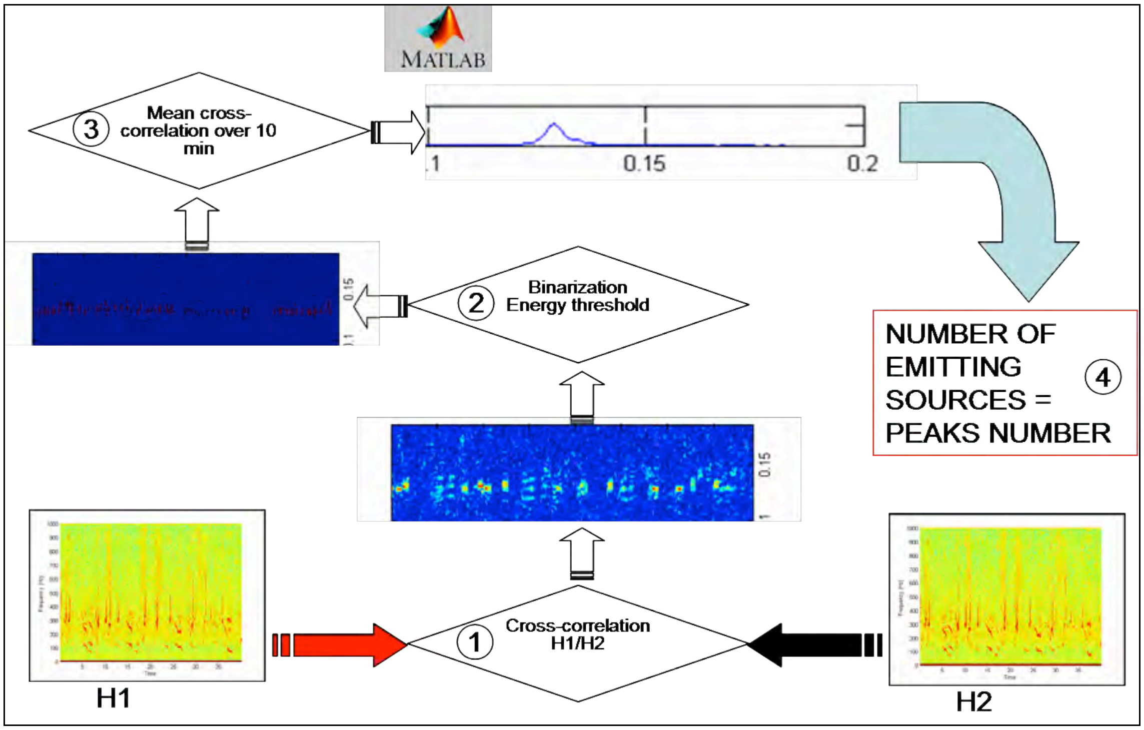

Figure 3. Block diagram showing the estimation of the number of sources using the customized Matlab Toolbox.

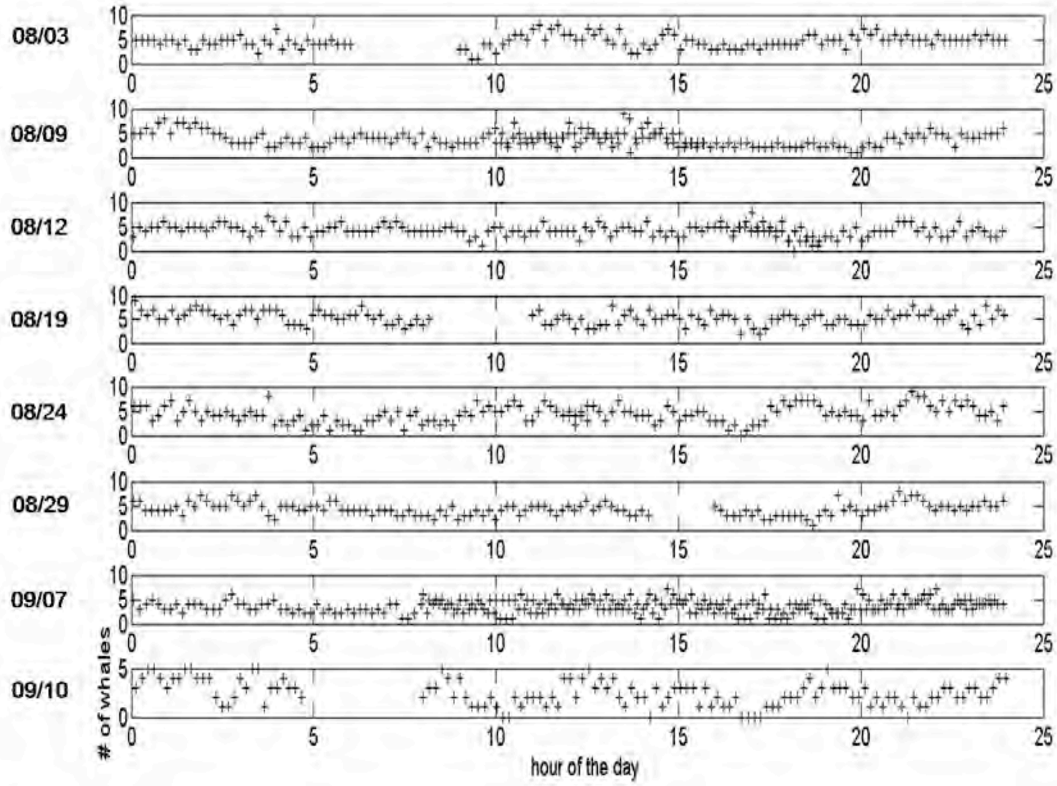

Figure 4. Raw estimations of the number of emitting humpback whales. Each line encompasses the results of one recording session and the hour of the day (date/month/day). Overlapping points mean the session lasted more than 24 h.

the 10 min period. The magnitude of the peaks is high and narrow if the source is static and active. The peak is wider if the source is moving. Step 4 - assuming the peaks correspond to distinctive emitting sources, the estimation of the number of emitting whales is given by the number of peaks included in the last representation. The peak magnitude threshold ensures that only sources likely to vocalize frequently are captured. In this way, occasional and continuous emitting sources, such as episodic vocalizations and boats, are not taken into account. Peaks appearing for $\tau_{ij} \approx 0$ should be viewed with caution as it could result from parasite noises caused by the acquisition device, or generated by independent random processes. Fluctuations in magnitude were observed throughout the analyses, suggesting there was no constant noise pollution.

Results

Number of emitting whales

A total of 218 hours were analyzed using the above mentioned processing methods. In order to compare each session, it is important to note that the thresholds (energy and mean cross-correlation) stayed the same, regardless of the sessions analyzed. Fig. 4 summarizes the raw estimation of the number of emitting whales resulting from each 10 min file. The values have been represented as a function of the hour of the day (not *vs.* recording time). Over a period of almost 5 weeks, the estimations vary between night and day from 0 to 10 detected individuals, with few values under 2 individuals. Short time variations are due to any new individual arriving or leaving the detection area. Some consecutive estimations are constant over 10 files (1 hour). A significant decrease in this number is observed toward the beginning of September, with 5 individuals being the maximum detected. These results also confirm the continuous presence of emitting whales, or singers, in the Sainte Marie channel.

Weekly variation in the number of emitting whales

Basic statistical processing was applied to the raw estimations. Fig. 5 (top) shows the normalized distribution of the estimations for each session. It shows similar shapes with one observed mode, but a progressive displacement of the maximum probability in time. The mean estimated number is continued in Fig. 5 (bottom). The estimations of the first session on 3 August seem to reflect a decreasing dynamic initiated in July. On 9 August, the number reaches a minimum of 4 individuals, then tends to increase until 5.5 whales on 19 August, which is the maximum estimated mean value. Then, it significantly decreases to around 2.5 individuals on 10 September (minimum value). The standard deviation (SD) is relatively steady over the time period, between 1.2 and 1.8, and does not seem to be correlated with the estimated number. However, a significant spreading of the estimation is found at 08/24, as the SD reaches the highest value. No weekly cyclic behavior was observed for the duration of the present study.

The mean normalized strength received from the raw recordings (red curve) has been added to the last representation after scale modifications. Both curves are highly correlated, probably due to the cumulative impact of the numerous singers, or because the song level was intentionally increased. An exception is found for the last session, as aural analysis reveals that one singer was very close to the hydrophones. It significantly increased the level received compared the previous sessions.

Daily distribution

The variation of the estimated individual number over 24 h has been investigated by pooling all the estimations. A two dimensional normalized histogram (bi-distribution) resulted, as shown on Fig. 6 (top). The observed probability of a couple (whales number, hour of the day) is not flat or uniform, and modulations are perceptible. Fig. 6 (bottom) represents the value of the estimated number resulting from the maximum probability for a given hour of the day. A general stepwise pattern seems to be apparent. The duration of the steps are about 4-5 h suggesting that regular changes in the spatial configuration of the animals may occur over a 24 h period. The number is higher during the night (from 8 pm to 5 am) and constant at around 4-5 individuals. During the day, estimations vary much more, from 2-5 individuals. The lowest number appears at the end of the day (from 3 to 8 pm).

Discussion

A. Estimation of the number of emitting whales

Few studies exist on whale distribution or density in the waters of Madagascar, and none by passive acoustics, which is restrictive for comparative purposes. A paper based on visual observation and historic

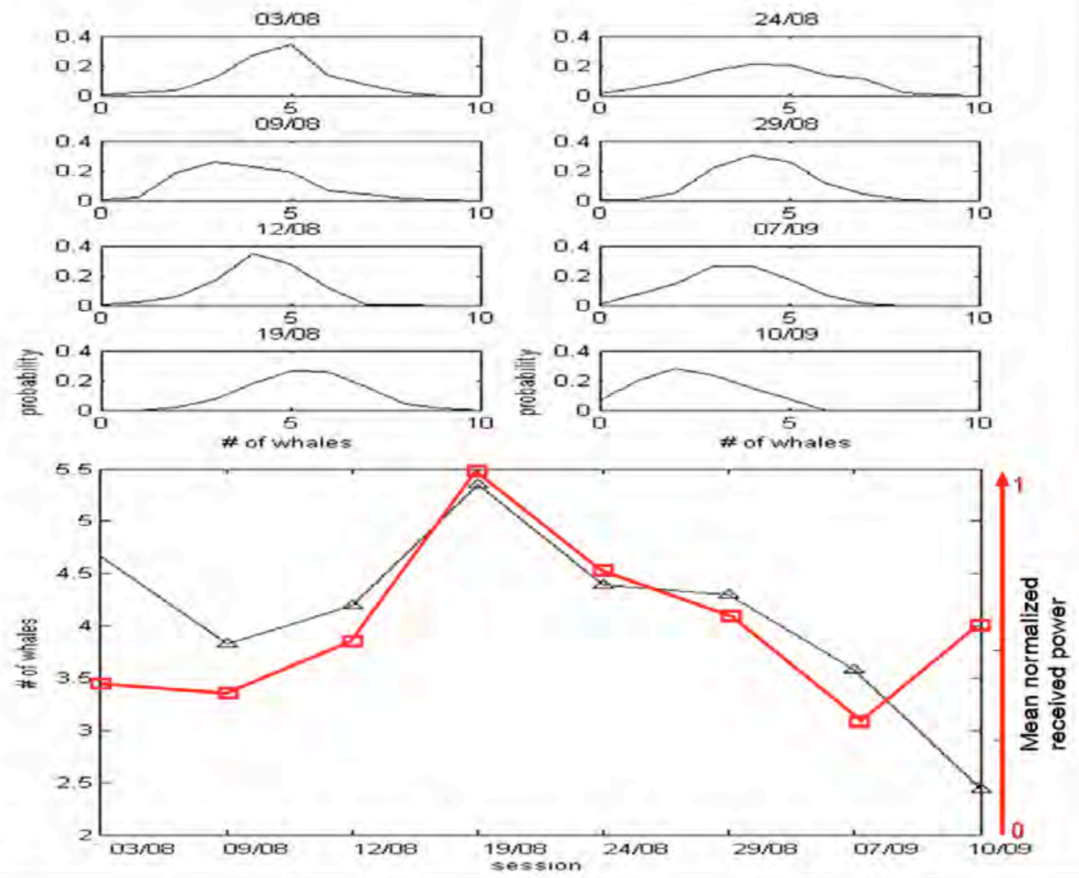

Figure 5. Top - Normalized distribution of estimated emitting whale number for each session (date/day/month). Bottom - mean estimated number of emitting humpback whales by session in comparison with the mean normalized acoustic strength received.

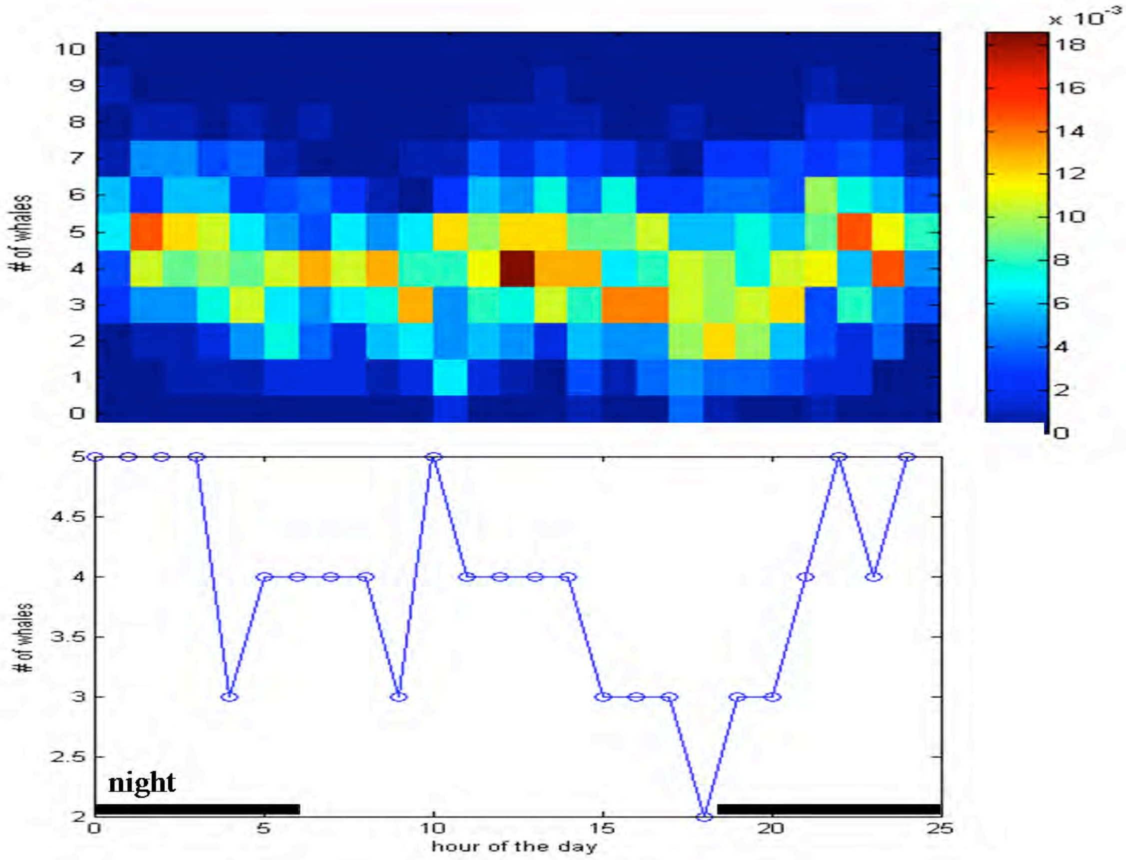

Figure 6. (Top) - Bi-distribution of the number of emitting whales vs the hour of the day. All data are pooled. (Bottom) - maximum probability of the previous bi-distribution.

catch data along the south and southeastern coast of Madagascar (Best, 1998), reports a bimodal seasonal distribution of humpback catches, which reflects seasonal abundance. One peak occurs in the third week of August and one wider peak, in July. This bi-modality would suggest that the population follows two waves of migration. The monthly distribution from the present study is very similar in the respective periods, with a peak occurring at the end of the second week of August. The estimated values at the beginning of August and in the middle of September remain almost equivalent. Despite the fact that the data seems to indicate fewer whales present before August 03, the second expected peak was not significantly apparent during the observation period in the present study.

The significant decrease in September could be explained by changes in the proportion of singers in the total population during the breeding season. As the end of the breeding season is approaching, more and more males achieve their mating goal, and these could then become less active as singers, or they could have left the area. Another study (Trudelle *et al.*, 2018) describes how the composition of the channel humpback population varies based on visual observations, and pointed to a 35% decrease in observed cases of singing among single individuals, couples, and competitive groups, between the middle of August and the middle of September. The current standard deviation anomaly detected in the distribution on August 24 corresponds to the first measurement after the maximum peak. This could be a consequence of a reorganization of the population, with more displaced individuals or individuals in transit in the study area.

Even though the raw acoustic strength received can be highly impacted by motor boats, bad weather, or whales singing close to the hydrophone, it is interesting to observe that the acoustic level measurement is consistent for qualitatively evaluating the density of emitting whales. Seger (2016) agrees that most of the ambient noise in generated by whale vocal activity.

An indisputable contribution of acoustic monitoring is highlighted when the objective is to detect diurnal/nocturnal effects, or fine temporal scale variations. Many previous studies can be found (often based on acoustic strength measured) concluding that there is more acoustic activity at night (e.g. Au, 2000), but none show clear trends during a complete 24 h period based on a significant amount of data. The current study provides the typical hour by hour pattern of the number of singers present. The reason for lower acoustic activity during the day could be a result of a relatively higher number of males involved in active surface groups during daylight hours. However, there are no studies suggesting a significant reduction of activity just before nightfall.

Consistency of the estimations

The toolbox developed uses an algorithm based on the spatial consistency of the acoustic sources. This method is efficient to filter out environmental noises such as rain, random clicks generated by coral reef organisms, and anthropogenic sources, as these are either occasional (short time duration) or of rapid motion. The estimations are also robust regarding time and frequency overlaps, and the changing SPL of the sound productions, once the sources are recognized as spatially distinctive. The known major limitations are if whales emit close together, or get into a different position but with the same bearing to the hydrophone. The consequence of this is an underestimation of the true number of whales. The results given in this study can be considered as minimally effected by these limitations. However, the precision of results could be increased by implementing a range estimation model.

Despite the fact that the detection function could not be evaluated, the detection threshold, materials and methods stayed unchanged, maintaining the same acoustic volume/area of coverage for all the sessions. Thus, the estimated number is likely to be proportional to the density of animals in the study area. The present results may be particularly reliable to describe the local fluctuation of the humpback population. A previous study (Helble, 2013) established the probability of detection using their own sound recording device. The resulting probability function was equal to 1 to 3 km for humpback whales. By taking into account this maximum distance, any emitting humpback whales should be detected within a surface area $S_{\max} = 14$ km^2. As an indicative overview, the ratio of the estimated number using this area gives a density ranging between 0.07 and 0.7 whale/km^2. Frankel *et al.* (1995) mentioned a comparable result of 0.62 whales/km^2 for an acoustic survey in the shallow waters of Hawaii.

Conclusions and further work

When and for how long does the whale emit sound? During the present study, actual investigations were conducted over a short time scale. Cross-correlations provided information on the position of the source and also on the duration that the source has been active. The toolbox developed here can be harnessed to extract basic features, such as the starting time of a continuous sound, its duration, and rhythm. Such an automatic analysis may be a significant contribution to this research topic as different levels of study might be available; from the scale of the song unit to the scale of a complete song. Although, several studies on song duration have been done in the past (Thompson, 1981; Payne, 1983; Fristrup, 2003), few have focused on the rhythm and silence duration. Additionally, previous work has been limited by the amount of continuous data and the fact they did not use automatic analysis. A complete song can last more than 22 h (Winn and Winn, 1978). The current dataset and further implementation of the toolbox provides the opportunity to shed some light on these questions, with the longest session duration available in the current dataset being 42 h.

As distinctive singing whales (not overlapping) are well separated by the cross-correlation, this method would offer perspectives to study soundscapes including multiple emitting humpback whales. Thus, it will be possible to consider the songs within a social context and to reveal important clues on acoustic interactions among the individuals. Although some research has highlighted such interactions associated with humpback social calls (Silber, 1986), or between singers and surface activity (Tyack, 1981), most previous works on songs are based on single singer sequences, and have not been able assess any element of communication between singing individuals present in a given area. Is there any accordance among the individuals on the song duration or rhythm? Do they overlap their sound production? Is it possible to observe a pattern as “emitter- receiver”? Such questions could be firstly investigated by the extraction of the previously mentioned parameters without any investigation into the frequency-temporal structure of the songs. Similarly to the detection of short term displacement of the sources, sound production and motion could also linked.

More acoustic surveys may be needed over a complete season (ie. from June to October) to observe cyclical behaviour or multi-modal distribution, while yearly measurements are needed to compare inter-annual variations and distribution, perhaps with the use of more acoustic stations along the Sainte Marie channel, in order to refine the current findings.

Acknowledgements

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Using passive acoustic monitoring to assess humpback whale occurrence and breeding activity around La Réunion Island

Laura Ceyrac[1], Emmanuelle Barreau[1, 2], Alexandre Modi[1, 2],
Vanessa Estrade[1], Violaine Dulau[1]

[1] GLOBICE Réunion
30, Chemin Parc Cabris
Grand Bois
97410 SAINT PIERRE
Ile de La Réunion

[2] Université de la Réunion

Corresponding author:
laura.ceyrac@globice.org

Abstract

Humpback whales use the coastal waters of La Réunion Island seasonally from June to October. Their distribution is relatively well-known on the west coast, which provides suitable breeding habitat, however little is known about their use and movement along the south and east coast of the island. Three autonomous acoustic recorders were deployed during the breeding season of 2016 off the west, south and east coasts to investigate spatial and temporal variations in humpback whale occurrence around the island. The dataset consisted of 10 minute acoustic recordings every hour, continuously from mid-June to early September from these three locations. Song and social call events were discriminated and their total durations were calculated and expressed as a percentage of the total recording duration per day. Off the west and south coast, social calls were distributed fairly homogenously over the season, while songs occurred over a shorter time period, with two significant peaks observed in mid-July and early-August. Off the east coast very few vocalizations were detected. These results demonstrated that humpback whales preferentially use the west coast of the island for breeding. In this area, daily variations in singing activity were observed. Singers appeared to be more active at night and during the morning, when less boat traffic was detected.

Keywords: humpback whale, song, passive acoustic monitoring, Indian Ocean, breeding activity, occurrence.

Introduction

Humpback whales (*Megaptera novaeangliae*) typically undertake latitudinal migrations, resulting in a strong and constrained annual cycle, where feeding and breeding activities are spatially and temporally segregated (Dawbin, 1966). In the south-western Indian Ocean (SWIO), humpback whales breed along the east coast of Africa, Madagascar and around small oceanic islands, and feed almost exclusively off Antarctica during the austral summer (Best *et al*., 1998).

La Réunion Island is a small (72 km long and 207 km of coastline) oceanic island, located 700 km east of Madagascar and 250 km west of Mauritius. The island shelf is very narrow (200 m depth contour which lies on average 3 km from the coast) and bottom depth increases rapidly from close to the shore, down to 3,000 m deep. This topography could restrict humpback whale breeding habitat to within 2km from the coast, except off Saint-Gilles where the 100 m contour lies 7 km from the coast (Dulau-Drouot *et al*., 2008). The humpback whale appears to be the most common species showing a clear seasonal pattern at La Réunion Island, and are present in coastal waters from early June to late October, with a peak in July-September. The consistent occurrence of newborn calves, competitive groups and typical humpback whale songs confirm that La Réunion Island represents a breeding area for the species in the south-western Indian Ocean (Dulau-Drouot *et al.,* 2008; 2012). Survey effort around La Réunion mostly covers the west coast and little is known about the occurrence of the species on the east coast of the island, leeward and where the shelf is very narrow (Dulau-Drouot *et al*., 2017).

Male humpback whales are well known for producing stereotypical sound pattern known as songs, composed of units, phrases and themes (Payne and McVay, 1971). Songs are associated with breeding areas although they have been recorded, to a lesser extent, during migration (Clapham and Mattila, 1990; Noad *et al*., 2000) and in feeding areas (Mattila *et al*., 1987; McSweeny *et al*., 1989; Clark and Clapham, 2004). Humpback whales are also known to produce social calls, which are emitted in bouts but are not structured, and produced in shorter events than songs (Payne and McVay, 1971). Social sounds are believed to be produced by both males and females (Dunlop *et al.,* 2007).

Passive acoustic monitoring can be a useful tool to detect the presence of cetaceans, particularly species that are acoustically very active, such as humpback whales on breeding grounds. It can provide valuable and quantitative information on timing of migration, occurrence patterns, and breeding activity, on a continuous time scale that is not dependent on weather conditions (Lammers *et al.,* 2011; Munger *et al*., 2012; Cerchio *et al.,* 2015).

The main objective of this study was to use passive acoustic methods to monitor the presence of humpback whales off the west, east and south coast of La Réunion Island over the breeding season, to assess spatio-temporal patterns of occurrence around the island. Daily patterns in song production and boat traffic were also investigated to provide further insight into humpback whale breeding activity and habitat use in coastal areas, where most human activity occurs.

Materials and methods

Data collection

Passive acoustic monitoring was conducted off La Réunion Island using 3 SoundTrap 300 STD autonomous recorders (manufactured by Ocean Instruments, New Zealand) deployed on the west (Saint Gilles), south (Saint Louis) and east coast (Saint Benoit), in water depth of around 30 m (Fig. 1, Table 1). The three recorders were located 70 to 80 km apart, therefore singers could not be recorded simultaneously at the three stations. The SoundTrap units were configured with a bandwidth of 20 Hz – 60 kHz and recorded at a sampling rate of 48 kHz which is adequate for humpback whale vocalizations, as the main frequency range is below 24 kHz (Thomson *et al*., 1979; Payne *et al*., 1983; Silber *et al*., 1986). The gain of the preamplifier was set to "high" to increase sensitivity, resulting in a maximum Sound Pressure Level (SPL) of approximately 172 dB re 1 µPa (SoundTrap user guide).

The recorder units deployed off the south and east coasts were duty-cycled to record 10 minutes every hour, and had a lifespan of a minimum of 57 days. The hydrophone deployed off the west coast was equipped with an external battery pack and was set to record continuously, resulting in a lifespan of around 33 days. Recorders were thus deployed several times during the study period. For comparison purpose, only the first 10 minutes of each hour of recording from Saint Gilles were taken into account in this study.

Vocalization detection

The occurrence of humpback whale sounds was assessed from the 15th of June to the 1st of September 2016. The "whistles and moans detector" module of Pamguard V.1.15.10 was used to detect humpback whale vocalizations from the recordings (Gillespie *et al*., 2008). A bandpass filter of 0-8000 Hz was applied to select frequencies corresponding to humpback whale sounds (Thomson *et al*., 1979; Payne *et al*., 1983; Silber *et al*., 1986; Clark *et al*., 1990). The detector extracts the contour of tonal sounds from the spectrogram display (Fast Fourier Transform (FFT) data). It was configured by testing different parameters: minimum frequency; maximum frequency; detection sensitivity; and numbers of connections for contour detection. Contour detections were visualized in real-time on the FFT spectrogram (FFT length 1024; FFT hop size 512 and Hann window). Each detection (contour and sound file) was saved into a database as both a binary (SQLite) and audio file (wav format). The "clip generator" module of Pamguard was used to visualize and play back all automatically-detected vocalizations. Each vocalization was validated by an acoustic operator and classified either as a humpback whale vocalization or as a false detection (Fig. 2). Only vocalizations with a good signal-to-noise ratio (vocalizations in which the signal was at least 10 dB higher than the background noise) were considered for analysis. Boats were also detected and categorized as "boat traffic". Motor boat signatures were characterized by broadband noise and harmonically related tones that correspond to engine and propeller specifications (Ogden *et al.,* 2011; Sorensen *et al.,* 2010).

Spatial and Temporal Occurrence

The duration of each event of successive vocalizations was measured by taking the time interval (in

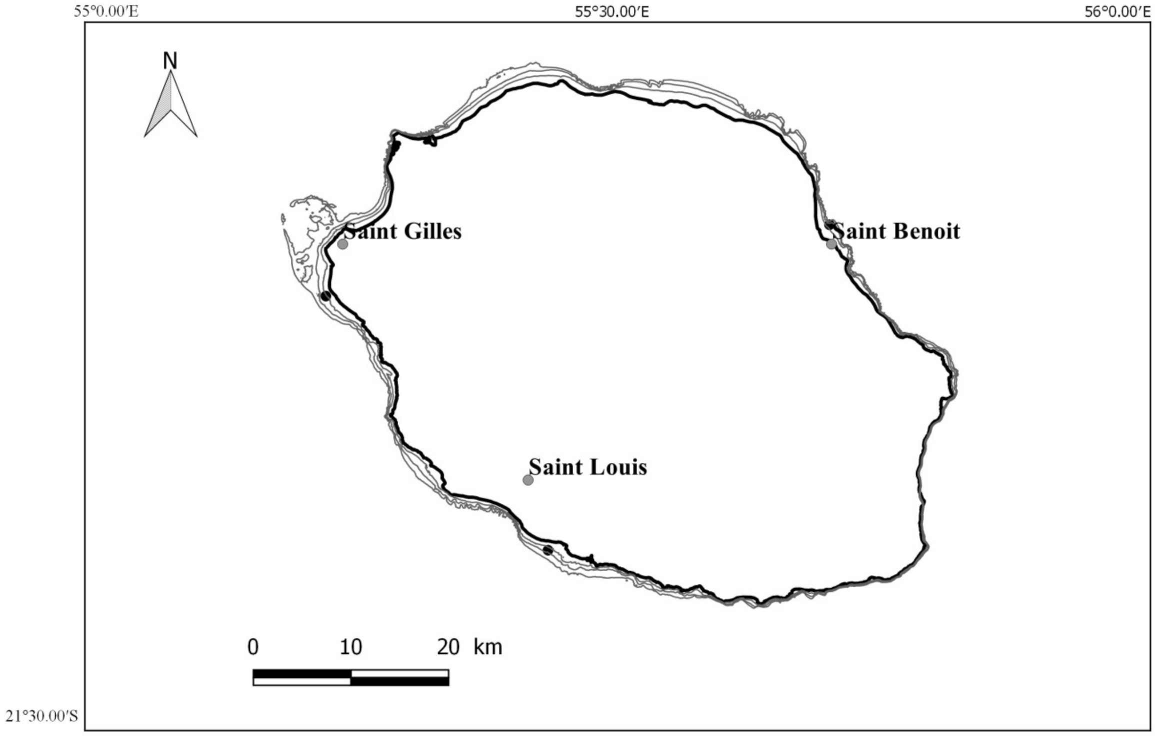

Figure 1. Map of La Réunion Island showing the position of the three hydrophones (black points) deployed around the Island.

mins) between the first and the last vocalization. Two events were considered as different after a lag time of more than 10 seconds between the last vocalization of the first event, and the first vocalization of the next event. This lag time was chosen because the time interval between two successive song units varied from 1 to 5 seconds. It was therefore considered that 10 s was a reasonable timeframe to consider two events as independent. Events were then classified into song or social call events, based on their structure and frequency. Song events were characterized by continuous, highly structured phrases and themes that contain sets of repetitive units above 4 kHz and generally showed harmonics (Payne and McVay, 1971; Darling, 1983; Helweg *et al.*, 1992; Au *et al.*, 2000; Fristrup *et al.*, 2003). In contrast, social call events were characterized by sounds ranging from 50 Hz to 3 kHz, which were produced erratically, in an unpredictable manner, without any rhythm and consistency (Tyack, 1981; Silber, 1986). The total duration of song and social call events were computed per day for each location (Saint Gilles, Saint Louis and Saint Benoît) and expressed as a percentage of the daily recording duration (240 minutes).

Table 1. Hydrophone stations used for temporal distribution and occurrence in 2016.
Days = number of days data were collected.

Site	Location (DMS)	Hydrophone depth (m)	Recording dates	Duration (Days)
Saint Gilles hydrophone	21° 5' 4.9999" S, 55° 12' 59.9976" E	33	29/06/2016-30/07/2016 02/08/2016-01/09/2016	61
Saint Louis hydrophone	21° 20' 10" S, 55° 26' 10.9968" E	33	17/06/2016-25/08/2016 26/08/2016-01/09/2016	76
Saint Benoit hydrophone	21° 0' 50.9998" S, 55° 42' 52.9999" E	33	15/06/2016-01/09/2016	78

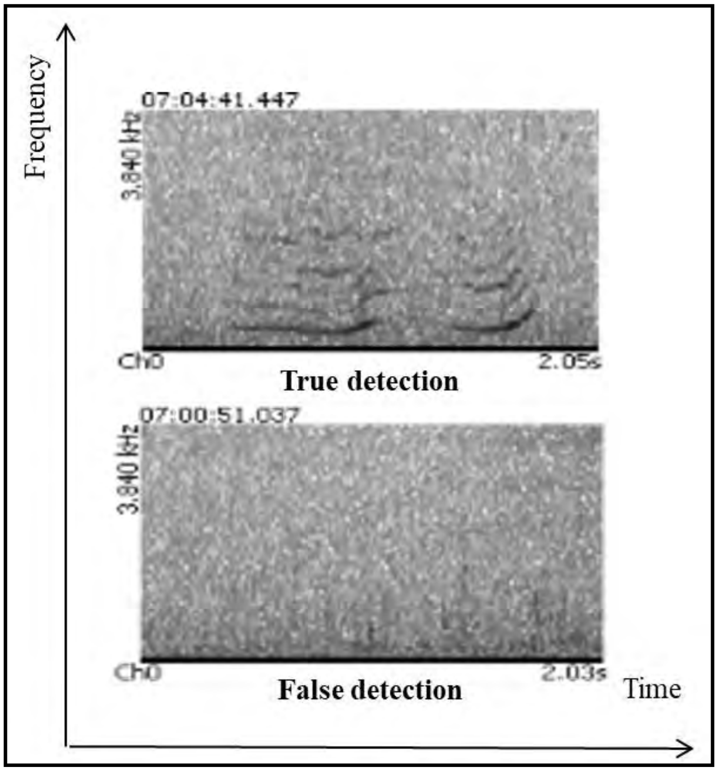

Figure 2. Examples of true (humpback whale vocalization) and false detections (noise).

Daily patterns in humpback whale singing activity and vessel traffic

Daily pattern of singing activity was investigated during the peak of the season, when songs were more frequently recorded (from the 29th of June to the 1st of September). For each location, a detection rate was computed for each hour of the day, by taking the proportion of recordings that included at least one song event, over the total number of 10 min recordings made at that hour, over the study period. Similarly, the detection rate of marine traffic (presence/absence of boat), was determined acoustically at the three sites.

Results

The hydrophone deployed off Saint Benoît (east coast) recorded for 78 days in a row. The hydrophones deployed off Saint Louis (south coast) and Saint Gilles (west coast) recorded for 76 and 61 days respectively, with 1 or 2 days of missing data (Table 1). Gaps in the recording occurred during recovery and re-deployment of the Sound Trap unit (for downloading data and recharging the batteries), which could not be undertaken on the same day.

A total of 860 hours of recording were analyzed: 244 hours from Saint Gilles; 304 hours from Saint Louis; and 312 hours from Saint Benoît. Humpback whale vocalizations were detected from all three recording locations, with some variability observed between sites (Fig. 3). Overall, humpback whale vocalizations were detected more often off the west coast (Saint Gilles) and the south coast (Saint Louis) compared to the east coast (Saint Benoît).

Temporal pattern of occurrence

For all sites, social calls were detected throughout the season, from July to early September, while songs were detected over a shorter period.

Songs were detected from the 14th of July to the 1st of September off the west coast, with two peaks observed in late July (song representing 100% of the recording duration) and in early August (87% of the recording duration) (Fig. 3). Off the south coast, songs were detected from the 15th of July only until the 14th of August. Two peaks were observed around the 16th of July and around the 2nd of August with song representing 70% and 81% of the recording duration, respectively (Fig. 3). Off the east coast, songs were detected from the 23th of July, and to a lower extent (35%), compared to the other sites. No peak was observed (Fig. 3). Very few humpback whale vocalizations were detected in general off this part of the island.

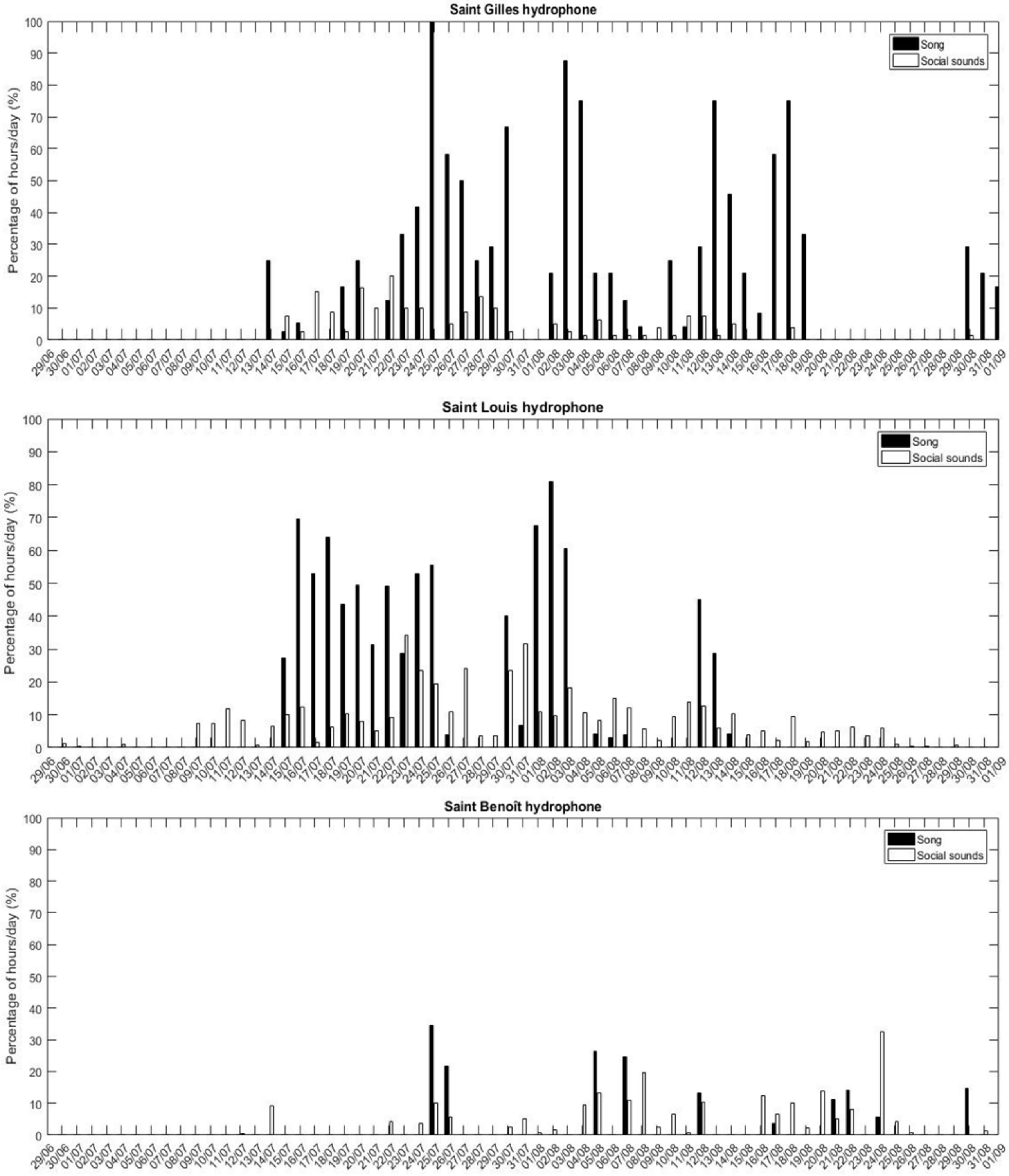

Figure 3. Percentage of hours of recording including humpback whale song (black bars) and social call (whites bars) over the breeding season of 2016 (late June to early September) at Saint Gilles (West), Saint Louis (South) and Saint Benoît (East).

Diel pattern in song activity

Songs were detected over the entire 24h period, but tended to increase at night off the west coast (Saint Gilles), more specifically between 7pm and 1am. The maximum detection rate (0.4) was observed in the evening, at 9pm and 10pm, and the minimum detection rate (0.2) was observed early in the afternoon, between 1pm and 3pm (Fig. 4). Off the south coast, songs were detected consistently throughout the day, and no clear daily pattern was observed. The detection

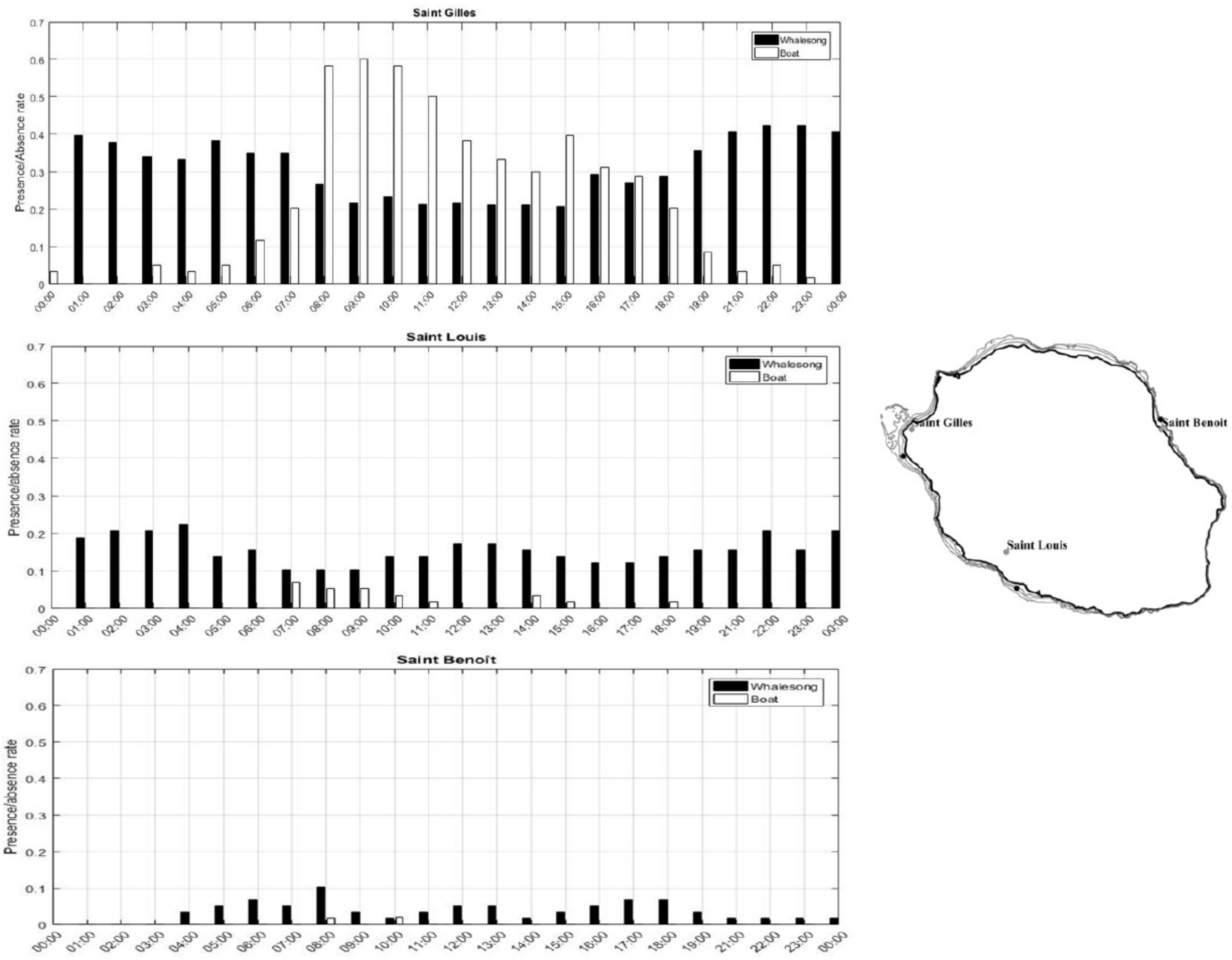

Figure 4. Detection rate of humpback whale songs (black bars) and boats (white bars) per hours, at each location, during the peak of singing activity (29th of June to the 1st of September 2016).

rate was lower than on the west coast, ranging from 0.1 to 0.2. Off the east coast, song detection rates were low (<0.1) and no diel pattern was observed (Fig. 4).

Diel pattern in vessel traffic

Vessel traffic was detected during daylight, from 7am to 6pm, with a peak (0.6) at 9am off Saint Gilles. On the south and east coast, marine traffic was less important, being almost absent. The maximum rate off Saint Louis (0.07) was at 7am, and only two boats were detected in Saint Benoit during the entire breeding season (Fig. 4).

Discussion

The results showed that humpback whales used the three study sites during the breeding season, with the west coast being used more extensively. Although the detection range of the hydrophone was unknown, the acoustic intensity of the sound received by the recorders was generally high compared to the background noise, and only good quality recordings were used, suggesting that the whales were detected within a few kilometers (up to a few tens of km maximum) from the recorders. Detection range might also have varied between sites, as sound propagation is largely influenced by local environmental characteristics. Due to a gentler slope, the recorder located on the west coast might have had a smaller detection range compared to those deployed on the east and south coast, although other factors might also have influenced sound propagation (e.g. type of substrate, topography, ambient noise). Assessing the detection range of the hydrophones at each location would require acoustic modelling based on oceanographic and environmental data, and could not be conducted in this study. Despite these uncertainties regarding the range of the hydrophones, the considerably higher detection rate recorded off Saint Gilles tends to indicate that the west coast of La Réunion represents a more suitable breeding habitat for the species, compared to the east coast that had been only poorly surveyed so far. This might be a result of lower habitat suitability in these areas, where underwater relief is very steep and the insular shelf is very narrow. Conversely, the west coast offers a larger shelf, particularly off Saint Gilles, where the 100m contour lies up to 7 km from the coast, offering an extended shallow water area, consistent with preferred humpback whale breeding habitat (Dulau-Drouot *et al*., 2008; 2012).

Social calls were detected at all three survey sites throughout the breeding season, from July to September, with no clear peak detected. Conversely, peaks in song production was observed from mid-July to early August off the south coast, and from mid-July to mid-August on the west coast, corresponding with the peak in breeding activity (increased sighting rate and presence of competitive groups) observed in La Réunion (Dulau-Drouot *et al*., 2008).

Furthermore, off the west coast, a diel pattern in song production was observed, with detection rates tending to increase during the night and decrease at around 8am. The rate of song detection was lowest during the day (between 9am to 3pm) and began to increase at around 4pm. These results suggest that, in breeding habitats, males spend more time singing at night, which is consistent with acoustic monitoring conducted in Maui, Hawaii (Au *et al*., 2000; Payne and Payne, 1985). Males might be less acoustically active during the day when they can engage in direct competition for females, within active groups, and may switch to other mating tactics such as song production at night, when visual cues are not possible (Au *et al*., 2000).

Interestingly, such a daily pattern in song production was not detected off the south and east coasts of La Réunion, which were used to a lesser extend compared to the west coast. Differences in song production between night and day might be less pronounced in areas providing less suitable breeding habitat, or when whale density is lower, as males might have less opportunity to switch between different mating tactics. Previous studies in Kauai, Hawaii (Helweg and Herman, 1994) and in the West Indies (Winn and Winn, 1978) also reported a lack of diel pattern in the number of singers. In Kauai, data were obtained at depth (700 meters) about 10-14 miles offshore, away from the breeding habitat (Helweg and Herman, 1994), and in the West Indies, the results were obtained from a large survey area from the Bahamas to Venezuela (Winn and Winn, 1978). The results from the present study may suggest that the detection of a daily pattern in song production could be representative of prime humpback whale breeding sites, providing suitable opportunities for males to engage in different mating behavior to maximize mating opportunities.
Alternatively, the daily pattern observed off the west coast could be linked to the increased number of boats using the area. As expected from visual observations and the location of the main harbours and recreational areas, boats were mainly present on the west coast, during daytime, from 6am to 6pm and with a peak in the morning. The increase in boat traffic corresponded to the time of the day when singing activity was lower off the west coast. The daily pattern observed off the west coast might be an artifact of the increased number of boats observed in this area during daytime, which could have masked part of the songs and thus decreased the detection range of the recorder. The question as to whether the decrease in song detection during the day resulted, in part, from an increase in disturbance from boat traffic might be asked, as engine noise may affect the acoustic environment of singers (Watkins, 1986; Norris, 1995; Sousa-Lima and Clark, 2008).

These preliminary results were based on a single breeding season (2016), during which a relatively low number of whales were observed compared to previous years (GLOBICE, unpub. data). Additional data should be collected over the coming years to confirm trends and further examine spatio-temporal variations in whale occurrence and song production in La Réunion. In particular, variation in humpback whale abundance between years might also have an impact on the breeding/singing behavior and the distribution of the species around the island, and would be worth investigating further.

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From universal to local law: prospects for the protection of whales in the western Indian Ocean through the Whale Route project

Stéphanie Sorby

University of Reunion Island
Institut de recherche pour de
développement de la Réunion,
La Réunion, France

Abstract

Whales are highly mobile animals, travelling long distances between breeding and feeding sites. They do not confine themselves to a specific area, crossing the waters and jurisdictions of multiple nations as well as areas beyond national jurisdiction. As a result, the conservation and management of these marine species is very challenging, requiring inter-institutional coordination, international and regional agreements. As an emblematic migratory species, whales are the subject of many international agreements, with a universal vocation, dedicated to their conservation and management. These include the Convention on International Trade in Endangered Species, and importantly, the International Convention for the Regulation of Whaling. A sanctuary was established in 1979 by the International Whaling Commission in the western Indian Ocean to implement and reinforce this latter universal convention at the regional level. However, these legal instruments do not guarantee the full protection of whales and their habitats from direct and indirect impacts of human activities such as pollution, ship strikes, overfishing, entanglement in fishing gear, disturbance, or even climate change. Consequently, a project for humpback whales, the whale route has emerged in the western Indian Ocean. This project is intended to protect humpback whales from many anthropogenic disturbances, to encourage their conservation, and to raise environmental awareness through sustainable tourism and outreach activities. The project requires the establishment of a road map to obtain the best possible marine protected areas for cetaceans through appropriate regional cooperation and governance arrangements in the western Indian Ocean. Indeed, because of the migratory pattern of whales, it is necessary to coordinate initiatives between many stakeholders such as States and Territories in this region, and also international organizations, transnational networks, public and private actors. This article aims to analyse the challenges and prospects of a regional protected area to contribute to the conservation of humpback whales. It also highlights the cooperation and the coordination required in the western Indian Ocean to resolve governance issues.

Keywords: whale route, sanctuary, marine protected area, whaling, global law, universal law, regional law, local law, transnational law, charter, label, governance, actors, agreements.

Introduction

Threats to whales occur in a vast area through which they migrate, both in the high seas and within the exclusive economic zones of coastal states in the northern and southern hemisphere. Therefore, measures to protect whales must operate at the same scale involving universal protection which does not have political borders.

The protection of whales reveals a multitude of legal and institutional frameworks, or "regimes", which together form an international convention for the protection of the environment. This includes institutions, secondary legislation, and sometimes the development of financial mechanisms (Maljean-Dubois, 2017). Using this kind of mechanism, certain uses such as trade (Convention on International Trade in Endangered Species of Wild Fauna and Flora), and whaling (International Convention for the Regulation of Whaling or "Whaling Convention"), which devastated whale populations due to the development of new technologies, were controlled, and sanctuaries were created to ensure protection of these great mammals.

These regimes are supplemented by soft law, generating non-binding obligations, often developed in the context of local characteristics. This applies, for example, to whale-watching charters, or labels awarded to companies for responsible whale watching activities. This variety of hard and soft laws which include global and local measures results in inconsistent and discontinuous protection. Indeed, the protection of whales varies according to their location during their migration, and to the disturbances they face, as many uses are not subject to global regulations (such as noise pollution, or vessel speed causing ship strikes). Thus, the protection of whales reflects a fragmented situation with regulations that do not adequately provide protection from anthropomorphic activities.

Given that the protection of whales is a global issue, a holistic approach is required, including special legal provisions at the international, regional and national level in the Indian Ocean. In this respect, the various theories of global law are useful (Frydman, 2012; Delmas-Marty, 2013) because they suggest approaching the law through a multiscale way with a variable normative intensity (Thierbierge, 2009).

The example of a whale route fits within these new approaches to law. A whale route project is currently under development in the western Indian Ocean (western Indian Ocean), led by the Council of Reunion Island. The objective of this route is to protect whales during their migration in the region through specific regulations while considering the variety of existing laws at various levels. To ensure some consistency in the level of protection afforded to whales, and given their long migration route through many exclusive economic zones (EEZs), collaboration between the States of the region is essential. The main countries involved in the whale route are France (for Reunion Island and Mayotte), Mauritius, Madagascar, Seychelles, Comoros, but countries from the East Coast of Africa are also concerned with whale migration, and could be part of the project. It is therefore a large-scale project, similar to the journey undertaken by these mammals each year.

The large scale nature and challenging context of whale migrations needs to be approached and understood at a regional level in the Indian Ocean. The protection of cetaceans by this whale route concept is part of this approach and incorporates not only a top-down approach (from global to regional law - I), but also a bottom-up approach (from local to trans-national law - II). Against this background, the goal of this paper is to critically assess whether the legal framework for creating and implementing the whale route can be considered a global law project.

From universal to regional law in the Indian Ocean

As a consequence of whaling, whale populations have been severely depleted, resulting in international conventions to protect them. Whaling itself, being the biggest threat, has been regulated through a universal convention (A), which has particular requirements for regional law for the protection of whales in the Indian Ocean (B).

Development of universal law against whaling

Whaling, whose first signs date back to the Neolithic (Lee & Robineau, 2004), has been so devastating for whales that many species are endangered (International Union for Conservation of Nature, Red List of threatened species, 2017). It was only with the conclusion of the International Convention for the Regulation of Whaling (ICRW) that whaling has been regulated.

The International Whaling Commission (IWC), set up under the International Convention for the Regulation of Whaling signed in 1946, is the multilateral intergovernmental body charged with the conservation of whales and the management of whaling. The purpose of the Commission, which is comprised of 89 representatives and a scientific committee, is to “establish a system of international regulation for the whale fisheries to ensure proper and effective conservation and development of whale stocks” (Whaling Convention, 1946) through catch limits, restrictions on hunting methods, and designation of whale sanctuaries. In other words, the IWC regulates whaling in order to increase stocks and thus to enhance whale catches. It appears that the Commission has a dual mandate; on the one hand, managing fisheries, and on the other hand, conserving whale species. These objectives are inherently linked as whaling will depend on healthy whale stocks.

In 1982, as several whale stocks has been decimated, the IWC adopted a moratorium on commercial whaling, which entered into force in 1986. Henceforth, whaling for commercial purposes was forbidden for Member States bound by the regulation. However, despite the ban, whaling remains legal in some cases:

A government can lodge a reservation to the moratorium, as Norway and Iceland did, to keep on whaling.

Indeed, the possibility of making a reservation to the moratorium was possible at the time of its adoption, but Iceland accepted the prohibition and then withdraws from the Convention to re-adhere it in 2002 by making a reservation to the moratorium, which can be legally questionable.

Aboriginal subsistence whaling, as it does not seek profit or excessive catches, is allowed despite the moratorium, as long as hunted whale populations stocks remain at a healthy level.

Whaling is also legal for scientific research purposes. The Convention does not define "scientific research", but it gives responsibility to Member State governments to issue permits to kill whales for this purpose. This exception to the ban has been widely used for decades by the government of Japan, but in 2014, in a historical decision, the International Court of Justice (ICJ) ordered Japan to end its research program (JARPA II) deciding that it was not for scientific purposes (ICJ, 2014). Since then, after following the Court's ruling which was limited to JARPA II, the Japanese government started a new 12-year research programme called "New Scientific Whale Research Program in the Antarctic Ocean" (NEWREP-A).

Each contracting government has to report to the IWC each time a permit is issued (Article VIII (3) of Whaling Convention), but the Commission does not regulate permits for scientific purposes, which can explain why this case (the Whaling case) was brought before the ICJ by anti-whaling nations to end the Japanese programme.

In addition to these exceptions allowing whaling, it appears that the moratorium is becoming increasingly weak. Indeed, to overturn the ban, a three-quarters majority vote by the commissioners is required and pro-whaling members have increased during recent years within the IWC, sometimes under political and financial pressure. It is alleged that Japan used its overseas development aid to convince developing countries to join the Commission in order to vote for the resumption of commercial whaling (Dippel, 2015).

To sum up, the ICRW was adopted to reduce whaling on overexploited stocks and to rebuild depleted stocks. The moratorium is not sufficient, on its own, to protect whales from whaling. Indeed, some countries still conduct whaling in defiance of the moratorium. Moreover, this pause in commercial whaling is fragile considering the increasing number of pro-whaling nations. The creation of whale sanctuaries could be a solution to this threat. This would be an example of regionalisation of a universal convention.

Manifestation of universal law in regional law

While the moratorium on whaling does provide protection for whales, it is not infallible and not permanent. Therefore, to strengthen the protection of whales in the western Indian Ocean, a whale sanctuary has been created by implementing the Whaling Convention directly in regional law. The IWC designated a whale sanctuary in 1979 (Paragraph 7 (b) of the Schedule of the Whaling Convention) where commercial whaling is forbidden, regardless of the status of whale stocks and of whether the moratorium is in force or not. It covers the whole of the South Indian Ocean. The sanctuary has been regularly revised since 2002 and, at its 54th annual meeting, the IWC agreed to continue this prohibition of commercial whaling in this specific area without setting a time for a further revision. This decision is a positive move for the Indian Ocean, given the proliferation of pro-whaling nations. A three-quarters majority of votes by IWC members is needed to overturn such decisions.

When the sanctuary was created, the Member States made no reservations. Thus, from a legal point of view, commercial whaling is prohibited by all Member States. However, the exception of scientific whaling does not seem to take into account the establishment of a sanctuary. When the ICJ condemned Japan, it was not because their scientific whaling programme was taking place in the Southern sanctuary, but because the Japanese scientific programme was not considered as such.

This second Southern sanctuary, created in 1994, appears more vulnerable than the South Indian Ocean sanctuary. This is because if the moratorium is lifted, sanctuaries will remain areas where commercial whaling is prohibited, but there is a legal loophole that can weaken this prohibition. In international law, governments can lodge an objection to circumvent a provision. This was the position taken by the government of Japan, which lodged an objection to the prohibition of commercial whaling in the Southern sanctuary for one species, the Minke whale (Whaling Convention, 1946). This means that, despite the moratorium, Japanese fishermen can kill minke whales for commercial purposes in this sanctuary. Japan did not object to any other baleen or toothed whale species, so their former scientific programme, JARPA II, could not be legal since Humpback and fin whales were also targeted (in addition to minkewhales) in this programme implemented in the Southern Ocean sanctuary.

Consequently, if the moratorium is lifted, sanctuaries would still protect whales from commercial whaling, except if a government lodged an objection to the prohibition. This is why anti-whaling nations are campaigning for more protected areas. However, creating a new sanctuary is not easy; a proposal for a sanctuary in the South Atlantic Ocean has recently been rejected as it did not achieve the three-quarters majority of votes required. Pro-whaling nations pointed out that there is already a moratorium on commercial whaling so this protected area would be unnecessary. However, as already highlighted, the moratorium does not guarantee protection.

The creation of a sanctuary in the Indian Ocean, decided almost forty years ago, is therefore an opportunity. It is an example of the development of a regional law resulting from a convention with universal reach. This means that regional specificities, such as the high abundance of whales in this area, can influence the creation of a regional law. Regional law would in this case be more protective than the universal law. Nevertheless, this sanctuary whose role is limited as long as the moratorium remains in force (as it prohibits commercial whaling too), represents increased legal protection justified by the need to protect humpback whales in the area. Even if humpback whales are not threatened by commercial whaling in the sanctuary, they are subject to other threats that need to be regulated. Making use of existing rules at the local level to create a regional law would be an appropriate approach for the creation of a whale route in the western Indian Ocean.

From local to regional law

Facing universal law, and sometimes thanks to it, new norms are emerging at the local level, as in the Reunion Island. These norms could be extended to the western Indian Ocean region for the creation of a whale route.

Emergence of local norms

Local law refers to rules that are restricted to limited areas or territories like Reunion Island. This law is characterized by being more specific than national law, and also by the emergence of new instruments, whose legal value is sometimes debated, but which nevertheless serve a particular purpose.

For example, in Reunion, as in Madagascar, a whale watching charter has been developed to ensure the protection of these large mammals. As such, operators involved in whale watching must respect several rules. These include: boats keeping a certain distance from cetaceans; not pursuing or cutting off whales; and reducing speed in their presence.

In order to reward good practice, an eco-label for the responsible Observation of Cetaceans in Reunion (O2CR) has been developed locally by public and private actors. The objective is to consolidate the charter and include whale watching as a contributor to sustainable development.

The objective of the charter is to better organise and regulate the whale watching industry, and include whale watching as a contributor to sustainable development. Nevertheless, the legal value of this charter is debatable, which impacts on the powers of sanction and punishment in the event of non-compliance.

In order to determine the extent to which the charter is binding, its scope, and thus its legal enforceability, it is necessary to identify its origin (Frydman & Lewkowicz, 2012). Indeed, the origin is critical for understanding the legal value of these rules and their place in the hierarchy of norms. The origin acts as a "pedigree", or a "certificate of origin" (Frydman & Lewkowicz, 2012).

The whale watching charter for marine mammals in Reunion was developed by a local non-governmental organization devoted to the study and awareness of cetaceans. The charter does not require formal accession by sea users, and contains simple "general and specific recommendations" without providing for sanctions in the event of non-compliance. It is a non-binding instrument relying on moral and ethical standards rather than a legal one. It would thus belong to soft law. The origin and the non-binding nature of the rules in the charter do not guarantee its effectiveness. According to Maljean-Dubois & Richard (2004), the charter will be considered as effective if it is implemented in practice by a group of people (brigade), but also if it has the capacity to encourage and eventually convince users to behave respectfully.

The charter is generally respected and is effective in Reunion, based rather on a sense of nationalism rather than a legal origin (Dworkin, 1977 in Frydman, 2012). The charter is a good example demonstrating that binding force is not always linked to effectiveness.

The charter was developed by non-state actors, to protect themselves from potential injuries during whale watching and, of course, to protect whales. The success of the charter relies on the environmental awareness of users, particularly around the risks of an inappropriate approach and its consequences. A bad approach can be dangerous for boaters as well as for whales and their calves, and is also likely to lead to the whales leaving the area, to the detriment of observers. In addition, a group (brigade) "Quiétude" ("Peacefulness" in English) is in charge of enforcing the charter by reminding the users about the rules of good conduct. This brigade is an indispensable component for the effectiveness of the charter through ensuring compliance. This brigade relies on the fear of users of being shamed for non-compliance to ensure the effectiveness of the charter. Although this brigade embodies a certain authority to enforce the charter, it does not have any power to impose sanctions. Moreover, as a "soft" instrument of law, the charter does not have binding legal value. However, the charter supports the hard legal instruments that exist, whose content is rather vague. The Environmental Code (article L411-1) and the Ministerial Decree of the 1st of July 2011 which prohibits the intentional disturbance, including the pursuit or harassment of animals such as mysticetes, in their natural environment (Decree, 2011), are considered as hard law, but have poorly regulations. For instance, there is no definition of harassment included. While the charter has no legal value, it is more specific in terms of harassment and navigation, making the hard law more consistent and coherent. Behaviour that is contrary to the charter can therefore always be sanctioned on this legal basis by the competent authorities, including the French Maritime Directorate of the southern Indian Ocean, Ecoguards of Reunion's Natural Marine Reserve, Coast Guard officers, the Indian Ocean Brigade, and the Gendarmerie). However, in general, the soft law contained in the Charter is useful to the situation in Reunion in that it effectively satisfies a need and provides some consistency to more general objectives stemming from both domestic and "traditional" international law, even without having a hard legal basis.

This local law developed in Reunion dedicated to the protection of whales is an interesting legal scheme that could be extended to the western Indian Ocean. As an instrument of soft law, this charter would be based on voluntary participation and compliance, and would gradually introduce and integrate rules for responsible whale watching. States would also have the freedom to adapt their domestic law to support the recommendations of the charter if they so wish.

The charter could then form the basis of an agreement between the western Indian Ocean countries (in the form of a treaty) or could result from an infra-state agreement. In this sense, an agreement could be concluded between the relevant administrative authorities or public bodies in the different countries, as in the case of the "Sister Sanctuary Agreement" established in French Antilles. In this way, local law could form the basis of the proposed whale route, and would be a first step towards the progressive, consistent and cooperative protection of whales migrating in this region.

From local to transnational law: towards the conclusion of an agreement for the whale route

The creation of the whale route could be achieved through the development of a local law at a transnational level through a multilateral or bilateral agreement and, regardless of the selected model, this route will need its own specific governance).

Implementation of local law at the transnational level through a multilateral agreement

Because of their long migrations, humpback whales can be observed in large parts of the western Indian Ocean and on the coasts of many countries. Regional co-operation between different territories is needed to protect them from the threats they face. The Convention on Migratory Species could play a major role in the development of regulated areas for whales in the western Indian Ocean.

The Convention on the Conservation of Migratory Species of Wild Animals (CMS), also known as the Bonn Convention, is an environmental treaty under the aegis of the United Nations Environment Programme, established in 1979, and entered into force in 1983 (CMS, 1983). It aims to conserve migratory species and their habitats, consequently its area of coverage is universal, from territorial waters, EEZ, to the high seas. As a framework convention, its key function is the creation of regional agreements to protect migratory species and their habitats in a large area. Agreements created under the CMS that are dedicated to cetaceans include the Agreement on the Conservation of Cetaceans of the Black Seas, Mediterranean and Contiguous Atlantic Area (ACCOBAMS) and the Agreement on the Conservation of Small Cetaceans in the Baltic, North East Atlantic, Irish and North Seas (ASCOBANS). ACCOBAMS was the first agreement binding the countries of that region to work together for the conservation of cetaceans (ACCOBAMS, 2001).

ACCOBAMS has twenty-four parties, and aims to reduce threats to cetaceans in a very large area by adopting resolutions. A whale watcher certificate has been created to reward and ensure sustainable tourism, an education programme has been published to create awareness of the cetacean species inhabiting the agreement area, and an application has been developed to help avoid ship strikes by real-time plotting of cetaceans (REPCET). Considering the threat posed by ship strikes, the French decree of the 8th of March 2017 (Decree, 2017) forms part of the hierarchy of French norms according to a classical normative approach (Kelsen pyramid) and is therefore based in hard law. This decree requires the mandatory use of the REPCET application in the PELAGOS sanctuary, a large area dedicated to the preservation of cetaceans in the Mediterranean that was established by a tripartite agreement between France, Monaco, and Italy (PELAGOS, 2002). Currently, only vessels flying the French flag are legally required to use REPCET as the other member states have yet to adapt their national legislation accordingly. Nevertheless, many Italian companies have decided to voluntarily equip their vessels with REPCET for use in the PELAGOS sanctuary.

No decree provides for the application of this system for French within the area of the ACCOBAMS agreement, as REPCET has to first demonstrate its effectiveness in the Pelagos sanctuary, which is a smaller area. The ACCOBAMS agreement is an interesting legal framework to protect whales, but it suffers from poor commitment from member states. Whilst the agreement may provide whale protection measures, it is the States which will have to implement them. International environmental law is often characterized by its ineffectiveness because of the softness of norms which is often linked to the insufficient priority given to environmental as compared to commercial issues. In environmental agreements, the commitment of the States is mainly limited to objectives to be achieved rather than to obligations to protect the environment. Many environmental agreements allow States great flexibility to design and implement protection measures without any obligations to produce results. As a consequence, international regulations are not always implemented (Petit, 2011).

The creation of a multilateral agreement in the Indian Ocean could suffer from a lack of commitment by States. However, countries may be incentivised by the economic benefits generated by whale watching tourism associated with such a sanctuary. In addition to the international links that the whale route will create, the tourist economy could expand considerably in the area by enhancing this natural heritage. This could include the establishment of a common regional charter for the responsible approach and observation of whales, or the creation of a common label awarded to companies for responsible whale watching. It is believed that it is legally feasible to provide for regional cooperation with the aim of improving the protection of whales, and associated ecotourism. “Strict” regulations, such as the adoption of specific rules on fishing types allowed in the area, or the adoption of anti-collision measures, which can sometimes be costly and constraining, could be more difficult to apply as illustrated by the use of REPCET in the ACCOBAMS sanctuary.

International cooperation through the medium of a multilateral agreement could therefore be an approach to consider for the whale route. Private actors such as non-governmental organisations or whale watching companies, and even transnational networks and fora, for instance the Humpback Whale World Congress (held in Reunion in 2017) or the Symposium of the Western Indian Ocean Marine Science Association, could be appropriate to promote international cooperation. Using a bottom-up approach, a locally-developed mechanism such as the whale watching charter of Reunion Island, could be adapted and made available for regional use in the western Indian Ocean through a soft law agreement such as a memorandum of understanding between countries. This cooperative approach would lead to coherent and directed protection of whales between States, with individual countries choosing to develop a legal basis for the charter if they so wish.

The difficulties experienced with implementing anti-collision measures for all members of ACCOBAMS illustrates the challenges of implementing a multilateral agreement with soft law. The cause of this ineffectiveness may be financial, but it can also be linked to the fear of losing sovereign rights.

A more gradual approach through bilateral agreements could also be considered to determine the most appropriate and effective mechanism to protect whales in the western Indian Ocean.

Development of regional cooperation through bilateral agreements

If regional cooperation through a multilateral agreement for the western Indian Ocean whale route appears too ambitious or constraining for the countries of the region, cooperation through bilateral agreements may be appropriate.

The contracting Parties would then be two States, which would establish protection objectives in a delimited area. Since the EEZ are adjacent between the islands of the western Indian Ocean, this would enable regulation of a large area without interfering with the principle of freedom of the high seas, according to article 87 of the United Nations Convention of the Law of the Sea (UNCLOS, 1982).

Because of their large adjacent EEZs, an agreement between Reunion and Madagascar would cover and regulate, for example, a large strategic area where numerous activities are taking place and where maritime traffic is abundant.

The whale route could be influenced by a protection mechanism developed in the French West Indies for the AGOA sanctuary. This is a protected area set up under the Cartagena Convention, more commonly called "SPAW" (Specially Protected Areas and Wildlife) which aims to ensure the favourable conservation status of marine mammals by protecting them and their habitats from direct or indirect negative impacts of human activities. The sanctuary was created in 2012 and currently covers the entire EEZ of the French West Indies. The declaration on the creation of the AGOA sanctuary expressly foresees cooperation between protected marine areas frequented by the same animals, such as humpback whales, which move into the waters of the sanctuary during the winter, but are also present in the northwest or northeast Atlantic in summer. "Sister agreements" have allowed decentralized cooperation between different marine areas frequented by whales to be developed to ensure consistent protection for whales during their migration. For example, AGOA has been officially "twinned" with the Stellwagen Bank National Marine Sanctuary since 2011 (United States of America), the Saguenay-St. Lawrence Marine Park (Canada) since 2015, and the Yarari Sanctuary (Netherlands) since 2017. A "sister sanctuary agreement" has been concluded between the United States National Oceanic and Atmospheric Administration's Stellwagen sanctuary and the former French Marine Protected Area Agency to protect humpback whales and to provide "new avenues for collaborative education, scientific and management efforts, including joint research and monitoring programs" (Special Agreement for the implementation of the Memorandum of Understanding, 2011).

This bottom-up approach by which States collaborate indirectly through legally constituted national administrative entities may be easier to implement. The "sister agreement" is established between two administrative authorities in different countries, which can help to avoid the potential procedural difficulties relating to the conclusion of an international agreement.
Applying a bottom-up approach and developing local law for use at an international level for the creation of a whale route could be an interesting option for the western Indian Ocean. However, marine areas dedicated to the protection of whales or large marine protected areas would have to exist within the waters under the jurisdiction of at least two countries to consider the development of a "sister agreement".

Whether the collaborative agreement chosen is part of a universal whale protection approach or based on local law, the whale route will have to be the subject to an appropriate governance system.

The Governance of the whale route

Several "platforms" or "fora" exist through which the whale route concept can be taken forward. These fora would provide the opportunity for discussion between relevant stakeholders and for decisions to be made to protect the whales in a delimited area.

The Convention for the Protection, Management and Development of the Marine and Coastal Environment of East Africa (Nairobi Convention, 1985) could function in this role. As a platform for discussing issues related to the marine and coastal environment in the western Indian Ocean, the Convention is also a legal and institutional forum that provides a framework for bringing the countries of the region together. The Convention coordinates the various strategies to protect the marine environment and in particular promotes the creation of a marine protected area network in its Article 10: "The Contracting Parties shall, individually or jointly, take all appropriate measures to protect and preserve rare or fragile ecosystems as well as rare, depleted, threatened or endangered species of wild fauna and flora and their habitats in the Convention area".

Also, a "Protocol Concerning Protected Areas and Wild Fauna and Flora in the Eastern African Region" signed in 1985 and entered into force in 1996, highlights the need for cooperation between Member States of the western Indian Ocean in order to coordinate their efforts to protect migratory species whose natural range extends over their territories, such as humpback whales. This direct reference to humpback whales provide a clear legal framework for the whale route that could be used in an appropriate governance system.

On the basis that the environment is increasingly perceived as having a common value for all mankind, the United Nations Educational, Scientific and Cultural Organization (UNESCO) could also potentially provide a forum for the governance of the whale route. The objective of working within the UNESCO system would be for the whale route to become designated as a World Heritage Site, provided the criteria drawn up by the UN agency are met for this inscription. Within UNESCO, the Intergovernmental Oceanographic Commission could play a major role in the governance of the whale route. States of the western Indian Ocean region, potentially involved in the whale route project, are also members of this Commission, whose objective is to promote international cooperation and to coordinate programmes in marine research, services, conservation and protection of the coastal and marine environments to understand and effectively manage the resources of the ocean and coastal areas. This institution could host meetings between state and non-state actors from many countries in the area which are involved in the implementation of the whale route in order to encourage inter-state cooperation for common and consistent decision-making.

This role could also be played by the Indian Ocean Commission, established by the 1984 Victoria Agreement, which has five island states in the southwest Indian Ocean as members. The Commission coordinates various programmes demonstrating its involvement in the protection of the marine environment. For instance, the Indian Ocean Commission's Marine Protected Area Network Programme is implemented by the World Wildlife Fund of Madagascar and the Western Indian Ocean Programme Office, and aims to contribute to the preservation of biodiversity and marine resources in the southwestern Indian Ocean eco-region through a network of well-managed Marine Protected Areas.

Like it does with this programme, the Commission could facilitate activities related to the whale route by providing institutional support and hosting experts to discuss and reach decisions. For example, non-governmental organizations operating in countries involved in the whale route project, and specialised brigades (cf. "Quiétude"), could then, at the local level, act as intermediaries for the implementation of new norms and standards. The Commission could also play a key role in financial support through the contribution of the European Union. The European Union which has observer status since October 2017, is the main donor of the Commission, and is particularly involved in the development of the island states in the western Indian Ocean. Because of this, the influence of the European Union in the Indian Ocean basin is significant (Tabau, 2017).

Transnational networks and fora such as the International Humpback Whale World Congress held in July 2017 in Reunion Island, and whose next meeting will take place in 2020, could also play a role in the governance of the whale route, mainly on a technical level. This is an opportunity for actors, scientists, politicians and researchers to meet each other on a regular basis during these congresses to discuss and come up with regulations to protect whales. In addition to the whale charter of Reunion Island, which was extended to include dolphins and turtles during this 2017 Congress, a common charter for western Indian Ocean States could introduced and discussed during the next Congress in 2020, in the context of the whale route.

In addition to governance platforms, actors have a decisive role to play in the implementation of the route. States, of course, must cooperate and commit themselves in a multilateral or bilateral agreement according to the chosen model. Since Reunion is not a state, but an overseas department and region of France, substate authorities could intervene in an international agreement, as allowed by the Letchimy law (French Law, 2016). As such, the Regional Council can negotiate an international convention with a neighbouring foreign state and then sign it with the authorization of the State provided that this treaty respects the international commitments of France (Tabau, 2018).

Private actors also have a significant role to play in assisting decision-makers. Experts, researchers and associations provide essential information on whale protection. For example, the work of scientists can guide the delimitation of the area to be protected according to the distribution range of the whales. They can also assist with the development of guidelines for approaching whales through information obtained from behavioural studies.

Conventions, international organizations, and transnational networks are all ways of ensuring the effective governance of the whale route, in which public and private actors will play a key role. This range of different possibilities for governance of the whale route demonstrates the existence of many diversified tools. These tools should not be regarded as competing with each other, but complementary, to be adapted to the realities and requirements of international community (Maljean-Dubois, 2017). Thus, a holistic approach to governance appears to be more appropriate than a single option (Maljean-Dubois, 2017).

Conclusion

Considering the migratory pattern of whales, their conservation and management require associations between existing institutions and agreements at different levels in order to enhance the consistency of the relevant law. However, legal instruments contribute but do not guarantee a full protection of whales and their habitats. Indirect impacts also imply to consider other legal frameworks. Therefore, the project of the "whale route" should take into account this complex legal environment. To develop regional cooperation around this project, it is necessary to use current legal frameworks but also to reveal links between them. These links may be considered from a top down approach (for example, implementation and adaptation at the local level of multilateral agreements) but also from a bottom up dynamic (for example, replication of the whale watching charter applied to Reunion Island coastal area). The latter could be more appropriate for the protection of whales at the regional scale considering the loopholes of the top-down approach. Beside these normative interactions, the governance of the "whale route" has necessarily to be analysed from a global perspective, emphasizing relationships between various actors, institutions, and networks.

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