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First song description of the humpback whales, *Megaptera novaeangliae* (Balaenopteridae: Artiodactyla), breeding off Nicaragua

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ABSTRACT

Introduction: Humpback whales belonging to the Central American (CA) Distinct Population Segment breed off the Pacific coast of Nicaragua. Knowledge on this endangered population and its conservation status is limited.
Objective: The aim of this study is to provide the first description of the CA humpback whale song off Nicaragua, which helps further understanding on the population's dynamics.
Methods: Acoustic recordings of songs were obtained during dedicated boat-based surveys at two locations on the Pacific coast of Nicaragua in 2018. Recordings were made from the boat using a portable system for a total of 23 hours and 56 minutes over 32 days from January to April 2018. A total of nine recordings of high enough quality for the song analysis were identified during this period from three different days at Padre Ramos (PR) (northern site) and four different days at San Juan del Sur (southern site). Song structure was described using standard humpback whale song elements, i.e. themes, phrases, and units.
Results: A total of seven themes, seven phrases, and 19 unit types were identified. Three of the themes were common and frequently repeated in a song cycle while the others were less common in the repertoire and were recorded only during the middle of the season. Song theme order was variable, both within and across song sessions.
Conclusions: This study provides the first song description of humpback whales along the Pacific coast of Nicaragua. Comparison of these songs with other datasets from the CA population and other breeding areas in the Northern Hemisphere could help understand the migratory patterns of these animals and the level of connectivity among populations since song can be socially learnt. Future data collection of humpback whale song recordings in Nicaragua is necessary to gain further understanding on the song structure variation within this population and the mechanisms of song transmission and dynamics across populations in the region.

Key words: Acoustics; Central America; Song structure; North Pacific; Reproduction.

RESUMEN

Primera descripción del canto de las ballenas jorobadas, *Megaptera novaeangliae* (Balaenopteridae: Artiodactyla) que se reproducen en Nicaragua

Introducción: La ballena jorobada del segmento poblacional Centroamericano se reproduce en la costa Pacífica de Nicaragua. El conocimiento sobre la biología y estado de conservación de esta población amenazada y su estado de conservación es limitado.
Objetivo: El objetivo de este estudio es generar la primera descripción del canto de las ballenas jorobadas de la población de Centroamérica observadas en aguas nicaragüenses.
Métodos: Se obtuvieron grabaciones acústicas durante salidas de investigación en dos localidades de la costa Pacífica de Nicaragua en el 2018. Las grabaciones se realizaron desde el bote utilizando un sistema portátil durante un total de 23 horas y 56 minutos en 32 días de enero hasta abril del 2018. Un total de nueve grabaciones de suficiente calidad para el análisis de los cantos fueron identificados durante este periodo en tres días en Padre Ramos (Norte) y cuatro días en San Juan del Sur (Sur). La estructura del canto se describió de acuerdo con los elementos estándares de canciones de ballenas jorobadas: temas, frases y unidades.
Resultados: Se identificaron siete temas, siete frases y 19 unidades. Tres temas eran comunes y se repetían varias veces dentro de una canción mientras que otras eran menos comunes en el repertorio de canto y se grabaron solo en la mitad de la temporada. El orden de los temas en la canción fue variable a dentro de la canción y entre las sesiones de canto.
Conclusiones: Este estudio representa la primera descripción del canto de las ballenas jorobadas en el Pacifico nicaragüense. La comparación de estos cantos con los de otras localidades de la población de Centroamérica y con otras áreas de reproducción de poblaciones en el hemisferio norte contribuirá a comprender mejor los patrones migratorios de estos animales y el nivel de conectividad entre poblaciones desde que la canción fue aprendida. La recolección futura de datos de cantos de ballenas jorobadas en Nicaragua es necesaria para mejorar la comprensión de la variación en la estructura del canto de esta población y el mecanismo de transmisión y dinámica de canto entre poblaciones de la región.

Palabras clave: Acústica; Centroamérica; Estructura de canción; Pacifico Norte; Reproducción.

INTRODUCTION

The humpback whale, *Megaptera novaeangliae* (Borowski, 1781) is known for its seasonal migration between breeding and feeding areas. There are 14 recognized Distinct Population Segments (DPS), of which seven located in the North Pacific, and amongst which the Central America DPS (Bettridge et al., 2015), the focus of this study. The Central America whales (hereafter CA whales) migrate to Central America between January and April, from their feeding areas on the West coast of the United States (Calambokidis et al., 1997; Calambokidis et al., 2000; De Weerdt et al., 2022). The waters off Nicaragua are considered important breeding habitats for CA whales with Padre Ramos being used mainly by mother-calf pairs, and San Juan del Sur mainly by adult whales (De Weerdt et al., 2022). CA whales are listed as endangered according to the National Marine Fisheries Service (NMFS) and little information is available on their ecology (Bettridge et al., 2015).

Humpback whale males produce structured and complex songs (Payne & McVay, 1971), and while singing activity occurs extensively during the breeding season, it has also been described along migration corridors and on feeding areas (Kowarski et al., 2022; McSweeney et al., 1989; Schall et al., 2022). Humpback whale songs are used as a parameter to study individual movements and population dynamics (Cerchio et al., 2001; Cholewiak & Cerchio, 2022; Darling, Goodwin, et al., 2019; Darling & Sousa-Lima, 2005). Males from the same population conform to similar songs, which evolve through the season. This evolution partially happens by the error accumulation of singers. Accumulation of changes, the sharing of such changes and culture are determined by the social interactions between singers (Garland et al., 2022).

Because only males are known to sing (Cholewiak & Cerchio, 2022; Darling & Bérubé, 2001; Darling et al., 1983), their songs are thought to be a male precopulatory display

(Dines et al., 2015) used to attract females and/or mediate male-male interactions (Herman, 2017; Smith et al., 2008; Tyack & Clark, 2000). Humpback whale songs are traditionally classified into themes, phrases, and units, allowing comparisons of song elements across geographical regions (Darling & Sousa-Lima, 2005; Payne & Payne, 1985; Payne et al., 1983) and between populations (Cholewiak & Cerchio, 2022; Garland et al., 2011; Schall et al., 2022). Within a breeding season, the song can vary, however, males eventually conform to the same song for their population (Herman, 2017). Songs sung by humpback whales undergo both an evolutionary and a revolutionary process (Owen et al., 2019). The evolutionary process consists of song modification over time by accumulation of small changes resulting in a progressive change (Cerchio et al., 2001; Garland et al., 2011), while revolution, or cultural diffusion, is a rapid change whereby a novel song appears and is adopted by the population (Noad et al., 2000). A song can therefore change within and between seasons in any given population.

Humpback whale song studies can provide valuable insights on population connectivity and function (Garland et al., 2011; Garland et al., 2022; Garland, Gedamke, et al., 2013). Understanding changes in humpback whale songs within and between seasons can help understand migratory routes, by comparing songs between regions. Furthermore, studying song composition within and between seasons can provide insights on the cultural transmission that occurs in different humpback whale populations (Darling, Acebes, et al., 2019; Garland et al., 2015; Zandberg et al., 2021). Presently, there is only one study describing songs of CA humpbacks at their breeding ground in 2016-2017 off Caño Island, Costa Rica (Chereskin et al., 2019). This present study provides additional information on the song of CA whales breeding in Central America; until now no description of song is available for animals breeding in Nicaraguan waters. Recent work comparing phrase compositions of humpback whale songs sung between 2011 and 2013 in Mexico, Hawaii, the Philippines and Japan showed that mixing of population throughout the North Pacific occurs (Darling, Acebes, et al., 2019).

Boat based surveys took place between January and April 2018 on two study sites along the Nicaraguan Pacific coast: Padre Ramos, northern Nicaragua and San Juan del Sur, southern Nicaragua. During the surveys, an omni-directional hydrophone (H2a Aquarian) connected to a recorder (Tascam DR-05V2) was deployed to determine presence/absence of singers every 30 minutes. Whenever a singer was detected, and if their song was audible above the background noise, a recording was made at a sampling rate of 92 kHz and 24 bits resolution for as long as the song was detectable.

A total of 108 recordings (San Juan del Sur, n = 66; Padre Ramos, n = 42) were made in 32 days of boat survey effort during the 2018 breeding season. Any recordings with multiple audible singers and/or with low signal-to-noise ratio (SNR) were excluded from further analyses. SNR was estimated by measuring NIST Quick Signal-to-Noise ratio (Sostres Alonso & Nuuttila, 2015) for each labeled unit in every recording (RAVEN 1.5; (K. Lisa Yang Center for Conservation Bioacoustics at the Cornell Lab of Ornithology, 2022)). Recordings that captured at least 10 minutes of a song were selected for the analysis as humpback whale songs are known to last on average 10-15 minutes (Cerchio et al., 2001). An additional criterion was that the SNR of the recordings had to be 14 dB or above. We considered a humpback whale song as a continuous recording containing at least one performance of each theme in that moment of the season (as it happens that themes are added or lost within the season) (Cholewiak et al., 2013). Songs recorded on different days were considered as samples of distinct individuals (Warren et al., 2020), while recordings from the same day were assumed to be from the same individual. Each analyzed recording contained either a song or a song fragment (i.e., part of a song composed of a stereotyped series of vocalizations, repeated at least once), as described in

Kowarski et al. (2019). Whether songs were incomplete because the animal moved away, stopped singing or did not perform the full song, could not be determined due to the logistical constraints of the setup (e.g. boat drifting substantially from original location). Only nine recordings were above 10 minutes in length and met our SNR criterion. The selected recordings totaled 3 hours and 30 minutes for the analysis. These recordings were collected on three different days at PR and four different days at SJDS; therefore, based on the assumption that each day represents a new singer, an estimated number of seven singers were recorded (Fig. 1).

Songs were manually analyzed in RAVEN Pro by generating spectrograms, with a Fast Fourier Transform (FTT) of 1 024 points resolution, and a Hanning window (50 % overlap), corresponding to frequency resolution of 43.1 Hz. Finer frequency resolution (2 Hz) was used for the graphical representations presented in this study. Following the method of Cholewiak et al. (2013), songs were classified into themes, phrases, and units. For the unit classification, the following acoustic variables were considered: fundamental frequency contour, tonal quality type (e.g. tonal or pulsed), duration (delta time), peak, low, high, and delta frequency (Malige et al., 2020). Each unit type was assigned a unique letter (Green et al., 2011). To test the consistency of the manual unit classification, a Random Forest Analysis (RFA) was applied on the measured variables of the units: low, high, Delta and peak frequencies and the duration (Delta time). A Random Forest model is a machine learning algorithm that combines multiple decision trees using "bagging" to create a final classification that averages all the decisions. The Out Of Bag (OOB) score is a way to validate a Random Forest model (Hastie et al., 2009).

Phrases were assigned only after reviewing multiple recordings to ensure consistency. The guidelines described in Cholewiak et al. (2013) were followed for the identification of phrases within the recordings. Transitional phrases were also identified and marked as such. However, these are not included in the results to clearly indicate the song sequence. Finally, themes were identified and assigned a unique color (Cholewiak et al., 2013), based on the phrase delimitations and sequence. A total of 19 unit types were identified based on the manual classification. The RFA of 1500 trees tested the manual classification of units and gave an OOB error rate of 31 %, showing duration and peak frequency as the most important measurable variables for unit classification. This OOB value indicates that manual classification was robust and reliable throughout the dataset. All unit types were shared on both Nicaraguan sites.

The CA male whales in Nicaragua sang songs made of seven themes represented by different colors in Fig. 1. The themes represented by the colors light and dark green are constituted of the repetition of phrases 4 or 3, respectively. These phrases differed by just one unit (j vs. n). However, since they were sung consistently separately, they were considered as unique themes (Fig. 1). The red and purple themes are made up of the repetition of phrases 1 and 2 respectively. These phrases share a common subphrase made of units a and b at the beginning of the phrase. At the start of the season, almost all themes were recorded on both sites. However, the sequence of themes varied between study sites (and within the season). In January, all themes were present in San Juan del Sur, except for the light green theme. However, the sample size at this location is limited to a single day of recording for January. The same themes observed in January in San Juan del Sur were present in Padre Ramos in February, except for the light green theme that appeared in Padre Ramos. Finally, the yellow and orange themes were not encountered in March at both sites and in April in San Juan del Sur only. There was only one common month of recording between sites (March), but both sites presented the same overall number of themes. Due to the lack of common recordings in the same months, it is challenging to compare the two sites.

The results of this study show a lot of variability in theme sequences. This indicates the 2018 Nicaragua CA song did not follow a

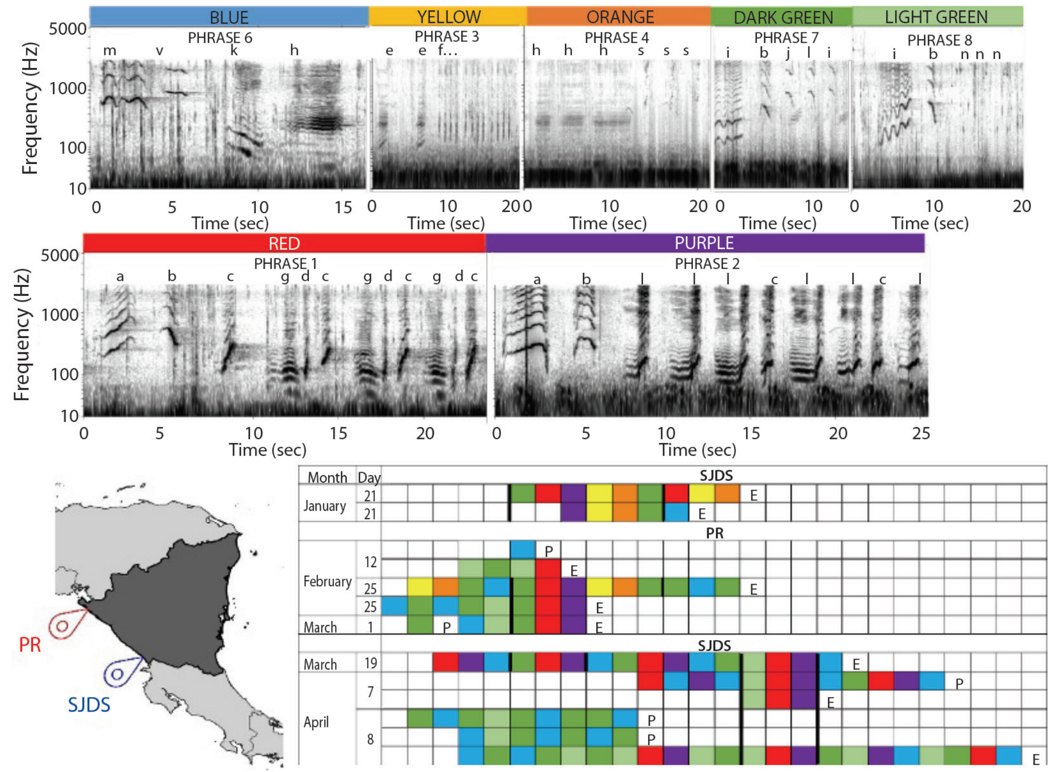

Fig. 1. Spectrograms of phrases identified in CA humpback whales singing off Nicaragua (hamming window, frequency resolution: 2 Hz, frame length: 0.128 s, time step: 0.032 s); the repetition of such phrases results in the theme identified at the top of each spectrogram. Distinct themes are represented by the colors red, yellow, orange, dark green, light green, purple and blue. The sequence of themes per recording are presented per site at Padre Ramos: PR (north) and at San Juan del Sur: SJDS (south) at the bottom of the figure (table) (P = Pause in whale singing; E = End of recording). A new line was started when there was a pause in the singing in the recording that was longer than the silence between phrases. The theme sequence was aligned (thick vertical black lines) arbitrarily to try to identify matching sequences across recordings.

strict theme order, as described for some other Southern hemisphere populations (Garland, Noad, et al., 2013). The presence of common themes at both sites suggests that a certain level of movement of males takes place; this is in contrast with the low level of photographic recapture observed between sites (De Weerdt et al., 2022). This inconsistency highlights the need for further research to understand whale movements in this area. To confirm if the same song is sung on both sites at the same time, synchronous recordings during the entire season would be needed. Gradual change of song along the season was observed in studies on other breeding grounds, such as Mexico and Hawaii (Cerchio et al., 2001; Darling, Acebes, et al., 2019). Compared to other Northern hemisphere songs, this study showed a more 'elaborate' and less organized song structure than previously reported for the 2016-2017 breeding season in Caño Island, Costa Rica (Chereskin et al., 2019). No further comparison with the song from Costa Rica could be achieved due to the limited information presented about individual unit characteristics and the resolution of the spectrograms. Within season comparison between breeding grounds would allow to gain a better insight on the dynamics and potential exchanges between animals in these breeding grounds.

Although our dataset was rather small, a poorly structured theme sequence could be observed in the second half of the season; this could be due to the mixing with other populations such as the Mexican DPS; furthermore, error accumulation over the entire season could be an alternative or concurrent explanation for the observed lack of structured sequence in the song (Mcloughlin et al., 2018; Mercado III et al., 2005) and/or the evolution of the song as the season progresses. In other words, whales may be rearranging themes and introducing or removing elements until the end of the season. A broader dataset would be required to determine if the pattern observed in this study is representative of the CA population in Nicaragua or if these are idiosyncrasies from individual singers. Interestingly, an extensive variability in the order in which themes are sung was also observed in some recordings from Socorro, Mexico, in unpublished work from Smith-Aguilar, as reported in Cholewiak et al. (2013). The gradual replacement of the yellow and orange themes by the more common blue theme as the season progressed, suggests that gradual song changes took place in the songs of Nicaraguan whales. This process is described as song evolution and it has been widely reported for other humpback whale populations in both hemispheres (Fournet et al., 2018; Garland et al., 2011; Mercado, 2021; Payne & Payne, 1985). The findings of this paper can be used for future regional song comparisons with whales from the North Pacific to assess population connectivity. Future work should explore song evolution and the seasonal dynamics within the Central America population.

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 Contributions: JDW, conceptualized the study, acquired the data, and contributed to analysis interpretation, and drafted the initial and revised versions of this manuscript. DD, RSL, and FP contributed to data analysis and interpretation of results, and contributed to the drafting of the manuscript at all stages.

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