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Intensive feeding of humpback whales (*Megaptera novaeangliae*) in the breeding ground of Banderas Bay, Mexico

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Humpback whales (*Megaptera novaeangliae*) are found in all major ocean basins and typically undergo seasonal migrations from feeding areas in mid and high latitudes to breeding areas in low latitudes (Mackintosh, 1942). In the North Pacific Ocean, humpback whales feed primarily along the Pacific Rim from California, USA to Kamchatka, Russia and migrate to breeding areas of Central America and Mexico (Eastern North Pacific breeding population), the Hawaiian Archipelago (Central North Pacific breeding population), and the Ryukyu and Ogasawara Islands of Japan, the Philippines, Taiwan and the Marianas Islands (Western North Pacific breeding population)[1].

In the Mexican Pacific waters there are three primary breeding aggregations: 1) Baja California Peninsula (from Cedros Island to Cabo San Lucas on the occidental coast to Loreto inside the Gulf of California); 2) the Revillagigedo Archipelago (Rice, 1974; Urbán and Aguayo, 1987; Steiger *et al.*, 1991); and 3) mainland Mexico's Pacific coast (from Mazatlán, Sinaloa in the north extending as far south as the Mexico-Guatemala border). Banderas Bay and its adjacent waters are therefore a region of dense seasonal humpback whale aggregation in the central Mexican Pacific, which congregates animals migrating from different summer feeding regions of the North Pacific (Medrano *et al.*, 1995; Urbán *et al.*, 2000).

During the summer, humpback whales feed upon different species depending on their geographical area and prey availability, which can vary widely by season and location. North Pacific humpback whales are generalist predators and likely exploit both fish and zooplankton species (Witteveen *et al.*, 2011). Their main prey is krill: *Euphausia pacifica*, *Thysanoessa spinifera* and *T. raschii* (Nemoto, 1957); and small fish schools: *Clupea harengus* (Nemoto, 1957; Rice, 1963; Krieger and Wing, 1984), *Engraulis mordax*, *Mallotous villosus*, *Theragra chalcogramma*, *Pleurogrammus monopterygius*, *Ammodytes hexapterus*, *Gadus microcephalus, Eleginus gracillis* (Nemoto, 1957; Rice, 1963; Witteveen *et al.*, 2008), *Sardinops sagax* (Clapham *et al.*, 1997), *Thaleichthys pacificus, Trichodon trichodon, Hypomesus pretoius* (Witteveen *et al.*, 2008) and *Stenobrachius leucopsarus*[2] (Neilson *et al.*, 2015). Humpback whale feeding behavior is extremely rare in low-latitude waters where whales typically fast for extended periods (Mackintosh, 1942; Chittleborough, 1965). Occasional winter feeding has been reported from a few breeding areas worldwide, including the Dominican Republic (Whitehead, 1981; Baraff *et al.*, 1991), Hawaii[3], Brazil (De Sá Alves *et al.,* 2009; Danilewicz

[1]Calambokidis, J., Falcone, E.A., Quinn, T.J., Burdin, A.M., Clapham, P.J., Ford, J.K.B., Gabriele, C.M., LeDuc, R., Mattila, D., Rojas-Bracho, L., Straley, J.M., Taylor, B.L., Urbán- R., J., Weller, D., Witteveen, B.H., Wynne, K., Yamaguchi, M., Bendlin, A., Camacho, D., Flynn, K., Havron, A., Huggins, J. and Maloney, N. (2008) SPLASH: Structure of Populations, Levels of Abundance and Status of Humpback Whales in the North Pacific. U.S. Dept of Commerce, Western Administrative Center, Seattle, Washington. *Final Report for Contract AB133F-03-RP-0078.*

[2]Neilson, J.L., Gabriele, C.M. and Vanselow, P.B.S. (2015) Humpback whale monitoring in Glacier Bay and adjacent waters 2014. Annual Progress Report. *Natural Resource Report NPS/GLBA/NRR-2015/949.* US Department of the Interior, National Park Service. Fort Collins, Colorado, USA.

[3]Salden, D.R. (1989) An observation of apparent feeding by a sub-adult humpback whale off Maui, Hawaii. Page 58 *in* Abstracts, *VIII Biennial Conference on the Biology of Marine Mammals*, 7–11 December 1989, Pacific Grove, CA, USA

Table 1. Reports of humpback whales feeding in their breeding grounds.

Year of feeding	Location	# of whales	Food source	Authors
1980	Dominican Republic	1 defecating	Unknown	Whitehead, 1981
1989	Dominican Republic	1 juvenile	Unknown	Baraff *et al.* 1991
1989	Hawaii	1 juvenile	Unknown	Salden, 1989
1989	South of Gulf of California, Mexico	1 adult	*Nyctiphanes simplex*	Gendrón and Urbán, 1993
1988-1991	Baja California Sur, Mexico	3 adults defecating	Unknown	Gendron and Urbán, 1993
2002	Brazil	1 juvenile carcass	*Acetes americanus*	Danilewicz *et al.*, 2009
2003	Costa Rica	1 adult	Unknown	Rasmussen *et al.*, 2012
2005	Brazil	2 juveniles	Unknown	De Sá Alves *et al.*, 2009
2012	Oaxaca, Mexico	1 juvenile	Clupeidae	Villegas-Zurita and Castillejos-Moguel, 2013
2014	Brazil	1 juvenile	*Peisos petrunkevitchi*	Bartolotto *et al.*, 2016
2017 and 2018	Nicaragua	1 to 20 adults	Unknown	Weerdt and Ramos, 2019

et al., 2009; Bortolotto *et al.*, 2016), Costa Rica (Rasmussen *et al.*, 2012) and Nicaragua (Weerdt and Ramos, 2019). Opportunistic feeding observations in the winter/breeding season of Mexican waters have also been reported in the Gulf of California (Urbán and Aguayo, 1987; Gendron and Urbán, 1993) and in Oaxaca (Villegas-Zurita and Castillejos-Moguel, 2013) (Table 1).

Here we report on an intensive feeding episode of humpback whales that occurred in the boreal winter months of 2011/2012 in Banderas Bay, a mainland Mexico breeding area. Between 19 December 2011 and 6 March 2012 over a 79-day period, humpback whales were documented feeding on 26 different occasions. Feeding activity was observed intensively and extensively for much of this period, with some feeding aggregations involving up to an estimated 50 individual whales. These are the first confirmed reports of feeding of humpback whales from Banderas Bay, which has been the focus of whale research since 1980 and a major whale watching industry site since the late 1990s.

Banderas Bay is located between 20º15'N and 20º47'N and 105º15'W and 105º42'W in the Mexican mainland Pacific coast with outer limits defined by Punta Mita, Nayarit in the north and Cabo Corrientes, Jalisco in the south. It is an open bay with a maximum width north to south of 31.5 km and east to west of 38.9 km (Figure 1). The sighting data in this report was collected on three-hour whale watching trips which departed between 08:00h and 17:00h daily. These vessel trips were conducted from 8 December 2011 until 23 March 2012, the legally defined period that commercial whale watching tours are permitted in the area by the Mexican Wildlife Ministry (SEMARNAT). This annual research has been ongoing in Banderas Bay since 1996 and is

Figure 1. Study area, Banderas Bay, Mexico.

coordinated by the non-governmental organization Ecología y Conservación de Ballenas, A.C. (ECOBAC). Vessels departed from Marina Vallarta and/or Marina Nuevo Vallarta randomly in search of whales. Additionally, on several occasions when a radio report of whales feeding was received, boats departed explicitly with the intention of locating and collecting data on feeding events. Date, geographic location, sighting start and end time, number of whales in the group, behavior and other species associated were recorded for every sighting. Whenever possible, fluke identification photographs were taken.

Humpback whales were recorded feeding on 26 occasions on 20 different days, over a 79-day period, between 19 December 2011 and 6 March 2012 (Table 2). Feeding observations occurred throughout daylight hours, with approximately half of the observations of feeding made before 12:00h (46.16%, 12/26 sightings) and approximately half of the observations after 12:00h (53.84% 14/26 sightings), with no obvious diurnal pattern. It is unknown if the humpback

Table 2. Humpback whale feeding events observed in Banderas Bay, Mexico. Feeding activity was confirmed by direct observation of whales feeding or inferred from indirect evidences of feeding. Number of whales represents the numbers of whales directly observed feeding. Other cetaceans *Tt: Tursiops truncatus, Sa: Stenella attenuata* and *Be: Balaenoptera edeni.* Approximate depth calculated from NOAA <http://coastwatch.pfeg.noaa>.

Event number	Date	Time of day	Approx. depth in meters	Number of whales feeding	SST °C	Feeding activity or associated activity	Associated species Sea birds / other cetaceans
1	19 Dec 2011	am	630	2 adults	22.6	Lateral lunge feeding	No / No
2	21 Dec 2011	pm	900	3 adults	23.3	Swimming in circles	No / Be
3	30 Dec 2011	pm	100	4-5 adults	24.5	Lateral lunge feeding	Yes / *Tt*
4	31 Dec 2011	am	840	30-40 adults		Lateral and vertical lunge feeding	Yes / *Sa*, *Be*
5	31 Dec 2011	pm	30	4-6 adults		Lateral lunge feeding	Yes / No
6	31 Dec 2011	pm	180	15 adults		Lateral and vertical lunge feeding	No / *Sa*, *Be*
7	1 Jan 2012	pm	910	4-6 adults		Swimming in circles	Yes / No
8	2 Jan 2012	pm	520	2 adults	26.4	Swimming in circles	No / No
9	3 Jan 2012	am	500	3 adults	25.6	Lateral lunge feeding	Yes / No
10	4 Jan 2012	am	450	2-4 juveniles and adults		Lateral and vertical lunge feeding	Yes / 2 *Be*
11	5 Jan 2012	am	515	3 adults	25.4	Lateral lunge feeding and swimming in circles	No / 3 *Be*
12	5 Jan 2012	pm	530	5-8 adults	25.4	Lateral lunge feeding and swimming in circles	No / *Be*
13	6 Jan 2012	am	490	5-6 adults	25.8	Vertical lunge feeding	Yes / No
14	7 Jan 2012	am	30	5-6 adults		Lateral and vertical lunge feeding	Yes / No
15	8 Jan 2012	pm	140	10-20 adults		Lateral and vertical lunge feeding	Yes / No
16	9 Jan 2012	am	250	3-4 adults		Vertical lunge feeding	Yes / No
17	9 Jan 2012	pm	395	5-6 adults		Vertical lunge feeding	Yes / No
18	12 Jan 2012	pm	≤ 25	20-40 adults	26.3	Lateral and vertical lunge feeding	Yes / No
19	14 Jan 2012	am	30	50 adults		Lateral and vertical lunge feeding	Yes / No
20	15 Jan 2012	pm	300	30 adults		Vertical lunge feeding	No / No
21	7 Feb 2012	pm	1,000	6 adults	24.3	Lateral lunge feeding and swimming in circles	No / No
22	8 Feb 2012	am	1,090	2 juvenile and adult	23.9	Feces	No / No
23	8 Feb 2012	am	1,200	5-9 adults	23.9	Swimming in circles and feces	No / No
24	8 Feb 2012	am	840	1 adult	23.9	Feces	No / No
25	5 Mar 2012	am	90	8-10 adults		Lateral and vertical lunge feeding	Yes / No
26	6 Mar 2012	pm	620	1 adult		Lateral lunge feeding	No / No

Figure 2. Images of humpback whale feeding behavior in Banderas Bay, Mexico. A) Single whale lateral lounge feeding on 31 December 2011; B) Single whale vertical lounge feeding on 4 January 2012; C) Two whales vertical lounge feeding on 12 January 2012. D) Feces trailing behind a diving whale on 8 February 2012.

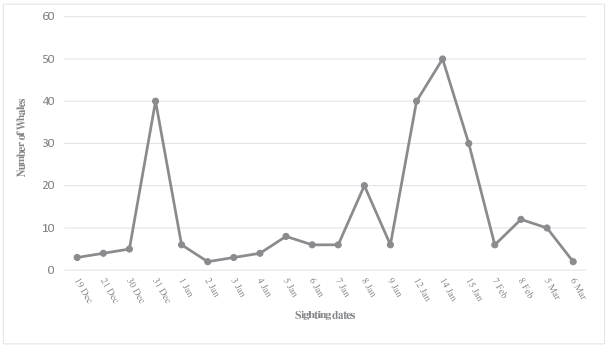

Figure 3. Number of humpback whales feeding in each sighting between December 2011 and March 2012.

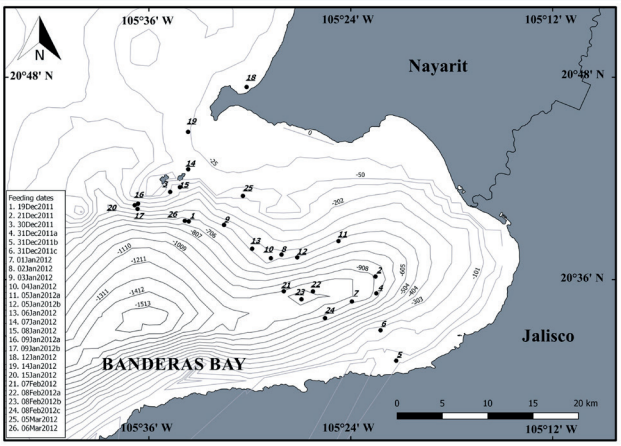

Figure 4. Humpback whales feeding locations within Banderas Bay from December 2011 to March 2012. Bathymetry obtained from <http://coastwatch.pfeg.noaa.gov>

whales continued to feed at night. There is photographic and/or video evidence of 16 of the 20 sightings (Figure 2), and four sightings were anecdotal reports from reliable and experienced witnesses who were privy to other humpback whale feeding sightings during that winter. Humpback whales were observed laterally and vertically lunge feeding at the surface, swimming in circles and/or defecating. In general, feeding involved mostly adults, based on in-situ size estimates of the age-class of individuals involved. In nearly two-thirds of feeding sightings (65.38%, 17/26 sightings) the whales were in small aggregations of two to six whales. However, in around a quarter of feeding sightings (23.07%, 6/26 sightings) from 15 to 50 humpback whales were involved (Figure 3). Multiple groups of whales were seen feeding in different locations at different hours of the day on 31 December 2011, 5 January, 9 January and 8 February 2012. The feeding events were recorded mostly in the central-south area of the Bay (Figure 4), an area where lower densities of humpback whales are typically found. Approximate depth of feeding sightings varied from ≤25 to 1,200 m and sea surface temperatures (SST) registered in situ ranged from 22.6 to 26.3ºC with an average of 24.7ºC.

Figure 5. Pacific anchovies (*Cetengraulis mysticetus*).

Three additional species of cetaceans were registered feeding alongside humpback whales in nine of the feeding events: one to three Bryde's whales (*Balaenoptera edeni*) in six sightings, pantropical spotted dolphins (*Stenella attenuata*) in two sightings and bottlenose dolphins (*Tursiops truncatus*) in one sighting. Moreover, nine species of marine birds were also recorded during 14 sightings: laughing gull (*Larus atricilla*), brown booby (*Sula leucogaster*), brown pelican (*Pelecanus occidentalis*), black-vented shearwater (*Puffinus opisthomelas*), common tern (*Sterna hirundo*), blue-footed booby (*Sula nebouxii*), Heermann's gull (*Larus heermanni*), magnificent frigate (*Fregata magnificens*), and Caspian tern (*Sterna caspia*). On two different occasions when humpback whale feeding activity was observed, samples of the whales' prey species were collected using a fishing net. It was determined in both cases that humpback whales were feeding on Pacific anchovies, *Cetengraulis mysticetus* (Figure 5).

This is the first report of humpback whales feeding intensively, over such a long time (20 days over a 79-day period) and in such large numbers (one to 50 whales) in any breeding ground worldwide, and it is also the first time that they were observed feeding in Banderas Bay, Mexico. Opportunistic feeding observations in the winter/breeding season of Mexican waters have been reported in the Gulf of California (Urbán and Aguayo, 1987; Gendron and Urbán, 1993) and in Oaxaca (Villegas-Zurita and Castillejos-Moguel, 2013). However, the feeding episode that we describe in this report from Banderas Bay, to our knowledge and to date, is the longest intensive feeding episode of humpback whales reported in Mexico or on any breeding ground anywhere in the world. Furthermore, reports of humpback whales feeding in breeding areas are usually of lone individuals, and/or isolated feeding events[1] (Whitehead, 1981; Baraff *et al.*, 1991; De Sá Alves *et al.,* 2009; Danilewicz *et al.*, 2009; Bortolotto *et al.*, 2016; Rasmussen *et al.*, 2012). The one exception are the reports from Nicaragua, which occurred in two successive years, over several weeks (Weerdt and Ramos, 2019). It has already been reported in other regions that climate change-related effects on oceanographic conditions are driving shifts in the behavior and distribution of migratory whales and their prey (Perry *et al.*, 2005, Simmonds and Isaac, 2007). Fleming *et al.* (2015) found that humpback whales trophically respond to ecosystem shifts and, as a result, their foraging behavior is a synoptic indicator of oceanographic and ecological conditions across the California Current System. During the 2011/2012 winter the region was under the effects of a moderate La Niña, (which had begun as a strong La Niña the previous winter). In the boreal winter of 2011/2012 in Banderas Bay, the La Niña effect caused the SST to drop to an average of 24.32°C[4], and by mid-December there was a noticeable abundance of Pacific anchovies, a subtropical non-migratory fish with a coastal pelagic distribution (Avendaño *et al.*, 2014), in the surface waters of the Bay. This prolonged period of colder SST in the bay might have led to an abundance of a humpback whale prey species, which resulted in the opportunistic exploitation of a plentiful and available food resource, and this unprecedented intensive feeding episode of humpback whales in Banderas Bay. The high degree of foraging flexibility shown by humpback whales may be a significant contributor to this species' resilience, as humpback whales have displayed some of the highest rates of population growth seen in any large whale over the last few decades (Barlow and Clapham, 1997; Zerbini *et al.*, 2010).

We conclude that historic and recent reports of humpback whales feeding in Mexican and Central American breeding areas (Urbán and Aguayo, 1987; Gendron and Urbán, 1993; Rasmussen *et al.*, 2012; Villegas-Zurita and Castillejos-Moguel, 2013; Weerdt and Ramos, 2019), combined with our report of an intensive feeding episode over 79 days in Banderas Bay, Mexico, suggest that the Eastern North Pacific humpback whale breeding population will opportunistically feed when prey resources are available to successfully exploit food sources. Humpback whales can provide insight into biological consequences of inter-annual climate fluctuations, fundamental for ecosystem predictions related to global climate change (Fleming *et al.*, 2015). With the Mexican humpback whale population now classified as "Threatened" and the Central American population as "Endangered"[5], it is essential that this phenomenon of regional feeding be investigated, to aid in successful population management and to better understand global consequences of climate change.

[4]UCAR (2019) NOAA NCEI *Extended Reconstructed Seas Surface Temperature.* Available on line <https://rda.ucar.edu/datasets/ds277.9/> Consulted on 9 August 2019.

[5]NOAA (2016) *Endangered and Threatened Species; Identification of 14 distinct population segments of the Humpback Whale* (Megaptera novaeangliae) *and revision of Species-wide listing*. Federal Register Government, USA. Available on line <https://www.federalregister.gov/documents/2016/09/08/2016-21276/endangered-and-threatened-species-identification-of-14-distinct-population-segments-of-the-humpback> Consulted on 19 August 2019.

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