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Decreases in encounter rate of endangered Northeast Pacific humpback whales in Southern Costa Rica: Possible changes in migration pattern due to warming events

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Warming events in the Pacific Ocean are becoming more frequent, intense, and on a larger temporal and spatial scale. This has caused critical habitats of marine species to lose their quality and marine organisms respond by modifying their critical feeding and reproduction behaviors, as well as their distribution. The Northeast Pacific humpback whale of the Central America distinct population segment (DPS) remains Endangered due to its small population size and because its response to climate change and human interventions is unknown. In this work, we showed the encounter rates of humpback whales in their breeding grounds in Costa Rica for breeding seasons comprised in the period 2000-2020. We analyze the influence of climatic indices that influence the Pacific and environmental variables related to temperature and productivity in the feeding grounds of this population (United States). We hypothesize that the more intense the warming events, the fewer humpback whales complete their migration to Costa Rica. We conclude that the humpback whales of this population could be finding thermally favorable areas in intermediate latitudes (p. e.g., Mexican-Guatemala coasts), which could be related to the decreases in the presence of humpback whale adults and calves in Costa Rica. These observed changes could inform how humpback whales might respond to climate change.

KEYWORDS

Central America DPS, climate change, El Niño, encounter rate, *Megaptera novaeangliae*, migration, Northeast Pacific, wintering grounds

Introduction

Marine warming events are becoming more frequent, lasting, and intense which has affected the quality of marine habitats and the population status of species (Wernberg et al., 2013; Scannell et al., 2016; Frölicher et al., 2018). The evaluation of the quality of critical habitats (feeding, reproduction, and migration areas) can be done through indicator species (Gregr and Trites, 2001; Bailleul et al., 2012; Trudelle et al., 2016). In this sense, the humpback whale (*Megaptera novaeangliae*) is considered an indicator species because its abundance, reproductive success, distribution, and diet are affected by abnormal environmental conditions (Fleming et al., 2016; Schall et al., 2021; Gabriele et al., 2022).

The humpback whale has been in recovery since 1985, after its near extinction by whaling; however, some of its populations remain listed as "Endangered" under the Endangered Species Act (81 FR 62259; September 2016; NMFS and NOAA, 2016). Among the main anthropogenic threats that have limited their recovery are fishing gear entanglement, vessel strikes, and the degradation of their critical habitats (Bettridge et al., 2015; NMFS and NOAA, 2016).

The Northeast Pacific humpback whales of the Central America DPS are classified as "Endangered" due to their small population size (approximately 1400 individuals) (Wade, 2021; Curtis et al., 2022). This population makes extensive migrations (≈ 5100 km) from their breeding grounds in Central America (southern Mexico, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, and Panama) to their feeding grounds off California-Oregon-Washington in the United States (Calambokidis et al., 2000; Rasmussen et al., 2011; NMFS and NOAA, 2016; Curtis et al., 2022). This region is under the influence of wind upwellings of the California Current System and different patterns of Pacific climate variability such as the El Niño-Southern Oscillation (ENSO), the Pacific Decadal Oscillation (PDO), and the North Pacific Gyre Oscillation (NPGO) (Jacox et al., 2014; Jacox et al., 2016).

During El Niño conditions the upwelling weakens, the thermocline deepens, and warm subtropical water enters the California Current, which causes low productivity and changes in prey availability for humpback whales (Fleming et al., 2016; Cartwright et al., 2019; Gabriele et al., 2022). Low prey availability can mean that humpback whales do not have sufficient energy reserves to complete the migration, gestation or to ensure the survival of their calves, which can have long-term negative effects on the population (Cartwright et al., 2019; Kershaw et al., 2021; Gabriele et al., 2022).

Humpback whale populations that have been monitored for decades showed that the abundance of mothers with calves at breeding grounds decreases considerably when abnormal warm conditions occur at their feeding grounds, as well as temporary changes in the arrival of whales to their feeding grounds related to the early melting of ice (Ramp et al., 2015; Cartwright et al., 2019; Frankel et al., 2021). Humpback whales are modifying the timing of their migration and their distribution, as well as their stay in their breeding and feeding grounds (Avila et al., 2020; Meynecke et al., 2021).

The Northeast Pacific humpback whale Central America DPS is one of them with the highest category of threat and it is unknown how this population has responded to warming events (Endangered Species Act, 81 FR 62259, September 2016; NMFS and NOAA, 2016). Therefore, in this work, we use the best available historical data on humpback whale encounter rates in their wintering grounds in Costa Rica, to describe the pattern of occurrence since the early 2000s. In addition, we address the possible effects of warming events on the migration and presence of humpback whales with calves in Costa Rica.

Method

Study area

Humpback whale wintering grounds are located on the coast of the Osa Peninsula, Costa Rica (Figure 1). This area is limited to the east by the coasts of the Térraba-Sierpe River System, Drake Bay, and Corcovado National Park up to Punta Salsipuedes, including the surroundings of Caño Island. The study area has an approximate size of 3800 km^2 and is within the 200 m isobath. In this area, there is a stable sea surface temperature (around 28°C) throughout the year (Rasmussen et al., 2007; Oviedo and Solís, 2008; Rasmussen et al., 2011).

Encounter rate of humpback whales

Opportunistic records of humpback whales were made during the breeding seasons 2000-2006, 2014-2015, 2015-2016, and 2019-2020 (Figure 1). The surveys have been carried out since 1998 by Fundación Vida Marina aboard their whale-watching vessels. The records were obtained from December to May on citizen science-oriented surveys focusing on cetaceans' fauna in the study area. The port of departure and landfall was at Drake Bay, Osa Peninsula. The boat trips were directed to areas of known predictable occurrence and the observations were performed from 08:00 to 15:00 hours. Information was recorded on group size, group composition, and geographic position. The encounter rate was assessed as group sightings per unit search effort; dividing the number of all groups of whales sighted and sub-groups containing mother-calf pairs by the effort made every 1000 km as in Palacios et al. (2012). The study used data from 2272 total hours of field efforts between breeding seasons 2000-2006, 2014-2015, 2015-2016, and 2019-2020 at an average speed of

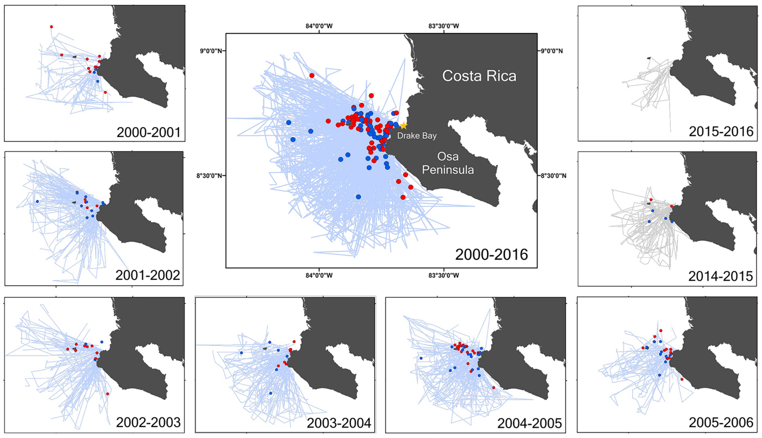

FIGURE 1
Breeding grounds of the Northeast Pacific humpback whales in Osa Peninsula, Costa Rica. Effort (blue lines); Adult humpback whale sightings (blue dots); Mother-calf pairs sightings (red dots). The port of departure and landfall was at Drake Bay, Osa Peninsula.

14.09(± 1.11) km/hr and an average search distance of 3526.55 (± 1442.27) km.

Climatic indices and environmental variables

Monthly values of the El Niño Multivariate Index (MEI), the Pacific Decadal Oscillation (PDO), and the North Pacific Gyre Oscillation (NPGO) for the 2000-2020 period were obtained through the ***rsoi*** package (Albers, 2020) in R version 4.2.0 (R Core Team, 2022). These indices consider large-scale ocean-atmosphere processes that influence the upwelling of the California Current System and cause changes in sea surface temperature, the concentration of nutrients, and abundance of marine species of different trophic levels whose effects can last from months to decades (Chenillat et al., 2012; Peterson et al., 2014; Fleming et al., 2016).

Sea surface temperature (SST), Chlorophyll a concentration (CHL-a), and coastal upwelling index (UPW) were analyzed for the period 2000-2020 given that they are good indicators of abundance and availability of zooplankton and small pelagic fish which are the main prey for humpback whales (Mackas et al., 2006; Munger et al., 2009). The area considered to extract the environmental information corresponds to the feeding grounds of humpback whales of the Central America DPS (34-48°N and 120-128°W, https://www.fisheries.noaa.gov/resource/map/humpback-whale-critical-habitat-maps-and-gis-data). Daily SST values were obtained through satellite images, level 4 and with a 0.25° resolution of Optimum Interpolation Sea Surface Temperature (https://www.ncei.noaa.gov/products/optimum-interpolation-sst). CHL-a data were monthly and from the NASA combined-satellite time series that are constructed from the SeaWiFS and MODIS-Aqua sensors (https://oceancolor.gsfc.nasa.gov/). Also, monthly values of the Biologically Effective Upwelling Transport Index (UPW) constructed with satellite and *in situ* data were obtained for the west coast of the United States (https://oceanview.pfeg.noaa.gov/products/upwelling/cutibeuti). A monthly series by environmental variable was obtained from 2000 to 2020. For each month, the average monthly value of the series was subtracted to calculate the time series of monthly anomalies. Positive values of anomalies indicate that environmental conditions were above the average historical conditions and vice versa, if anomalies present negative values, the conditions were below the historical average. Finally, annual and semi-annual averages of the climatic indices and anomalies of environmental variables were calculated to analyze their relationship with the annual encounter rates of humpback whales in Costa Rica.

To assess the influence of climatic indices and environmental variables on the encounter rate of humpback whales Spearman correlations were performed (Robinson et al., 2009; García-Morales et al., 2017).

Results

Encounter rate of humpback whales

The humpback whale records were consecutive between 2000 and 2006, then there was a seven-year gap and were resumed on 2014-15, 2015-16, paused again, and restarted on the breeding season 2019-20. The highest encounter rates were recorded in the breeding seasons 2000-01, 2004-05, and 2005-06 while the lowest encounter rate was during the 2015-16 breeding season (Figure 2). Although the effort was not the same in all

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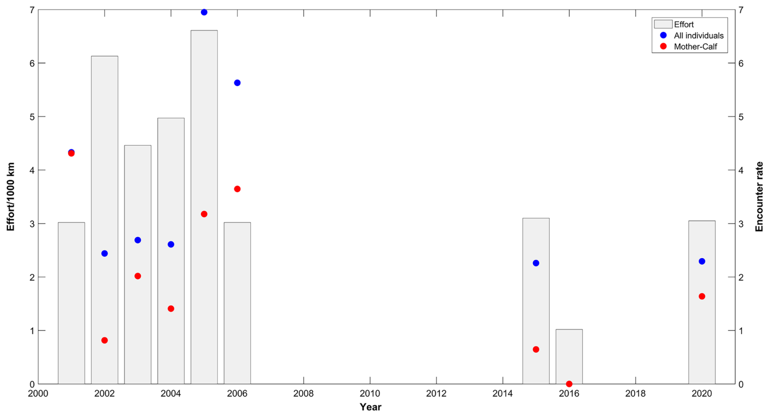

FIGURE 2
Encounter rates of humpback whales in the Osa Peninsula, Costa Rica. Effort made in each breeding season (gray bars); Encounter rate including adults and mother-calf pairs (blue dots); and Encounter rate of mother-calf pairs (red dots).

years and opportunistic data was retrieved, the entire wintering ground in southern Costa Rica was covered, so these data represent the best available estimates of the occurrence of this population in the area.

Climatic indices and environmental variables

During the study period, there were two warm phases of the PDO during 2002-2005 and 2014 to 2020. During these periods there were negative phases of the NPGO that represent low productivity in the feeding grounds of the humpback whale. Also, during the study period, moderate and strong El Niño events occurred in 2002-03, 2009-10, and 2015-16. Positive anomalies of SST were observed in the feeding grounds of humpback whales from 2014 to 2020. During this period there was great variability in CHL-a anomalies and mostly negative anomalies in UPW between 2014-2016 (Figure 3).

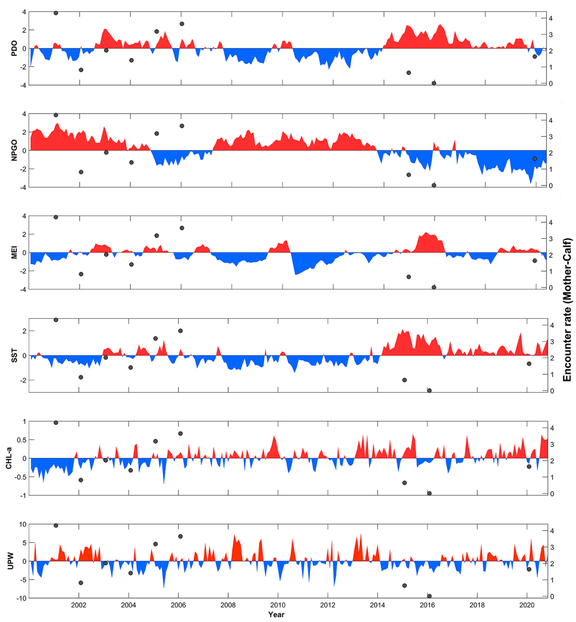

FIGURE 3
Monthly values of the Pacific Decadal Oscillation index (PDO), the North Pacific Gyre Oscillation index (NPGO), and the Multivariate ENSO Index (MEI) and anomalies of Sea surface temperature (SST), Chlorophyll a concentration (CHL-a), and the coastal Upwelling Index (UPW) obtained from the feeding grounds of humpback whales off California-Oregon-Washington in the United States (area graphs). Encounter rate of humpback whale mother-calf pairs recorded during the breeding season in the Osa Peninsula, Costa Rica (gray spots).

Influence of environmental conditions on encounter rates

Negative trends were detected between the annual averages of the MEI (Spearman's rank coefficient: r = –0.65, $p = 0.05$), SST (Spearman's rank coefficient: r = – 0.64, $p = 0.06$), and CHL-a (Spearman's rank coefficient: r = – 0.68, $p = 0.04$) with the encounter rates of humpback whales' mother-calf pairs. As MEI and SST anomalies intensity increases fewer whales were observed on the wintering grounds. Positive CHL-a anomalies were related to lower encounter rates in the wintering grounds (Figure 4). No relationships were found with the PDO, NPGO, and UPW values nor with semi-annual averages calculated for all the variables.

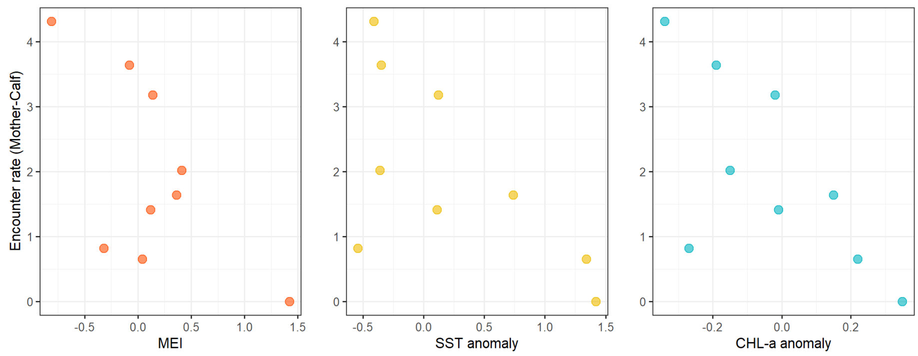

FIGURE 4
Relationships between encounter rates of humpback whales' mother-calf pairs and the averages of the Multivariate ENSO Index (MEI), anomalies of sea surface temperature (SST) and Chlorophyll a concentration (CHL-a).

Discussion

Opportunistic data in the study of cetaceans has been widely used due to the difficulties associated with the costs to carry out systematic surveys to obtain accurate estimates (Embling et al., 2015). The main limitations of the use of this type of data are the error associated with the analysis due to the lack of data standardization, non-consecutive information, and gaps in spatial coverage (Richardson et al., 2012). However, thanks to the use of opportunistic data, it has been possible to make inferences about general population trends, abundances, and distribution of some species or populations whose aspects of their population ecology are unknown, and which have been used in species conservation plans (Williams et al., 2006).

The Northeast Pacific humpback whales of the Central America DPS is one of the four DPSs that remain endangered, mainly due to its reduced population size (NMFS and NOAA, 2016; Curtis et al., 2022). The estimates of the population size of the Central America DPS have been assessed considering the sightings of humpback whales in their breeding grounds from southern Mexico to Central America, and whose most recent data date from 2021 (Calambokidis et al., 2008; Barlow et al., 2011; Curtis et al., 2022).

In this work, we incorporated data from humpback whale sightings in Costa Rica during the breeding seasons of 2000-2006, 2014-15, 2015-16, and 2019-20. This information is relevant because, in addition to having recent occurrence estimates for this area, it allows us to make inferences about the responses of humpback whales to current climate change and about their critical behaviors of migration and reproduction.

The feeding grounds of the humpback whale, Central America DPS are off California-Oregon-Washington in the United States (Steiger et al., 1991; Calambokidis et al, 2000). Environmental conditions in these areas are often affected by interannual warming events such as El Niño and the presence of marine heatwaves (Bond et al., 2015; Tseng et al., 2017; Newman et al., 2018). In addition to these phenomena, the warm phase of the PDO generates positive SST anomalies in the area and the negative phase of the NPGO is related to a decrease in productivity in this region (Di Lorenzo et al., 2008). These conditions cause changes in prey distribution and availability for humpback whales, which has induced the species to modify their local distribution and feed at higher latitudes or in more coastal areas, increasing their exposure to bycatch or vessel strikes (Fleming et al., 2016; Santora et al., 2020).

According to the analysis, the more intense the El Niño events and the greater the SST anomalies, the fewer whales and calves are observed in their southern breeding grounds in Costa Rica. The most drastic decrease in the encounters rate of adult and mother-calf pairs occurred during intense and long-lasting warming events such as the 2015-16 El Niño and the 2014-2016 marine heatwave (Gentemann et al., 2017). An independent study recorded two sightings that included mother-calf pairs of humpback whales during the 2010 breeding season in Golfo Dulce, Costa Rica, and during the 2020 breeding season there were three encounters, but all the sightings were single adults with no calves (Brooke Bessesen, *pers comm*). These dramatic declines were also recorded in the Hawaiian DPS during the same period (Cartwright et al., 2019; Frankel et al., 2021). In addition, a recent study showed that the breeding areas of the Central America DPS are the ones with the warmest conditions in the North Pacific (temperatures greater than 28°C) and that it is possible that if these high temperatures are maintained through the years can cause habitat shifts (von Hammerstein et al., 2022).

Humpback whales migrate to their breeding grounds looking for warmer and shallower waters without turbulence to optimize the use of their energy for gestation and lactation and not for thermoregulation, thereby ensuring the survival of the calf (Braithwaite et al., 2015; Meynecke et al., 2021). The energy needs of whales vary according to their sex and reproductive status, being reflected in the temporal variability at the time of arrival to their breeding grounds and in the length of stay (Craig et al., 2003; Avila et al., 2020). In other humpback whale populations, it has been observed that individuals that do not have sufficient energy reserves do not migrate to their breeding grounds so that the abundance of adults and calves decreases in these areas (Frankel et al., 2021; Meynecke et al., 2021; Schall et al., 2021).

The monthly values of the PDO, as well as the monthly anomalies of SST show a warming period from 2013, which continued until 2017. This warming period, in addition to having a large temporal scale, also had a great spatial scope (Menne et al., 2018; Yu et al., 2019). It is possible that presence of warmer conditions recorded in intermediate latitudes (Mexican coasts) could have favored humpback whales in finding thermally favorable areas for calving and could be one of the causes of decreases in the encounter rates in Costa Rica (Cavole et al., 2016; Robinson, 2016). In previous years, humpback whales from Central America DPS have been observed off Mexican coasts, which leads us to hypothesize that the whales are responding to these warming events by modifying their migratory behavior (Calambokidis et al., 2008; Taylor et al., 2021).

Climate change is modifying the conditions of the critical habitats of the humpback whales (Askin et al., 2008; De Weerdt and Ramos, 2019; Dey et al., 2021). The increase in SST has triggered several responses in humpback whales, such as changes in the timing of their migration, and variations in the length of stay in their feeding and breeding areas, humpback whales have also been observed feeding in more coastal areas and forming aggregations from tens to hundreds of individuals to feed (Ramp et al., 2015; Findlay et al., 2017; Avila et al., 2020; Santora et al., 2020).

Humpback whales are organisms considered resilient due to their ability to modify their feeding and migration behaviors mainly in response to thermally abnormal conditions (Moore and Huntington, 2008; Meynecke et al., 2021; Cabrera et al., 2022). It is possible that the Northeast Pacific humpback whale population might be modifying its critical migration behaviors (shortening the migratory route) in response to warming events in the Pacific Ocean. Therefore, it is necessary to increase efforts in carrying out systematic surveys and studies that address migration and the quality of their critical habitats in terms of environmental conditions and human interventions such as vessel disturbance, fishing gear, and ocean pollution to have a solid scientific basis that allows for improving conservation strategies for humpback whales of the Central America DPS.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

Ethical review and approval were not required for the animal study because we were based on observational data in situ, following current guidelines in place in Costa Rica for marine mammals sightings, the majority of it from 2000-2006.

Author contributions

LP-G, LO, and HG contributed substantially to the conceptualization, data analysis, document writing, and figure editing. DH-M, JP-P, and SG contributed to the logistics and data collection. DH-M, JP-P, and SG contributed to the writing and revision of the manuscript. All authors agree that this work be submitted for publication.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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