ARTICLE

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Cooperative feeding and foraging lateralization by Eden's whales off southern China

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Abstract

We investigated surface feeding behaviors of Eden's whales (*Balaenoptera edeni edeni*) in northern Beibu Gulf, southern China, between April 3, 2018, and April 26, 2021. During 122 days at sea, 1,065 individual feeding events were recorded, and eight feeding behaviors were identified: two nonlunging (tread-water and/or trap-feeding, 7.7%, and a novel behavior we call "pirouette feeding," 15.3%) and six lunging (right lateral lunging, RLL, 10.9%; left lateral lunging, 0.2%; upright lunging, 6.3%, vertical lunging, 18.5%; inverted lunging, 0.3%; cooperative lateral lunging, COL, 40.9%). During COL, 2–8 whales swam clockwise around a fish school and simultaneously performed RLL on surfacing—the first cooperative feeding behavior recorded for a *Balaenoptera* whale. Five lateralized feeding behaviors (entailing either a left or right rotation on the long-body axis) accounted for 65.8% of individual feeding events, with a strong right-side bias (99.7%). Lateralized behavior is prevalent in many vertebrates, including several species of rorquals, and we suggest that the right-biased foraging

lateralization among rorquals specifically allows them to keep their right eye on their prey (i.e., a sensory versus motor lateralization), and that this shared asymmetry among conspecifics may have preadapted Eden's whale for cooperative foraging.

1 | INTRODUCTION

Rorquals (Balaenopteridae) currently comprise eight species of *Balaenoptera* whales, plus the widely divergent humpback whale (*Megaptera novaeangliae*). The defining characteristic of balaenopterids is their massively distensible throat pleats that allow them to gulp in huge volumes of water, which they force back out through their baleen plates to filter out small, shoaling prey, mainly fish and krill (Goldbogen et al., 2017; Pivorunas, 1979; Werth, 2000). Collectively, rorquals are globally distributed, inhabiting a wide range of marine habitats, from oligotrophic tropical oceans to immensely productive polar waters, and from shallow, nearshore habitat to deep, offshore waters. As a result, they are exposed to a wide range of prey types, which has, in turn, given rise to a diverse array of feeding methods (Kot et al., 2014; Pivorunas, 1979).

Among the rorquals, humpback whales exhibit the greatest diversity of described feeding behaviors (Goldbogen et al., 2015), including, and probably not limited to, lunge-feeding (Jurasz & Jurasz, 1979; Watkins & Schevill, 1979), bubble-net feeding (D'Vincent et al., 1985; Hain et al., 1982; Ingebrigtsen, 1929; Jurasz & Jurasz, 1979), bubble-cloud feeding (Hain et al., 1982), bubble-curtain feeding (Acevedo et al., 2011), flick-feeding (Ford, 2014; Jurasz & Jurasz, 1979), circular swimming/thrashing (Hain et al., 1982), lobtail-feeding (Weinrich et al., 1992), bottom-feeding/ rolling and prey flushing (Hain et al., 1995), double-loop feeding and spiraling (Canning et al., 2011; Wiley et al., 2011), subsurface skimming (Acevedo et al., 2011), and trap-feeding (McMillan et al., 2018). The distinctions between these behaviors are sometimes blurred—some tend to be variations on a theme that can grade into each other (e.g., bubble-curtain and bubble-net feeding), and two or more behaviors are sometimes used in combination during the same feeding event (e.g., double-loop behavior with bubble-netting, followed by lunge-feeding; Wiley et al., 2011). Additionally, these behaviors can involve single animals or groups feeding in concert.

It has been suggested that the slow swim speed and over-sized appendages of the humpback give it the maneuverability required to perform these often-complex feeding behaviors (Edel & Winn, 1978; Wiley et al., 2011; Woodward & Winn, 2006). On the other hand, the speedy but less-maneuverable *Balaenoptera* rorquals are limited mainly to lunge feeding (Goldbogen, 2010; Goldbogen et al., 2006). Nevertheless, they do exhibit a diversity of inter- and intraspecific feeding behaviors, which, as in the humpback, are presumably adapted to the characteristics of their prey (e.g., species, density, behavior; Acevedo et al., 2011; Alves et al., 2010; Friedlaender et al., 2009; Hain et al., 1982; Jurasz & Jurasz, 1979; Kot et al., 2014; Watkins & Schevill, 1979). Despite having a broad understanding about how rorquals feed, new foraging behaviors continue to be described (e.g., Acevedo et al., 2011; Goldbogen et al., 2017; Iwata et al., 2017; Izadi, 2018; McMillan et al., 2018; Wiley et al., 2011).

Toothed whales and dolphins, due to their durable social alliances (often involving related individuals) exhibit a remarkable diversity of what is often described as cooperative feeding behavior (e.g., Benoit-Bird & Au, 2009; Engleby & Powell, 2019; Oliveira et al., 2013; Pitman & Durban, 2012; Rossi-Santos & Flores, 2009; Similä & Ugarte, 1993; Würsig, 1986). Baleen whales, on the other hand, are often solitary (Mann & Karnisky, 2017), and even when they do aggregate where prey is abundant, they tend to feed independently (Kot et al., 2014; Tershy

et al., 1993). Among nonrorqual baleen whales cooperative feeding is largely unknown: southern right whales (*Eubalaena australis*) and bowhead whales (*Balaena mysticetus*) sometimes forage in echelon formation (Fish et al., 2013; Würsig & Clark, 1993), and bowheads have also been reported diving and surfacing synchronously, with groups of 3–4 animals lunging "upwards out of the water with their heads together in a manner similar to that of cooperatively feeding humpback whales" (Moore et al., 2010).

Among rorquals, only the humpback is regularly reported to engage in cooperative feeding (e.g., D'Vincent et al., 1985; Jurasz & Jurasz, 1979; Ramp et al., 2010; Sharpe, 2001; Weinrich & Kuhlberg, 1991). Humpback whales feeding on herring (*Clupea harengus*) schools in southeastern Alaska used a uniform vocalization, that was closely associated with the initiation of the cooperative feeding behavior (D'Vincent et al., 1985; Jurasz & Jurasz, 1979; Sharpe, 2001). There has been little or no evidence of cooperative feeding among any of the *Balaenoptera* species other than occasional reports of echelon swimming and synchronous lunging among small groups of fin whales (*B. physalus*) and possibly blue whales (*B. musculus*; Kot et al., 2014; Tershy et al., 1993).

Lateralized behavior, i.e., behavior performed preferentially by one side of the body, is widespread in the animal kingdom (Rogers, 2002), including marine mammals. More specifically, right-biased lateralized behavior is practiced by a wide range of marine mammal taxa (Karenina et al., 2016; MacNeilage, 2014), including odontocete cetaceans (e.g., Hoese, 1971; Karenina et al., 2016; Lewis & Schroeder, 2003; Marino & Stowe, 1997; Silber & Fertl, 1995; Vaughn et al., 2010), bowhead whales (*Balaena mysticetus*; Fish et al., 2013), gray whales (*Eschrichtius robustus*; Woodward & Winn, 2006), pinnipeds (walrus, *Odobenus rosmarus*; Levermann et al., 2003; California sea lion, *Zalophus californianus*; Wells et al., 2006), and manatees (*Trichechus manatus*; Tyler-Julian et al., 2016).

Right-side bias is also common among lunge-feeding rorquals, including all the largest species: blue whale, fin whale, sei whale (*B. borealis*), Bryde's whale (*B. edeni*), and humpback whale (e.g., Canning et al., 2011; Clapham et al., 1995; Kot et al., 2014; Tershy & Wiley, 1992; Wiseman, 2008). The smallest rorqual, the common minke whale (*B. acutorostrata*), exhibited right-side foraging bias only 56.7% of the time in the Gulf of California (Tershy & Wiley, 1992) but 98% of the time in the Gulf of St. Lawrence, Canada (Kot et al., 2014).

Bryde's whale (*B. edeni*) is a medium-sized rorqual that inhabits tropical and warm temperate waters around the world, generally between latitudes 40°N and 40°S (Kato & Perrin, 2018). Currently, two subspecies are recognized: the pantropical Bryde's whale (*B. e. brydei*; maximum length 15.6 m), which occurs mainly in deep, oceanic waters, and the smaller Eden's whale (*B. e. edeni*, 11.5 m), which inhabits shallow, neritic areas of the Indo-West Pacific (Committee on Taxonomy, 2021; Kershaw et al., 2013; Rice, 1998). Genetic evidence, however, strongly supports recognizing these as two separate species (Rosel et al., 2021; Sasaki et al. 2006; Wada et al. 2003). Although various feeding behaviors have been attributed to Bryde's whales (sensu lato), lunge-feeding is by far the most common (e.g., Anderson, 2005; de Mello Neto et al., 2017; Izadi, 2018; Miyazaki & Wada, 1978; Notarbartolo di Sciara, 1983; Penry et al., 2011; Steiner et al., 2008; Tershy et al., 1993). To date, nearly all observations have been of whales feeding at the surface, but instrumented Bryde's whales also are documented to lunge at depth (Alves et al., 2010).

Lunge feeding by rorquals has been subdivided into various categories depending on the body orientation of the feeding whale; these include upright lunge, right and left lateral lunges, vertical lunge, and inverted lunge (see Methods for definitions). In conjunction with various forms of lunge feeding, Bryde's whales employ other prey corralling methods, including a novel head-slapping behavior (Izadi, 2018) and various "bubbling" behaviors (Hain et al., 1982), including bubble-net or -curtain feeding (Kot et al., 2014; Lodi et al., 2015; Wiseman, 2008) and bubble-cloud feeding (Baker & Madon, 2007; Neumann & Orams, 2003; Wiseman, 2008). In addition, other, nonlunge-feeding behaviors have been described. Wiseman (2008) reported two instances of Bryde's whales skim feeding in Hauraki Gulf, New Zealand, where whales on two different days were seen swimming slowly, on their sides, at the surface, with their mouths open, through presumed krill patches (see also Thompson et al., 2002). Iwata et al. (2017) described a novel "tread-water feeding" behavior (see Methods) by Bryde's whales (i.e., Eden's whales) from the Gulf of Thailand. In addition, Bryde's whales from the Gulf of California, Mexico, and in Hauraki Gulf, New Zealand, showed a clear right-side bias when lunge feeding (Tershy & Wiley, 1992; Wiseman, 2008); to date, however, lateralized feeding behavior has not been reported specifically for Eden's whale.

Unless accompanied by a calf, Bryde's-type whales tend to occur mainly as solitary individuals (e.g., Anderson, 2005; Gonçalves et al., 2015; Izadi, 2018; Lodi et al., 2015; Steiner et al., 2008; Tershey et al., 1993), and, although they regularly aggregate in areas where prey is abundant, there are no reports of cooperative feeding that we are aware of. A pair of Bryde's whales tagged and tracked for 14 hr by Alves et al. (2010) stayed together continuously, including when diving and surfacing, and the same pair were seen together over three separate years. Although the whales' movements, including diving, were clearly synchronized during the tracking period, it was unknown if they were cooperatively foraging.

Chen et al. (2019) reported on a feeding aggregation of Bryde's whales near Weizhou Island, northern Beibu Gulf, southern China, which was subsequently genetically identified as Eden's whales (Li et al., 2019). Although Eden's whales occur year-round in Beibu Gulf, their numbers increase near Weizhou Island during January–April (Chen et al., 2019). Herein, we detail the feeding behaviors of Eden's whales in Beibu Gulf, including various types of lunge feeding, tread-water and/or trap-feeding, and a novel "pirouette feeding" method. We also describe "cooperative lateral lunge feeding" by Eden's whales, which is the first report of cooperative feeding by a *Balaenoptera* whale. We also discuss a strong, right-side bias in their foraging behaviors.

2 | METHODS

2.1 | Data collection

We conducted vessel-based surveys for Eden's whales during 122 days between April 3, 2018, and April 26, 2021, in the nearshore waters around Weizhou Island, in northern Beibu Gulf, southern China (Figure 1; for additional
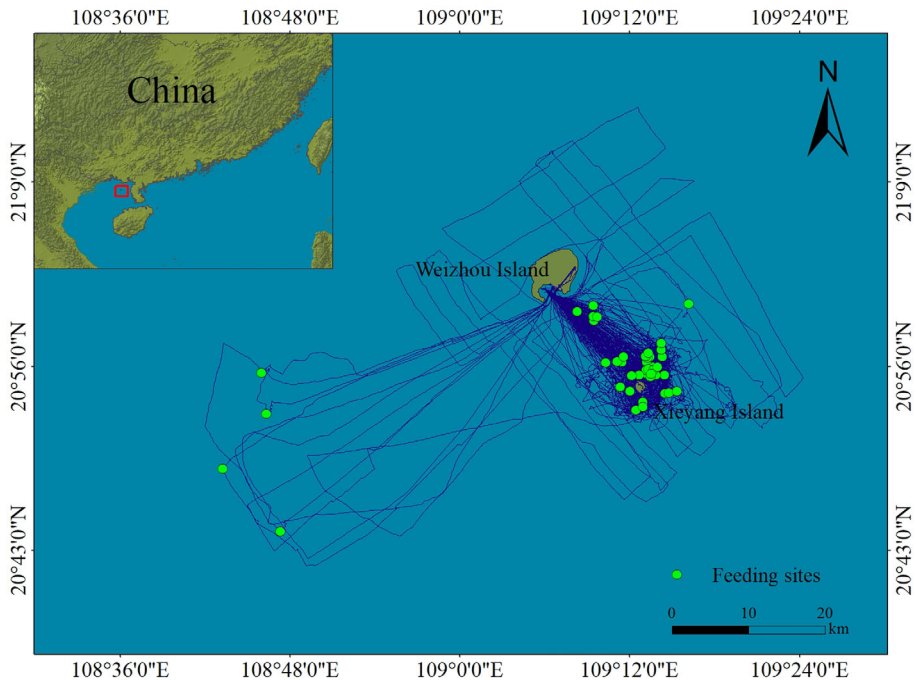

FIGURE 1 Locations of Eden's whales observed feeding off Weizhou Island, northern Beibu Gulf, southern China, between April 3, 2018, and April 26, 2021.

survey details see Chen et al., 2019). Annual sea surface temperature ranged from 17.8°C to 30.7°C and averaged 23.2°C (Huang & Li, 2008). Weather permitting (Beaufort Sea State ≤3; swells ≤1 m), we conducted field work from 8.3–11 m vessels with 150–180 hp outboard engines; our normal survey speed was 13–15 km/hr. Usually, four observers (two to seven) searched for whales with unaided eye. When whales were detected, the vessel reduced speed to 2–9 km/hr to approach the whales, and further observations were made from >100 m to avoid interfering with the whales' behavior. Data recorded included time, location, and estimated group size, along with detailed notes on feeding behaviors.

Whales were photographed using a Canon EOS-1Dx Mark II camera with a 100–400 mm zoom lens. Individual whales were photo-identified using their dorsal fins and compiled into a catalog and feeding behaviors were documented. Video of individuals and feeding events were recorded using a hand-held Sony PXW-FS5 video camera and from unmanned aerial vehicles (UAVs, Dajiang Phantom 3 or 4 Professional).

2.2 | Feeding behavior terminology

We classified surface-feeding behaviors of Eden's whale based on our videos, photographs, and contemporaneous field notes. A whale was recorded as feeding if the animal was at the surface with its mouth open or its ventral pouch distended. We classified individual feeding behaviors based on terminology borrowed from Kot et al. (2014), Iwata et al. (2017), and McMillan et al. (2018), with some modification. Below we define each of the terms we use to describe the various feeding behaviors referred to in the text.

Lunge feeding. The whale accelerates and as it swims into a prey aggregation, it opens its mouth, inflating the throat pouch with prey-laden water; the mouth is closed immediately, and water pressed out through the baleen. Variations on lunge feeding refer to the orientation of the whale relative to the sea surface. These include:

Upright lunge feeding (UPL, Figure 2a). A forward trajectory with the head projecting out of the water at an angle of approximately 45° (10°–75°) relative to the sea surface and little (<30°) or no rotation on the long axis of the body. The mouth is open when the whale breaks the surface, but is rapidly closed before reentering, typically chin-first.

Right lateral lunge feeding (RLL, Figure 2b). A forward trajectory with the head exiting the water at a low angle (<30° in our observations) relative to the sea surface, with an approximately 90° roll to the right. The mouth opens rapidly just before or during surfacing; sometimes there is a counterclockwise roll to the left as the whale rights itself before diving.

Left lateral lunge feeding (LLL, Figure 2c). The same as RLL but to the left side, sometimes with a clockwise roll to right itself before diving.

Vertical lunge feeding (VTL, Figure 2d). The head emerges from the water nearly vertically (76°–90°). The mouth is open as it breaks the surface and often closes rapidly during the ascent. The whale typically reenters falling forward, onto its chin, but sometimes falls backward, or laterally, to either side.

Inverted lunge feeding (INL, Figure 2e). The whale lunges and rolls over at least 180°, with the belly up, at the surface or just underwater.

Cooperative lunge feeding (COL, Figure 3). Two or more whales swim clockwise in a circle around a ball of baitfish; as they surface, they lunge synchronously while rotating toward the right on the body axis—a simultaneous RLL. The whales then close their mouths, right themselves, and swim away from the circle. Sometimes, one of whales in COL operated trap-feeding or tread-water feeding (see definition below).

Nonlunge-feeding behaviors include:

Trap-feeding (TPF, Figure 4). A whale rises slowly and vertically out of the water amid a prey swarm at the surface, exposing its head and closed mouth. While stationary, the lower jaw is opened widely, until it is at, or just below, the waterline. At that time, small fish that are attempting to escape from underwater predators (e.g., fish,
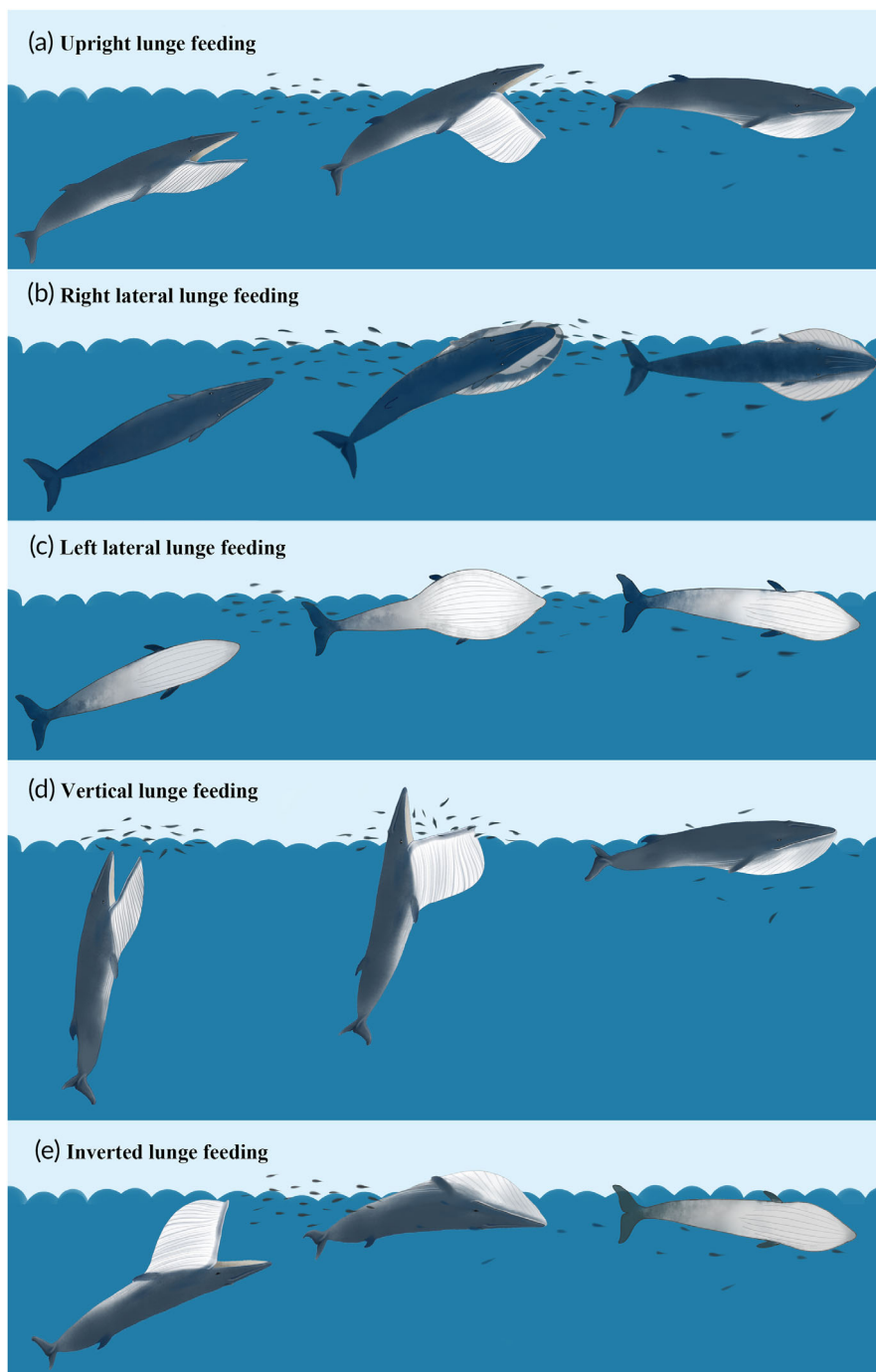
FIGURE 2 Five lunge-feeding behaviors by Eden's whales observed in waters near Weizhou Island, China; see Methods for detailed behavioral descriptions.

seabirds, other whales; see Discussion), jump into the whale's open mouth. After holding this position for "about 20 s" (Greenfelder & Pitman, 2013), the whale closes its mouth and rolls forward, sieving and swallowing the prey underwater. McMillan et al. (2018) described some variation on this behavior for humpbacks, whereby the whale

FIGURE 3 Four Eden's whales cooperatively lunge feeding near Weizhou Island, China. The whales all swim clockwise and right lateral lunge when they surface, with their bellies facing outward.

remained stationary at or just below the surface, apparently not necessarily in a vertical position, with its mouth open. The feeding whale was frequently noted to spin in place and/or use its flippers to direct prey into its mouth.

Tread-water feeding (TWF, Figure 4). The whale rises vertically out of the water, exposing its head and closed mouth. The lower jaw is lowered to 90°, until it is at, or just below, the waterline. The proximal ends of the lower jaws are lowered just below the surface causing water and associated prey to be sucked into the rear of the whale's mouth. After holding this position for an average of 14.5 s (maximum 32 s; Iwata et al., 2017), the whale closes its mouth and rolls forward, sieving and swallowing the prey underwater. The main difference between TPF and TWF is that for TPF, foraging predators make prey available to the feeding whale, and this is reportedly not the case for TWF (see Discussion).

Pirouette feeding/Spin Scoop (PIF). The whale rises vertically out of the water amid a swarm of baitfish, exposing its head and closed mouth. The lower jaw is lowered to 90°, until it is at, or just below, the waterline (Figure 5a). The whale then tilts its head to the right (or, potentially, to the left), lifts the left edge of the lower jaw out of the water and lowers the right edge below the surface; the whale then swings around nearly 180° (potentially 1–3 circles) to the right (or, potentially, left), scooping up fish at the surface. The mouth is closed after about 5 s (Figure 5b), and, with its throat pleats inflated, the whale sinks briefly backward into the water before it rights itself and rolls forward (Figure 5c). After a quick breath, the whale continues forward, with its throat pleats still distended and water being expelled between its lips (Figure 5d).

It should be noted that some of these behaviors grade into others, or the whale can switch from one to another, apparently depending on the nature of the prey.

2.3 | Statistical testing of behavioral frequencies

We used the statistical program R to analyze behavior data. Depending on the context, COL events were considered either a single event, or each participating whale was counted as a separate event. Proportion and count data were calculated to compare the frequencies of each feeding behavior. The Shapiro–Wilk test was used to test normality with the "shapiro.test" package in R. All statistical tests were conducted in RStudio. Chi-square analyses tested for significant differences between observed feeding behaviors and the expectation of equally distributed proportions (null hypothesis). Package "bartlatt.test" was used to determine the assumption of equal variance.

3 | RESULTS

We obtained approximately 77,000 photographs, 58 hr of hand-held video footage, and 72 hr of drone video over 122 separate days. From these, we recorded 1,065 separate feeding events. Surveys occurred during September–April, and the number of feeding events/hour was highest during March–April (2.21 events/hr) (Figure 6).

3.1 | Feeding behaviors

A minimum of eight different feeding behaviors was recorded, including six types of lunging ($n = 820$, 77.0%), pirouette feeding ($n = 163$, 15.3%), and tread-water/trap-feeding ($n = 82$, 7.7%). There were significant differences in percentages for those eight feeding behaviors (Chi-square test, $\chi^2 = 1,032.9$, $df = 7$, $p < .001$).

Lunging behaviors included COL ($n = 435$ lunges by individual whales, 40.9%, during 149 COL events; of these, 18 individuals were TPF or TWF, this number was subtracted in laterization analyses), RLL ($n = 116$ events, 10.9%), UPL ($n = 67$ events, 6.3%), VTL ($n = 197$ events, 18.5%), LLL ($n = 2$ events, 0.2%), and INL ($n = 3$ events, 0.3%).
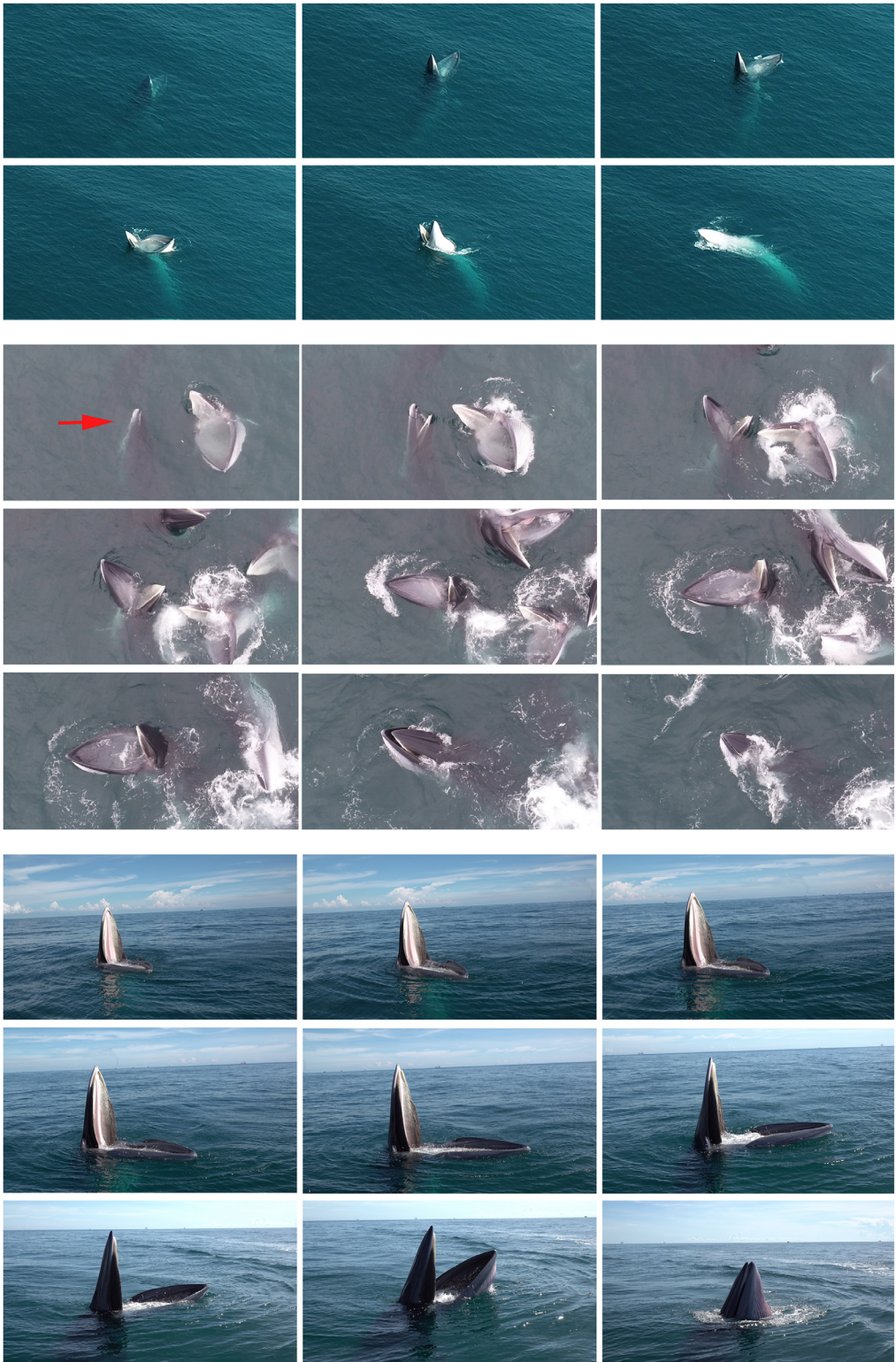
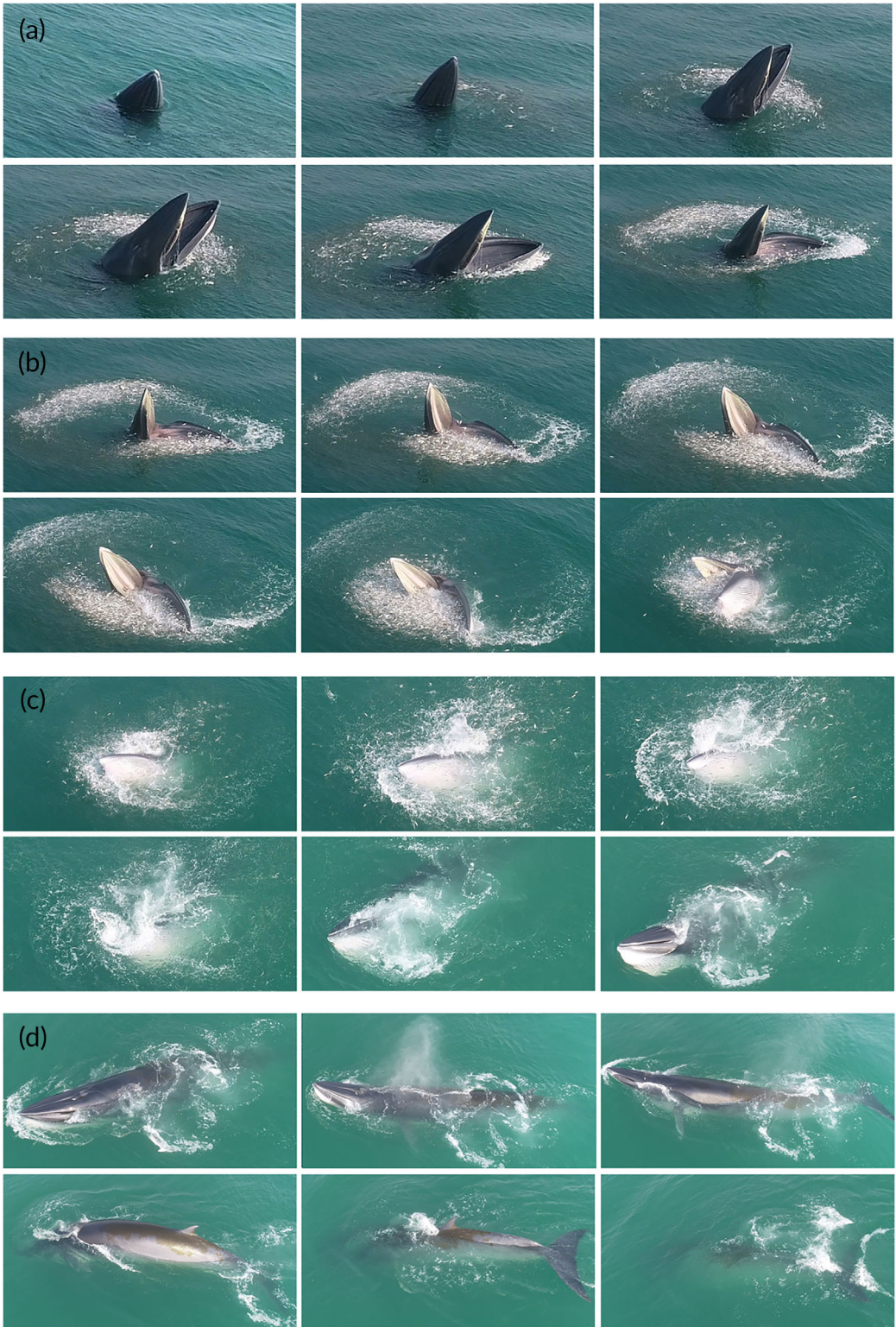**FIGURE 4** Eden's whale tread-water or trap-feeding near Weizhou Island, China.

FIGURE 5 Pirouette feeding by an Eden's whale near Weizhou Island, China; see text for detailed description.
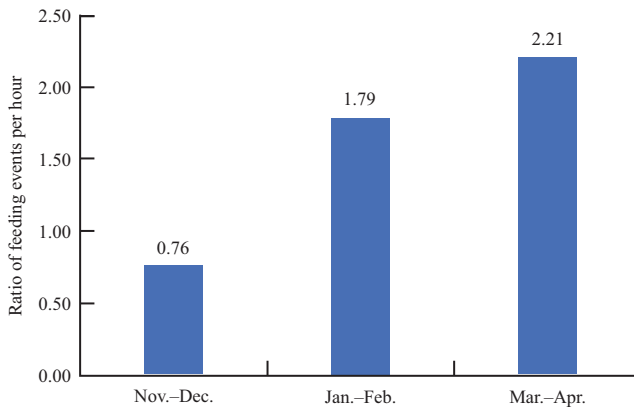
FIGURE 6 Eden's whale feeding events/hour observed near Weizhou Island, China, during 2-month intervals, November–April 2018–2021.
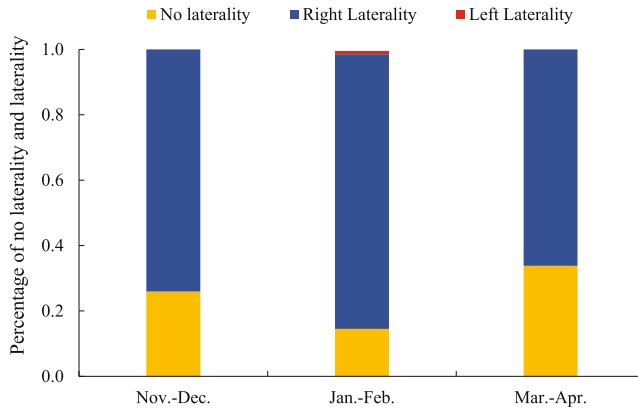
FIGURE 7 The percentage of lateralized (both right and left) versus nonlateralized feeding behavior by Eden's whales, by 2-month intervals, near Weizhou Island, China, during November–April 2018–2021.

TWF/TPF took an average of 13.8 s (range 10–22 s, $n = 5$ events); it was performed most often by single whales (59.8% of the time). PIF took an average of 6 ± 2.8 SD s (range 4–10 s, $n = 42$ events). After a single PIF event, whales switched feeding behavior on 17 occasions (40.5%), continued feeding by PIF on 5 (11.9%), and ended feeding on 20 (47.6%).

3.2 | Lateralized feeding behavior

Of the eight feeding behaviors, five had a potential for lateralization (i.e., having an option for a left or right rotation on the longitudinal body axis); these included four lunging behaviors (RLL, LLL, INL, and COL) and one nonlunging behavior (PIF). Three feeding behaviors had no potential for lateralization, including two lunging behaviors (VTL and UPL) and one (possibly two) nonlunging (TWF/TPF). Of the 1,065 feeding events recorded for individual whales (i.e., with each COL event considered a multiple event according to the number of whales present), the potential for lateralization was significant (Chi-square test, $\chi^2 = 106.6$, $df = 1$, $p < .001$). Furthermore, lateralized feeding behavior occurred more often than nonlateralized during every month of our surveys, especially during January and February
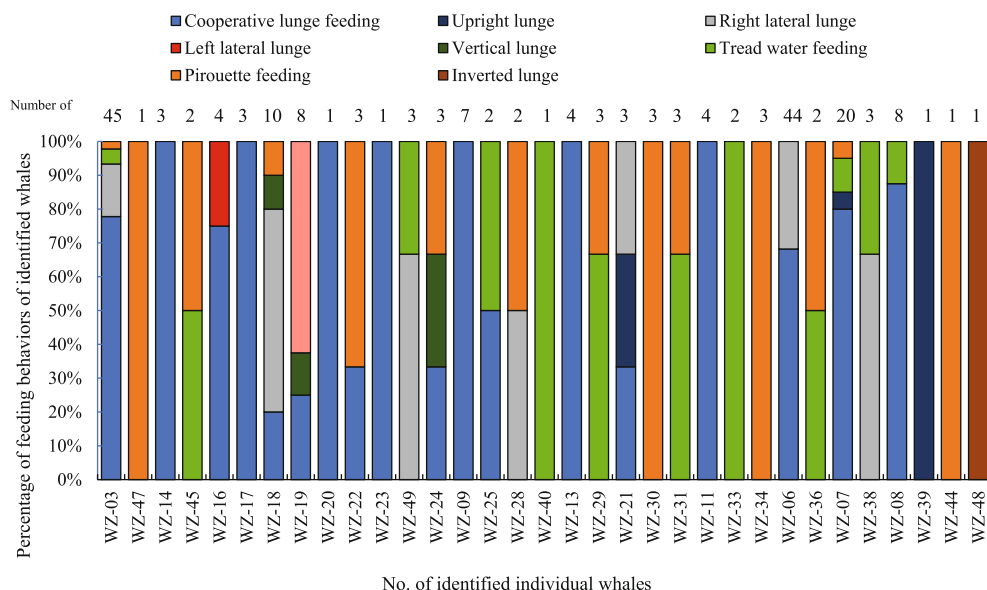
FIGURE 8 The percentage of different types of feeding behaviors for 33 individually identified Eden's whales near Weizhou Island, China.

(Figure 7). Eden's whales showed a strong right-side bias: of 701 lateralized feeding events, 699 (99.7%) were rotated to the right; 2 (0.3%) rotated left. During COL events ($n = 149$), most surfacing whales ($n = 417$, 95.9%) always circled clockwise and when they lunged, they always rotated to the right.

3.3 | Cooperative lunge-feeding behavior

An average of 2.9 whales (range 2–8) participated in COL events ($n = 149$). The mean time that whales were at the surface during COL was 6.9 ± 1.9 SD s (range 6.0–12.0 s, $n = 102$ individual whales). During 19 events, whales conducted COL behaviors more than once (range 2–7 times). The dives that occurred between COL surfacings were synchronous with a mean of 146.1 ± 81.9 SD s (range 41.0–280.0 s, $n = 8$). During six COL events, the same group of whales participated in each of the repeat events with 5, 3, 3, 4, 3, and 2 whales participating in 3, 2, 4, 3, 4, and 2 events, respectively. During the other 13 events, some of the participating whales either changed to other feeding behaviors, such as RLL, joined the next COL with other whales, or swam away; changes in behavior were sometimes difficult to assess due to difficulty in reidentifying individual whales. We did not observe more than one group engaged in COL in the same general area at the same time.

Among our photographs of feeding whales, 33 were individually identifiable, and they fed in different ways at different times. The average number of different feeding behaviors recorded for individually identifiable whales was 1.8 (range 1–4; Figure 8). Eighteen of the 33 (54.5%) individually identifiable whales engaged in COL feeding, 15 whales (45.5%) participated in PIF behavior, and 12 (36.4%) performed TWF/TPF (Figure 8).

4 | DISCUSSION

Our study of Eden's whale foraging habits in northern Beibu Gulf, China, revealed a variety of feeding behaviors, including the first observations of lateralized foraging behavior by this taxon and the first documentation of cooperative feeding by a *Balaenoptera* whale. We discuss each of these in turn below.

FIGURE 9 A Bryde's whale trap-feeding inside a tuna purse-seine net, north of Papua New Guinea, Western Pacific, in March 1978; three additional whales were feeding on a bait ball underwater. The whale is hanging vertically in the water with its rostrum jutting straight up. Baleen is visible in the mouth roof, while the lower jaw extends out at a 90° angle just below the surface. The splashing around the whale is a feeding school of yellowfin tuna (photo by G. L. Friedrichsen).

4.1 | Feeding behaviors

Lunge feeding is by far the most common feeding behavior reported for rorquals (Goldbogen et al., 2017; Kot et al., 2014). It was also the commonest behavior (80.7%) recorded for individual Eden's whales in Beibu Gulf. We did, however, observe other feeding behaviors that are uncommon or previously unknown among *Balaenoptera* whales.

What we call PIF was first described for humpback whales off western Canada by McMillan et al. (2018), although they considered it a variation on TPF. For Eden's whales in Beibu Gulf, PIF consists of a single whale surfacing vertically in the middle of a school of small fish. The fish react by swimming away from the whale, thereby forming a ring, and the whale responds by sweeping its lower jaw around in an arc and skimming fish near the surface into its mouth. In Figure 5, the skimmed arc is approximately 180°. PIF is not a lunge-feeding behavior, nor is it the largely, or entirely, passive prey capture of TPF (see below). As such, we have identified PIF as a separate behavior, and although it clearly works for single whales feeding on small fish schools, it is not known why one of the lunge-feeding behaviors would not be more appropriate most of the time.

There is some confusion about TPF and TWF feeding behaviors that needs to be addressed here. McMillan et al. (2018) coined the term "trap-feeding" to describe a novel feeding behavior by humpback whales off northern Vancouver Island, Canada. This entailed a whale remaining stationary at or just below the surface with its mouth open as foraging seabirds, including diving auks (Alcidae) and flying gulls (Laridae), pursued juvenile Pacific herring (*Clupea pallasi*) that sought refuge by swimming or jumping into the whale's mouth. After an average of 18 s (*SD* 14 s; range 4–82), the whale closed its mouth and rolled forward (McMillan et al. 2018).

There is additional evidence that TPF is more widespread - geographically and taxonomically. Figure 9 shows a previously unreported observation of TPF by a rorqual, and the first of which we are aware. The photo was taken in March 1978 by fisheries observer Gary L. Friedrichsen, near the equator, north of Papua New Guinea, in the Western Pacific (0°50′S, 144°27′E). It shows a Bryde's whale inside a tuna purse-seine net, hanging vertically in the water with its rostrum pointing straight up, and its lower jaw (not visible) extending out just below the waterline. Splashing in the water around the whale is a school of small yellowfin tuna (*Thunnus albacares*) that were feeding on a bait ball. When the photograph was taken, three other Bryde's whales were below the surface, also feeding on the bait ball, and baitfish pursued by tunas and the whales were jumping into the whale's mouth. This same behavior was observed in the same general area, over several days, by different groups of whales (G. L. Friedrichsen, personal communication, July 2020).

In April 2005, a single Bryde's whale was photographed in the western Caribbean foraging among a school of unidentified tunas that were feeding on baitfish at the surface (Greenfelder & Pitman, 2013). The whale had positioned itself vertically with its mouth open, and small baitfish, which were fleeing from the tunas, were leaping into its mouth. After about 20 s, the whale lifted its lower jaw, closed its mouth, rolled over, and dove. This was the first published observation of a purely passive foraging behavior by a baleen whale of which we are aware. Because the whale is stationary, for TPF to be effective, other predators need to be present to drive prey toward the waiting whale, and to date these predators have included tunas (Greenfelder & Pitman, 2013; Figure 9), seabirds (McMillan et al., 2018), and other whales (supplemental video in Iwata et al., 2017; video link cited above; Figure 9; see below).

McMillan et al. (2018) described TPF as a "feeding innovation" because humpbacks had been monitored at their study site since the mid-2000s, and the behavior was first observed in 2011. As further evidence of a recent onset, they also documented a rapid spread of the behavior through the local humpback population via cultural transmission. Although the humpback whale is by far the most widely studied large whale in the world (Clapham, 2000; Mann & Karniski, 2017), the observations of McMillan et al. (2018) are, to date, the only reported observations of TPF by this species anywhere, and it may represent a feeding innovation for humpbacks globally. Although TPF may be a recent addition to the feeding repertoire of the humpback whale, it is also clear that: (1) Bryde's whales have been performing TPF for at least decades (since at least 1978); (2) this behavior is widespread (occurring at least in the western Pacific and the western Caribbean); and (3) in addition to humpbacks, it is practiced by at least two species/subspecies of rorquals (Eden's and Bryde's whales).

Iwata et al. (2017) used the phrase "tread-water feeding" to refer to a novel feeding behavior they described for Bryde's (i.e., Eden's) whales in the northern Gulf of Thailand. TWF is like TPF in that the feeding whale holds a stationary, vertical posture in the water with its mouth agape, but, while TPF involves other predators driving prey toward the feeding whale, for TWF the whale purportedly surfaces in a concentration of prey, opens its mouth, and lowers the proximal portion of the lower jaw to create suction and draw the prey in.

It is unclear how TWF would work for foraging Eden's whales because, in the absence of predators, prey that remain next to a feeding whale put themselves at risk. On the other hand, there is no doubt that Eden's whales engage in TPF, at least at times. Iwata et al. (2017) did not report other predators present around feeding whales, but their Figure 1 shows a "TWF" whale with prey jumping out of the water all around it; the whale's calf is just a few meters away, lunging toward it with its mouth open, and undoubtedly driving prey in its direction. In a supplemental video, Iwata et al. (2017) show another TWF whale, with a whale swimming less than a body length away that could also be driving prey toward it. Additionally, drone footage from a separate source and posted on the internet shows another Eden's whale feeding in the northern Gulf of Thailand (https://www.instagram.com/p/CJ_NfTtnLMV/?utm_source=ig_embed&utm_campaign=embed_video_watch_again). In the video, the whale is vertical in the water with its mouth wide open, and baitfish, which are apparently trying to escape another Eden's whale lunge-feeding just a few meters away, are leaping into its mouth.

In our study, the second most common feeding behavior by Eden's whales, after COL, was TWF/TPF. Although we did not specifically record TPF, during at least 30.3% of the TWF feeding events that we recorded (n = 33), other Eden's whales were lunge-feeding in the immediate area, and potentially driving prey to the vertically oriented whale; in the case of solitary whales, predatory fish could have been present but undetected. Additional observations will be necessary to determine if Eden's whales are capable of TWF (i.e., vertical, stationary feeding in the absence of other predators).

Iwata et al. (2017) also noted that the deeper waters of the upper Gulf of Thailand were hypoxic due to anthropogenic eutrophication; they suggested that this might restrict the whales' prey to surface waters and could have led to the novel development of purported TWF behavior by Eden's whales in the Gulf of Thailand. As additional evidence that TWF/TPF was a local innovation, they also stated that this behavior had not been reported for Bryde's whale elsewhere. As we report above, TPF behavior is widespread, if uncommon, among Bryde's whales (sensu lato), including offshore waters (Greenfelder & Pitman, 2013; Figure 9), which makes it less likely that it originated in the Gulf of Thailand or for the reasons cited by Iwata et al. (2017).

4.2 | Lateralized foraging behavior

Lateralized behavior at the population level is widespread among cetaceans and usually expressed as a right-side feeding bias (Karenina et al., 2016). According to MacNeilage (2014), humans and marine mammals have the "strongest manifestations of what is apparently a vertebrate-wide tendency toward a rightward action asymmetry associated with routine behavior," which he suggested for marine mammals was primarily feeding behavior.

Among baleen whales, a strong, right-side foraging bias has been documented for gray whales and most rorqual species (e.g., Canning et al., 2011; Clapham et al., 1995; Kasuya & Rice, 1970; Kot et al., 2014; Ridgway, 1986; Tershy & Wiley, 1992), including, now, Eden's whale. Among the five feeding behaviors that had a potential for lateralization by Eden's whales (i.e., RLL, LLL, INL, COL, and PIF; $n = 719$ events), there was a clear right-side bias (99.7%) versus left (0.3%). Left lateral lunging has been occasionally observed among all rorquals studied to date, including Eden's whale, which we view as evidence that right-side feeding bias among baleen whales is a facultative behavior.

It is not known why feeding lateralization is so prevalent among rorquals, or why it is right-biased. Vision is important to foraging rorquals (e.g., Torres et al., 2020), and Goldbogen et al. (2013) suggested that rolling behavior in blue whales might enhance visual processing otherwise hampered by laterally placed eyes. Baleen whales have evolved enormous mouths to support a massive water-filtration apparatus (Goldbogen, 2010), and this has resulted in the most widely spaced eyes in the animal kingdom and largely nonoverlapping fields of vision (Rogers, 2002)—a considerable disadvantage for a mobile predator. Once a rorqual has become constrained by monocular vision, using the same eye all the time would have some advantages, including enhanced neural efficiency and motor abilities (Rogers, 2002). It remains to be explained, however, why rorquals, and many other vertebrates, have come to rely on their right eye (MacNeilage, 2014; Rogers, 2002; Siniscalchi et al., 2012).

There is also debate about whether right-biased feeding lateralization among whales has primarily a motor ("handedness") versus sensory ("eyedness") function. Karenina et al. (2016) argued that feeding lateralization in cetaceans is used for prey perception and therefore, sensory; and Jaakkola et al. (2021) also concluded that "right side-down bias commonly reported in cetaceans might be better characterized as a right-eye bias for tracking prey." A recent study on blue whales seems to support this conclusion: although blue whales show a strong right-side bias when lateral lunging at the surface (Kot et al., 2014; Tershy & Wiley, 1992), instrumented individuals foraging at depths of <70 m (but not at the surface) consistently rolled on their left sides when lunging, and whales foraging >70 m reverted to right lunging (Friedlaender et al., 2017). Although motor lateralization (i.e., the roll direction) varied with depth, sensory lateralization remained constant, such that whales were consistently able to view their prey with their right eye, either by rolling to the right and looking down when surface-lunging, or by rolling left and looking up when foraging at intermediate depths. When the whales descended to depths where they could no longer see (or be seen by) their prey, they resumed right lateral lunging, which is perhaps their default orientation.

4.3 | Cooperative feeding behavior

Although there is some debate as to the distinction between "coordination" and "cooperation" among feeding groups of cetaceans (Benoit-Bird and Au, 2009; Pearson, 2019), we will use the definition of cooperation offered by Connor (2000), i.e., "to denote individuals doing better by acting in concert than alone, but not including exchanges of altruism." A few cetaceans (notably killer whales *Orcinus orca*) sometimes hunt cooperatively for large, individual prey (Guinet et al., 2007; Pitman & Durban, 2012), but most purported cooperative hunting involves groups of conspecifics herding up small prey into dense aggregations. This behavior is commonly observed among delphinids (e.g., Connor, 2000; Rossi-Santos & Flores, 2009; Wells, 2019), but among baleen whales, the humpback had been the only species reported to hunt cooperatively (see Introduction).

Balaenoptera whales are fast, but not very maneuverable (Ford & Reeves, 2008), which probably limits their opportunities for cooperative feeding, but we suggest that the at times repetitive, tightly maneuvered, and highly

synchronous movements of Eden's whales (Figure 3) represents cooperative feeding behavior, which is to our knowledge the first reported for a *Balaenoptera* whale. Moreover, this behavior would probably not be possible without the foraging lateralization that we also documented; as Karenina et al. (2013) state: "when asymmetrical individuals need to coordinate their behavior with each other, uniformity in side preferences within a population is advantageous." Also, it seems unlikely that lateralized foraging behavior evolved in rorquals specifically to allow for cooperative feeding, because blue whales and Bryde's whales, for example, both show lateralized lunging behavior (Friedlaender et al., 2017; Tershy & Wiley, 1992, respectively), but neither has been reported foraging cooperatively. Instead, it seems more likely that among rorquals, lateralized behavior evolved first, making species like Eden's whales and humpbacks preadapted to develop cooperative feeding (Canning et al., 2011).

AUTHOR CONTRIBUTIONS

Bingyao Chen: Conceptualization; funding acquisition; investigation; methodology; project administration; supervision; writing – original draft; writing – review and editing. **Caiwen Wu:** Investigation; writing – original draft. **Lisa T. Ballance:** Writing – review and editing. **Dagmar Fertl:** Writing – review and editing. **Huiping Jiang:** Investigation; visualization; writing – review and editing. **Ying Qiao:** Investigation; writing – review and editing. **Guang Yang:** Conceptualization; supervision; writing – review and editing. **Robert L. Pitman:** Conceptualization; supervision; writing – original draft; writing – review and editing.

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