



# Humpback whale feeding behavior and defecation observed on the Hawaiian breeding grounds

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The traditional paradigm of humpback whale (*Megaptera novaeangliae*) behavior involves migration annually between low latitude breeding grounds and high latitude feeding grounds, with limited or no feeding during migration (see Owen et al., 2017), and individuals fasting on the breeding grounds (e.g., Baker et al., 1986; Chittleborough, 1965; Clapham, 2000; Dawbin 1966; Katona & Beard, 1990; cf. Mikhalev, 1997). Humpback whales have been recognized as dietary generalists since the examination of stomach contents during commercial whaling operations (e.g., Clapham et al., 1997). While at high latitudes in the northern hemisphere, humpback whales, known commonly as lunge feeders, typically consume krill (*Euphausia* sp.) and small schooling fish such as capelin (*Mallotus villosus*), herring (*Clupea* sp.), sand-lance (*Ammodytes* sp.), and juvenile salmon (*Oncorhynchus* sp.) (Straley et al., 2018; Szabo, 2015; Witteveen et al., 2008, 2011; Reidy et al., 2022). In the southern hemisphere, researchers have historically maintained that humpback whales rely largely on Antarctic krill (*Euphausia superba*; Groß et al., 2020). However, recent data employing stable isotope techniques have revealed that like the northern hemisphere humpbacks, they too are generalists (Bury et al., 2024), exploiting small schooling fish such as jack mackerel (*Trachurus declivis*), pilchards (*Sardinops neopilchardus*), and redbait (*Emmelichthys nitidus*) along their migration route (Owen et al., 2017). Shifts in the dominant prey source in response to location, variations in ocean temperatures and ecosystem conditions reinforces this dietary flexibility (Fleming et al., 2016). Humpback whales and other baleen whales are considered capital breeders, and during migration and breeding, their metabolic needs are thought to be met by breakdown of adipose tissue, resulting in a loss of body mass while migrating thousands of kilometers and engaging in breeding behaviors (Christiansen et al., 2016).

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While most humpback whales, including all age classes and reproductive conditions, do migrate annually between feeding and breeding grounds (e.g., Chittleborough, 1965; Craig et al., 2003; Straley et al., 1994), there is a growing body of evidence that there may not be strict adherence of foraging behavior to only high-latitude habitats and that there may be more plasticity in these behaviors than previously thought. First, as noted earlier there is evidence of feeding along migratory routes in both hemispheres (Baraff et al., 1991; Owen et al., 2024; Stamation et al., 2007; Swingle et al., 1993). Second, behavior and other evidence of foraging, like defecation and stomach contents of stranded whales, have been observed in winter in tropical waters of the eastern Pacific Ocean off Nicaragua (De Weerdt & Ramos, 2020), Ecuador (Garcia Cegarra et al., 2021), and Mexico (Frisch-Jordan et al., 2019; Gendron & Urban, 1993), as well as in the western Atlantic off the coast of Brazil (Bortolotto et al., 2016; Danilewicz et al., 2009; De Sá Alves et al., 2009) and in the Dominican Republic (Baraff et al., 1991). Thus, although documentation of foraging on low-latitude breeding grounds among migrating whales is limited, opportunistic feeding may not be uncommon (De Sá Alves et al., 2009; Gendron & Urban, 1993).

The principal breeding habitat for humpback whales in the North Pacific is the Hawaiian Islands (Barlow et al., 2011), with large numbers of whales traditionally aggregating particularly in the Maui Nui region that includes the islands of Maui, Moloka'i, Lanai, and Kaho'olawe (Herman & Antinoja, 1977; Mobley et al., 1999). On the Hawaiian breeding ground, this well-studied population exhibits behaviors such as male song, male-male competition, males escorting females, and females nursing their newborn calves (see Herman, 2017 for a review). Foraging behavior by humpback whales in Hawai'i has only rarely been reported anecdotally, including a single apparent feeding lunge by a juvenile whale on a school of Pacific chub mackerel (*Scomber japonicus*) photographed off Maui in 1989 (Salden, 1989, 1990). Here, we report two recent documented instances of humpback whales lunge feeding on schools of fish and on observations of whale defecation in Hawaiian waters during the winter breeding season.

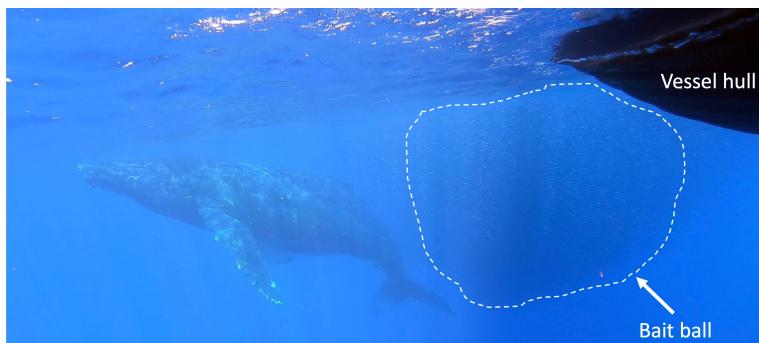
On January 23, 2023, a collaborative research team representing the National Oceanic and Atmospheric Administration's (NOAA) Hawaiian Islands Humpback Whale National Marine Sanctuary, Syracuse University, and the University of Hawai'i at Hilo conducted a mission to deploy instrumented suction-cup data logging tags (CATS, Acousonde & Dtags; see Burgess et al., 1998; Cade et al., 2016; Johnson & Tyack, 2003) on humpback whales off west Maui. A single juvenile-sized (~7–9 m in length) whale was sighted and approached approximately 5.1 km southwest of Olowalu, Maui (20.77°N, 156.65°W). From several hundred meters away, the whale could be seen performing surface lunges, giving the impression of socially engaging with another whale. However, as the research vessel approached closer to attempt to deploy a tag on the whale, the whale performed a distinctive lateral surface feeding lunge <10 m from the bow of the vessel. The whale was observed lunging towards the surface on its right side with its mouth open and its ventral pleats distended, and then closing its mouth once at the surface (Figure 1). A large (~5–8 m diameter) bait ball of darkly colored, slim fish approximately 5–7 cm in length was observed in the location where the whale was feeding (Figure 2). The whale continued to perform feeding lunges after a failed attempt to deploy a tag.

Multiple GoPro video cameras and smartphones were used to film the encounter from the surface and underwater, capturing 13 feeding lunges with an average interval between lunges of  $43.3 \pm 18.3$  s. After about 20 min of feeding, the whale began moving away from the bait ball and was not resighted. We were unable to identify the species of the prey.

Nine days later, on February 1, 2023, the pilot of a commercial helicopter tour operated by GoFly Maui reported an adult-sized whale off the northeast coast of the island of Moloka'i, near Cape Halawa (21.17°N, 156.71°W) apparently lunge-feeding on a bait ball at the surface. A passenger took photographs of the activity using a digital single-lens reflex camera with a zoom lens and documented two lunge-feeding events. In the resulting sequence of images (Figure 3), the whale can be seen approaching a bait ball of fish from below, at which point the fish begin to scatter at the surface. The whale is then seen engulfing a large portion of the bait ball while lunging laterally on its right side. The images show the whale with its mouth open showing baleen and distended ventral pleats. Following the feeding lunge, the whale can be seen expelling air and water out of the sides of its mouth.

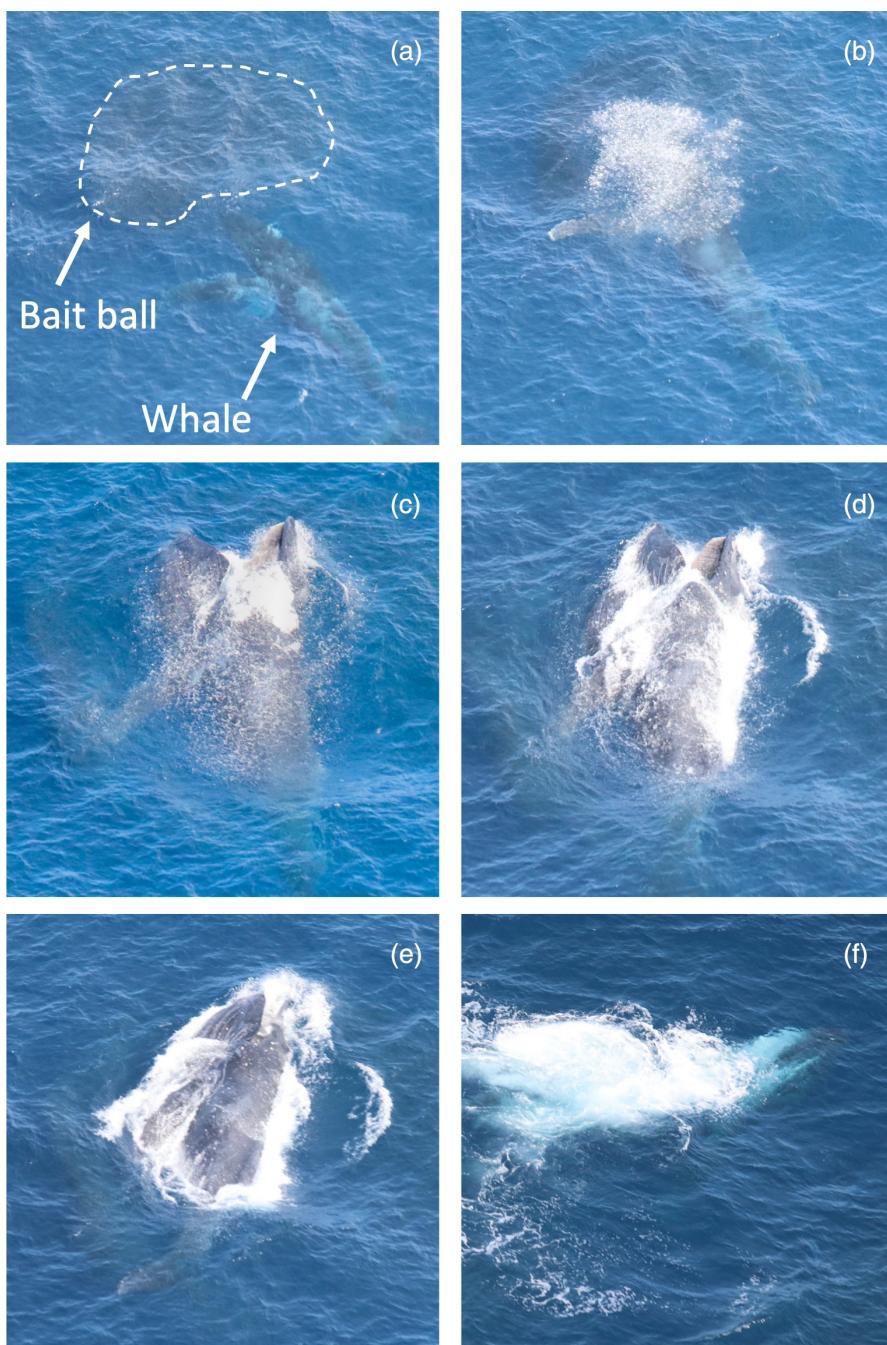


**FIGURE 1** Juvenile humpback whale lunge-feeding on a bait ball off Olowalu, Maui documented from two cameras aboard the NOAA R/V Koholā (Photo: Julia Zeh/Marc Lammers, NOAA permit #19655).



**FIGURE 2** Underwater image of the whale and the bait ball off Olowalu, Maui (Photo: Eden Zang, NOAA permit #19655).

Although documented cases of whales feeding are historically rare on the Hawaiian breeding ground, documentation of whale defecation is more common (Figure 4). Table S1 in the supplementary materials summarizes 27 observed defecation events compiled from the archives of the authors' field notes from 1998 to 2023. Except in rare cases, no collections of fecal materials were made and no analyses of composition were conducted. Defecation events were observed both from the surface and underwater while researchers gathered video and audio data while snorkeling. Defecation was observed during the four principal months (January–April) of the breeding season in both non-competitive and competitive groups. Both male and female humpback whales occupying various behavioral roles were observed defecating. Defecations were never observed from calves, and only two were from juvenile-sized whales; most were from adult-sized whales (estimated visually). Defecations were observed while whales were slowly traveling as well as when they dove or surfaced. When reported, defecations were brown or brownish green in color, likely reflecting the composition of their prey (e.g., fish). None were red or purple as reported often from humpback whales defecating in the feeding grounds, where the dominant prey is often krill (e.g. Reidy et al., 2022). The consistency of humpback whale feces varied from fine matter in the form of a large dark cloud to, slick-like viscous material, to large cube-like fibrous chunks. In one instance, defecation was associated with a pungent scent at the surface.



**FIGURE 3** Sequence of images of a humpback whale feeding off Cape Halawa, Molokai showing (a) the bait ball and the whale approaching, (b) fish scattering at the surface as the whale begins to lunge, (c–e) the whale engulfing portions of the bait ball, and (f) expelling water and air from the sides of the mouth following the lunge (Photo: Erin Ehinger).

The rarity of documented feeding by humpback whales in Hawai'i suggests that it is not a common behavior. However, how uncommon it is, remains an open question. The more frequently observed cases of whale defecation dating back to at least 1998 suggests that more feeding may be occurring in Hawai'i than is witnessed, although it



**FIGURE 4** Juvenile whale observed defecating off Lahaina, Maui while milling upside-down at the surface on February 24, 2018 (Photo: NOAA).

remains unclear whether feces could simply represent byproducts of adipose tissue metabolism or fish consumed during migration (e.g., Owen et al., 2017). On high latitude feeding grounds, humpback whales are known to influence the health of the ecosystem by cycling important nutrients via their feces, which contribute to local biological productivity (Roman & McCarthy, 2010) and earning them the label of “marine ecosystem engineers” (Roman et al., 2014). If the observed events of defecation do represent feeding while in Hawai‘i, it suggests similar ecological processes could be occurring and raises some critical questions, namely: what are whales eating, where and when are they eating, and why are they eating while in Hawai‘i?

To be clear, the answers to these questions are unknown. However, clues exist that could point to answers. Salden (1990) described a juvenile whale lunge-feeding on a school of Pacific chub mackerel. This species is not common in Hawai‘i, so it is possible that it may instead have been misidentified for the more prevalent mackerel scad (*Decapterus macarellus*), known in Hawai‘i as ‘opelu, or bigeye scad (*Selar crumenophthalmus*), known as akule. ‘Opelu and akule are commonly found in coastal Hawaiian waters. Thus, it is possible that whales may target larger aggregations of these fish under certain circumstances. However, unlike in the two most recent feeding cases, only one feeding lunge was observed by Salden (1990), despite having visually tracked the whale prior to and after the event. So, if they occur, feeding attempts on these species are likely rare and opportunistic.

In the more recent case of feeding observed off Olowalu, Maui, the bait ball was composed of small, slim fish estimated to be approximately 5–7 cm in length and, darkly colored dorsally. These were neither ‘opelu nor akule, which measure approximately 20 cm in length and have bluish or silver coloration. In winter of 2023 fishermen reported unusually frequent sightings of schools of Hawaiian anchovy (*Engraulisaustralis*), known locally as nehu (Brian Ishida, personal communication, February 21, 2023), that match the description of the fish observed. Another possibility is that these may have been remnant members of the nocturnally present mesopelagic boundary community (MBC; Reid et al., 1991), which migrates from deep offshore waters during the day to shallow coastal waters at night (Benoit-Bird & Au, 2004; Benoit-Bird et al., 2001). Members of the family Myctophidae, which are a major component of the MBC, can also be approximately 5–7 cm in length, darkly colored dorsally, and slim (Benoit-Bird & Au, 2006). Although no direct evidence of whales feeding on the MBC exists, Henderson et al. (2022) report that humpback whales instrumented with satellite-monitored location-dive tags that transited between Hawaiian Islands conducted long, deep dives to depths of 100–300 m during nighttime hours. They hypothesized that whales could be diving to meet the rising MBC, as has been observed in certain odontocete species (Benoit-Bird & Au, 2003; Copeland et al., 2019). This suggestion has also been made by Derville et al. (2020) for humpback whales showing similar diving behavior in New Caledonia.

The question of where and when whales feed in Hawai'i is of course related to the species they may be consuming. If feeding is restricted to daytime hours, then opportunistic exploitation of nearby schools of *Nehu*, *'opelu*, or *akule* may be the primary circumstance in which feeding takes place. These are likely to be rare, stochastic events not tied to specific locations and probably only occur when a whale is simply in the right place at the right time. On the other hand, if whales target the MBC at night, as speculated by Henderson et al. (2022) and Derville et al. (2020), then this would give them regular opportunities for foraging, since the MBC predictably enters shallow coastal waters in Hawai'i nightly (Benoit-Bird & Au, 2003, 2006). If periodic nocturnal feeding does occur, it could help explain the comparatively more common observations of defecation. Future analyses to determine the identification of prey species present in humpback whale fecal samples collected in the Hawaiian breeding grounds (e.g., Reidy et al., 2022), as well as stable isotope analysis of skin/blubber biopsy samples (e.g., Witteveen et al., 2011) could help reveal what humpback whales are consuming in Hawaiian waters.

Why some whales may choose to spend time feeding while in Hawai'i is difficult to surmise but may be informed by the age class of the whales observed. Two out of the three cases described or cited here involved juvenile whales. Juveniles have limited body resources to metabolize and thus typically have shorter residency times in the Hawaiian breeding grounds and earlier departures for the breeding grounds than adult males and mothers of newly born calves (Craig et al., 2001, 2003). It may be that, unlike mature adults, which are primarily focused on reproductive behaviors, juveniles may need to spend some time supplementing their energy reserves built up over the summer on high latitude feeding grounds to sustain themselves on the breeding grounds and facilitate their migration back to the feeding grounds. Alternatively, they may simply be more inclined to capitalize on a feeding opportunity. Moreover, this might be more necessary during some years than others, depending on how productive the feeding season was during the summer. Thus, climate factors such as marine heat waves and El Nino/Southern Oscillation events, which influence productivity on the summer feeding grounds (Frankel et al., 2022; Gentemann et al., 2017), could help determine the need for whales to supplement energy reserves while in the breeding grounds.

Although there is much more that needs to be understood about humpback whale feeding behavior in the Hawaiian breeding grounds, the fact that it does occur, coupled with observed defecation, suggests that the whales may be interacting with the local marine ecosystem in ways that have not been previously examined. The extent to which humpback whales are influencing the Hawai'i marine ecosystem through feeding and defecation is presently unknown but may be a fruitful area of future research.

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## AUTHOR CONTRIBUTIONS

**Marc O. Lammers:** Conceptualization; data curation; investigation; supervision; writing – original draft. **Julia Zeh:** Conceptualization; investigation; writing – original draft. **Adam A. Pack:** Conceptualization; data curation; writing – original draft. **Ed Lyman:** Conceptualization; data curation. **Eden Zang:** Investigation.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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