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Fish Feeding and Rapid Foraging Behavior Switching by Gray Whales (*Eschrichtius robustus*) in California

Marc A. Webber,[1,2] William Keener,[1] Tim M. Markowitz,[1,3] David Chamberlin,[4] Darrin Allen,[1] Rebekah S. Lane,[1] Josephine M. Slaathaug,[1] Pilar N. Rodriguez,[1] Kathi George,[1] and Julia E. O'Hern[1]

[1]*The Marine Mammal Center, 2000 Bunker Road, Sausalito, CA 94965, USA*
E-mail: webberm@tmmc.org
[2]*California Academy of Sciences, Department of Ornithology and Mammalogy, Golden Gate Park, 55 Music Concourse Drive, San Francisco, CA 94118, USA*
[3]*University of California, Berkeley, Department of Integrative Biology, Berkeley, CA 94720, USA*
[4]*Bay Area Underwater Explorers, PO Box 320673, Los Gatos, CA 95032, USA*

Abstract

Gray whales (*Eschrichtius robustus*) evolved to suction feed on benthic invertebrates and typically do not consume adult fish. Yet, these whales are flexible foragers, occasionally skim feeding on planktonic invertebrates and rarely lunge feeding on fish, the latter according to anecdotal accounts. We documented the unusual phenomenon of multiple gray whales predating dense schools of anchovy over a sustained period (22 days) in June 2022 at Pacifica, California, in the Gulf of the Farallones. Analysis of 11,265 photos and 11 video clips (totaling 4 min 16 s) for behavior and whale identification resulted in a total of 165 foraging events by six identified gray whales. Attribution of foraging behavior to the most active individuals was achieved by matching left pectoral fins, visible during lateralized feeding behavior. Whales rolled onto their right sides in 96% of near-surface side-swimming bouts. Another behavior, first photographed here, was dynamic surface lunge feeding by one gray whale. Five gray whales interspersed fish feeding with benthic suction feeding evidenced by sediment streaming: prey type switching was executed rapidly, in less than 1 minute in several instances, the shortest intervals reported for a baleen whale. Similar results were obtained for foraging behavior switching (continuous side-swimming or intermittent lunging) in pursuit of fish. Four photo-identified Pacifica whales were sighted in San Francisco Bay/Gulf of the Farallones, one of which was also matched to the Pacific Coast Feeding Group. Such local and regional connections warrant efforts to determine whether gray whales use this area as a migratory stopover site or for summer foraging, or both. Our observations confirm gray whale behavioral plasticity and opportunistic exploitation of food resources in mid-latitudes, which may enhance their resilience to climate change.

Key Words: gray whale, *Eschrichtius robustus*, fish, feeding, foraging, foraging behavior, behavior switching, lunge feeding

Introduction

The Pacific Ocean coast near San Francisco, California (United States), is part of the migration route of the Eastern North Pacific stock of gray whales (*Eschrichtius robustus*; Rice & Wolman, 1971; Jefferson et al., 2015). Most of the whales travel 10,000 km from their breeding lagoons in Baja California, Mexico, to their summer feeding grounds in the Bering and Chukchi Seas and are commonly sighted in California in December through May (Allen et al., 2011; Swartz, 2018). A subpopulation (~212 individuals), known as the Pacific Coast Feeding Group (PCFG), spend the summer and fall from far northern California through British Columbia, Canada, between 41° to 52° N (Darling, 1984; Calambokidis et al., 2002b; Harris et al., 2022). Farther south, smaller numbers of lesser-studied summering gray whales have also occurred in California at the Farallon Islands, Pigeon Point, and Point Arena (Rice, 1963; L. Newton, pers. comm., as cited by Rice & Wolman, 1971; Dohl et al., 1983; Sullivan et al., 1983; Mallonée, 1991; Avery & Hawkinson, 1992; Hawkinson, 1992; Pyle & Gilbert, 1996; Jenkinson, 2001; Jones & Ota, 2011; Ingman et al., 2021; Mercer et al., 2022). Recent observations by The Marine Mammal Center (TMMC) in San Francisco Bay indicate gray whales also use this estuarine habitat from February through June (Markowitz et al., 2022).

Eastern North Pacific gray whales recovered from whaling-era exploitation but are subject to boom-bust cycles of abundance (Reamer, 2022; Stewart et al., 2023). They recently suffered a sharp population decline, accompanied by a severe drop in calf production (Eguchi et al., 2022). The stock's current abundance is 14,526, a 46% reduction from the 2015/2016 estimate (Eguchi et al., 2023). A ten-fold increase in the number of dead gray whales stranded on their coastal migration route in 2019 prompted the declaration of a federal Unusual Mortality Event (UME) for the West Coast of the U.S. (Christiansen et al., 2021; National Oceanic & Atmospheric Administration [NOAA] Fisheries, 2022). Necropsies found that several stranded gray whales showed signs of malnutrition, especially on the northbound leg (Christiansen et al., 2021; Raverty et al., in press).

Diet and Feeding Behavior

Gray whales are known to be bottom feeders, typically consuming a wide variety of benthic and epibenthic invertebrates such as amphipods and mysids (Nerini, 1984; Werth, 2007). Gray whales can also feed in the water column on pelagic zooplankton, such as krill, mysids, and spawning squid, and at the surface on crab larvae, krill, and occasionally Pacific herring (*Clupea pallasii*) eggs and larvae (Pike, 1962; Darling et al., 1998; Benson et al., 2002; Dunham & Duffus, 2002; Moore et al., 2022).

Outside their traditional feeding grounds in the Arctic, gray whales may engage in limited foraging in their breeding areas, based on stable isotope analysis (Caraveo-Patiño & Soto, 2005; Gelippi et al., 2022). Feeding during migration is considered less common, although shallow seafloor pits, evidence of benthic feeding, have been detected by side-scan sonar in northern California (Cacchione et al., 1987). In a thorough study conducted in the 1960s, almost all stomachs examined (99%; n = 314 of 316) were empty in gray whales migrating south and north through northern California waters; the two stomachs with food contained crab larvae (Rice & Wolman, 1971). Shore whalers operating in central and northern California in the 1920s caught seven gray whales and reported stomach contents for five: four were empty and one contained the pelagic krill (*Euphausia pacifica*; Howell & Huey, 1930; Clapham et al., 1997). Feeding is well-documented for the PCFG, which forages on invertebrate prey during the summer season well south of Arctic primary feeding grounds (Darling et al., 1998; Calambokidis et al., 2017). These summer-resident whales consume benthic amphipods, swarms of epibenthic mysids, and, less commonly, crab larvae (Newell & Cowles, 2006; Allyn et al., 2024). Biomass density of benthic amphipods in regions where PCFG whales feed are lower than in the Arctic, requiring PCFG whales to consume a more varied diet (Carruthers, 2000).

Gray whale dietary flexibility is facilitated by a range of foraging behaviors. In reviewing its feeding ecology, Nerini (1984) remarked on the species' ability to employ all three main baleen whale filter feeding behaviors: (1) suctioning, (2) skimming, and (3) engulfing. Suctioning is the most common gray whale feeding technique in which the whale rolls onto one side (usually the right) as it suctions sediment from the seafloor and strains out infaunal prey with coarse baleen (Nerini, 1984; Woodward & Winn, 2006). Excess water and sediment expelled from the mouth generate characteristic plumes visible at the surface (Rugh & Fraker, 1981; Nerini, 1984; Moore et al., 2022). Skimming is continuous ram feeding with an open mouth, interrupted by pauses to filter prey-laden water and swallow (Werth & Potvin, 2016; van der Hoop et al., 2019). This feeding strategy, used by right (*Eubalaena* sp.), bowhead (*Balaena mysticetus*), and sei (*Balaenoptera borealis*) whales, is occasionally observed in gray whales feeding on zooplankton at the surface (Newell & Cowles, 2006; Croll et al., 2018; Segre et al., 2021). Another form of continuous ram feeding is side-swimming, performed as the whale feeds while swimming forward on its side just beneath the surface; this posture has been referred to as "sharking" when part of the fluke extends into the air (Torres et al., 2018). Engulfing is intermittent ram feeding, referred to as lunge feeding, and involves acceleration before the mouth is opened to greatly expand the buccal cavity, followed by prey filtration (Goldbogen et al., 2017). It is mainly seen in rorquals (Balaenopteridae) and reported rarely in gray whales (Sund, 1975; Nerini, 1984).

Prior Cases of Fish Feeding

Gray whales generally do not eat adult schooling fish (in contrast to icthyplanktonic eggs and larvae), but necropsy findings of intestinal endoparasites that may require fishes as intermediate hosts suggest such consumption happens occasionally (Rice & Wolman, 1971). Instances of presumed foraging on fish by gray whales over the past 75 y compiled by Nerini (1984) are updated below:

- *Stomach Contents*
    - Local fishermen found "barrels of sardines" in the gut of a gray whale stranded in San Ignacio Lagoon (Mexico) (Walker, 1949; C. Hubbs, pers. comm., as cited by Pike, 1962, p. 831).

- In a sample of 70 gray whales taken by Soviet-era whalers, one had a small amount of Pacific sand lance (*Ammodytes hexapterus*) that may have "entered the stomach accidentally" and *Clupea* sp. was also included in a list of their prey (Zimushko & Lenskaya, 1970, p. 208; also see Klumov, 1963).

- A gray whale stranded near Grays Harbor, Washington (USA), had several gallons of rainbow smelt (*Osmerus mordax*) in the digestive tract (K. Balcomb, pers. comm., as cited by Ray & Schevill, 1974).

- *Historic Field Observations*

  - On rare occasions off San Diego, California, gray whales have been seen criss-crossing through a "dense school of small fish, like anchovies" (Gilmore, 1961, p. 11).

  - During two aerial cetacean censuses in Monterey Bay, California, in 1973, three to four gray whales were seen engulfing small bait fish at the surface (Sund, 1975).

  - During a herring survey in Kuskokwim Bay, Alaska (USA), a gray whale was seen "chasing a ball of herring" (Frost et al., 1982, p. 455).

  - Off Point Mugu, California, gray whales were observed swimming erratically through bait fish (S. Leatherwood, pers. comm., as cited by Nerini, 1984).

  - In San Ignacio Lagoon, gray whales were seen circling and engulfing bait fish (J. Sumich, pers. comm., as cited by Nerini, 1984).

  - Gray whales have been reported to feed on seasonal herring runs at Vancouver Island, British Columbia (Canada) (J. Oliver, pers. comm., as cited by Guerrero, 1989).

  - On a whale-watch trip off Half Moon Bay, California, in the mid-1980s, a gray whale was seen surface lunging on bait fish (P. Jones, pers. comm., 21 September 2023).

The bait fish referred to above were not identified to species, and there are no images of prey taxa or described feeding behaviors for any of the examples listed. A photograph taken off Vancouver Island in 2000 purports to show a gray whale feeding on herring (Pyenson & Lindberg, 2011, Figure 5), but reddish material accumulated at the base of the baleen rack suggests the gray whale was skimming small crustaceans floating at the surface.

Study Objectives

In June 2022, we were alerted to gray whales feeding nearshore on schooling fish at Pacifica, California. Recognizing this as an unusual and ephemeral phenomenon, we sought to achieve the following:

- Photograph the foraging activity and characterize the frequency of foraging bouts and their durations.

- Track the individual gray whales involved using photo-identification.

- Describe foraging behaviors and document changes in tactics.

- Compare images of individual gray whales observed in Pacifica to previously established photo-identification catalogs to determine whether they have been recorded elsewhere in the San Francisco Bay Area or in the PCFG range.

Documenting local gray whale foraging, particularly when it occurs outside the core migration season and established feeding grounds, adds to our knowledge of the species' diet, habitat use, and behavioral ecology.

Methods

Study Area

The city of Pacifica, California, is situated on the San Mateo County coast approximately 17 km south of the entrance to San Francisco Bay. Gray whales were active in June 2022 along the 5-km stretch of coast between Mori Point to Mussel Rock (just north of the border with Daly City) and frequently in the vicinity of the Pacifica Municipal Pier (37° 38.0' N, 122° 29.8' W; Figure 1). The pier extends 345 m from shore where water depth is approximately 10 to 12 m. This area is at the eastern edge of the Gulf of the Farallones, a wide, relatively shallow section of the continental shelf. While the majority of the Gulf is within the Monterey Bay and Greater Farallones National Marine Sanctuaries, Pacifica lies within an exclusion zone outside federal marine sanctuary protections (Batha et al., 2013). The seafloor substrate is composed of sand and silt (coarse and fine-grained sediments) impacted by outflows from San Francisco Bay (San Francisco Public Utilities Commission, 2006).

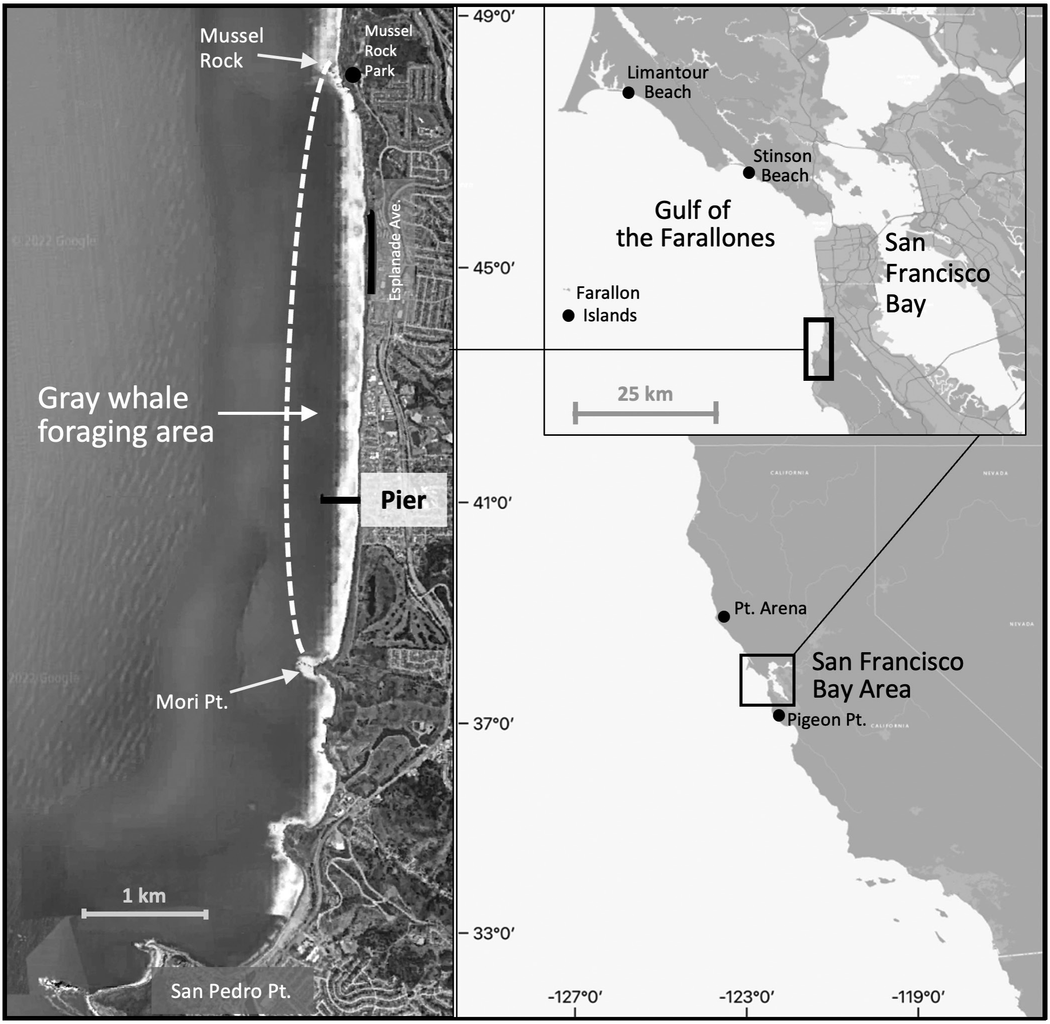

Figure 1. Gray whale (*Eschrichtius robustus*) observation area, June 2022: (left) Pacifica, with main feeding area indicated; and (right) insets showing location of Pacifica in the San Francisco Bay Area and in California. Principal photography platforms were the Pacifica Municipal Pier, Esplanade Avenue, and Mussel Rock Park.

The marine environment is heavily influenced by the California Current Ecosystem (CCE), which features wind-driven upwelling that brings cold, nutrient-rich water to the surface in spring and summer, creating one of the most biologically productive areas in the world, and is an important foraging area for migrating rorquals (Checkley & Barth, 2009; Calambokidis et al., 2015).

Data Collection and Analysis

From 6 to 27 June 2022, the research (co-authors) team conducted nonsystematic visual scans from shore that yielded 38 sessions over 20 d to document gray whale behavior and individual identifications. Session durations varied from 1 s (single images; n = 5 sessions) to 3 h 40 min (mean = 30.9 min), with photographic effort defined by times of first and last images in each session. Duplicate records (n = 9 of 174 behavioral events), possible because multiple researchers took photographs of a gray whale simultaneously from the same location, were excluded from data analysis, prioritizing retention of the best quality images and longest uninterrupted behavioral sequences. High-resolution Nikon and Canon digital SLR cameras equipped with telephoto lenses (≥ 300 mm focal length) were used to capture images and video clips. Platforms were the Pacifica Municipal Pier (10 to 12 m above sea level [asl]) and nearby coastal bluffs, principally along Esplanade Avenue (25 m asl) and at Mussel Rock Park (60 m asl; Figure 1). Observations were conducted in daylight hours (time range: 0710 to 1942 h), though sea fog occasionally hampered visibility. Additional photographs were contributed by vetted citizen scientists, and a member of the general public provided incidental video footage recorded at 30 frames/s on an Apple iPhone 11 Pro. Of the 11,265 still photographs obtained, 86% (n = 9,743) were taken by the research team.

Photographs and video clips were archived in *Adobe Lightroom Classic*. All photographs were analyzed for gray whale activity, as well as for the occurrence of fish, seabirds, and all other marine mammals. Humpback whale (*Megaptera novaeangliae*) activity was collected from daily observations posted on the Pacifica Whalespotting Facebook page (https://www.facebook.com/groups/352947586172817). No prey fish or fecal samples were collected, but photographs were reviewed by an expert at San Francisco State University's Estuary & Ocean Science Center to confirm species identification (W. Kimmerer, pers. comm., 23 July 2023). Gray whale behavioral assessment focused on the description and duration of foraging events, with three feeding tactics defined as the following:

1. *Side-swimming* – Gray whale swimming on its side with its head underwater and a half fluke (i.e., a lobe), pectoral fin, or both fluke and fin visible above the surface (Torres et al., 2018).

2. *Lunging* – The gray whale's head rises above the surface, followed by the expulsion of water from the whale's mouth (Sund, 1975).

3. *Sediment streaming* – Plumes of sediment emanating from the gray whale's mouth or washing along its sides mid-body following a dive, indicating the occurrence of benthic suction feeding (Rugh & Fraker, 1981; Nerini, 1984; Torres et al., 2018; Moore et al., 2022).

Lunges were rated for intensity (high, moderate, low) based on the relative size of the splash generated by the gray whale as its head contacted the water at the conclusion of the lunge. Durations of all behaviors were calculated based on image timestamps reviewed in *Lightroom* (minimum interval displayed = 1 s). Events for which only a single image was taken of a behavior (n = 20) were binned with events of 1 s duration. Side-swimming bouts lasting ≤ 3 s were categorized as short duration and tallied separately from longer duration bouts. A limitation of this study is that series of high frame rate still images may have missed the start of a behavioral sequence as the photographer adjusted the camera to focus on a gray whale that suddenly surfaced. Therefore, calculated durations for some behavioral events may be somewhat shorter than what actually occurred.

Angles of the head of a lunging whale relative to the horizontal sea surface were measured by the *ImageJ* software, Version 1.54 (National Institutes of Health). Gray whale behavioral data were tabulated, and summary tables, charts, and statistics (means, standard deviations) were produced in *Microsoft Excel*. Maps were created with Google Earth satellite imagery and through *QGIS*, Version 3.18 (https://qgis.org).

Photo-Identification

Photographs of both sides, including the dorsal hump, of the gray whales encountered were taken—a standard mark-recapture procedure for this species (Calambokidis et al., 2002a; Newell & Cowles, 2006; Gosho et al., 2011). Identifications were based on natural skin pigmentation patterns and scars, and gray whales that showed unique characteristics were assigned numbers in TMMC's regional gray whale catalog. The best quality photographs were visually compared to others entered into the dataset to detect local resightings. Images of all individuals documented in Pacifica were compared to TMMC's gray whale catalog and the online catalog of known PCFG whales maintained by Cascadia Research Collective (CRC) and other collaborators in the PCFG Consortium (https://pcfgconsortium.org). The limited number of Pacifica whales identified (n = 7) reduced the potential for errors in matching good to high-quality images, and the short duration of the study period, approximately 3 wks, minimized the probability of mark change (Elliser et al., 2022). Pigmentation patterns on the dorsal and ventral surfaces of pectoral fins showed more detail and contrast than flank pigmentation. Pectoral fins (averaging 1.74 m in length in mature animals; Woodward et al., 2006) raised vertically into the air as the whales rolled at the surface provided consistent, unambiguous resighting matches of the three most active foraging whales.

Results

This opportunistic observational study conducted at Pacifica from 6 to 27 June 2022 documented the presence of gray whales on 20 of the 22-d study period. The 19 h 35 min of effort resulted in 11,265 still photographs and 11 video clips (4 min 16 s of footage).

Photo-Identification of Whales

Photo-identification efforts resulted in an observational image set of seven gray whales of unknown sex and age, all estimated as > 10 m in length. Individual whale presence ranged from 1 to 13 d. Behavioral analysis of the photo collection confirmed that six of the seven whales engaged in foraging (Figure 2).

The six gray whales for which foraging was documented appeared to be in fair to good body condition; however, the individual not observed feeding, TMMC-4, was in poor condition. It was visibly emaciated, showing extreme depression of subcutaneous fat in the postcranial (nuchal) area and along the dorsal aspect of its lateral flanks (using body condition assessment methods developed by Bradford et al., 2012). TMMC-4 was seen in the area on a single day, 8 June. The only gray whale observed on 14 June remained unidentified due to low light conditions.

Foraging Behaviors

The gray whales foraged in depths estimated at 3 to 20 m, and from the surf zone to 500 m offshore, but most activity occurred within 100 m from the coast where fish shoals appeared to be concentrated. The whales moved mainly parallel to the shore as they foraged.

Three baleen whale foraging behaviors, or tactics (Torres et al., 2018), were observed: (1) side-swimming, (2) engulfing, and (3) sediment streaming (an indication of benthic suctioning). The 165 foraging events consisted of side-swimming (*n* = 117 bouts); surface lunging, a form of engulfment (*n* = 30 lunges); and sediment streaming (*n* = 18 dives). Foraging activity varied considerably between whales (Figure 3). Three gray whales (TMMC-3, 5, and 6 in Figure 2) accounted for a combined 94% (*n* = 155) of all documented foraging events, and one of these whales (TMMC-3) performed half (52%; *n* = 86) of all observed foraging behaviors.

Side-Swimming—The most common foraging behavior was side-swimming, observed in a total of 117 bouts by six identified gray whales. The whales swam on their sides just below the surface displaying three postural variations: (1) exposure of a pectoral fin only (Figure 4A), (2) exposure of a fluke only (Figure 4B), and (3) exposure of a fluke and pectoral fin simultaneously (Figure 4C). Both a fluke and pectoral fin were visible at the same time in 47% (*n* = 51) of bouts, fluke only in 29% (*n* = 31) of bouts, and pectoral fin only in 24% (*n* = 26) of bouts. Nine whales progressed from showing the fluke only to pectoral fin only, or vice versa. Whales rolled to the right extending left appendages into the air in 96% (*n* = 112) of bouts and rolled to the left in 4% (*n* = 5) of bouts. Side-swimming was performed as the whales continued to swim forward into areas where fish appeared to be concentrated, signaled by increased

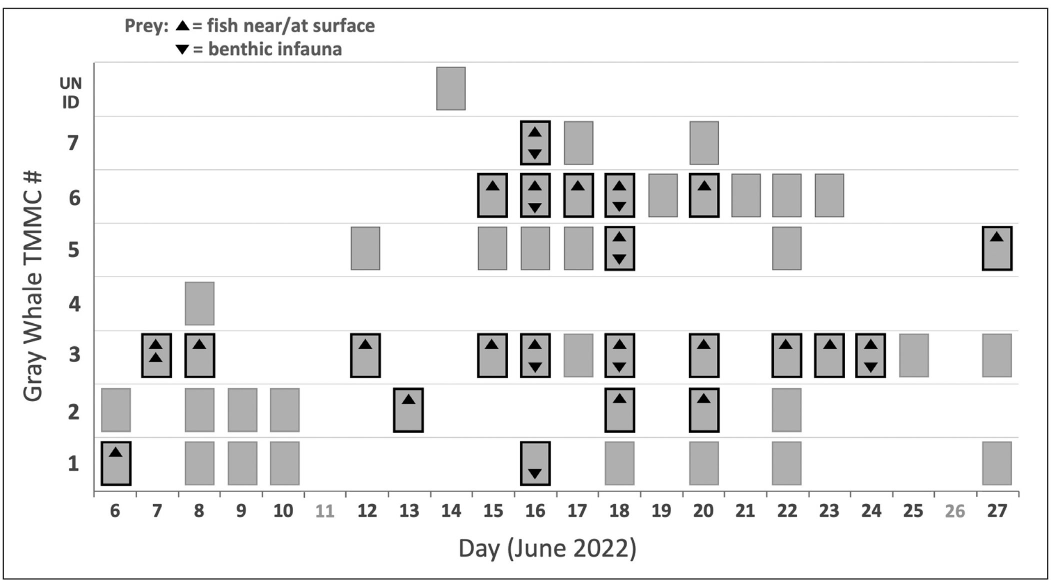

Figure 2. Timeline diagram of gray whale activity at Pacifica, California, June 2022. Daily occurrences of seven identified whales are displayed as boxes by TMMC catalog #, plus one unidentified whale (UN ID). Bold outlines on boxes indicate foraging observed. *Prey types:* upper triangles = fish targeted while side-swimming; lower triangles = sediment streaming indicating foraging on benthic infauna. On 7 June, TMMC-3 foraged on fish by surface lunging and by side-swimming (denoted by two upper triangles in box).

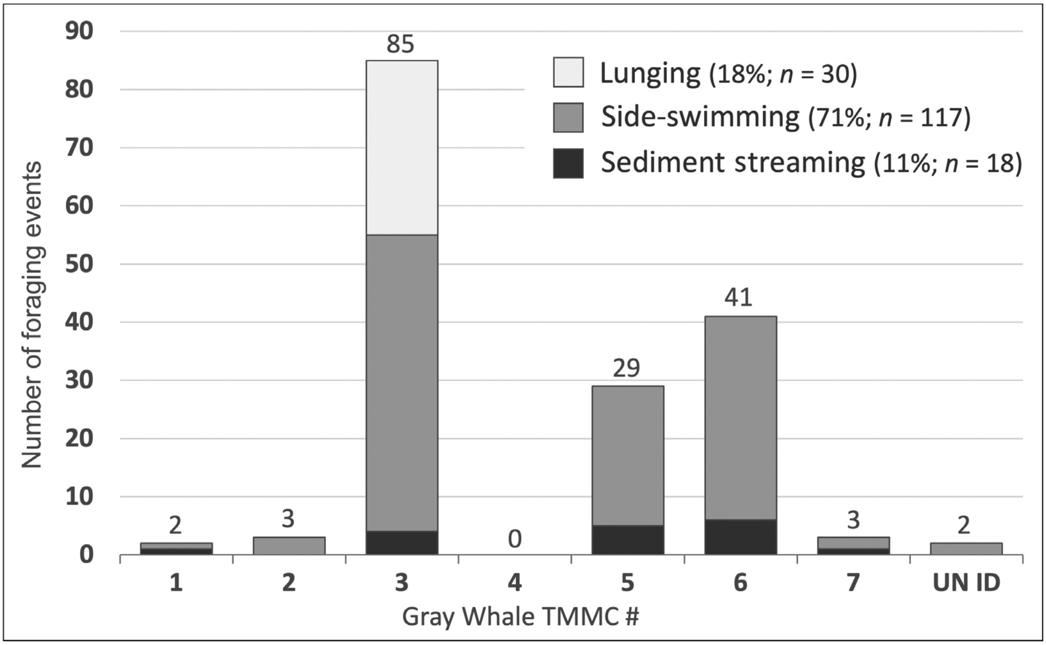

Figure 3. Foraging behavior events (n = 165) of seven identified gray whales at Pacifica, California, June 2022. Events are displayed by individual whale and categorized by behavior type: surface lunging, side-swimming, and sediment streaming indicating a benthic suctioning dive. TMMC-4 was not observed foraging, and the column at far right, UN ID, represents two events in which whales were unidentified. Values above columns are foraging event totals for that whale. TMMC-3, 5, and 6 accounted for 94% (n = 155) of all events.

seabird activity and fish leaping above the surface near the whale in 22% (n = 26) of these events. It was common for pectoral fins to be in motion and flexing as the whales actively swam near the surface and through breaking waves. In some instances, flukes were seen moving from side to side with sufficient force to produce a strong wake. Sediment plumes were not generated by side-swimming activity. The extent of the mouth gape underwater was not visible, and jaw movements or pauses to process prey and flush excess water were not detected. (See Supplemental Video footage; the video for this article is available on the *Aquatic Mammals* website.)

Durations of side-swimming bouts (n = 117) ranged from 1 to 59 s (mean = 9.3 s ± 12.3 SD). Short bouts (n = 55) lasting ≤ 3 s may have been executed partly to aid in turning as gray whales traveled back and forth along the shore. Longer bouts (n = 62) of > 3 s (mean = 16.3 s ± 13.6 SD) constituted 53% of all bouts. Whales engaged in side-swimming usually did so singly, but on a few occasions, two whales in proximity (within two to three body lengths) foraged simultaneously, though not apparently cooperatively. Pair coordinated surfacings (per ethogram in Torres et al., 2018) were infrequent (observed in < 5% of cases).

Lunging—Lunge feeding was executed by a single gray whale (TMMC-3) in 30 instances during a 2 h 13 min session on 7 June 2022 (Figure 5). Bouts of one to 12 consecutive lunges lasted from 1 s to 28 min 37 s before the whale's behavior changed. The lunging behavior consisted of rapid surfacing when the whale propelled itself upwards and forward with its head raised out of the water at a maximum angle of 40° relative to the sea surface before becoming parallel to the surface. While the head was above the surface, water was forcefully squeezed through one or both sides of the mouth, often at the mouth gape, with the jaws in a closed, or nearly closed, position. Of the 20 lunges in which both sides of the mouth were visible, water was ejected on both sides in 60% (n = 12) of the lunges, primarily on the left side in 25% (n = 5) of the lunges, and on the right side in 15% (n = 3) of the lunges. The whale's sudden surfacing caused fish to leap into the air near the whale's head in every lunge; and in a few instances, fish appeared to be expelled from the mouth along with water.

More than half the lunges (53%; n = 16) were rated as moderate intensity, 33% (n = 10) were low, and 13% (n = 4) were high. Distention of the throat and its grooves was visible in high intensity

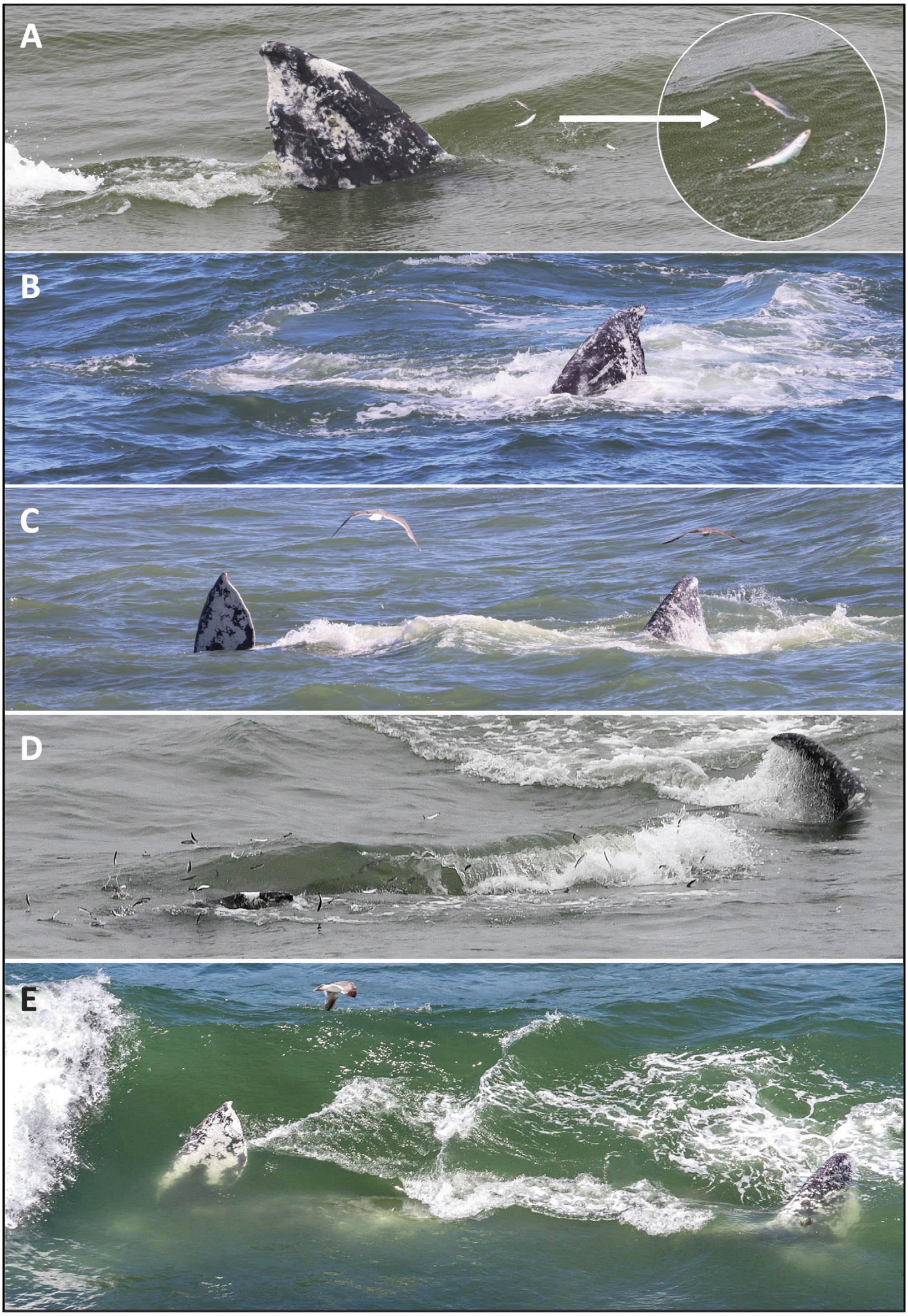

Figure 4. Gray whales side-swimming at Pacifica, California, June 2022: (A) TMMC-3 – pectoral fin only visible, with northern anchovy (inset); (B) TMMC-7 – fluke only visible; (C) TMMC-6 – fluke and pectoral fin visible; (D) TMMC-3 fluking to accelerate into a fish shoal; and (E) TMMC-6 side-swimming along breaking wave. (*Photo credits:* [A] D. Allen, 23 June 2022; [B] & [C] M. A. Webber, 16 June 2022; [D] C. Campo, 12 June 2022; and [E] S. Siebert, 18 June 2022)

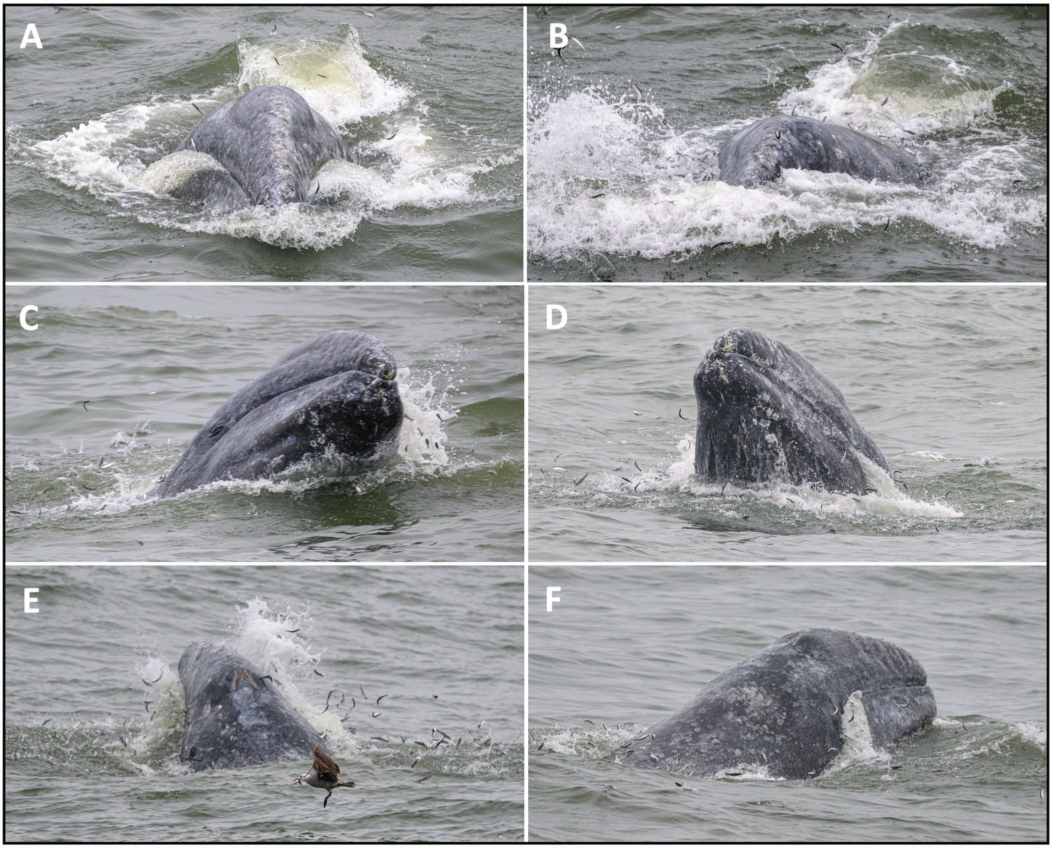

Figure 5. Gray whale TMMC-3 surface lunge feeding on northern anchovy off the Pacifica Municipal Pier, California, 7 June 2022: (A & B) high-intensity lunges with intense splashes; (C & D) high-angle lunges, with distention of throat grooves visible in (D); (E) moderate intensity lunge—note Heermann's gull (*Larus heermanni*) with anchovy in bill; and (F) low-intensity lunge. No spouts were visible during lunges; blowholes are closed in (E) and (F). (Photos provided by D. Chamberlin)

lunges (Figure 5D). It was not possible to determine the extent of the mouth gape as it was presumed to have reached its maximum underwater just prior to surfacing. Of 20 instances in which the blowholes were visible, they were closed during 17 (85%) of these bouts. No spouts were visible during lunges. Between lunges, the gray whale occasionally surfaced normally to breathe and also engaged in side-swimming.

Sediment Streaming—Sediment streaming was observed for five identified gray whales. In 18 instances, plumes of brownish water were apparent as a whale surfaced, evidence of typical gray whale suction feeding on benthic prey (Rugh & Fraker, 1981; Nerini, 1984; Torres et al., 2018; Moore et al., 2022). Muddy sediment-laden water originated near the head after 89% (n = 16) of dives and washed along the sides of the whale in the remaining 11% (n = 2). Of the 16 cases where sediment was seen near the mouth, it was expelled from both sides in 75% (n = 12) and from the left side in 25% (n = 4). No fish were observed during these events (Figure 6).

Prey Fish

Photographs of small fish escaping gray whale feeding bouts permitted identification of the species as northern anchovy (*Engraulis mordax*), the only prey observed (Figure 4A inset).

Foraging Behavior Switching

Five gray whales (TMMC-1, 3, 5, 6, and 7) employed two different feeding tactics depending on prey habitat: (1) side-swimming in the water column, apparently targeting fish, and (2) suctioning bottom sediment, evidenced by sediment streaming. Four gray whales (TMMC-3, 5, 6, and 7) switched prey habitat rapidly, often in less than 1 min. Summary data are provided for all foraging sessions in which these four whales switched

Figure 6. Gray whale TMMC-6 streaming sediment from both sides of the mouth, Pacifica, California, 18 June 2022 (*Photo credit:* S. Siebert)

habitat (Table 1). Observed intervals between switches ranged from 7 to 113 s. Another whale (TMMC-1) was observed side-swimming once on 6 June and streaming sediment once on 16 June.

Even when prey habitat was not switched, foraging tactics could change rapidly. One gray whale (TMMC-3) alternated between side-swimming and lunging for the same fish prey in the water column as it foraged in water 10 to 12 m deep near the end of the Pacifica Municipal Pier. This whale engaged in 12 side-swimming bouts over four events ranging from 32 s to 15 min 41 s. Thus, the whale switched foraging behaviors eight times over the total 2 h 35 min session; and on one occasion, it switched to side-swimming as rapidly as 17 s after executing a lunge. It was the only whale to employ all three feeding tactics observed (i.e., side-swimming, lunge feeding, and benthic suctioning based on sediment streaming), but it never used more than two tactics in a single day (Figure 2).

Co-Foraging Birds and Mammals

Gray whale foraging activity occurred in the context of multiple species targeting fish. Dense anchovy shoals nearshore attracted numerous (~5,000) piscivorous seabirds. In descending order of flock composition, they were western gull (*Larus occidentalis*), Heermann's gull (*Larus heermanni*), California gull (*Larus californicus*), Brandt's cormorant (*Urile pencillatus*), brown pelican (*Pelecanus occidentalis*), Caspian tern (*Hydroprogne caspia*), and common murre (*Uria aalge*). Gulls usually followed whales overhead as the whales' movements in many events drove fish to the surface, and at times into the air. Small numbers of other marine mammals were sighted in the area, including pinnipeds: California sea lion (*Zalophus californianus*) and harbor seal (*Phoca vitulina*); and cetaceans: harbor porpoise (*Phocoena phocoena*), California coastal bottlenose dolphin (*Tursiops truncatus*), and humpback whale. Humpback whales engaged in surface lunge feeding on the fish shoals, usually farther offshore than the area preferred by gray whales, but on a few occasions, they approached gray whales (to within 3 m in one instance). Humpback whales were in the study area on a total of 15 of 22 observation days, with a maximum count of four near the Pacifica Municipal Pier on 25 June, a day when no gray whales were seen.

Post-Study Observations

Four days after the gray whales left the Pacifica area, an additional observation of a gray whale feeding on small schooling fish was made on 1 July 2022 at Limantour Beach in Point Reyes National Seashore, Marin County (Figure 1, upper inset), ~57 km northwest of Pacifica (P. Pyle, pers. comm., 27 February 2023). A solitary whale engaged in side-swimming close to shore (20 m off the beach), and small fish (presumably northern anchovy) were visible in photographs as they

Table 1. Foraging behavior switching by four gray whales (*Eschrichtius robustus*) foraging nonsynchronously at Pacifica, California. Number of consecutive foraging events, with begin/end times and durations, are categorized as side-swimming for fish near the surface or sediment streaming, indicating the suctioning of benthic infauna. Observed interval is the maximum time elapsed between the last behavior and the beginning of the alternate behavior.

June 2022	TMMC #	Begin	End	Duration (s)	Observed interval (s)	Side-swim bout	Sediment stream
16	3	0:00:00	0:00:01	1		1	
	3	0:00:36	0:00:37	1	35		1
	3	0:01:11	0:01:16	5	32	1	
	6	0:00:00	0:06:49	409		5	
	6	0:06:57	0:06:57	1	8		1
	7	0:00:00	0:00:02	2		1	
	7	0:00:15	0:04:15	240	13		2
18	5	0:00:00	0:17:05	1,025		5	
	5	0:17:24	0:17:25	2	19		1
	5	0:19:18	0:19:48	30	113	2	
	5	0:20:37	0:23:44	187	49		2
	5	0:24:02	0:25:50	108	18	2	
	6	0:00:00	0:00:43	43		4	
	6	0:00:52	0:00:52	1	9		1
	6	0:01:34	0:20:10	1,116	42	6	
	6	0:20:20	0:20:20	1	10		1
	6	0:20:27	0:20:57	30	7	1	
	6	0:21:36	0:30:25	529	39		3
	6	0:34:49	1:53:56	4,747	24	5	
24	3	0:00:00	0:21:45	1,305		4	
	3	0:22:46	0:25:26	160	61		2

leaped into the air. Images of this gray whale (right side only) did not match those of the identified gray whales at Pacifica in June 2022.

Photo-Identification Catalog Matches

Comparisons to TMMC's gray whale catalog revealed four of the seven June 2022 Pacifica whales were observed at other sites, or years, in the local area. TMMC-1 and TMMC-2 were seen foraging at Stinson Beach, Marin County, on 3 July 2022. TMMC-5 was first seen on 10 July 2021 at the Farallon Islands, and then in San Francisco Bay in May 2023. TMMC-6 was first sighted on 17 April 2022 in San Francisco Bay, and then on multiple occasions in the bay from February to May 2023, where it was observed streaming sediment (TMMC, unpub. data, 2021-2023; Markowitz et al., 2022). Comparisons to the PCFG online catalog revealed one positive match (TMMC-2 = CRC-840), which had a > 10 y sighting history in the PCFG range from northern California to British Columbia.

Discussion

Our results confirm gray whale foraging opportunism and dietary flexibility. Three filter-feeding tactics were observed: (1) side-swimming, (2) surface lunging, and (3) benthic suctioning evidenced by sediment streaming. Surface skimming with the head out of the water partially exposing baleen in a dorsal up body position, as illustrated by Moore et al. (2022), was not observed in this study. Certain gray whale feeding-related behaviors described from aerial drone footage by Torres et al. (2018) were not recorded, such as headstands, bubble blasts, defecation, or fully submerged side-swimming, the latter perhaps due to our relatively horizontal perspective from shore or pier.

Foraging Behaviors

The gray whales in Pacifica in June 2022 targeted fish in the water column, although fish consumption could not be confirmed, and no fecal samples were collected for prey analysis. Nevertheless, these whales appeared to have the functional ability to pursue fast-moving prey fish, a reasonable inference based on our observations: one whale lunged multiple times in dense shoals of anchovy with fish leaping from the streams of ejected water as the mouth closed; and all six whales spent extended periods of time side-swimming near the surface, causing fish to leap into the air as they made repeated passes through anchovy shoals. In addition, these whales were persistent in their foraging efforts, remaining in the area where the anchovies were massed nearshore for nearly a month. Six days after the anchovies, seabirds, and whales departed Pacifica, we documented two of the same whales farther north off the Marin County coast foraging (side-swimming) in anchovy shoals.

The dynamic surface lunges were similar, to a degree, to lunges performed regularly by feeding rorquals. Gray whales have a reputation as a relatively slow-moving species with a constraint imposed by baleen sieve size (Dunham & Duffus, 2001; Woodward et al., 2006). Yet, despite lacking anatomical adaptations found in rorquals, such as elastic ventral groove blubber, engulfment by gray whales was aided by their two primary throat grooves that allowed a limited expansion of the buccal cavity (see Figure 5D; Johnston & Berta, 2011; Berta et al., 2015; Shadwick et al., 2019; Friedlaender, 2022). These lunging behaviors may have been more dynamic and splashier than the engulfing described by Sund (1975) in which gray whales feeding on bait fish rose vertically above the surface with mouth open and water streaming from the mouth sides, a position held momentarily before the whale "settled back into the water" (p. 265). In our observations, water was not flushed in a predominantly right-sided manner as reported by Wellington & Anderson (1978) regarding a gray whale feeding on mysids at the surface in a kelp forest. Rather, water was mostly expelled from both sides of the mouth.

Lunge feeding was the least common behavior recorded, exhibited by one of the six foraging gray whales at Pacifica, occurring on a single day compared to 14 d for side-swimming. Individual variation in feeding technique may account for the fact that only one of the whales performed lunges (Witteveen et al., 2015; Heithaus et al., 2018). It is also possible that prey density was a factor. Lunge feeding is energetically costly, and threshold prey density has been implicated in foraging technique choices by humpback whales (lunge feeding vs trap feeding; Goldbogen et al., 2011; McMillan et al., 2019). Lunge feeding occurred near the beginning of the 22-d study period when anchovy shoals may have been at their most dense, prior to intensive seabird and marine mammal predation. From this sample, it was not possible to gauge the lunges' energetic efficiency, but closed blowholes observed in most of the lunges suggested the energy expended by the whale did not require breathing at each surfacing.

Side-swimming was the most common foraging behavior observed. Despite the fact that the mouth was not visible underwater, a reasonable inference is that the gray whales were feeding on fish while side-swimming as they swam forward into areas where anchovies were concentrated, with fish seen leaping near the whale in 22% of these bouts. Neither sediment-laden water nor plumes were observed during side-swimming, indicating the whales were foraging higher in the water column and not on or near the substrate (cf. Darling et al., 1998). In Oregon, gray whale side-swimming was only seen in a foraging context (Torres et al., 2018). Postural variations observed (e.g., pectoral fins only visible, flukes only, both appendages partly out of the water) may have been dependent on the depth of target anchovy schools as these behaviors were observed in water depths ranging from 2 to 12 m. Newell & Cowles (2006) and Torres et al. (2018) reported only flukes were observed above the water, though Darling et al. (1998) described gray whales feeding on herring eggs while they were on their sides with a pectoral fin and half fluke above the surface. Although, based on our observations, the whales in Pacifica were targeting fish while side-swimming, it is possible that the whales (and the anchovies) were foraging on epibenthic or pelagic crustaceans (e.g., mysids).

The gray whale's morphological design is suited for precise maneuvering, and sculling of the pectoral fins and fluke may help with positioning and making turns (Woodward et al., 2006). Side-swimming whales exhibited a strong right-sided preference, rolling in that direction in 96% of bouts. This concurs with previous reports of gray whale lateralized feeding, rolling right side down (Newell & Cowles, 2006; Woodward & Winn, 2006), and heavier wear on right-side baleen plates (Kasuya & Rice, 1970).

Duration of side-swimming bouts were all < 1 min, ranging to a maximum of 59 s with nearly half (47%) lasting 1 to 3 s. Such short bouts may have been executed as the gray whale rolled to make a tight turn in shallow water, exposing a raised pectoral fin. Even in longer bouts, the gape was not visible underwater, so it was not possible to ascertain the continuity of filter feeding or how evasively anchovy reacted to the approaching whale (Cade et al., 2020). Jaw openings/closings have been reported during side-swimming viewed aerially (Torres et al., 2018). It is possible that the whales may have used an instinctive feeding behavior, suctioning (negative intraoral pressure), created by strong gular muscles, expandable throat grooves, tongue, and lips, to augment the ram effect as they swam forward through the fish shoal (Ray & Schevill, 1974; Johnston & Berta, 2011; Kienle et al., 2015). Suctioning was proposed as a way for side-swimming gray whales to feed on herring egg masses but was not confirmed (Darling et al., 1998). Combination ram-suction feeding has been found in odontocetes (e.g., belugas [*Delphinapterus leucas*]; Kane & Marshall, 2009).

Northern anchovy can be added to the lengthy list of prey items targeted by gray whales (Nerini, 1984). This short-lived planktivorous schooling fish is common, at times abundant, in the CCE, where they comprise a major part of the coastal forage fish community (Thayer et al., 2017; Fennie et al., 2023). The species occupies coastal pelagic habitat from the surface to 300 m deep, where it is capable of spawning multiple times per year, peaking from February through April (Schwartzkopf et al., 2022). Northern anchovy are strongly influenced by climate variability in the CCE, and favorable habitat is occasionally compressed shoreward (Ralston et al., 2015; Santora et al., 2020). In 2019, as the anchovy population reached its highest level since the 1960s (Thompson et al., 2022), the CCE began to experience a 3-y La Niña (the cool phase of the El Niño-Southern Oscillation climate pattern) when upwelling and colder water preferred by anchovies tend to prevail (Muhling et al., 2020; Thompson et al., 2024). Compared to recent years (2014 to 2019), nearshore Pacifica sea surface temperatures were relatively low during this June 2022 observation period, ranging from 12.8° to 13.59°C (Pacifica State Beach Sea Temperature, 2022, based on Huang et al., 2020). Acoustic-trawl surveys by National Oceanic and Atmospheric Administration (NOAA) Fisheries revealed a large biomass of northern anchovy off the San Mateo coast in summer 2022 (Stierhoff et al., 2023). During that same timeframe, the species' superabundance in the San Francisco Bay Area reached its highest levels in 40 y, with seabirds and marine mammals feeding on schools in San Mateo County in early to mid June before moving up the coast to San Francisco during the last half of June, then farther north to Marin County during the last week of June and first week of July (P. Pyle, pers. comm., 27 February 2023). This activity culminated in news reports of fish "falling from the sky" due to being dropped by seabirds flying inland (Mauhay-Moore, 2022).

To maximize energy gain, gray whales may select prey based on its quantity and quality (caloric content; Darling et al., 1998; Hildebrand et al., 2022). The energy density of northern anchovy (6.6 ± 0.5 kJ g^{-1}) exceeds that of several other potential gray whale prey items (Glaser, 2010; Gallagher et al., 2018). By comparison, zooplankton, such as Dungeness crab (*Cancer magister*) larvae, have a mean value of 4.21 ± 1.27 kJ g^{-1}, the mysid *Neomysis rayii* has a mean value of 2.42 ± 1.06 kJ g^{-1}, and the Arctic benthic amphipod (*Ampelisca macrocephala*), a typical gray whale prey species, has a mean energy density of 2.02 kJ g^{-1} (Hondolero et al., 2012; Hildebrand et al., 2021). Fish shoals in Pacifica during June 2022 may have been dense enough to offer an efficient calorie-rich feeding opportunity (Piatt & Methven, 1992; Feyrer & Duffus, 2015).

Benthic Feeding

Sediment plumes streaming from gray whales were evidence of benthic foraging at Pacifica, but the question arises whether the five whales that engaged in this activity were able to find infauna to consume. Potential benthic food resources in the study area were sampled by the Environmental Protection Agency (EPA) in 2009 after gray whales were observed trailing sediment plumes at Pacifica (Jones & Ota, 2011). Benthic community analysis showed sediments dominated by polychaete worms (density = 1,776/m^2), crustaceans (e.g., cumacean shrimps, amphipods, mysids; 1,227/m^2), and mollusks (e.g., clams, snails; 206/m^2; EPA, 2009). Organisms in this assemblage, at higher densities, were similar to those found in the substrate and in gray whale fecal samples off Humboldt County, California, and Kodiak Island, Alaska, where the whales fed on benthic infauna outside their primary feeding grounds in the Bering and Chukchi Seas (Hawkinson, 1992; Moore et al., 2007; Gosho et al., 2011). Therefore, it is possible that the whales at Pacifica were able to supplement their diet benthically. Given their high caloric values, anchovies would be a preferred food target (Glaser, 2010). This conjecture is supported by the fact that once the fish were depleted or departed, based on the absence of seabird foraging activity, the whales left the area and did not remain to bottom feed.

Foraging Behavior Switching

Results herein show that gray whales can switch from targeting fish in the water column to suctioning the benthos for invertebrates quickly and can readily go back and forth between these behaviors. Gray whales have been known to switch prey, prey habitat, and feeding techniques to take advantage of the short-term availability of food (Nerini, 1984; Dunham & Duffus, 2001; Moore et al., 2022; Allyn et al., 2024). Prey type switching also occurs in other species of baleen whales—for example, humpback, fin (*Balaenoptera physalus*), and sei whales (Jefferson et al., 2015; Witteveen et al., 2015). Switching between planktonic crustaceans and pelagic fish in humpback whales may be driven seasonally by changes in patchy prey availability, particularly in marine ecosystems prone to fluctuate such as the CCE (Fleming et al., 2016; Rockwood et al., 2020; Santora et al., 2020). Apart from foraging variation intra- and inter-seasonally, there is little in the scientific literature on the exact timing of prey type switching by baleen whales. In humpback whales, survey results suggested that small groups of migrants in Australia consumed krill and fish in the same foraging area on consecutive days (Owen et al., 2015). One study asserted that gray whales could switch prey "in the matter of a day" (Nelson et al., 2008, p. 367), referring to investigations of foraging at Vancouver Island where switching from planktonic prey to benthic prey was seen in groups of gray whales from one day to the next as they shifted foraging sites (Duffus, 1996; Dunham & Duffus, 2001). Our observations showed that gray whale foraging tactics can switch very rapidly (< 1 min), which has not been previously reported for baleen whales.

In contrast to some baleen whale species that employ a single feeding strategy, we observed four gray whales that used two tactics in a single day: (1) side-swimming and (2) benthic suctioning. A fifth whale used three: (1) side-swimming, (2) engulfing, and (3) benthic suctioning. Foraging tactic switching in a single day has been observed in humpback whales pursuing sand lance (*Ammodytes* spp.) as the whales switched from surface lunging to side-rolling at the bottom as the depth of fish varied in response to diel changes in ambient light (Friedlaender et al., 2009).

The study of baleen whale foraging behaviors has benefitted from recent advances in biologging tags incorporating 3D movement sensors, with research focused on two families: Balaenopteridae (rorquals) and Balaenidae (right and bowhead whales; Goldbogen et al., 2017; Shadwick et al., 2019). Gray whales (family Eschrichtiidae), as relatively accessible coastal dwellers, are well-studied and their morphology described, yet much remains to be learned regarding their fine-scale feeding biomechanics. This may explain, in part, contrasting views of gray whales as generalist feeders or ecological niche specialists (Johnston & Berta, 2011; Segre et al., 2021). Investigations into the kinematics of the species' multiple modes of foraging and engulfment capacity will add to our understanding of the diversity of baleen whale feeding mechanisms (Johnston & Berta, 2011; Cade et al., 2016).

Connections to San Francisco Bay and PCFG Whales

Typically, gray whales reach their Arctic feeding grounds by June when the PCFG also arrives in the Pacific Northwest (Newell & Cowles, 2006; Swartz et al., 2006; Calambokidis et al., 2017). Yet, gray whales have been observed foraging during summer months in California at the Farallon Islands from 1973 to 2016, and at Pacifica and Point Arena—locations south of the PCFG feeding areas (Pyle & Gilbert, 1996; Jones & Ota, 2011; Ingman et al., 2021; Mercer et al., 2022). Of the seven Pacifica whales, only one had a history of summering along the Pacific Northwest coast, which suggests that most of these individuals are not PCFG members. At the same time, sighting records of four Pacifica whales at the Farallon Islands, Stinson Beach, and in San Francisco Bay suggest local occupancy, warranting efforts to determine whether gray whales use this area as a migratory stopover site or for summer foraging, or both. We recommend future investigations include wider catalog comparisons and studies of foraging behavior, habitat preferences, prey availability, and morphological measurements for body condition assessments and length estimations.

Conservation Issues

The benthic infauna prey preferred by gray whales on their Arctic feeding grounds have been in decline (Grebmeier et al., 2018; Stewart et al., 2023). Warming at high latitudes is predicted to result in more pelagic prey; and gray whales, which show some ability to feed on both prey types, may fare better than trophic specialists (Bluhm & Gradinger, 2008). Our observations, albeit a small sample size over a short time period, add to previous findings that these whales can exploit a wide variety of food resources across a wide latitudinal range, which may enhance their resilience to future climate change (Darling et al., 1998; Moore et al., 2007; Torres et al., 2022). Gray whale behavioral plasticity, demonstrated in an impressive display of facultative switching between multiple feeding tactics at Pacifica, may have ensured the species' survival across the Pleistocene as sea levels and habitat changed in response to glacial advances and retreats (Pyenson & Lindberg, 2011). However, there is a concern that ongoing climate change may occur too fast for gray whales to adapt as they search for sufficient alternate food resources and feeding areas (Torres et al., 2022; Stewart et al., 2023).

Nearshore feeding in a busy maritime area exposes gray whales to human-related threats such as vessel strikes and entanglement in pot/trap fishery gear, sources of potentially lethal injury (Carretta et al., 2020; Ingman et al., 2021). Effective management depends on accurate information about habitat use, phenology, foraging behavior, and diet (Dunham & Duffus, 2001). This is especially crucial when assessing the eastern North Pacific gray whales, which recently experienced abnormally high mortalities (Eguchi et al., 2022, 2023). Monitoring is therefore prudent, with the goal of providing insight into the capacity of a baleen whale species to exploit foraging opportunities and respond to environmental change (Moore et al., 2007; Torres et al., 2022).

Note: The supplemental video for this article is available in the "Supplemental Material" section of the *Aquatic Mammals* website: https://www.aquaticmammalsjournal.org/index.php?option=com_content&view=article&id=10&Itemid=147.

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