



<https://doi.org/10.15517/rev.biol.trop..v71i54.57280>

## Southern Hemisphere humpback whales (*Megaptera novaeangliae*) (Artiodactyla: Balaenopteridae) singing activity at Caño Island Biological Reserve, Costa Rica before, during, and after COVID-19 lockdowns

Laura J. May-Collado<sup>1, 2\*</sup>;  <https://orcid.org/0000-0002-4790-9524>

Sawyer Bottoms<sup>1</sup>;  <https://orcid.org/0000-0002-8821-7348>

Grace Durant<sup>1</sup>;  <https://orcid.org/0000-0002-1896-3900>

Jose David Palacios-Alfaro<sup>3</sup>;  <https://orcid.org/0000-0002-0315-094X>

Juan Jose Alvarado<sup>4, 5, 6</sup>;  <https://orcid.org/0000-0002-2620-9115>

1. Department of Biology, University of Vermont, Burlington, VT 05405, USA; sawyer.miller-bottoms@uvm.edu, grace.durant@uvm.edu
2. Smithsonian Tropical Research Institute, Panama, Panama; lmaycoll@uvm.edu (\*corresponding author)
3. Fundación Panacetacea, St Paul Minnesota, 55118, USA; pala1611@gmail.com
4. Escuela de Biología, Universidad de Costa Rica, San José, Costa Rica, juan.alvarado@ucr.ac.cr
5. Centro de Investigación en Ciencias del Mar y Limología (CIMAR), Universidad de Costa Rica, San José, Costa Rica.
6. Ecología Tropical (CIBET), Universidad de Costa Rica, San José, Costa Rica.

Received 21-IX-2022.

Corrected 13-II-2023.

Accepted 11-IV-2023.

### ABSTRACT

**Introduction:** Boat traffic is recognized as a major contributor of underwater noise. Increasing presence of boats in coastal habitats is predicted to have important repercussions on the communication of marine mammals. In Costa Rica, the waters of the Caño Island Biological Reserve are an important breeding area for humpback whales from the Breeding-Stock G (BSG). Their predicted and abundant presence has fueled the development of whale watching activities as an important component of the local economy, and while the country has norms of conduct for this activity, whales often interact with multiple boats at the same time. The lockdowns associated with the COVID-19 pandemic provided a unique opportunity to study the potential impacts of noise associated with boat traffic on the singing activity of humpback whales.

**Objective:** Determine whether noise levels and boat acoustic presence around Caño Island Biological Reserve changed during the COVID-19 lockdowns, and if it did, what is the impact on song detection of BSG humpback whales.

**Methods:** Acoustic recordings were made using a bottom-mounted autonomous underwater recorder for 30 days in September 2019, 2020, and 2021, resulting in a total recording effort of 480 hours.

**Results:** Our results show that broadband underwater noise levels ( $\text{dB}_{\text{RMS}}$ ) during pre-lockdown were significantly higher, particularly at frequencies below 1kHz, than during and post-lockdown. This is likely due to a decrease in the proportion of boat acoustic presence during the lockdown. Although the proportion of whale songs detected did not vary among years, whale songs were detected similarly throughout the day during the lockdown, compared to pre-and-post lockdown where the proportion of whale song presence decreased during hours when more boats were present.

**Conclusions:** This study shows a clear change in underwater noise levels during the COVID-19 lockdown, likely due to a decrease in boat presence. The study also highlights the potential impact of noise associated with boat traffic on humpback whale singing activity. The results of this study can inform the Conservation Areas of Osa



(ACOSA) in charge of managing Caño Island Biological Reserve, to develop and implement mitigation measures to regulate underwater anthropogenic noise associated with tour boats.

**Key words:** ambient noise levels; boat traffic; whale-watching; tourism; bioacoustics.

## RESUMEN

**Actividad de canto de las ballenas jorobadas (*Megaptera novaeangliae*) (Artiodactyla: Balaenopteridae) del hemisferio sur en la Reserva Biológica de la Isla del Caño, Costa Rica, antes, durante y después de los cierres asociados a la pandemia de COVID-19**

**Introducción:** Se reconoce que el tráfico de embarcaciones es uno de los principales contribuyentes al ruido marino. Se predice que la creciente presencia de barcos en los hábitats costeros tendrá importantes repercusiones en la comunicación de los mamíferos marinos. En Costa Rica, las aguas de la Reserva Biológica Isla del Caño son un hábitat reproductivo importante para las ballenas jorobadas de la población reproductiva G (BSG). Su presencia ha impulsado el desarrollo de las actividades de observación comercial de ballenas, lo cual es un componente importante de la economía local. Aunque el país tiene normas de conducta para esta actividad, las ballenas a menudo interactúan con múltiples barcos turísticos al mismo tiempo. Los cierres y limitaciones de movilización de botes asociados a la pandemia de COVID-19 brindan una oportunidad para estudiar el impacto potencial del ruido asociado al tráfico de embarcaciones en la actividad de canto de las ballenas jorobadas.

**Objetivo:** Determinar si los niveles de ruido ambiental bajo el agua y la presencia de botes cambiaron antes, durante y después de los cierres y cuarentena por COVID-19, y si estos cambios influyen en la detección de cantos de machos de ballenas jorobadas.

**Métodos:** las grabaciones acústicas se realizaron con una grabadora autónoma montada en el fondo marino durante 30 días en septiembre de 2019, 2020 y 2021, resultando en un esfuerzo de grabación de 480 horas.

**Resultados:** Nuestros resultados muestran que los niveles de ruido ambiental ( $\text{dB}_{\text{RMS}}$ ) antes del cierre (2019) fueron significativamente más altos, particularmente a frecuencias bajas ( $<1\text{kHz}$ ), que durante y después de los cierres asociados a la pandemia de COVID-19. Es probable que esto se deba a una reducción en la presencia de embarcaciones durante el cierre. Aunque la detección de cantos de ballenas jorobadas no varió entre años, durante la cuarentena se detectaron los cantos de ballenas de forma uniforme durante el día, mientras que antes y después de la cuarentena se notó un decrecimiento en la proporción de cantos a horas donde hay más detección de botes presentes.

**Conclusiones:** Este estudio muestra un cambio claro en los niveles de ruido ambiental durante el cierre de COVID-19, probablemente debido a una disminución en la presencia de embarcaciones. El estudio también muestra el potencial impacto del ruido asociado al tráfico de embarcaciones en la actividad del canto de las ballenas jorobadas. Los resultados de este estudio pueden informar al Área de Conservación de Osa (ACOSA), la cual está a cargo de la Reserva Biológica Isla del Caño, a desarrollar e implementar medidas que regulen el ruido antropogénico bajo el agua asociado a tráfico de botes turísticos.

**Palabras clave:** ruido ambiental; tráfico de botes; observación de ballenas; turismo; bioacústica.

## INTRODUCTION

Boat traffic (i.e., ecotourism, personal use, fishing, water-taxis) is increasing rapidly in many coastal environments contributing to an increasingly noisier ocean (Erbe et al., 2019). Concerns about the potential repercussions of underwater noise impacts on whale communication are increasing among scientists worldwide (e.g., Cholewiak et al., 2018, Erbe et al., 2019). High noise levels can reduce the distance at which these animals can communicate (e.g., Cholewiak et al., 2018, Rey-Barquero et

al., Laude et al., 2022) and can interrupt biologically important behaviors (e.g., Amrein et al., 2020; Sprogis et al., 2020). For example, Rey-Barquero et al., (2021) developed a model based on empirical data that showed that even in the presence of a single whale-watching boat, humpback whale, *Megaptera novaeangliae* (Borowski, 1781) song communication could be reduced by as much as 63 %. Another study found whale-watching activities to be one of the factors contributing to a decrease in communication space, with humpback whales experiencing masking levels of 80% or more

(Cholewiak et al., 2018). These studies show the potential negative impact of noise associated with boat traffic, particularly that of activities that directly target these animals, such as whale watching activities.

Whale-watching is a major catalyst of the local economy in Latin America (Tambutti & Gómez, 2020). The most recent review of the state of whale watching in Latin America is by Hoyt and Iñiguez (2008). The authors find that between 1996 and 2006, boat-based whale watching activities in the region grew at a rate three times higher than the rate of world tourism and five times higher than the rate of all Latin American tourism over the same period. Although many countries have adopted whale watching guidelines, compliance and enforcement remains limited (Gagne et al., 2022). As a result, whales might be exposed to noisy soundscapes.

In March 2020, the COVID-19 pandemic led to a global and national lockdown in Costa Rica to limit the spread of the virus. Widespread mandatory lockdowns and stay-at-home orders severely limited human mobility and activities in land and in the ocean. Costa Rica's economy shrank by 4.1% in 2020 as a consequence of these measures, and among the factors driving this trend was the sharp drop in tourism (Economic Survey of Latin America and the Caribbean, ECLAC, 2021). According to the CEIC Global Economy Database (2022), the number of air transported passengers dropped from 2,033,146 to 455,830 passengers. Worldwide, this drop in human mobility resulted in an increase in animal communication ranges; for urban songbirds, their communication range doubled in some places (Derryberry et al., 2020) and for dolphin and fish it increased to up to 65 % (Pine et al., 2021).

Male humpback whales are highly vocal animals that perform acoustic displays primarily during the breeding season (Herman et al., 2013). The South Pacific waters off the coast of Costa Rica, and particularly the north and east side of Caño Island, are an important breeding area for Southeastern Pacific humpback whales, also known as the International

Whaling Commission, designated Breeding Stock G (BSG) (Palacios-Alfaro et al., 2012; Rasmussen et al., 2007) as well as for whales from the "Central America" distinct population segment (DPS) (Bettridge et al., 2015). The BSG whales observed in Costa Rica migrate from feeding areas off the Antarctic Peninsula and the Fuegian Archipelago in Chile (Acevedo et al., 2017; Rasmussen et al., 2007). Multiyear boat surveys in this area indicate that BSG whales are particularly abundant in September (Palacios-Alfaro et al., 2012), and for this reason coastal communities in the area celebrate a whale festival during this month (Palacios-Alfaro, personal communication, 1 september 2022).

A previous study using passive acoustic monitoring data near Caño island found that male song activity occurred throughout the day, with a drop in singing activity during the morning hours, suggesting a potential response to whale watching tour boats presence (Chereskin et al., 2019). In other breeding areas in Brazil, increased boat traffic was shown to have a negative effect on humpback whale singing activity, with whales singing less when the number of boats increased (Sousa-Lima & Clark, 2008). In a recent study, Laute et al. (2022) found that on Icelandic foraging areas during the COVID-19 pandemic, whale watching trips were reduced by 68.6 %, and humpback whale call detection increased by nearly twofold. In this study we examine whether noise levels and boat acoustic presence around Caño Island Biological Reserve changed during the COVID-19 lockdowns, and if it did, how the detection of BSG humpback whale song was impacted.

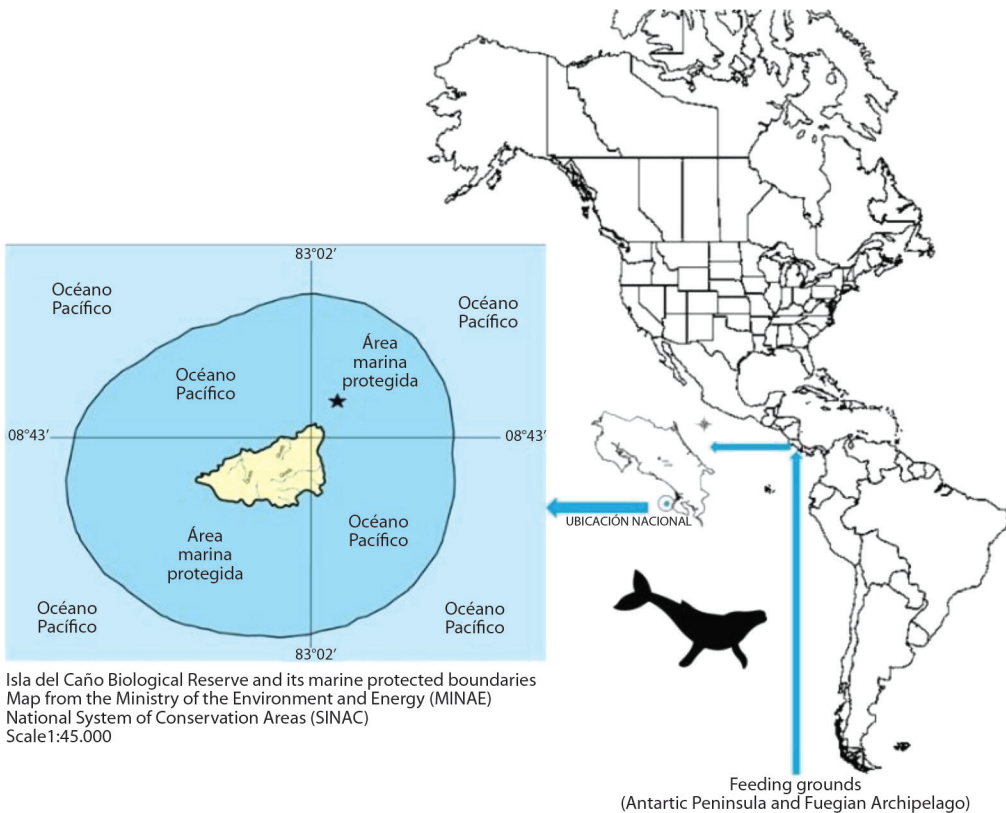
## MATERIALS AND METHODS

**Study Area:** This study took place at Caño Island Biological Reserve, 16 km northeast off the Osa Peninsula in the south Pacific coast of Costa Rica. This reserve protects approximately 58 km<sup>2</sup> of marine habitat around the island (Executive Decree 20790-MIRENEM, 1991). An autonomous underwater recorder was deployed in a location at the northeast side of

the island called El Jardín (8.719N/-83.863W, Fig. 1) at a depth of 25 m. This location is approximately 0.8 km from the island and is characterized by a sandy bottom (Chereskin et al., 2019). This area of the island has been highlighted by previous studies as an important reproductive habitat for BSG humpback whales (e.g., Rasmussen et al., 2007; Palacios-Alfaro et al., 2012). The island is also a tourist attraction with tour boats arriving to the island throughout the day to observe whales and dolphins, snorkel, and scuba dive.

**Data Collection:** An autonomous underwater recorder, a Soundtrap model 300 SD (Ocean Instruments; frequency range 20 Hz-150 kHz  $\pm$ 3dB; self-noise of less than sea-state in the bandwidth 100 Hz-2 kHz, and sensitivity of

-203 dB re V/ $\mu$ Pa) was deployed in El Jardín for the entire month of September 2019, 2020, and 2021. The recorder was programmed to record the soundscape at a sampling rate of 48 kHz for five minutes every 30 minutes in 2019, and for 15 minutes every 60 minutes in 2020 and 2021, resulting in a total of 480 hours recording effort. For this study, we only analyzed the first five minutes of every hour for each year, resulting in a total of 180 hours analyzed. These 5-min files were uploaded to RFCx ARBIMON (Rainforest Connection, 2020) for cataloguing and spectral inspection for presence/absence of whale songs and boats. The proportion of acoustic files with song and boat presence was calculated by dividing the number of 5-min files with whale songs and boats by the total number of 5-min files per year and time of day.



**Fig. 1.** Location of Caño Island Biological Reserve off the Osa Peninsula in the South Pacific of Costa Rica. The figure also shows a cartoon of a straight-line from Costa Rica towards the feeding areas off the Antarctica Peninsula and the Fuegian Archipelago in Chile to Caño Island, Costa Rica. The black star represents the deployment site of the autonomous underwater recorder.

**Ambient Noise Levels:** To measure broadband ambient noise levels we used the software dBWav from Marshall-Day Acoustics (<https://www.marshallday.com>) which is tailored for Ocean Instrument Soundtrap hydrophones. Upon calibration following Ocean Instruments instructions, the first five minutes of every hour were selected manually. Manual selection was done because dBWav does not automatically select the region of interest. We selected a subsample of days for this part of the data analysis including the following days for each year: 4, 7, 10, 13, 16, 19, 22, 25, and 28. The average root-mean-square ( $RMS_{dB}$ ) was then generated for each 1/3 octave bands ranging from 12.5 Hz to 10 kHz.

**Statistical analysis:** The statistical software SPSS 25 (IBM, 2017) was used for summary statistics and statistical analyses. An ANOVA test for multiple independent variables (n-way) was used to study the effect of year (pre, during, and post lockdown), time of day (hour), and 1/3 octave frequency bands on noise levels ( $RMS_{dB}$ ). Broadband noise levels were compared among years using a non-parametric Kruskal-Wallis' test. The 1/3 octave bands were grouped into two categories: below and above 1kHz frequency categories. Below 1 kHz included bands from 12.5 to 800 Hz and above 1 kHz bands from 1 to 10 kHz. A Kruskal-Wallis test was also used

to assess if there are differences in these two frequency categories among years. A Chi-Square one sample test for goodness of fit was used to compare the proportion of recordings with whale song and boat presence per year. Finally, the proportion of noise levels, whale song, and boat presence were plotted against time of day using a smoothing spline with a bootstrap confidence of fit using a lambda of 0.05 to look for diel patterns in ambient noise levels and whale song and boat presence within each year.

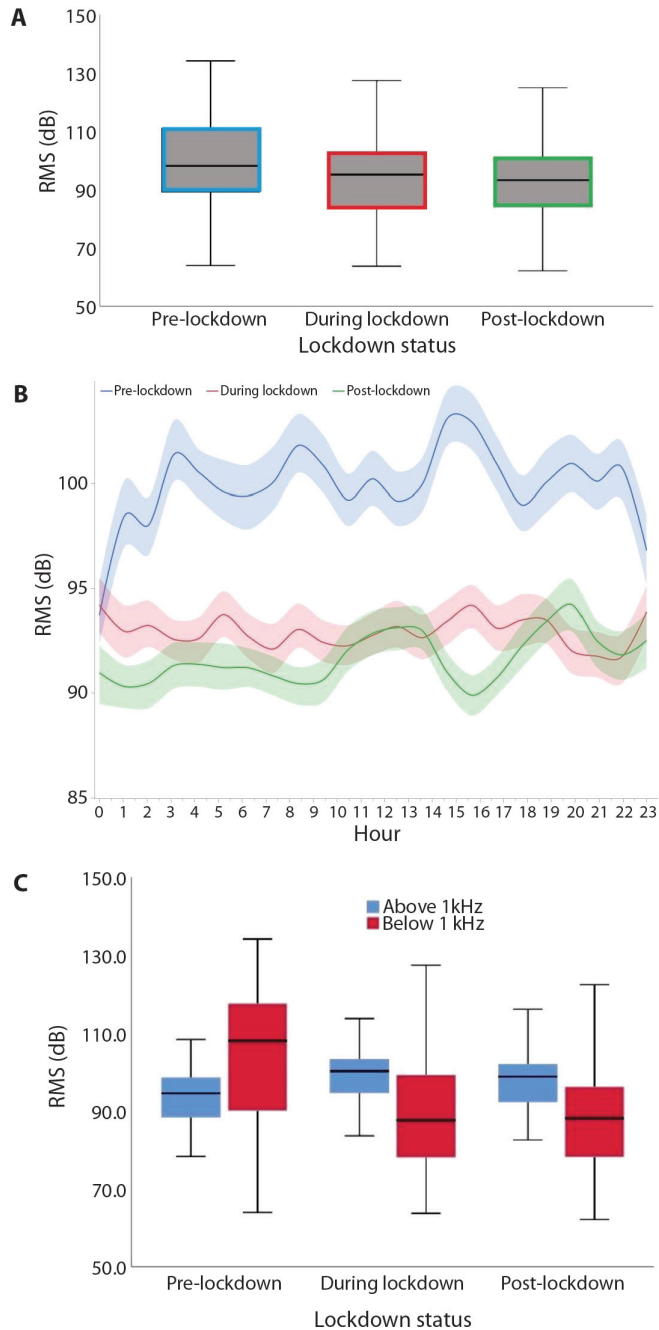
## RESULTS

**Ambient Noise Levels:** The results from the ANOVA analysis suggest that year ( $F=1610.5$ ,  $df=2$ ,  $p<0.001$ ), time of day (hour) ( $F=4.8$ ,  $df=23$ ,  $p<0.001$ ), 1/3 octave frequency bands ( $F=369.8$ ,  $df=27$ ,  $p<0.001$ ), and the interactions between year\*time of day ( $F=9.6$ ,  $df=46$ ,  $p<0.001$ ) and year\*1/3 octave frequency bands ( $F=176.7$ ,  $df=52$ ,  $p<0.001$ ) influenced the variation in ambient noise levels. Broadband ambient noise levels varied significantly among years (Kruskal-Wallis=876.06;  $df=2$ ,  $p<0.001$ , Table 1, Fig. 2A, Fig. 2B). In general, ambient noise levels were higher in pre-lockdown than during and post-lockdown (Table 1, Fig. 2A) and these differences among years were maintained throughout the day (Fig. 2B). When accounting for frequency categories

**Table 1**

Summary statistics of ambient noise levels (in dB) and the proportion of whale song and boat presence in pre-lockdown, during lockdown, and post-lockdown at Caño Island Biological Reserve.

	Pre-lockdown (2019)	During lockdown (2020)	Post-lockdown (2021)
<b>Ambient noise levels (dB)</b>			
Mean±SD	99.8 ± 15.3	93.0 ± 11.6	92.0 ± 11.0
Coefficient of Variation (CV)	15.3	12.5	11.8
Range (minimum-maximum)	63.9 -- 134	63.7 -- 127.4	62.1 -- 126.8
<b>Acoustic boat presence</b>			
Mean±SD	0.08 ± 0.13	0.03 ± 0.06	0.04 ± 0.09
Coefficient of Variation (CV)	152.8	169.6	193.9
Range (minimum-maximum)	0 – 0.44	0 – 0.22	0 – 0.30
<b>Acoustic whale song presence</b>			
Mean±SD	0.98 ± 0.02	0.99 ± 0.01	0.97 ± 0.04
Coefficient of Variation (CV)	2.0	0.8	4.2
Range (minimum-maximum)	0.93 – 1	0.96 – 1	0.86 – 1



**Fig. 2. A.** Broadband ambient noise ( $RMS_{dB}$ ) levels by year. **B.** Broadband ambient noise levels ( $RMS_{dB}$ ) by time of day. **C.** Broadband ambient noise levels ( $RMS_{dB}$ ) by year and frequency category. Broadband noise levels measured as the average root-mean-square ( $RMS_{dB}$ ) (a) by year and (b) time of day, in blue pre-lockdown (2019), in red during lockdown (2020) and in green post-lockdown (2021), and by (c) 1/3 octave frequency bands grouped into two categories below 1 kHz (12.5 to 800 Hz) and above 1 kHz in blue (1-10 kHz) and year, at Caño Island Biological Reserve, Costa Rica. The box plots display median, first and third quartiles, and maximum and lower values (excluding outliers) and the line plot uses a smoothing spline and bootstrap confidences of fit with a lambda of 0.05.

above and below 1 kHz we find significant differences among years. Ambient noise levels below 1 kHz were significantly higher in pre-lockdown (Kruskal-Wallis=1138.5;  $df=2$ ,  $p < 0.001$ , Fig. 2C) while ambient noise levels above 1 kHz were significantly higher during and in post-lockdown (Kruskal-Wallis=465.5;  $df=2$ ,  $p < 0.001$ , Fig. 2C).

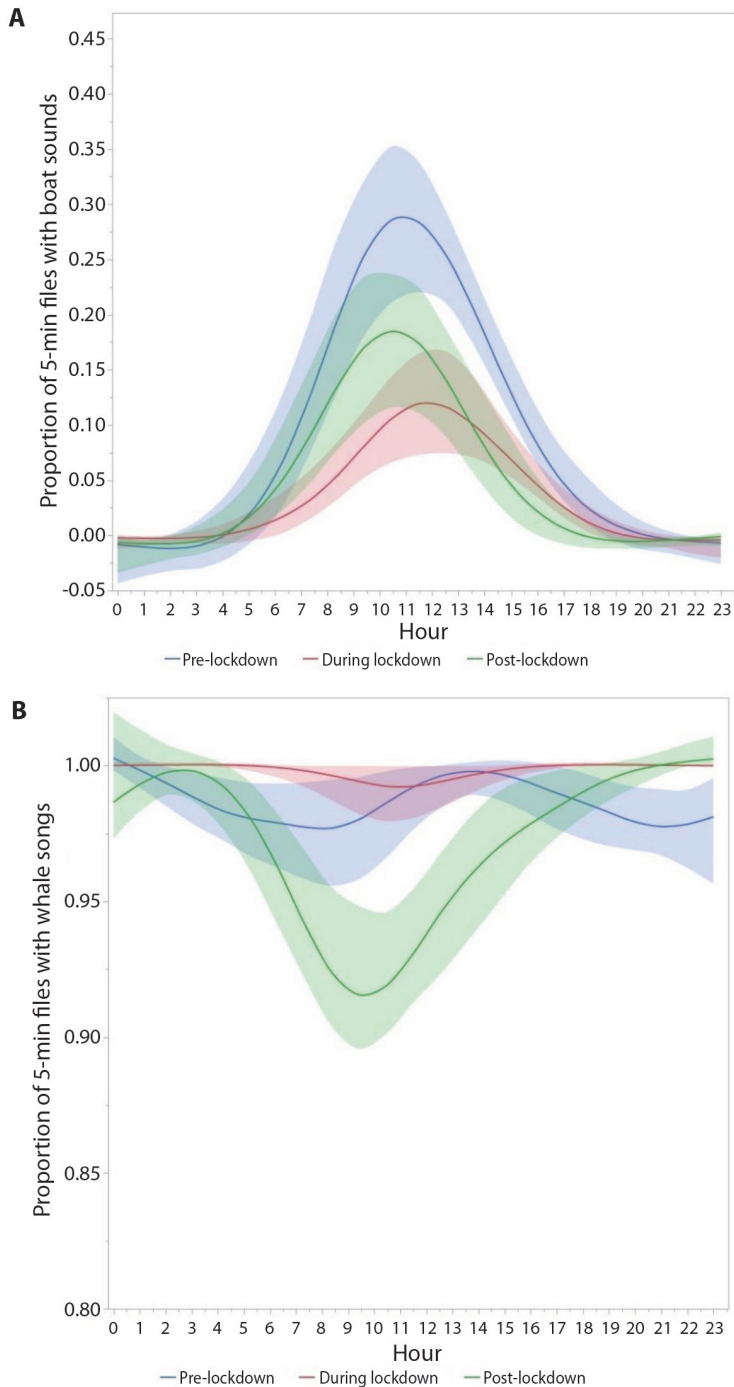
**Acoustic presence of whale songs and boats:** A total of 2 058 5-min per hour files were used for this analysis (2019 = 695 files, 2020 = 643 files, 2021 = 720 files). Of these, a total of 2 028 5-min files had an acoustic presence of whale song (2019 = 686 files, 2020 = 642 files, 2021 = 700 files) and 117 5-min files contained sounds of passing boats (2019 = 60 files, 2020 = 22 files, 2021 = 35 files). The proportion of 5-min files with boats passing by was significantly lower during lockdown than in pre-lockdown and post-lockdown ( $\chi^2=61$ ,  $df=2$ ,  $p = 0.003$ , Table 1). Interestingly, the diel acoustic presence of boats across years followed a similar pattern, with a peak in presence between 9 a.m. and noon for all years (Fig. 3A). No significant differences ( $p > 0.05$ ) were found in the proportion of 5-min files with whale songs across years, but pre-lockdown and post-lockdown years showed the greatest reduction in the proportion of files with whale songs compared to during the lockdown (Table 1, Fig. 3B). In addition, we found differences in diel patterns of the proportion of whale song presence among years. During pre-lockdown, the highest proportion of recordings with whale songs occurred at midnight and around 2 p.m. During the lockdown, the presence of whale songs was almost constant throughout the day, with a slight decrease between 9 a.m. and 2 p.m., and in post-lockdown a sharper decrease in whale song presence occurs approximately between 5 a.m. and 6 p.m., with the lowest proportion of whale song presence occurring between 10 a.m. and noon (Fig. 3B).

## DISCUSSION

This study shows that underwater ambient noise levels and boat presence changed between pre-lockdown, during lockdown, and post-lockdown periods around Caño Island Biological Reserve. The year before the COVID-19 pandemic had the highest mean underwater noise levels, particularly at low frequency below 1 kHz, and a higher proportion of boat presence. Although the proportion of whale song presence did not vary significantly among years, but we did observe a decrease in the proportion of acoustic files with whale songs during pre-and-post-lockdown. We also found differences in the diel pattern of song presence by time of day among years, suggesting a potential impact of tour-boat traffic in the area.

Boat traffic and shipping activities are the most dominant sources of underwater noise at low frequency (Southall et al., 2017). During the COVID-19 pandemic these activities were significantly reduced due to a slowdown of the global trade activity in order to mitigate and minimize the spread of the virus (Ryan et al., 2021; Thompson & Barclay 2020). This decrease in low-frequency underwater noise levels resulted in a potential increase in animal communication ranges during the COVID-19 lockdowns. For example, in New Zealand, underwater ambient noise levels dropped nearly threefold, resulting in an increased in dolphin and fish communication ranges to up to 65 % (Pine et al., 2021), while in Iceland a reduction of whale watching trips resulted in a twofold increase in humpback whale call (Laute et al., 2022), and a similar increase in dolphin whistle detection rates were found in Panama (Gagne et al., 2022).

Caño Island Biological Reserve is an important breeding area for humpback whales (Rasmussen et al., 2007). Therefore, it is not surprising that their overall presence did not change between periods. However, Caño Island



**Fig. 3.** Diel song detection of BSG humpback whale songs (a) and boat sounds (b) measured as the proportion of 5-min files per hour with songs and boat sounds during pre-lockdown (2019 in blue), during lockdown, (2020 in red) and post-lockdown (2021 in green) at Caño Island Biological Reserve, Costa Rica. These figures were done using a smoothing spline and bootstrap confidences of fit (light read and blue colors) with a lambda of 0.05. To facilitate visualization of the data, notice that scales for the proportion of boats and whale song detections are different.



Biological Reserve is also an important tourist destination, and while whales are not the primary target for all tour activities, boat presence is high in the area (Chereskin et al., 2019). A previous study showed that in September at Caño Island, BSG humpback whale singing activity happens primarily at nighttime hours (Chereskin et al., 2019). Similar diel singing activity patterns have been described in other humpback whale populations and appears to be widespread (e.g., Cholewiak 2008; Homfeldt et al., 2022). However, in this study we found that during the COVID-19 lockdown, the proportion of whale song presence was similar throughout the day (i.e., Fig. 3B). This suggests that in 'normal' times tour-boats might be reducing whale singing activity during the day, leading to higher rates during nighttime hours. For example, we observed a decrease in the proportion of whale song detections when boat presence increased during the day, particularly in pre-and-post-lockdown years. A high presence of tour-boats could lead to signal masking, which can lower the proportion of time that whale songs are detected by passive acoustic monitoring sensors, and similarly impacting detection among whales. Alternatively, whales may invest less in singing when there is a high presence of boats (and associated noise) and invest more time in singing at nighttime hours when boat presence is low (e.g., Parks et al., 2014). Such decision-making tradeoffs have been shown in humpback whales off the Ogasawara Islands in south Tokyo, where whales stopped singing when boats were nearby (Tsuji et al., 2018), and in humpback whales from the Abrolhos National Marine Park in Brazil, where humpback whales sang less when the number of boats increased (Sousa-Lima & Clark 2008).

The function of humpback whale song continues to be a subject of debate. Songs have been proposed to function as a reproductive display, by which males compete among themselves and attract potential mates (Herman 2017, Garland & McGregor 2020; Whitten 2019). That these songs can be masked by the underwater noise from human activities or

that whales stop their acoustic displays when there is a high presence of boats is of concern. The high proportion of acoustic files with whale songs during the COVID-19 lockdown suggests that whales have the potential to sing similarly throughout the day, but nighttime is likely the most efficient time to sing when boat traffic is high during the day, and highlights the potential impact boat traffic can have in their reproductive displays (i.e., males singing less) (Sousa-Lima & Clark 2008; Tsuji et al., 2018,) and habitat use (i.e., changing behavioral activities) (Sprogis et al., 2020).

As lockdown restrictions are lifted, tour boat presence is expected to return to normal at Caño Island. This study shows the potential impacts of unregulated tour boat presence on this important reproductive environment. These impacts are an important consideration for mitigation efforts and government investment in the enforcement of whale-watching regulations, as well as in the design and implementation of measures to regulate anthropogenic noise levels in this protected area.

**Ethical statement:** the authors declare that they all agree with this publication and made significant contributions; that there is no conflict of interest of any kind; and that we followed all pertinent ethical and legal procedures and requirements. All financial sources are fully and clearly stated in the acknowledgments section. A signed document has been filed in the journal archives.

**Author Contribution:** LJMC conceptualized the study, collected data in the field and the lab, coordinated data collection, performed data analysis, interpreted the data, and drafted and revised the manuscript. SB generated noise level data, and contributed to the drafting of the manuscript. GD, generated presence-absence data, and contributed to the drafting of the manuscript. JDP and JJA collected data in the field, recovered and deployed soundtraps, and contributed to the drafting of the manuscript.



## ACKNOWLEDGMENTS

We thank the University of Costa Rica and University of Vermont for funding this study. Data was collected under the research permit number ACOSA 60-SINAC-ACOSA-DASP-PI—R-060 2019 to 2022. We also thank Kristin Rasmussen and two anonymous reviewers for their feedback, edits, and suggestions.

## REFERENCES

- Acevedo, J., Aguayo-Lobo, A., Allen, J., Botero-Acosta, N., Cepella, J., Castro, C., Dalia Rosa, L., Denkinger, J., Felix, F., Florez-Gonzalez, L., Garita, F., Guzman, H. M., Haase, B., Kaufman, G., Llano, M., Olavarria, C., Pacheco, A. S., Plana, J., Rasmussen, K., Scheidat, M., Secchi, E. R., Silva, S., & Stevick, P. T. (2017). Migratory preferences of humpback whales between feeding and breeding grounds in the eastern South Pacific, *Marine Mammal Science* 33, 1035–1052. <https://doi.org/10.1111/mms.12423>
- Amrein, A., Guzman, H. M., Surrey, K. S., Polidoro, B., & Gerber, L. R. (2020). Impacts of whale watching on the behavior of humpback whales (*Megaptera novaeangliae*) in the coast of Panama. *Frontiers Marine Science*, 7, 601277. <https://doi.org/10.3389/fmars.2020.601277>
- Bettridge, S., Baker, C. S., Barlow, J., Clapham, P. J., Ford, M., Gouveia, D., Mattila, D. K., Pace, R. M., Rosel, P. E., Silver, G. K., & Wade, P. R. (2015). Status review of the humpback whale (*Megaptera novaeangliae*) under the Endangered Species Act, U. S. *Department of Commerce* [Report No. NOAA-TM-NMFS-SWFSC-540]. National Oceanic and Atmospheric Administration.
- CEIC. Global Economy Database. <https://www.ceicdata.com/en>. Last accessed 2022.
- Chereskin, E., Beck, L., Gamboa-Poveda, M., Palacios-Alfaro, J., Monge-Arias, R., Chase, A., Coven, B., Guzman, A., McManus, N., Neuhaus, A., O'Halloran, R., Rosen, S., & May-Collado, L. J. (2019). Song structure and singing activity of two separate humpback whales populations wintering off the coast of Caño Island in Costa Rica. *Journal of the Acoustical Society of America*, 146, EL509–515. <https://doi.org/10.1121/1.5139205>
- Cholewiak D. M. (2008). Evaluating the role of song in the humpback whale (*Megaptera novaeangliae*) breeding system with respect to intra-sexual interactions. Faculty of the Graduate School of Cornell University.
- Cholewiak, D., Clark, C.W., Ponarakis, D., Frankel, A., Hatch, L. T., Risch, D., Stanistreet, J. E., Thompson, M., Vu, E., & Van Parijs, S. M. (2018) Communicating amidst the noise: modeling the aggregate influence of ambient and vessel noise on baleen whale communication space in a national marine sanctuary. *Endangered Species Research*, 36, 59–75. <https://doi.org/10.3354/esr00875>
- Derryberry, E. P., Phillips, J. N., Derryberry, G. E., Blum, M. J., & Luther, D. (2020). Singing in a silent spring: Birds respond to a half-century soundscape reversion during the COVID-19 shutdown. *Science*, 370, 575–579. <https://doi.org/10.1126/science.abd5777>
- Economic Survey of Latin America and the Caribbean (ECLAC). (2021). *Labour dynamics and employment policies for sustainable and inclusive recovery beyond the COVID-19 crisis*. Santiago, United Nations.
- Erbe, C., Marley, S. A., Schoeman, R. P., Smith, J. N., Trigg, L. E., & Embling, C. B. (2019). The effects of ship noise on marine mammals—A review. *Frontiers in Marine Sciences*, 6, 606. <https://doi.org/10.3389/fmars.2019.00606>
- Executive Decree 20790-MIRENEM, 1991, Gaceta N.210, 4/11/1991.
- Frisk, G. (2012). Noiseconomics: The relationship between ambient noise levels in the sea and global economic trends. *Scientific Reports*, 2, 437. <https://doi.org/10.1038/srep00437>
- Gagne, E., Perez-Ortega, B., Hendry, A. P., Melos-Santos, G., Walmsley, S. F., Rege-Colt, M., Austin, M., & May-Collado, L. J. (2022). Dolphin communication during widespread systematic noise reduction—a natural experiment amid COVID-19 lockdowns. *Frontiers in Remote Sensing*, 3, 934608. <https://doi.org/10.3389/frsen.2022.934608>
- Garland, E. C., & McGregor, P. K. (2020). Cultural transmission, evolution, and revolution in vocal displays: Insights from bird and whale song. *Frontiers in Psychology*, 11, 544929. <https://doi.org/10.3389/fpsyg.2020.544929>
- Herman, L.M. (2017). The multiple functions of male song within the humpback whale (*Megaptera novaeangliae*) mating system: review, evaluation, and synthesis. *Biological Reviews*, 92, 1795–1818. <https://doi.org/10.1111/brv.12309>
- Herman, Louis M., Pack, Adam A., Spitz, Scott S., Herman, Elia K.Y., Rose, Kathryn, Hakala, Siri, & Deakos, M. H. (2013). Humpback whale song: who sings? *Behavioral Ecology Sociobiology* 67, 1653–1663. <https://doi.org/10.1007/s00265-013-1576-8>
- Homfeldt, T. N., Risch, D., Stevenson, A., & L. A. Henry. (2022). Seasonal and diel patterns in singing activity of humpback whales migrating through Bermuda. *Frontiers in Marine Science*, 9, 941793. <https://doi.org/10.3389/fmars.2022.941793>
- Hoyt, E., & Iñíguez, M. (2008). The state of whale watching in Latin America. Chippenham, UK, WDACS.

- Jones, N. (2019). Ocean uproar: saving marine life from a barrage of noise. *Nature*, 568, 158–161. <https://www.nature.com/articles/d41586-019-01098-6>
- Mercado, E. III. (2022). The humpback's new songs: diverse and convergent evidence against vocal culture via copying in humpback whales. *Animal Behavior and Cognition*, 9, 196–206. <https://doi.org/10.26451/abc.09.02.03.2022>
21. Laute, A., Grove, T. J., Rasmussen, M.H., Smith, A., Loisa, O., and Fournet, M. E. H. 2022. Impact of whale-watching vessels on humpback whale calling behavior on an Icelandic foraging group during the Covid-19 pandemic. *Marine Ecology Progress Series*, 701, 159-173. <https://doi.org/10.3354/meps14202>
- Lineamientos Nacionales para la vigilancia de la infección por Coronavirus (COVID-19). (2022). Ministry of Health of Costa Rica. <https://www.ministeriodesalud.go.cr/>
- Palacios-Alfaro, J. D., Martínez-Fernández, D., Sánchez-Godínez, C., & Venegas, R. (2012). Distribution and behavior of humpback whale (*Megaptera novaeangliae*, Borowski, 1781) (Breeding BSG), in the southern Pacific of Costa Rica [Report No. SC/64/SEP16]. *International Whaling Commission*.
- Parks S. E., Cusano D. A., Stimpert A. K., Weinrich M. T., Friedlaender A. S., & Wiley, D. N. (2014). Evidence for acoustic communication among bottom foraging humpback whales. *Scientific Reports*, 4, 1–7. <https://doi.org/10.1038/srep07508>
- Pine, M. K., Wilson, L., Jeffs, A. G., McWhinnie, L., Juanes, F., Scuderi, A., & Radford, C. A. (2021). A Gulf in lockdown: How an enforced ban on recreational vessels increased dolphin and fish communication ranges. *Global Change Biology*, 27, 4839–4848. <https://doi.org/10.1111/gcb.15798>
- Rainforest Connection (2020). RFCx Arbimon: Bio-Acoustic Analysis Platform. [Web-Based Platform]. Arbimon. <https://arbimon.rfcx.org>
- Rasmussen, K., Palacios, D. M., Calambokidis, J., Saborio, M. T., Dalia Rosa, L., Secchi, E. R., Steiger, G. H., Allen, J. M., & Stone, G. S. (2007). Southern hemisphere humpback whales wintering off Central America: Insights from water temperature into the longest mammalian migration. *Biological Letters*, 3, 302–305. <https://doi.org/10.1098/rsbl.2007.0067>
- Ryan, J. P., Joseph, J. E., Margolina, T., Hatch, L. T., Azzara, A., Reyes, A., Southall, B. L., DeVogelaere, A., Reeves, L. E. P., Zhang, Y., Cline, D. E., Jones, B., McGill, P., Baumann-Pickering, S., & Stimpert, A. K. (2021). Reduction of low-frequency vessel noise in Monterey Bay National Marine Sanctuary during the COVID-19 pandemic. *Frontiers in Marine Ecosystems Ecology*, 8, 656566. <https://doi.org/10.3389/fmars.2021.656566>
- Rey-Barquero M. P., Huertas-Amaya L. V., Seger K. D., Botero-Acosta N., Luna-Acosta A., Perazio C. E., Boyle J. K., Rosenthal S. & Vallejo, A. C. (2021). Understanding effects of whale-watching vessel noise on humpback whale song in the North Pacific coast of Colombia with propagation models of masking and acoustic data observations. *Frontiers in Marine Sciences*, 8, 623724. <https://doi.org/10.3389/fmars.2021.623724>
- Sousa-Lima, R. S. & Clark, W. C. (2008). Modeling the effect of boat traffic on the fluctuation of humpback whale singing activity in the Abrolhos National Park, Brazil. *Canadian Acoustics*, 36, 174-181. <https://jcaa.caa-aca.ca/index.php/jcaa/article/view/2008>
- Southall, B. L., Scholik-Schlomer, A. R., Hatch, L., Bergmann, T., Jasny, M., Metcalf, K., et al. (2017). Underwater Noise from Large Commercial Ships—International Collaboration for Noise Reduction. *Encyclopedia of Maritime and Offshore Engineering*. Hoboken, NJ: John Wiley & Sons, Ltd.
- Southall, B. L., Scholik-Schlomer, A. R., Hatch, L., Bergmann, T., Jasny, M., Metcalf, K., Weigart, L., and A. J. Wright. (2017). Underwater Noise from Large Commercial Ships—International Collaboration for Noise Reduction. *Encyclopedia of Maritime and Offshore Engineering*. John Wiley & Sons, Ltd.
- Sprogis, K. R., Vidense, S., & P. T. Madsen. (2020). Vessel noise levels drive behavioural responses of humpback whales with implications for whale-watching. *eLife*, e56760. <https://doi.org/10.7554/eLife.56760>
- Steiger, G. H., Calambokidis, J., Sears, R., Balcomb, K. C., & Cabbage, J. C. (1991). Movement of humpback whales between California and Costa Rica. *Marine Mammal Science*, 7, 306–310. <https://doi.org/10.1111/j.1748-7692.1991.tb00105.x>
- Tambutti, M., & Gómez, J. J. (2020). The outlook for oceans, seas and marine resources in Latin America and the Caribbean: Conservation, sustainable development, and climate change mitigation. *America* [Report LC/TS.2020/167.]. *Economic Commission for Latin America and the Caribbean* (ECLAC).
- Tujii, K., Akamatsu, T., Okamoto, R., Mori, K., Mitani, Y., & N. Umeda. (2018). Change in singing behavior of humpback whales caused by shipping noise. *PloS One*, 13, e0204112. <https://doi.org/10.1371/journal.pone.0204112>
- Whiten, A. (2019). Cultural evolution in animals. *Annual Review of Ecology, Evolution, and Systematics*, 50, 27–48. <https://doi.org/10.1146/annurev-ecolsys-110218-025040>