Vol. 726: 161–179, 2024
https://doi.org/10.3354/meps14464

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published January 11

Environmental drivers of persistent humpback whale *Megaptera novaeangliae* feeding events in a Mexican breeding area

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ABSTRACT: Humpback whales *Megaptera novaeangliae* typically fast for several months in low-latitude breeding areas. Here we report on persistent feeding events during 5 wintering seasons between 2013 and 2020 in a known upwelling region of Banderas Bay of the mainland Mexico breeding area. In total, there were 76 unique feeding events documented (group size = 1 to ~100 individuals), involving 201 photo-identified whales, of which 18 were documented feeding in multiple years. The most prolific years of documented feeding in 2017 and 2018 (based on number of reports/individuals photo-identified feeding) followed the strongest marine heatwave ever recorded in the North Pacific. Whales documented feeding in Banderas Bay had significantly shorter mean sighting histories (2.3 yr) than a non-feeding sample (8.7 yr) and were reported to be of small size, suggesting they were predominantly younger whales. Most high-latitude recaptures of Banderas Bay feeding whales were in more northern North Pacific feeding grounds (50.8% were resighted in Russia, Alaska, and northern British Colombia, Canada). A binomial general linear model revealed a significant relationship between the probability of whales feeding in Banderas Bay and sea surface temperature (SST). Specifically, feeding consistently occurred in years of lower than average winter SST (<25°C), associated with La Niña years of the El Niño Southern Oscillation (ENSO). We conclude that feeding of humpback whales is now a predictable occurrence in the upwelling region of Banderas Bay in years that ENSO fluctuations lead to lower regional SST. The magnitude of several years of low-latitude feeding events reported here was likely influenced by climate change induced marine heatwaves that occurred during the study period.

KEY WORDS: Global warming · Climate change · El Niño Southern Oscillation · Marine heatwave · Migratory species · Recovering population

1. INTRODUCTION

The long-distance annual migration of animals has evolved independently in a wide variety of taxa (Baker 1978). The driver of such migrations is typically to maximise survival by exploiting seasonal environments and resources (Chapman et al. 2014), particularly food but also access to mates or shelter, and to avoid predators, parasites, or unfavourable environmental conditions (Cresswell et al. 2011).

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Seasonal migrations will be favoured by natural selection and may evolve in populations or species where the benefits of moving surpass the costs of staying (Lack 1954). However, for migration to evolve it is essential there is long-term predictability of seasonal resources and environmental features in all habitats the population occupies (Jónzen et al. 2011, Riotte-Lambert & Matthiopoulos 2020). This reliance on habitat predictability in multiple locations makes migratory species especially vulnerable to environmental/climate change (Robinson et al. 2009). Extreme climatic events may temporarily transform regional habitats, often in very short periods, and therefore pose a significant threat to species that travel long and energetically costly distances and rely on seasonal food resources that are only temporarily available (Ramp et al. 2015). Long-term effects of climate change may, however, irrevocably alter seasonal habitats, lead to failed migrations and changes in population distributions and movement patterns, and even threaten species survival (Robinson et al. 2009).

A marine heatwave is defined as a period of extreme elevation in sea surface temperature (SST) which may last weeks, months, and even years (Hobday et al. 2016). Global warming has been linked to the increase in strength and frequency of marine heatwaves in the last 2 decades (Oliver 2019, Scannell et al. 2020). Between 2013 and 2016, the North Pacific experienced the strongest marine heatwave on record (Di Lorenzo & Mantua 2016). Beginning in the autumn of 2013, the marine heatwave that earned the moniker 'the Blob' had peak values ~2.5°C (or 3 SD) above normal (Di Lorenzo & Mantua 2016). Originating in Alaska and spreading as far south as California, the Blob persisted through to the summer of 2016 (Gentemann et al. 2017), with warmer waters lasting through to 2018 in some of the deep-water northern regions of the ocean basin (Jackson et al. 2018). In 2019, a resurgence of extreme warm SST around the Alaskan coasts was recorded and named 'the Blob 2.0' (Chen et al. 2021). These 2 marine heatwaves had extreme effects on all facets of marine and coastal ecosystems regionally. This included reduced ocean productivity (Whitney 2015), widespread toxic algal blooms (McCabe et al. 2016), decreased abundance of some species of small schooling fish and krill (Cavole et al. 2016, von Biela et al. 2019, Rogers et al. 2021), increased abundance of gelatinous zooplankton (Brodeur et al. 2019), and a shift in the distribution of a wide range of marine taxa (Cavole et al. 2016). Mass die-offs of several species of seabirds and marine mammals were also documented (Cavole et al. 2016, Jones et al. 2018, Piatt et al. 2020). Humpback whales *Megaptera novaeangliae* in the North Pacific were also greatly impacted in some regions, with evidence of reduced calving rates, abundance, and even survivorship associated with the marine heatwaves (Cartwright et al. 2019, Neilson & Gabriele 2019, Wray & Keen 2020, Frankel et al. 2022, Gabriele et al. 2022, Pelayo-González et al. 2022).

The humpback whale has a global distribution and undertakes some of the most extensive migrations of all mysticete species (Stone et al. 1990, Rasmussen et al. 2007, Robbins et al. 2011), moving annually between summer high-latitude feeding (H-LF) areas and low-latitude winter breeding areas (Dawbin 1966). Whaling data established that humpback whale populations globally have the same basic annual migration, with Northern and Southern Hemisphere population migrations following the respective boreal and austral seasons (Dawbin 1966), with the exception of a resident population in the Arabian Sea (Mikhalev 1997). In H-LF areas, humpback whales feed intensively on fish and zooplankton found in nutrient rich waters, resulting in substantial net gains in body mass (Chittleborough 1965). During the winter months on their breeding grounds, they mate and give birth in comparatively less productive tropical and sub-tropical waters (Dawbin 1966). The benefits of humpback whale migration to the productive waters of summer feeding areas are clear, yet there is still no consensus on the drivers behind the species' winter migration to the tropics (Corkeron & Connor 1999, Clapham 2001, Rasmussen et al. 2007, Pitman et al. 2020). During winter at low latitudes, all age classes except dependent calves mainly fast (some individuals for many months), with dramatic decreases in body mass during this time (Russell et al. 2022). The humpback whale is therefore considered a capital breeder, supporting reproductive costs with previously stored energy supplies, contrasting with income breeders, such as most small cetaceans, which feed constantly to support reproduction (Jonsson 1997). Notably, in the Arabian Sea, an upwelling affords year-round feeding for humpback whales; therefore, this population is unique for the species in that they are income breeders (Mikhalev 1997, Papastavrou & Van Waerebeek 1997).

The North Pacific humpback whale population is one of the best studied of all the species' populations globally. Despite being heavily harvested by 20th century whalers (Rice 1978), the population has made a strong recovery (US Federal Register 2016). Using data collected between 2004 and 2006 during the ocean basin-wide SPLASH (Structure of Populations, Levels of Abundance and Status of Humpback whales in the North Pacific) project, it was estimated to number over 21 000 (CV = 0.04) animals using a Chapman-Petersen estimate (Barlow et al. 2011), and to be increasing by 4–6 % per annum (Calambokidis et al. 2008). The regions recognized as feeding areas occur in the coastal areas of southern California (USA), extending up the west coast of North America to Alaska, and west across the Gulf along the Aleutian Islands to the seas of the Russian Far East (Calambokidis et al. 2008, Titova et al. 2018). The breeding areas of the North Pacific extend across the ocean basin from the Philippines, Japan, and the Mariana Islands in the west, through the Hawaiian Islands centrally, to Mexico and Central America in the east (Calambokidis et al. 2008, Hill et al. 2020).

In Mexico, there are 4 main winter breeding areas: Baja California, the Revillagigedo Archipelago, southern Mexico, and the central region known as mainland Mexico (Urbán & Aguayo 1987, Taylor et al. 2021a,b, Zavala-Alarcón et al. 2021; Fig. 1). Banderas Bay sits at the southern end of the mainland Mexico region (Fig. 1), and is used for mating (Calambokidis et al. 2008), calving (Ransome et al. 2022a), and nursing (Ransome et al. 2022b). Photo-identification and genetic studies have shown that the Bay receives whales from all known feeding areas of the North Pacific (Calambokidis et al. 2008, Baker et al. 2013, Titova et al. 2018, Ransome et al. 2023). However, it is predominantly the feeding areas in the waters of the USA, between California and the Washington state border with Canada, that have the strongest migratory connections to the Bay (Urbán et al. 2000, Calambokidis et al. 2008). The SPLASH project (2004–2006) found 72.6 % (119 / 164) of feeding area matches for whales from the Banderas Bay area were within the California to Washington region (Calambokidis et al. 2008).

Over the past few decades there have been increasing reports of a change in the foraging behaviour of some humpback whale populations. While there was only limited historic evidence, from a mid-latitude whaling station, of humpback whales feeding on migration (Dawbin 1966), documentation of feeding is now becoming an expected annual phe-

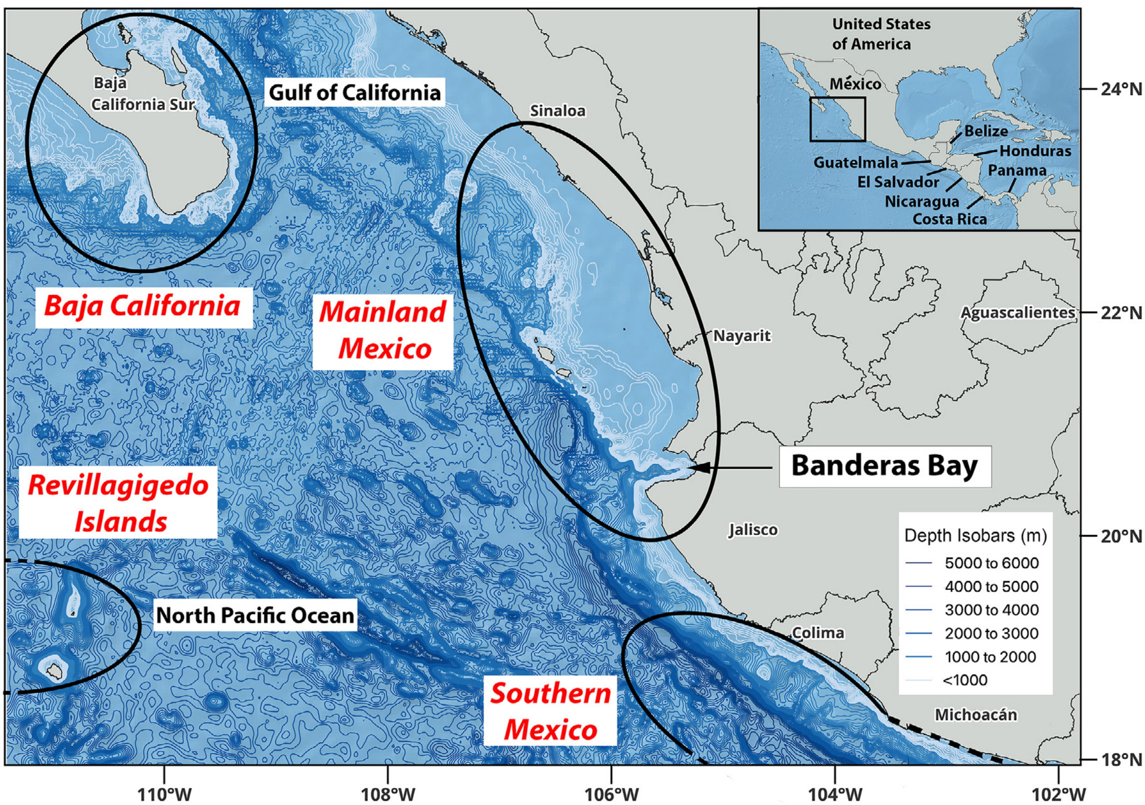

Fig. 1. Location of Banderas Bay and 4 recognized humpback whale *Megaptera novaeangliae* breeding areas (red names/ black polygons) in Pacific Mexico. Depth contours are 100 m isobaths sourced from General Bathymetric Chart of the Oceans (GEBCO; www.gebco.net)

nomenon on some Southern Hemisphere humpback whale migratory pathways, which are associated with seasonal upwellings. This includes both coasts of South Africa (Best et al. 1995, Barendse et al. 2010, Findlay et al. 2017, Dey et al. 2021) and southeast Australia (Stamation et al. 2007, Gales et al. 2009, Owen et al. 2017, Pirotta et al. 2021). This annual documentation of feeding whales in areas outside established well characterised H-LF areas is challenging the traditional 'feast or famine' theory (sensu Gales et al. 2009) of the foraging cycle of most humpback whale populations (Chittleborough 1965 cf. Arabian Sea, e.g. Mikhalev 1997). Furthermore, evidence of sporadic feeding of humpback whales in breeding areas during the winter continues to accumulate (Barraf et al. 1991, De Sá Alves et al. 2009, Bortolotto et al. 2016, De Weerdt & Ramos 2020, García-Cegarra et al. 2021). Such changes have been suggested to reflect the effects of climate change on prey abundance and distribution (Simmonds & Issac 2007, De Weerdt & Ramos 2020). However, increased reporting or greater competition in H-LF areas have also been put forward as plausible explanations for this apparent change in foraging behaviour (Findlay et al. 2017).

In the winter season of 2011/2012 (Dec–Mar), Frisch-Jordán et al. (2019) reported the longest ever intensive feeding episode of humpback whales in a breeding area to date, which occured in Banderas Bay over 79 d. This was the first time feeding had been reliably documented in the area during winter, despite over 15 yr of regular data collection (since 1996) and a large whale watching industry. Here we report on continued seasonal feeding documented in Banderas Bay for an additional 5 breeding seasons between 2013 and 2020. We investigate the migratory connections and sighting histories of feeding whales, and the environmental and demographic factors that may be influencing continued feeding events regionally.

2. METHODS

2.1. Study area

The documentation of humpback whales *Megaptera novaeangliae* feeding in Pacific Mexico in this study was exclusively from Banderas Bay, within the mainland Mexico breeding population (Fig. 1). Although there have been no modern abundance estimates (Bettridge et al. 2015), the mainland Mexico population was estimated to have reached ~4100 (in 2006) using data collected over 15 yr ago and to be growing by approximately 5.7% per annum (Calambokidis et al. 2008, Martínez-Aguilar et al. 2018). The bay is situated on the Mexican Pacific coast at the mouth of the Sea of Cortez in the Tropic of Cancer (~20° N) and covers an area of ~1100 km^2 (Mortera Gutiérrez et al. 2016). This is the northernmost extent of the eastern tropical Pacific (which extends south to Peru), which is considered one of the most productive oceans in the world (Fiedler et al. 1991), and also the start of the temperate North Pacific. Consequently, Banderas Bay is situated in an area where several biogeographic regions meet and is influenced by the cool Californian Current, warm equatorial currents, and the Mexican Coastal Current (Kessler 2006, Gómez-Valdivia et al. 2015).

The northern part of Banderas Bay is very shallow, with an average depth of 30 m (Mortera Gutiérrez et al. 2016). The continental shelf narrows at the southern end of the Bay and a deep sub-marine canyon drops down to approximately 1100 m (Fig. 2), which constitutes the northern section of the Middle America Trench (Mortera Gutiérrez et al. 2016). At the beginning of the 100 m isobar in the south part of the bay, there is an area of wind-driven seasonal upwelling caused by the tidal current interacting with the beginning of the slope of the submarine canyon (De La Torre Vázquez 2017). Consistent semi-annual regional upwellings occur, predominantly from January to June, with a peak in primary productivity from February to May (López-Sandoval et al. 2009, Domínguez-Hernández et al. 2020).

2.2. Data collection and effort

All sighting data was collected opportunistically from whale watch vessels (open hulled, 8–10 m vessels with 70–200 hp outboard motor engines) between 2013 and 2020. There is a large whale watching and tourism industry in the area that had been growing continuously until the COVID-19 global pandemic in 2020. During the whale watching season, vessels that collect data leave daily from Nuevo Vallarta and Puerto Vallarta marinas in the centre of the Bay (Fig. 2). Data were collected from 4 whale watch companies, with each company conducting typically between one and four 3 h whale watch trips a day throughout the official whale watch season (when permits for approaching and following whales can be obtained) in the Bay, from 8 December to 23 March each year (SEMARNAT 2010). We estimate therefore that each season (105 d), these vessels were on the ocean actively searching for or watch-

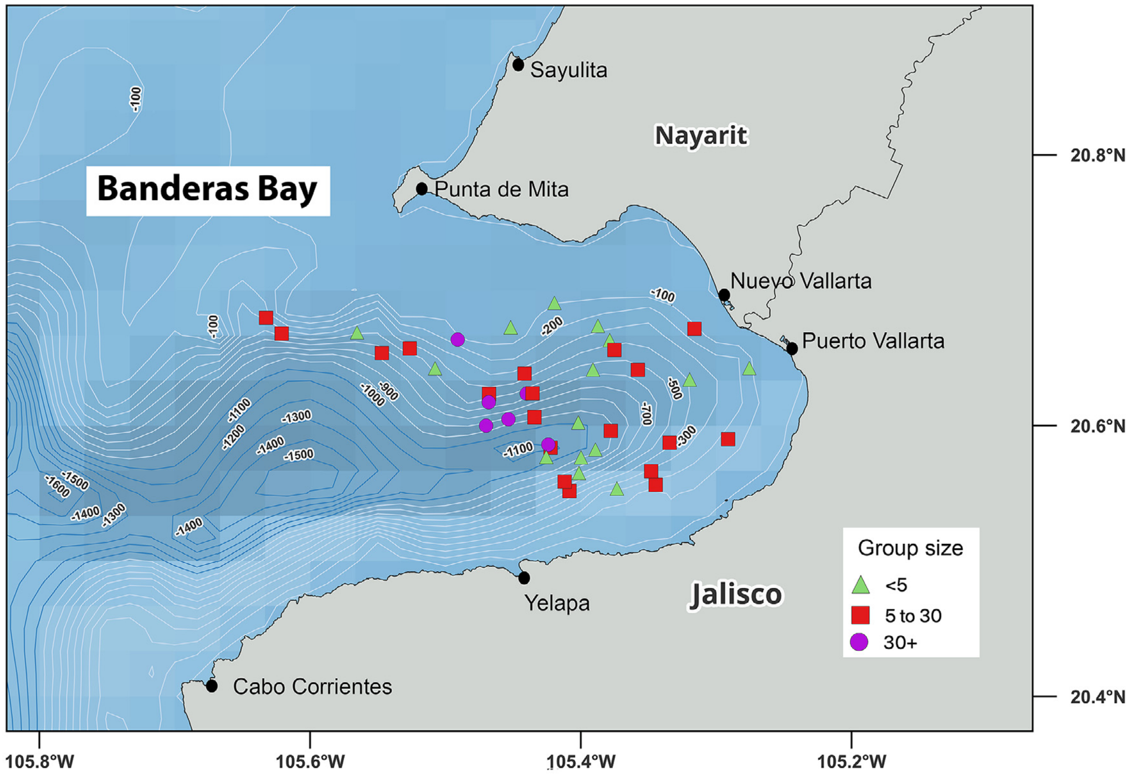

Fig. 2. Location and group size (estimated number of individual whales) of feeding groups of humpback whales in the waters of Banderas Bay, Mexico between 2013 and 2020. Only sightings with GPS locations are included on this map (n = 43). Contours are 100 m isobaths sourced from GEBCO (www.gebco.net)

ing whales in Banderas Bay for a minimum of 3150 h, or on average approximately 30 trip-hours per d. Data was also obtained from a whale watch company with 2 daily departures throughout the permitted season, from Sayulita, Nayarit, 15 km north of Banderas Bay (Fig. 2).

Data collection by whale watch vessels is a local initiative established in Banderas Bay in 1996, and coordinated by the non-governmental organization Ecología y Conservación de Ballenas, A.C. (ECOBAC, www.ecobac.org). It mainly involves the collection of photo-identification images and sighting data for the maintenance of a humpback whale photo-identification catalog. All data and photographs were collected by experienced guides and researchers using DSLR cameras (Canon/ Nikon) and telephoto lenses. The following data were recorded for each whale encounter where whales were documented feeding: time, GPS location (only available for some feeding events, n = 43; Fig. 2), estimated age class of whales, group size, group type, and behaviour. Water depth for sightings with recorded GPS positions were obtained using General Bathymetric Chart of the Oceans (GEBCO) of 2019 in QGIS 3.24 Tisler. The humpback whale watching season runs across calendar years (Dec–Mar), and hereafter we refer to the season by the year in which the most substantial part of the season occurred (i.e. season 2012/2013 is referred to as the 2013 season).

2.3. Classification of feeding

All unique sightings of whales documented feeding (encounter of either a lone whale or group of multiple whales) were classified as a feeding event. To identify whales involved in feeding events, a distinction was made between direct observations of whales feeding and displaying foraging behaviour and indirect measures of feeding, based on the following criteria:

(1) Direct evidence of feeding: Whales observed at the ocean surface, exhibiting foraging behaviour of mouth agape and lunge feeding and/or filtering water and prey species through baleen, or;

(2) Indirect evidence of feeding: Whales displaying foraging behaviour and (a) observed defecating, or (b) in close association with defecating whales, with all whales in the group displaying foraging behaviour and surfacing together (<1 min apart).

Foraging behaviour was classified as small groups of whales that had short dive times (<5 min), surfaced in the same area, and had very short surface times (<1 min) before diving again. Foraging behaviour is very different from typical breeding ground behaviour of humpback whales in Mexico (e.g. travelling, resting, singing, nursing, or courtship behaviour). Whales were not included in this study if they were described as displaying foraging behaviour but no defecation was observed from any individuals in the group. A conservative approach to identification of feeding whales was used due to the nature of the data collection from whale watch vessels. We note that many of the whales identified as involved in feeding activities were documented extensively in and around the feeding area during the feeding episodes, but we only included sightings where feeding could be reliably confirmed. We define a super-group after that first described by Findlay et al. (2017) as large groups of humpback whales estimated to be within 5 body lengths of their nearest neighbour. However, we used the estimated group size of 30 or more individual whales as the definition of a super-group (cf. 20 used by Findlay et al. 2017), as this was a group size estimate category used by some researchers at the time of field work.

Visual estimations of age class of feeding whales were categorised into 3 classifications (calf, juvenile, and adult) based on vessel based protocols established in the SPLASH program (Calambokidis et al. 2008). Calves can be recognised by their size and close association with their mother. They are on average ~4–4.5 m at birth and ~8–10 m at independence (Clapham et al. 1999a) after just under 1 yr with their mother (Clapham 1996). Whaling data suggests adults at physical maturity are on average ~13.3 m in length (males 13.1 ± 0.2 m [mean ± SD] and females 13.5 ± 0.2 m; Chittleborough 1955). Based on the approach by Craig et al. (2003), whales were classified as juveniles only when experienced observers visually estimated the whale was too large to be a calf of the year, but unambiguously small compared to adults, i.e. between 10 and 13 m (Chittleborough 1955, Clapham et al. 1999a). All whales not classified as calves or juveniles were classified as adults.

Photo-identification images of whales were collected from each sighting of feeding whales and the best fluke image for each individual whale was uploaded to the online platform Happywhale (www.happywhale.com). Happywhale matched each fluke via automated image recognition (Cheeseman et al. 2022) to a global humpback whale fluke photo-identification catalogue of 66 043 individuals, of which 27 536 were identified in the North Pacific Ocean. Images were matched with an expected accuracy of 97 to 99% of potential matches and successful matches were manually confirmed by trained observers (Cheeseman et al. 2022). An identification code was given to unmatched individuals with fluke identification photos of sufficient quality to be confirmed as new to the database. When images were matched to whales found on Happywhale that were not the intellectual property of one of the authors of the present study, the owner of the image was contacted as part of the North Pacific Humpback Whale Photo-ID (NPPID) collaboration (Cheeseman et al. 2023). Under the NPPID collaboration, each researcher with matches to whales in this study was contacted, the study explained, and permission requested for use of match information.

2.4. Statistical analyses

A general linear model (GLM) in R v.4.0.3 (R Core Team 2020) was used to investigate the influence of sea surface temperature (SST) and chlorophyll concentration (CC) on the occurrence of feeding events by whales in Banderas Bay. These 2 dynamic marine environmental variables were used as a proxy for predictors of upwelling conditions and investigated at a coarse spatial scale of 1° of latitude/longitude, which covered the entire area of the Bay. Note that in this analysis only, feeding data were included from Frisch-Jordán et al. (2019) on the 2012 feeding event. The merit of including this data was that it allowed for greater investigation of the influence of these potential environmental drivers on regional low-latitude feeding of humpback whales by including an additional 26 feeding events and 14 wk in the analysis. Methodology and study area for data collection and identification of feeding whales in 2012 was concordant with our methodology (Frisch-Jordán et al. 2019). The study period for this model was from 2012 to 2020 and included 140 wk of humpback whale breeding seasons. Due to the opportunistic nature of the data collection by whale watch vessels, and with insufficiently precise GPS location data for many of the feeding reports (n = 33), fine scale geographic modelling of feeding whales' distribution and static physical features was not possible.

Counts of individual humpback whales observed feeding were considered potentially unreliable due to opportunistic data collection and multiple researchers, and therefore not used in the model. Instead, we used a binomial GLM with presence/

absence of feeding whales as the dependent variable and weekly SST and CC during the breeding season as independent variables. If whales were seen feeding at any time during the week (Monday to Sunday), that week was classified as positive for feeding. Weekly SST and CC (scale = 1° of latitude/longitude) for the region across the whole breeding season were obtained from the US National Oceanic and Atmospheric Administration's (NOAA) National Environmental Satellite Data and Information Service (https://www.nesdis.noaa.gov).

To investigate the likely age class of whales observed feeding in Banderas Bay, the sighting history length (yr) of the identified whales observed feeding (hereafter referred to as feeding whales) was compared to a sample of photo-identified humpback whales not observed feeding (non-feeding whale sample, n = 157). Whales in the non-feeding sample were sighted during the feeding period in 2017, 2018, and 2020 in the same breeding population in nearby Sayulita, Nayarit. Sayulita is approximately 15 km north of the northern point of Banderas Bay and is part of the mainland Mexico breeding area (Fig. 2). Sayulita was used as a control region because no feeding behaviours were observed during the study period in this area. To provide robust statistical testing and reduce potential bias, RStudio (version 1.2.1335) was used to randomly select individual whales from the non-feeding whale sample to compare to feeding whales to provide equal sample sizes for comparison. Sighting history length was measured in years, from the date of the first sighting registered on Happywhale to the date of first feeding sighting (or sighting date in Sayulita of the non-feeding sample during 2017, 2018, or 2020). Welch's 2-sample *t*-test was then used to compare mean sighting history length in the two groups.

We further investigated the identity of feeding whales in Banderas Bay by assessing their migratory connections to H-LF areas. For each whale in the feeding sample, the furthest known sighting in an H-LF area recorded in Happywhale was classified as the foraging destination of the whale. If no documented sightings were recorded in a H-LF area, the foraging destination was recorded as unknown. Pearson's chi-square test for independence was used to test whether the H-LF migratory destinations of whales differed significantly between the feeding and non-feeding samples. We also compared the migratory distance between Banderas Bay and the centre of the H-LF area for the 2 groups, based on calculating the shortest oceanic great-circle distance (not crossing land) after the methodology of Bowditch (1994). A migratory distance was calculated for each whale seen in an H-LF area, and Welch's 2-sample *t*-test was used to compare the mean migration length (great-circle distance) between the feeding and non-feeding whale samples.

3. RESULTS

3.1. Feeding episodes

In total, there were 76 humpback whale *Megaptera novaeangliae* feeding events documented in Banderas Bay, Mexico, during 5 breeding seasons (each of 105 d) between 8 Dec 2012 and 23 Mar 2020, with 201 individually identified whales documented feeding (Table 1). No feeding was reported during the 2014, 2015 and 2016 seasons. In 2019, feeding was observed over an 8 d period (Table 1) although there were no images of photo-identified whales available for use in this study. Of the 76 documented feeding events, only one was of direct feeding of a lone whale gulp feeding at the water surface. In all other cases, indirect feeding was recorded, with whales confirmed to be feeding/have fed due to defecation by at least one whale in the group being observed (Fig. 3a,b), and associated with foraging behaviour.

In 3 cases involving solitary feeding whales, bubble clouds or bubble nets were reported being used during feeding events (Fig. 3c). Generally, the feed-

Table 1. Sightings of feeding humpback whales from 2013 to 2020 in the waters of Banderas Bay, Mexico. *reports not supported by photo documentation available to authors; NA: not applicable

Season	First feeding report	Last feeding report	Time span of reports (d)	Number of reports	Unique whale IDs (total IDs)
2013	08-Mar	21-Mar	14	4	14 (15)
2017	23-Feb	31-Mar	37	41	116 (154)
2018	22-Jan	15-Mar	45	26	66 (77)
2019*	27-Feb	06-Mar	8	NA	NA
2020	28-Feb	07-Mar	9	5	22 (23)

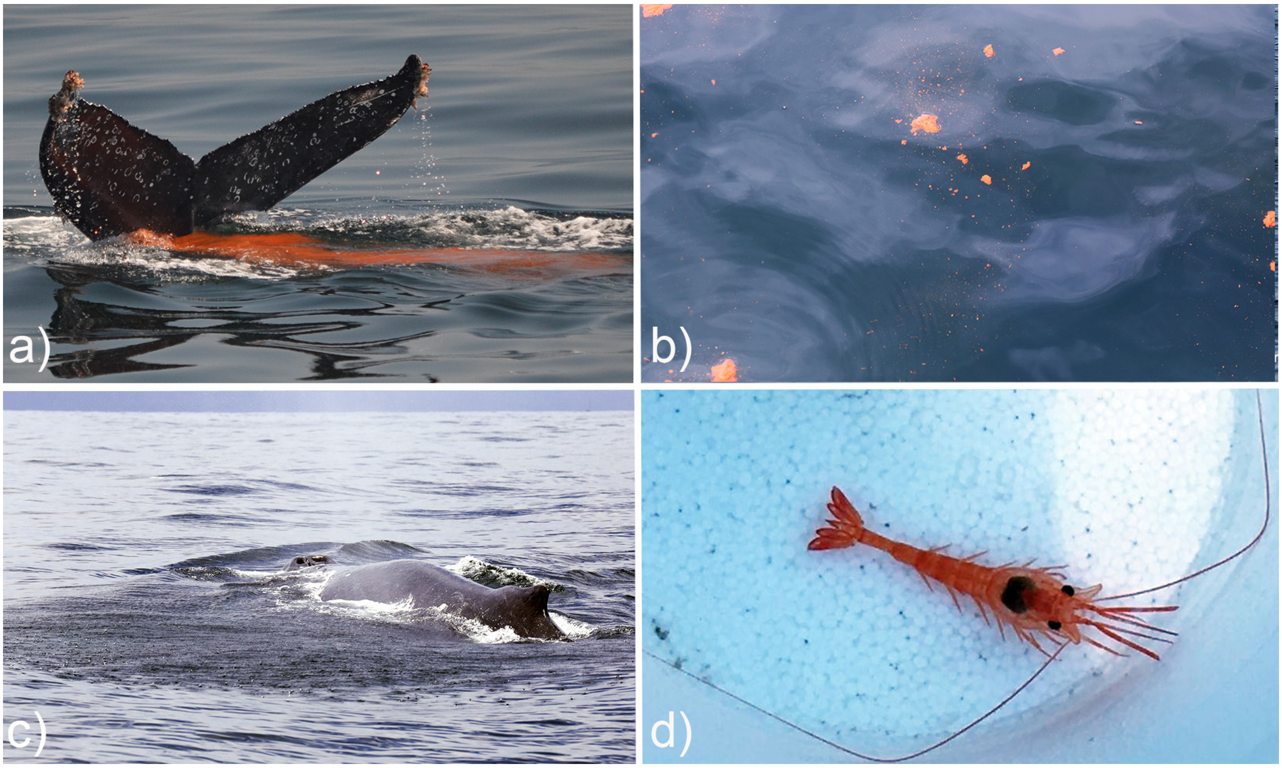

Fig. 3. (a) Humpback whale defecating (image: Astrid Frisch-Jordán); (b) faeces (image: Nicola Ransome); (c) bubble cloud around feeding whale (image: Nicola Ransome); and (d) sample of the presumed prey species in 2017 (image: Whale Watch Vallarta)

ing whales had short surfacing intervals of ~20 s and 3 to 5 exhalations before diving, and on surfacing, the exhalations of the feeding whales were notably loud. When fluking to dive, the whales would arch their peduncle steeply and lift their tail high in the air, which was commonly associated with defecation of a bright red-orange cloud that appeared from the peduncle (Fig. 3a,b). A very strong and pungent fishy odour was associated with the whales' defecations. On several occasions in February 2017 and 2018, small shrimp-like crustaceans appeared at the surface when whales surfaced during foraging behaviour (Fig. 3d). While samples were collected and photographed, the species was not able to be identified due to sample deterioration.

Feeding was typically associated with foraging behaviour, involving many small groups of whales consisting of 2 to 5 individuals. Small groups were sometimes dispersed over several km, making up large feeding aggregations. Feeding group size estimates ranged between 1 and ~100 individuals, with group sizes of 5 to 30 individuals documented most commonly (n = 44, 58%). Large aggregations of >30 feeding whales, termed 'super-groups' (n = 9), were observed in 3 of the 5 years (2017, 2018, and 2020; Figs. 2 & 4a). In the analysis of feeding whale events that had GPS locations (n = 43), feeding predominantly occurred in the region of known upwelling (Fig. 2) in the mid to south of Banderas Bay at depths typically greater than 100 m. Based on GPS positions (Fig. 2), the depth of the area where whales were reported feeding ranged between 58 and 1127 m, with an average depth of 436 m. In most reports (n = 47), observers classified the groups of whales as consisting predominantly of juvenile whales. No direct measurements were taken of body length, which precludes absolute confirmation of the age class of feeding whales. There were no confirmed cases of mothers with calves feeding or defecating during the feeding episodes. Only 9 (4.5%) feeding whales were of known sex (determined by past genetic studies or inferred from social roles in historical sighting data in Mexico), and all were male.

3.2. Identified individuals, group size, and duration of feeding events 2013–2020

Across the 5 yr when whales were documented feeding, 2017 and 2018 had noticeably larger numbers of feeding events. In total, 41 reports were made of feeding whales in 2017 over a 37 d period (Table 1),

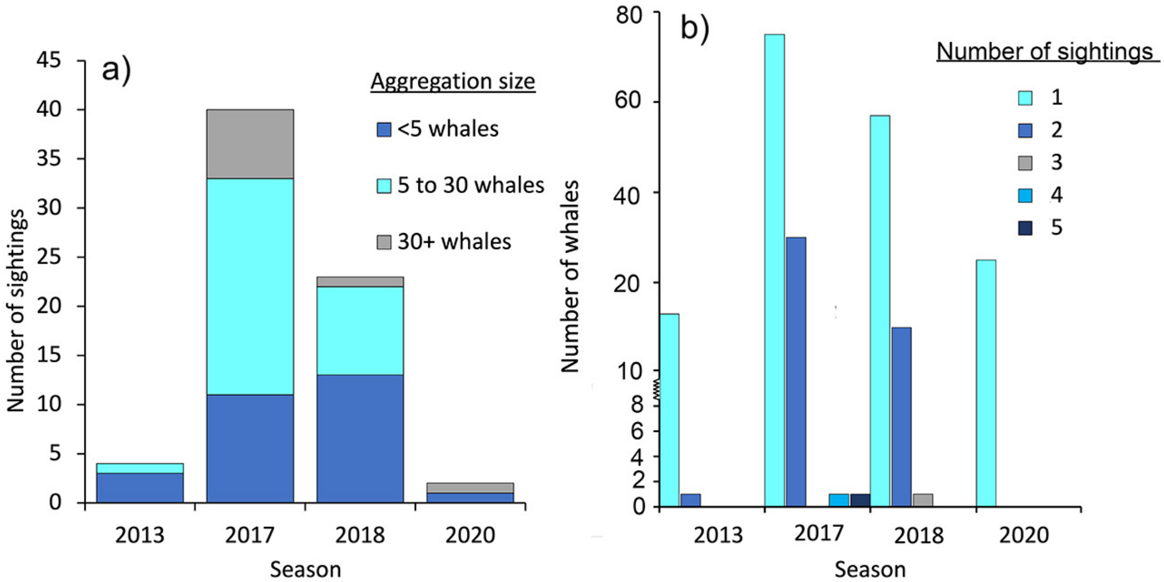

Fig. 4. Sighting summary for humpback whales in Banderas Bay, Mexico. (a) Reported aggregation sizes of feeding whales; and (b) number of feeding sightings each season for each individually photo-identified whale

with group size known for all but one report. This compares with 2018, the second most prolific year of feeding, with almost half the number (n = 26) of feeding reports compared to 2017 (Table 1), reported over a longer period of 45 d. In 2017, there were greater numbers of both individuals and groups documented feeding, larger group sizes, and a greater number of resighted feeding whales (Fig. 4, Table 1). In total, there were 7 d (17.1% of reports that year) that super-groups were reported in 2017 and 1 d in 2018 (Fig. 4a). Although a super-group was reported on only one day in 2018 (Fig. 4a), observers conservatively estimated a minimum of 100 individual whales feeding in the area. One observer collected 31 unique fluke identification images in less than 1 h, and reported difficulty in vessel travel due to constant, unexpected, surfacing of whales. Similarly, even though there were only 5 reports of whales feeding in 2020, one day involved a super-group (Fig. 4a), from which 22 individual whales were identified.

Between 2013 and 2020, there were a total 201 feeding whales photo-identified from Banderas Bay, with the greatest number (n = 166) occurring in 2017 (Table 1). During all events 72% (n = 84) were confirmed feeding just once, 25% (n = 29) were seen feeding twice, and 3 individuals were documented feeding on 3, 4, and 5 different days respectively (Fig. 4b). We also note that 2 dyad groups (i.e. 2 whales) and 2 trio groups (i.e. 3 whales) were seen feeding together on different days. The length of time between same season sightings of individual whales seen feeding varied from 1 to 30 d (mean = 6.2 d). During the sustained feeding events of 2018, fewer whales were photo-identified (n = 66; Table 1) and nearly half of those (n = 31, 47.0%) occurred on one day. There were a total 18 whales documented feeding in multiple years (Table A1 in the Appendix) and 3 events involving a dyad feeding together in 2 different years (Table A1).

3.3. Influence of sea surface temperature on feeding

Whales were present feeding in 21 of the total 140 wk (15%) across the 9 breeding seasons (2012–2020) included in the model. Weekly SST varied between 22.7 and 28.3°C, and weekly CC varied from 0.1 to 9.6 mg l^{-1} (Appendix, Fig. A1). There was a highly significant relationship between SST and the weekly presence/absence of feeding by humpback whales reported in Banderas Bay (GLM; z_{139} = −4.186, $p < 0.001$), although not with CC (GLM; z_{139} = −0.839, p = 0.402). The binomial model predicted a steep increase in the probability of whales feeding (>~20%) when SST was below 25°C, based on an increase in the slope of the curve, and a predicted 50 to 90% probability between 24 and ~23°C (Fig. 5).

The model predictions were consistent with the raw data and lower SST was generally associated with La Niña years of El Niño Southern Oscillation (ENSO). No feeding was observed in weeks when SST was >25°C, and longer feeding episodes (more consecutive weeks of feeding) typically occurred during extended periods of SST < 25°C (Fig. 6). However, we

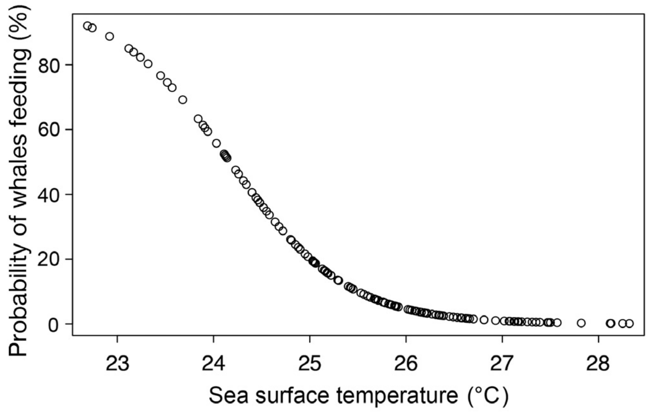

Fig. 5. Probability of humpback whales feeding modelled on sea surface temperature (SST), in Banderas Bay between wintering seasons of 2012 and 2020, via a binomial general linear model of feeding whale presence. SST obtained from US National Oceanic and Atmospheric Administration's (NOAA) National Environmental Satellite data and Information Service (https://www.nesdis.noaa.gov) at a spatial scale of 1° of latitude/longitude

note in 2013 (a very weak La Niña year), SST was below 25°C for 1 mo and yet only 14 d of feeding were documented (Fig. 6). Feeding may have been occurring earlier than the first confirmed report, with large numbers of whales and foraging behaviours reported in the feeding area 2 wk prior, although no defecation was documented to confirm feeding and it was therefore not included in the analysis. Lastly, even in neutral years or weak El Niño years (2020) when SST dropped below 25°C, feeding still occurred although there were fewer reports over a shorter duration (Fig. 6).

3.4. Sighting histories of individual whales documented feeding

Of the 201 whales photo-identified feeding in the Banderas Bay (between 2013 and 2020), 90 (44.8%) had no previous sightings recorded on Happywhale in the North Pacific, and to date have only ever been documented during these feeding events in Mexico. Furthermore, 62.7% (n = 126) of feeding whales had less than a 2 yr sighting history in the North Pacific when seen feeding in Banderas Bay for the first time. The mean sighting history length of the feeding

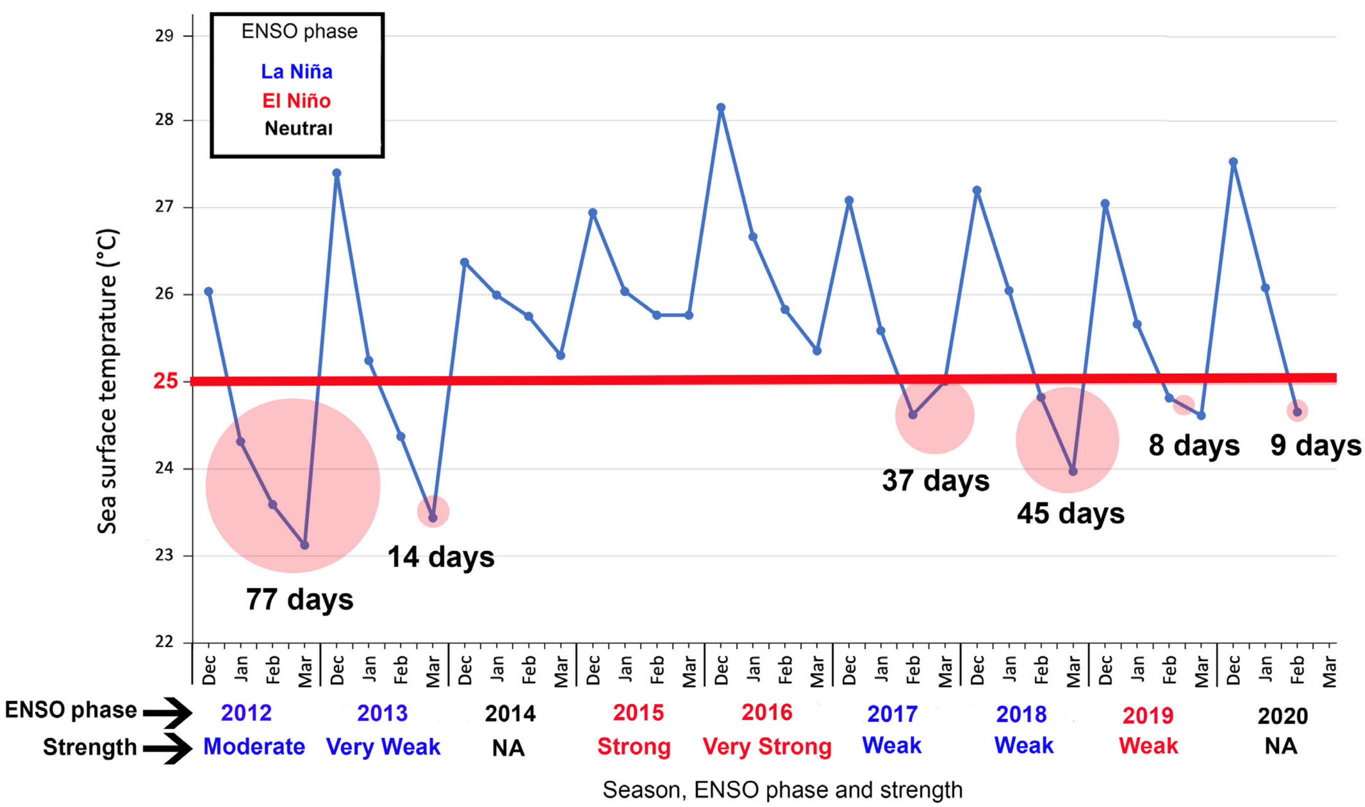

Fig. 6. Average monthly sea surface temperatures (SST, °C) during the winter breeding seasons between 2012 and 2020. Red circles indicate feeding episodes, size is relative to duration, and number below indicates length of episode. Solid red line indicates 25°C. X-axis also includes information on El Niño Southern Oscillation (ENSO) phase and strength during each season. SST sourced from NOAA NCEI Extended Reconstructed Sea Surface Temperature (https://doi.org/10.5065/JZ08-3W17; accessed 12 Jan 2021)

whale sample (mean ± SD = 2.3 ± 4.1 yr, median = 0 yr, range = 0–16 yr) was significantly lower (Welch's t-test; t = 10.827, df = 288.19, $p < 0.001$) than that of the non-feeding whale sample (mean ± SD = 8.7 ± 6.7 yr, median = 8 yr, range = 0–29 yr).

Of the 111 feeding whales with a sighting history, only 61 had been identified in a H-LF area of the North Pacific and over half (n = 31, 50.8%) of those were from northern regions from Russia to northern British Columbia (BC), Canada (Fig. 7). In contrast, less than a third (n = 20, 32.8%) had been sighted in the California to Oregon area. A Pearson's chi square test showed that the migratory destinations of the feeding whale group differed significantly from those of the random non-feeding whale sample (χ^2 = 14.193, df = 6, p = 0.028). Of the non-feeding sample of whales (n = 61), 75.4% (n = 46) had been sighted between California and Oregon, and only 4 were from the northern H-LF feeding areas, including 3 from the Aleutian Islands and 1 from the Western Gulf of Alaska (Fig. 7). The average migratory distance for the feeding whales of 4821.1 km (95% CI = 4363.1–5279.1) was significantly greater (t = −7.043, df = 93.728, $p < 0.0001$) than the non-feeding whale sample mean of 2923.6 km (95% CI = 2669.6–3177.6), with a difference of 1897.5 km.

4. DISCUSSSION

Capital breeding, such as the classic humpback whale *Megaptera novaeangliae* migratory model (Chittleborough 1965, Dawbin 1966), is considered an adaptation for survival in adverse conditions, rather than a preferred mammalian breeding strategy (Houston et al. 2007). This is primarily due to the energetic costs of maintaining and converting fat stores, the dangers of any error in estimates of required capital, and the reliance on habitat and resource predictability (Jonsson 1997, Ramp et al.

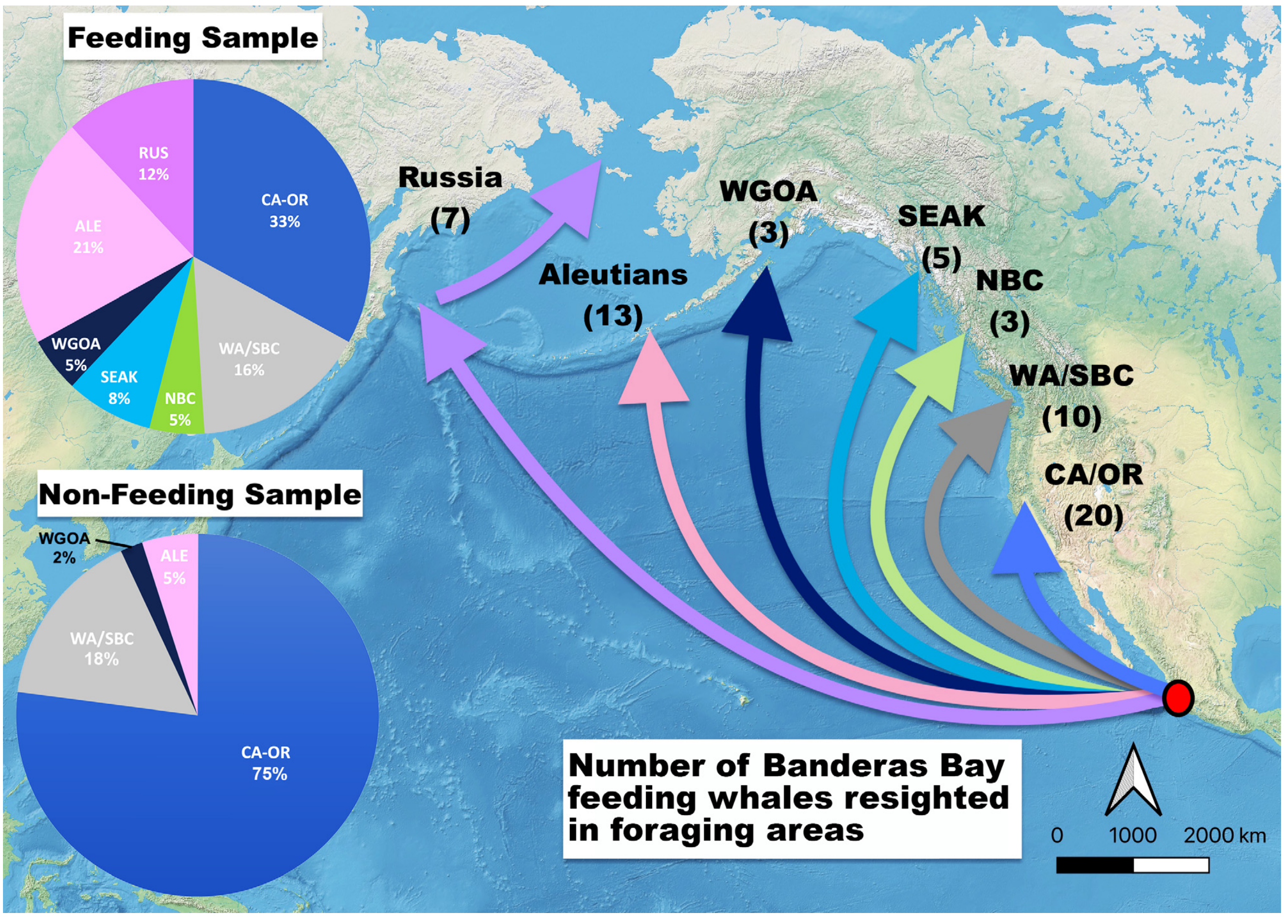

Fig. 7. Migratory destinations of the 61 Banderas Bay feeding humpback whales (*M. novaeangliae*) sighted in high-latitude feeding (H-LF) areas. Pie charts show the proportion of whales from different H-LF areas in the feeding (n = 61) and non-feeding sample (n = 61). ALE: Aleutians; RUS: Russia; WGOA: Western Gulf of Alaska; SEAK: Southeast Alaska; NBC: northern British Colombia; WA/SBC: Washington state and southern British Colombia; CA/OR: California and Oregon

2015). The resident Arabian Sea humpback whale population highlights that if suitable prey resources are available at low latitudes, humpback whales may be resident year-round (Mikhalev 1997). However, with the exception of upwelling areas, most (sub-) tropical humpback whale breeding areas worldwide typically have poor productivity and low densities of potential humpback whale prey species (Papastavrou & Van Waerebeek 1997). Feeding of humpback whales during winter in breeding areas has been very rarely documented. This is despite humpback whales being the most extensively studied large whale globally and the most popular target species of whale watch industries worldwide. Here we report on continued feeding episodes of humpback whales for extended periods in Banderas Bay within the mainland Mexico breeding area, a region formerly believed to be used only for mating, calving, and nursing by the species. This extends our preliminary understanding of extensive feeding in the region initially reported in 2011/2012 (Frisch-Jordán et al. 2019) and establishes for the first time a persistent change in humpback whale seasonal cycles and behaviour in a low-latitude breeding area. To date, this is the only published report of such prolific and ongoing feeding documented in a breeding area globally. Similar to other areas where feeding occurs at lower latitudes, i.e. non-migratory Arabian Sea population (Mikhalev 1997) and on migratory pathways (Gales et al. 2009, Barendse et al. 2010, Findlay et al. 2017, Dey et al. 2021), it is a region associated with seasonal upwellings.

All feeding reports in this study were made between late January and March in the area of seasonal upwelling over the slope of the submarine canyon in the mid- to southern area of Banderas Bay (Lluch-Cota 2000, Pennington et al. 2006). A regional study into primary productivity of this upwelling found localized phytoplankton biomass and production rates up to 2 times higher than the surrounding area (López-Sandoval et al. 2009). Ambriz-Arreola et al. (2012) showed a strong negative correlation between SST and seasonal patterns of zooplankton abundance associated with the upwelling (February to May). In other North Pacific upwellings, colder regional SST related to the La Niña phases of ENSO also leads to elevated levels of nutrients and more abundant zooplankton (Chenillat et al. 2012, Fleming et al. 2016). Faeces colour and consistency (C. Gabriele pers. comm.), the high incidence of repetitive fluke-up dives (which implies diving to some depth; Findlay et al. 2017), depth of area where whales were documented feeding, the volume of exhalations, the lack of observed surface feeding behaviour, and the collection of a small unidentified shrimp-like crustacean which surfaced with whales (Fig. 3d), suggest the whales were feeding on a zooplankton species, likely at some depth. Feeding was documented consistently over the last decade during winters when SST in the bay dropped below 25°C, at times associated with La Niña years of ENSO. No feeding was documented in the bay during the whale breeding seasons of 2014, 2015 and 2016 (Fig. 6). This correlated with the period of a strong phase of El Niño, when SST remained above 25°C. Our results show that feeding of humpback whales can be predicted to occur in years that ENSO fluctuation cause colder SSTs, with whales likely opportunistically exploiting increased localized productivity and higher abundance of a zooplankton prey species around the upwelling region of Banderas Bay. That no correlation was found between chlorophyll concentration (CC) and presence of feeding whales may be related to the coarse scale of CC data used in the model. Finer scale satellite data at weekly intervals was not able to be used in the models due to incomplete spatial coverage (from cloud masking).

There is no published documentation of feeding of humpback whales in Banderas Bay before 2011, nor are there anecdotal reports (Frisch-Jordán et al. 2019). This is despite regular seasonal data collection since 1996. Therefore, we believe the drivers of this now persistent change in humpback whale behaviour likely involve a combination of demographic and ecological factors influencing resource availability to individual whales in H-LF areas, and not just the abundance of suitable prey in the Banderas Bay region. One obvious factor to consider is the strong recovery of the North Pacific humpback whale population from commercial whaling (Clapham et al. 1999b). Using data from ~15 yr ago, Calambokidis et al. (2008) estimated that North Pacific humpback whales had already surpassed the approximate pre-whaling estimate of ocean basin abundance of 15 000 to 20 000 mature (i.e. non-calf) individuals (Rice 1978). This pre-whaling estimate did not include modern data from the recently uncovered illegal Soviet whaling of humpback whales in the ocean basin (Ivashchenko et al. 2016). Nevertheless, the North Pacific humpback whale population is likely nearing carrying capacity. Therefore, with increased intraspecific competition in H-LF areas, exploitation of available prey resources in other areas of seasonal humpback whale habitat with high productivity (i.e. upwelling regions) may be a necessity for individuals' survival and may play a greater future role in the species' foraging ecology regionally.

Fluctuations in abundance and/or quality of food resources in H-LF areas is another major factor likely to have driven feeding events. Unreliability of prey resources in H-LF areas may threaten survival of individuals that fast for long periods and travel extensive distances, arriving to forage with a limited window of time to replenish essential energy stores (Jonsson 1997, Ramp et al. 2015). The most prolific humpback whale feeding events in Banderas Bay (greatest number of individual whales documented feeding, number of reports, size of feeding groups, and length of feeding episodes) occurred in the breeding seasons of 2017 and 2018 immediately after the Blob dissipated. These were the same years that atypical feeding was reported in nearby Nicaragua of the Central America breeding area, associated with another upwelling system (De Weerdt & Ramos 2020). It seems likely that the record-breaking period of prolonged elevated SST of the Blob, which is known to have affected humpback whale prey availability and quality in some North Pacific H-LF areas (Jones et al. 2018, von Biela et al. 2019), led to even more prolific feeding of whales in Banderas Bay in 2017 and 2018. We note that within the first 2 wk of the 2017 breeding season in mainland Mexico, several severely emaciated and/or heavily lice infested whales were documented in the region (Appendix, Fig. A2; N. Ransome unpubl. data). This was a new phenomenon and suggests some whales had not been able to feed sufficiently during the prior summer feeding season in H-LF areas.

Our study reports that the migratory connections of whales documented feeding in Banderas Bay differed significantly from the expected migratory destinations of the breeding population (Urbán et al. 2000, Calambokidis et al. 2008) and individuals migrated significantly further. While 75.4% (n = 46) of the non-feeding sample were from the California-Oregon region (which corresponds well with the results of SPLASH, where 72.6% (n = 119) of Banderas Bay whales matched between California and the Washington border with Canada; Calambokidis et al. 2008), over half of feeding whales in the bay resighted in H-LF areas (50.8%, n = 31) were from the more northern foraging areas of Russia, Alaska, and Northern BC. Our results provide further support to our speculation that the now persistent feeding in Banderas Bay may be related to availability and/or quality of prey in some H-LF foraging areas, with a notably distinct subset of the population being the whales predominantly identified feeding. The Blob has been widely reported to have had the most severe ramifications on humpback whales that feed in the higher H-LF areas of the North Pacific (Cartwright et al. 2019, Neilson & Gabriele 2019, Wray & Keen 2020, Frankel et al. 2022, Gabriele et al. 2022). Therefore, these results align with those of previous studies, and suggest that prey scarcity was potentially further exacerbated in these areas as a result of marine heatwaves.

The occurrence of mother and calf humpback whales involved in feeding events were noticeably absent from reports in this study. Due to energy demands of gestation and lactation (Lockyer 1984), it might be expected that lactating females would exploit prey resources when available. Mothers with calves are regularly part of feeding groups on the migratory pathways off both east Australia and South Africa (Gales et al. 2009, Barendse et al. 2010) and opportunistic feeding of a lactating female has been reported in the Central America breeding area of Costa Rica (Rasmussen et al. 2012). However, most of the feeding whale reports in Banderas Bay between 2013 and 2020 were of whales described to be of a small size and visually estimated to be juveniles. A current limitation of this aspect of the data is that we cannot be certain of the age class of these whales, given no measurements were taken and no feeding whales were of known age. Nevertheless, approximately half of feeding whales photo-identified were not previously registered on Happywhale (n = 90, 44.8%) and those that were had significantly shorter sighting histories (mean = 2.3 yr) than non-feeding whales. This provides some support for a conclusion that these were likely younger, juvenile whales that had not reached physical maturity.

In other areas of the world, sporadic sightings of whales historically documented feeding in breeding areas have most commonly involved individuals visually estimated to be juveniles (Gendron & Urbán 1993, De Sá Alves et al. 2009, Bortolotto et al. 2016). Smaller and younger animals likely face greater competition from larger, more experienced whales in times of low prey quality/abundance (Weinrich et al. 1997), need extra energy for growth (Kyriazakis & Emmans 1992), have lower capacities to store blubber based on body size constraints (Iverson 2002), and have reduced efficiency in thermal regulation and energy conservation (Castellini 2002, Iverson 2002). Extended periods of fasting may therefore be particularly challenging for juvenile humpback whales, and during times of low resource abundance in H-LF areas they will likely be the first age class to seek out opportunistic resources for survival in other regions (Gabriele et al. 2022). The use of drone videogrammetry in marine mammal research (Christiansen et al. 2016) has grown in popularity since much of this data was collected. To continue to investigate the feeding phenomenon of humpback whales in Banderas Bay more efficiently, it is essential that body length measurements are taken of feeding whales via drone videogrammetry to confirm their age class.

We conclude that these persistent low-latitude feeding episodes were likely related to multiple factors on the terminal ends of humpback whale seasonal migrations, and the magnitude of feeding was linked to climate change-induced marine heatwaves which occurred during the study period. With evidence of individually photo-identified whales (n = 18) returning to feed over several seasons, we have shown that the area once considered used only for breeding may now be utilized regularly for feeding by a subset of the population. This suggests a persistent change in migratory behaviour, the first of its kind reported in a breeding area. Our analyses enable predictions of humpback whale feeding occurring based on Pacific-wide ENSO conditions and localized SST in Banderas Bay. We hypothesize that fluctuations in H-LF area resource abundance (especially in more northern areas) have intensified intraspecific competition, resulting in opportunistic feeding by predominantly younger whales in Mexico's Banderas Bay in years that ENSO fluctuations lead to lower regional SST and increased productivity of an upwelling. Continued research into this phenomenon should include tagging feeding whales to reveal foraging behaviour, using drone technology and videogrammetry to measure the length of feeding whales (Christiansen et al. 2016), and increased effort to sample and identify prey species.

With ongoing growth of most global humpback whale populations (NOAA 2016), feeding in highly productive areas such as upwelling regions of humpback whale seasonal habitat, independent of latitude, is likely to become more common. Ongoing climate change may lead to permanent changes in annual migrations and habitat use of humpback whale populations (von Hammerstein et al. 2022). Large whale species are especially vulnerable to vessel strike while foraging (Laist et al. 2001), which is a known threat to humpback whales in Banderas Bay and the greater Mexican Pacific (Ransome et al. 2021). High densities of foraging large whales in areas not traditionally recognised as supporting this behaviour may introduce unmanaged spatial conflict with fishing industries and heavy vessel traffic (e.g. shipping lanes, transport, and tourism) and lead to spikes in whale mortality (Berman-Kowalewski et al. 2010). With vessel strike and entanglement recognised as the primary modern threats to recovering large whale populations (Clapham et al. 1999b, Thomas et al. 2016), identifying and understanding changes in foraging behaviour of humpback whales will be an essential consideration for future effective management of populations globally.

Acknowledgements. We thank all collaborators of the FIBB Catalogue from Banderas Bay: Ecotours Vallarta, Vallarta Adventures, Cielo Abierto, Ocean Friendly, Vallarta Natours, Biocean, Alfredo Herrera, CRIP_INP, Whale Watch Vallarta, and the Instituto Tecnológico de Bahía de Banderas. Special thanks to Frank McCann, Liliana González, Marisel González, Carlos Joel Villasenor, Mylene Digeny, Ashley Clarke, and Ricardo Farkas. We also thank all the contributors of Happywhale, especially the following people: Alaska Coastal Marine, Alaska Sea Adventures, CINBR, Glacier Bay National Park, Ingmar Lee, Jeff Jacobsen, Pacific Wildlife Foundation, Wil Holmes-Roy, Adam Ernster, Bree Witteveen, Dale Frink, Erin Falcone, Greg Schorr, Jack Springer, James Moskito, Jodi Frediani, Joshua Meza-Fidalgo, Kate Cummings, Kate Spencer, Laurence Fischer, Leigh Torres, Marilia Olio, Peggy Stapp, Robert Perry, Selena Rhodes Scofield, Tim Huntington, Todd Chandler, Adam Pack, Blue Ocean Whale Watch, Douglas Sandilands, Hurtigruten Expeditions, International Whaling Commission, Lindblad/National Geographic Expeditions, Marine Education & Research Society, NOAA National Marine Mammal Laboratory, OSU Marine Mammal Institute WHET Lab, Pacific Wildlife Foundation, UAF Marine Advisory Program, Janice Straley, University of Alaska Southeast, Vincent Shay, Craig Hayslip, Chris Gabriele, Janet L Neilson, Tasli Shaw, and Jeff Moore. We also thank the reviewers and associate editor for their constructive comments, suggestions and careful edits, as well as Gloria Harvey for help with final review. Funding was awarded by the Cetacean Society International (CSI) to N.R. for some of the field work in Mexico. Additionally, the planning, research, and completion of this paper was supported by the Post-graduate International Scholarship of Murdoch University, Perth, Western Australia granted to N.R. Some independent research from Sayulita was conducted under SEMARNAT research permission SGPA/DHVS/9375/19.

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Appendix

Table A1. Humpback whales resighted feeding in Banderas Bay in different years between 2013 and 2020 (n = 18). *whales seen feeding with the same conspecifics in multiple years. In **bold** are dates and ID codes of whales seen feeding together in multiple years

Whale ID	2013	2017	2018	2020	Seen with same whale in 2 seasons?
4	12-Mar	26-Feb			No
9	12-Mar		15-Mar		No
16		23-Feb, 3-Mar	15-Mar		No
22		24-Feb	20-Mar		No
33*		**1-Mar***, 2-Mar, **3-Mar***, 4-Mar	**26-Feb***, 27-Feb		**34, 56**
34*		**1-Mar***, 20-Mar	**26-Feb***, 1-Mar		**33**
55		3-Mar, 04-Mar		02-Mar	No
56*		**3-Mar***	**26-Feb***		**33**
84		06-Mar		2-Mar, 7-Mar	No
95		07-Mar	15-Mar		No
96		08-Mar	8-Feb, 16-Feb		No
116		21-Mar	09-Mar		No
131			26-Feb, 8-Mar	02-Mar	No
161		02-Mar	15-Mar		No
162*		**20-Mar***	**15-Mar***		No
163			15-Mar	02-Mar	**183**
183*		**20-Mar***	**15-Mar***		**162**
205		20-Mar		07-Mar	No

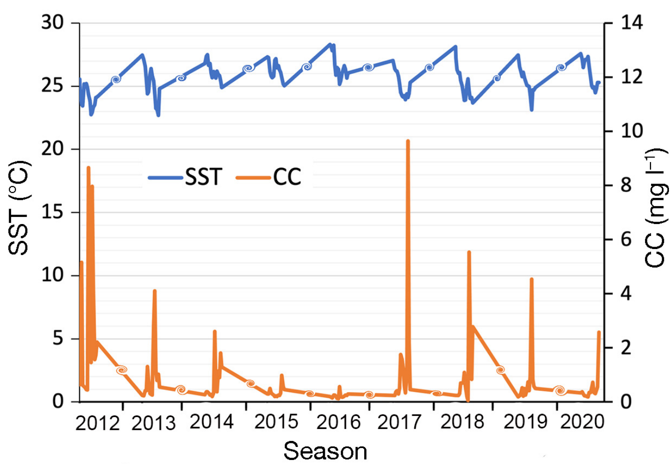

Fig. A1. Sea surface temperature (SST, °C) and chlorophyll concentration (CC, mg l^{-1}) data used in binomial GLM for humpback whale seasons from 2012 to 2020. A noted discrepancy in SST between our study and Frisch-Jordán et al. (2019) for 2 wk in Jan 2012 is likely due to different sources of data (satellite vs. collected *in situ*), and variation in temporal and spatial scale

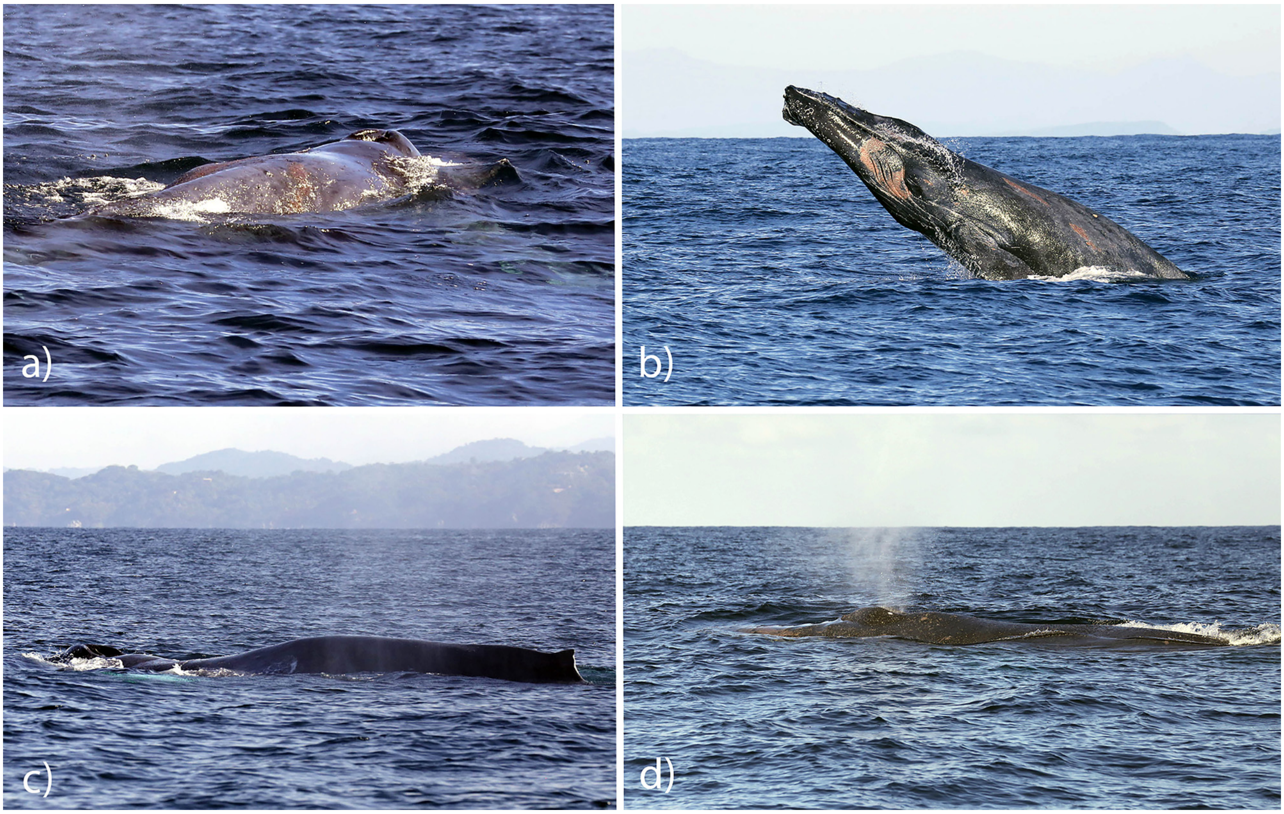

Fig. A2. Images of 4 emaciated and/or parasitized humpback whales (*M. novaeangliae*) seen in the first 3 wk of the 2017 breeding season in mainland Mexico (images: Nicola Ransome)

Editorial responsibility: Peter Corkeron,
Nathan, Queensland, Australia
Reviewed by: C. Gabriele and 2 anonymous referees

Submitted: September 8, 2022
Accepted: October 11, 2023
Proofs received from author(s): January 9, 2024