



Use and prevalence of novel bubble-net foraging strategy in Western Antarctic humpback whales

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ABSTRACT: The innovation of new foraging strategies allows species to optimize their foraging in response to changing conditions. Humpback whales provide a good study species for this concept, as they utilize multiple novel foraging tactics across populations in diverse environments. Bubble-net feeding (BNF), commonly seen in the Northern Hemisphere, has emerged as a foraging innovation in the past 20 yr within the Western Antarctic Peninsula. Using sightings data from 2015–2023, we found that BNF was present in every study year, with an annual average of 30% of foraging sightings. This data was supplemented with 26 animal-born tags deployed over the same study period. Of these tags, 12 detected instances of BNF, with BNF making up an average of 19% of the foraging lunges detected. There were seasonal trends in BNF sightings, as it was observed significantly more often at the beginning of the feeding season (January) before declining. BNF group sizes (mean: 3.41) were significantly larger than non-BNF surface feeding groups (mean: 2.21). This observation is consistent with BNF in the Northern Hemisphere, which also appears to primarily be a group foraging strategy. The seasonal pattern and relatively recent emergence of BNF suggests that its use is likely tied to specific environmental conditions, which should be investigated by comparing BNF with variables such as prey density and light availability. The social transmission of novel foraging strategies across other populations further suggests that the prevalence of this strategy likely occurs through social learning.

KEY WORDS: Behavioral plasticity · Foraging strategy · Optimal foraging theory · Group foraging · Humpback whales

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1. INTRODUCTION

Foraging has more direct and immediate fitness implications than other aspects of a species' biology and ecology (Stephens et al. 2008) — if individuals do not eat, they will die. Successful foraging affects not only immediate physical health, but broader aspects such as dominance competition or reproductive capa-

bilities (Stephens et al. 2008). As a result, foraging ecology encompasses a wide diversity of behaviors and strategies both within and across taxa (Calhoun & Hayden 2015). Strategies must account for the needs of the species (i.e. if they are specialist feeders or capital breeders) as well as those of the individual (i.e. age, size, or reproductive status) (Stephens et al. 2008). Some strategies are individualistic, such as the

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solitary predation observed in white sharks *Carcharodon carcharias* (Findlay et al. 2016), while others require group cooperation, such as the honeybee *Apis mellifera* dance, which communicates foraging sites to the hive (Beekman & Lew 2008). These strategies often change based on external factors such as prey availability, competition, or habitat shifts, sometimes resulting in novel innovations (Tuomainen & Candolin 2011). Studies of foraging behavior, therefore, provide valuable insights into a range of questions involving individual and group-level fitness, behavior, evolution, and ontogeny.

Following optimal foraging theory, individuals often utilize multiple strategies when feeding. Which strategies they use depend on several intrinsic and extrinsic factors. Strategies are commonly tailored to a specific habitat type. For example, bumblebee species *Bombus vosnesenskii* can have highly variable foraging patterns driven by the diversity of species found in floral patches (Jha & Kremen 2013), while Galapagos sea lions *Zalophus wollebaeki* have 3 distinct foraging patterns utilized in different areas of their habitat (Villegas-Amtmann et al. 2008). Strategies can also target specific food sources or prey types. Colombian woolly monkeys *Lagothrix lagotricha lugens* will pick fruit as well as actively capture arthropods (Fonseca et al. 2022). Demographics and social dynamics can also play a role in which strategies are used and how often. Adults in the aforementioned woolly monkey population capture arthropods more often than juveniles (Fonseca et al. 2022), while bottlenose dolphin populations show social preferences or even segregation based on preferred foraging tactics (Daura-Jorge et al. 2012, Methion & Díaz López 2019). This can often be due to the role of social learning in the transmission and use of certain strategies or prey types. New Caledonian crows will use different designs in their foraging tools based on what they learned from their immediate family members (Rutz et al. 2018). Similarly, a portion of bottlenose dolphins in Shark Bay, Western Australia, use sponges as a foraging tool by learning the techniques from their mothers (Krützen et al. 2005). An understanding of the drivers behind foraging tactic diversity and use is therefore key to the spectrum of species' ecologies.

Humpback whales *Megaptera novaeangliae* serve as an excellent study species for foraging behavior and strategy due to their high degree of behavioral plasticity (Jurasz & Jurasz 1979). The suite of strategies documented in humpback whales include surface or subsurface lunging (Ware et al. 2011), the use

of bubbles (Hain et al. 1982) or body parts to corral prey (McMillan et al. 2019), or scooping prey from the substrate (Ware et al. 2014). Multiple strategies are often employed within single populations, demonstrating the whales' ability to adapt and innovate in response to surrounding environmental conditions such as prey behavior and abundance (Weinrich et al. 1992, Allen et al. 2013) or water temperature (Owen et al. 2019). For example, changes in the distribution or depth of krill swarms due to sea-ice coverage can result in a shift in foraging behavior (Friedlaender et al. 2013, Riekkola et al. 2019). Some strategies appear distinct to specific feeding populations, such as lobtail feeding in the Gulf of Maine (Allen et al. 2013) or trap feeding in British Columbia (McMillan et al. 2019). These 2 strategies show evidence that such distinctions may be at least partially due to cultural trends, as both show evidence of social transmission between individuals who spend time together (Allen et al. 2013, McMillan et al. 2019). Lobtail feeding, in particular, is considered one of the strongest examples of cultural learning in an animal species (Allen 2019).

One strategy for which humpback whales are well known is their bubble-net feeding (BNF). An individual will dive below prey and emit bubbles from their nares while moving in a spiral pattern to encapsulate the prey. They then lunge at or near the surface on the contained prey. Bubbles can be emitted by one or more individuals, with multiple animals foraging within the net, exhibiting synchronized lunges evidenced by surface timings (Jurasz & Jurasz 1979). Bubble nets are thought to either reduce the amount of prey that escapes or increase the density of the prey within, thus maximizing engulfment per lunge on a given prey field. This strategy occurs primarily at and around the surface, potentially further trapping prey by vertically compressing them against the surface. Previous work has supported that bubble nets aid in the prevention of prey escape in fish (Sharpe & Dill 1997) and krill (Finley et al. 2003), and some spiraling behavior by the whales appears to horizontally corral prey with a cone-shaped net, likely increasing prey density within the net (Wiley et al. 2011). Bubbles are also used in other feeding formations besides nets, such as clouds (i.e. production of a large, single mass of very small bubbles (Hain et al. 1982, Wiley et al. 2011) or curtains (i.e. a straight line of bubbles; Hain et al. 1982, Acevedo et al. 2011).

BNF has primarily been documented in populations across the Northern Hemisphere, including the North Atlantic (Hain et al. 1982), North Pacific (Jurasz &

Jurasz 1979), and Arabian Sea (Baldwin et al. 2011) feeding stocks. While populations often use different variations of the strategy (Sharpe 2002, Wiley et al. 2011, Allen et al. 2013), certain features seem to remain consistent. It appears to predominantly be a group feeding strategy, often occurring in groups of 3 or more. Coordination among individuals also seems relatively common, with the possibility of role specialization proposed in several separate populations (Sharpe 2002, Mastick et al. 2022). These populations all primarily feed on various species of small schooling fish (Jurasz & Jurasz 1979, Hain et al. 1982, Baldwin et al. 2011), although the Gulf of Alaska population also employs BNF on euphausiids such as Pacific krill (Jurasz & Jurasz 1979). Despite commonalities to the BNF strategy, these populations are geographically and genetically distinct from one another (NOAA 2016). It is possible that each population developed the strategy independently, with common conditions driving the similarities between them. However, individuals are occasionally known to move between populations, even over distances in excess of 4000 km (Stevick et al. 2016). Another possibility is that the strategy was transmitted between populations through this individual movement, where it then spread socially through the population as other strategies do.

Over the last 2 decades, the employment of BNF has emerged within Southern Hemisphere populations and has been documented in recent studies (Findlay et al. 2017, Pirotta et al. 2021, Cade et al. 2022). Previously, it was thought to be unique to the Northern Hemisphere, as Southern Hemisphere populations have historically shown less overall diversity in their tactics, primarily using lunging either at the surface or at depth (Friedlaender et al. 2013, 2016). This is likely due to their focus on Antarctic krill as a high-fidelity prey source (Nicol et al. 2008), while Northern Hemisphere populations often feed on a diversity of krill and schooling fish species (Jurasz & Jurasz 1979, Hain et al. 1982). Documentations to date are incidental, with no focal studies that describe or quantify its use and prevalence on the Antarctic feeding grounds. The overall aim of this study is to present the first detailed description of BNF and its prevalence and use in a Southern Hemisphere population that feeds around the Western Antarctic Peninsula (WAP). This will address 2 objectives: (1) to provide a baseline understanding of foraging diversification and innovation in a recovering humpback whale population and (2) to improve our understanding of Southern Hemisphere humpback whale foraging ecology, which is key to their role as sentinels for the Antarctic ecosystem.

2. MATERIALS AND METHODS

2.1. Data collection

2.1.1. Sightings

Data collection occurred along the WAP during the austral summers and autumns (December–April) from 2015–2023 (excluding 2021–2022 due to the COVID-19 pandemic) as part of the Palmer Long-Term Ecological Research (PAL LTER) program. We used 2 specific platforms: the Palmer US Antarctic Research Station and the PAL LTER annual research cruises. Sightings data were collected opportunistically from small vessels (<7 m). A sighting was defined as any group of humpback whales that were approached by the research vessel for active data collection. Date and location were recorded, as well as group size and composition. Photos for identification and behavior were taken using a DSLR camera with a zoom lens. Beginning in 2018, uncrewed aerial systems (UAS) collected aerial photos and videos of each sighting when weather conditions permitted. UAS models included LEM-HEX44 (20 MP RGB camera), DJI Phantom 4 (internal camera), and DJI Inspire 2 (Zenmuse X5S camera).

Feeding strategies were classified into 3 categories: BNF, other surface feeding (OSF), and deep feeding. OSF was identified as any instance where at least one individual in a sighting was observed exhibiting aspects of feeding such as lunging, open mouth, distention of throat pleats, or straining of water out of the mouth. BNF was specified in instances where the presence of bubbles was observed coincident with or preceding any of the previously identified aspects of feeding. Deep feeding was classified only from tag data, as there were no reliable surface indicators of the behavior.

2.1.2. Individual identification

Humpback whale individuals were identified using 2 primary methods: photo-ID and DNA profiling. These tactics were combined whenever possible but at least one was required to give the individual a unique identifier. Photo-ID was used to identify individuals using the unique markings on the tail flukes and, in some cases, dorsal fins (Katona & Whitehead 1981). Photos were uploaded to the open-source platform HappyWhale (<https://happywhale.com>), which uses an AI algorithm to match individuals sighted globally (Cheeseman et al. 2022). This ensured that

any resightings, both within and between seasons, had been accounted for. Skin–blubber biopsy samples were collected to obtain genetic identification using DNA profiling (e.g. determination of genetic sex and microsatellite genotyping). Samples were collected using standard practices (see Palsboll et al. 1991). Crossbows were used to project arrows modified with a 40 mm stainless steel tip to sample individuals along the dorsal flank. DNA was extracted from samples with a commercially available kit (DNeasy 96 Blood & Tissue Kit; Qiagen) and genotyped following previous studies (see Pallin et al. 2023 for full details)

2.1.3. Tags

A total of 33 animal-borne suction cup tags (Customized Animal Tracking Solutions [CATS]; Cade et al. 2016, Goldbogen et al. 2017) were deployed between January and March from 2015 to 2020. These inertial-measurement unit tags were equipped with tri-axial accelerometers and integrated video cameras (1290 × 720 or 1920 × 1080 pixel resolution). Tags were deployed opportunistically from inflatable zodiacs using a 6 m carbon-fiber pole to place tags dorsally, with the video facing forward. Once tags detached from the animal, an ARGOS satellite location would transmit so that the tags could then be located and retrieved using a VHF signal with a Telonics R1000 radio receiver and a directional Yagi radio antenna. All data from tags were downloaded and decimated (down-sampled) to 10 Hz, the tag orientation was corrected for based on placement on the animal, and the 3-dimensional orientation (pitch, roll, heading) of the animal was calculated with custom-written scripts in MATLAB v.2023a (Cade et al. 2021).

Video footage from tags was audited for specific instances of BNF behavior using Behavioral Observation Research Interactive Software (BORIS) (Friard et al. 2016). The audit was conducted by 2 expert auditors (J.A.A. and R.C.N.) who were familiar with humpback whale behavior. For each tag video, auditors marked each instance of a bubble event, defined as an emission of at least 2 bubbles emitted 1 s apart by the tagged animal. The start of a bubble event was marked as the first frame in which the initial blast of bubbles can be seen in view, and the end of an event was marked as the first frame in which the terminal blast of bubbles can be seen in view. To address inter-auditor variability, we conducted a validation audit of a

single deployment consisting of bubble events. The results of the validation determined that inter-auditor effects were insignificant, as both the number of bubble events detected and the timing of events differed between auditors by less than 5%.

To differentiate bubble net events from the broader audited bubble events, we removed bubble events with duration <7.0 s to remove bubble emissions unaffiliated with a bubble net. A Jenks classification was used to determine the threshold duration, identifying natural breaks in duration distribution (Jenks 1967); data binning was determined using the Freedman-Diaconis rule (Freedman & Diaconis 1981). Other feeding events were identified as any instance where a lunge was detected in the tag sensor data. Lunges are identified in this manner by a stereotyped pattern of acceleration followed by rapid deceleration (Cade et al. 2016, Kahane-Rapport et al. 2020). These were split into 2 categories: OSF (as with the sightings data), defined as lunges detected at less than 25.5 m (95th percentile of bubble event start depths as found in this study to maintain consistency), and deep feeding, defined as lunges detected at greater than 25.4 m (Cade et al. 2016).

To make a direct comparison with non-BNF tactics, BNF lunges were defined as lunges detected through tag sensor data adjacent to a bubble event. This is because not all bubble events were accompanied by a lunge, and video analysis occasionally identified lunges adjacent to bubble events that were not detected through tag sensors. This discrepancy between detected and video-identified lunges is likely due to the slower speed at which BNF occurs, making lunge detection less effective (Allen et al. 2016). However, as lunge detection has been reliably validated for non-BNF tactics (Cade et al. 2016), it has been used here as a proxy across all tactics to maintain consistency. Linear regression between lunge depth and both starting and ending bubble event depth found correlation coefficients of 0.69 and 0.89, respectively, ensuring that lunge depth was representative of the depth at which BNF occurs.

Hourly feeding rates were calculated as the number of lunges detected by the tag sensors over the total number of tag deployment hours. Hourly BNF rates were calculated by the number of bubble-net events over the 7 s threshold over the total hours of video audited. Feeding strategies were broadly placed into 3 categories: BNF (as defined above), OSF (lunges < 25.4 m with no bubble nets), and deep feeding (lunges > 25.5 m) (Cade et al. 2016).

2.2. Data analyses

All analyses were conducted in R v.4.1.2 (R Core Team 2021) or MATLAB 2023a. Sightings data were tested for normality using the Shapiro-Wilk test (Shapiro et al. 1968) from the 'stats' package, and variance was tested using Levene's test (Levene 1960) from the 'car' package. As these data were found to be neither normally distributed nor having equal variance, comparisons were made using the non-parametric Kruskal-Wallis test (Kruskal & Wallis 1952) from the 'stats' package. Pairwise comparisons were then made using the Dunn test from the 'rstatix' package with a Benjamini-Hochberg p-value adjustment method to correct for multiple testing. Each of these tests required a p-value of <0.05 for significance. Effect size was quantified with the epsilon-squared test from the 'rcompanion' package, in which values greater than 0.04 are considered a moderate effect and those greater than 0.64 are considered a very strong effect (Rea & Parker 2014, Tomczak & Tomczak 2014). For analyses related to group size, sightings with groups of 10 or more individuals were removed to account for potential inaccuracies in assessing the number of individuals present. To assess seasonal patterns, sightings were pooled by ordinal date regardless of year.

3. RESULTS

3.1. Description of BNF prevalence

3.1.1. Sightings data

A total of 2268 individuals (including repetitions) were observed across 1108 sightings over the course of the study period (Fig. 1). Of these sightings, 378 were identified as foraging, with 86 BNF and 292 OSF observations. A breakdown of sightings across years and foraging tactics is provided in Table 1. The number of BNF occurrences remained relatively consistent, neither clearly increasing nor decreasing in observed use over time (count of sightings, mean: 12; range: 5–24; proportion of all sightings, mean: 8%; range: 4–13%; Table 1). BNF typically made up a minority of foraging occurrences (proportion of foraging sightings, mean: 30%; range: 9–71%) apart from the 2014–2015 season, most likely due to the low number of foraging sightings (Table 1).

The proportion of individuals observed using BNF showed no clear pattern across the study period,

ranging from 4–22% (mean: 13%, including unidentified and resighted individuals). This held true for the proportion of those BNF events just among individuals observed foraging, with a range of 11–82% (mean: 35%, including unidentified and resighted individuals). See Table 2 for a breakdown of individual data. There were 1363 individuals uniquely identified through photo and/or genetic identification. Among these, 227 were observed using BNF and 485 were observed using OSF. Nine of these individuals were observed using both BNF and OSF techniques, indicating that individuals can switch between tactics.

3.1.2. Tag data

A total of 26 tags were deployed (2015–2020) on unique individuals and used for lunge and depth analysis (Table 3). A total of 114.5 h of video footage were analyzed, and 493 BNF events were detected. The duration of individual BNF events averaged 14.4 s (range: 7–152.4 s; Fig. 2). Bubble emissions began and terminated at shallow depths, averaging 12.9 m for both (start range: 0.0–138.4 m; end range: 0.2–93.5 m; Fig. 3). A total of 2045 lunges were detected during the video footage portions of tag deployments. As with the surface observations, BNF made up the smallest proportion (13.9%) of the total number of lunge events, followed by deep feeding (21.7%), while OSF made up the majority of lunge events (64.1%). BNF lunges were predominantly in the shallow portion of the water column at an average of 12.3 m (range: 0.0–38.0 m), comparable to the depths of OSF lunges (mean: 12.3 m; range: 0.0–25.4 m). Deep feeding lunges were substantially deeper than either surface feeding tactics (mean: 124.0 m; range: 25.4–438.6 m) and were not accompanied by bubbles.

3.2. Patterns in group size

Of the 376 foraging sightings with group size data available, the majority (84.6%) were composed of groups that contained 3 or fewer individuals (singles: 23.7%; pairs: 39.4%; trios: 21.5%), while only 15.4% were in groups larger than 3. There were 370 sightings with a group size of less than 10 used to assess the relationship with foraging tactic. Significantly larger groups were observed using BNF compared to OSF (Kruskal-Wallis $\chi^2 = 30.93$, $p < 0.001$; Fig. 4), with a moderate effect size ($\epsilon^2 = 0.0838$).

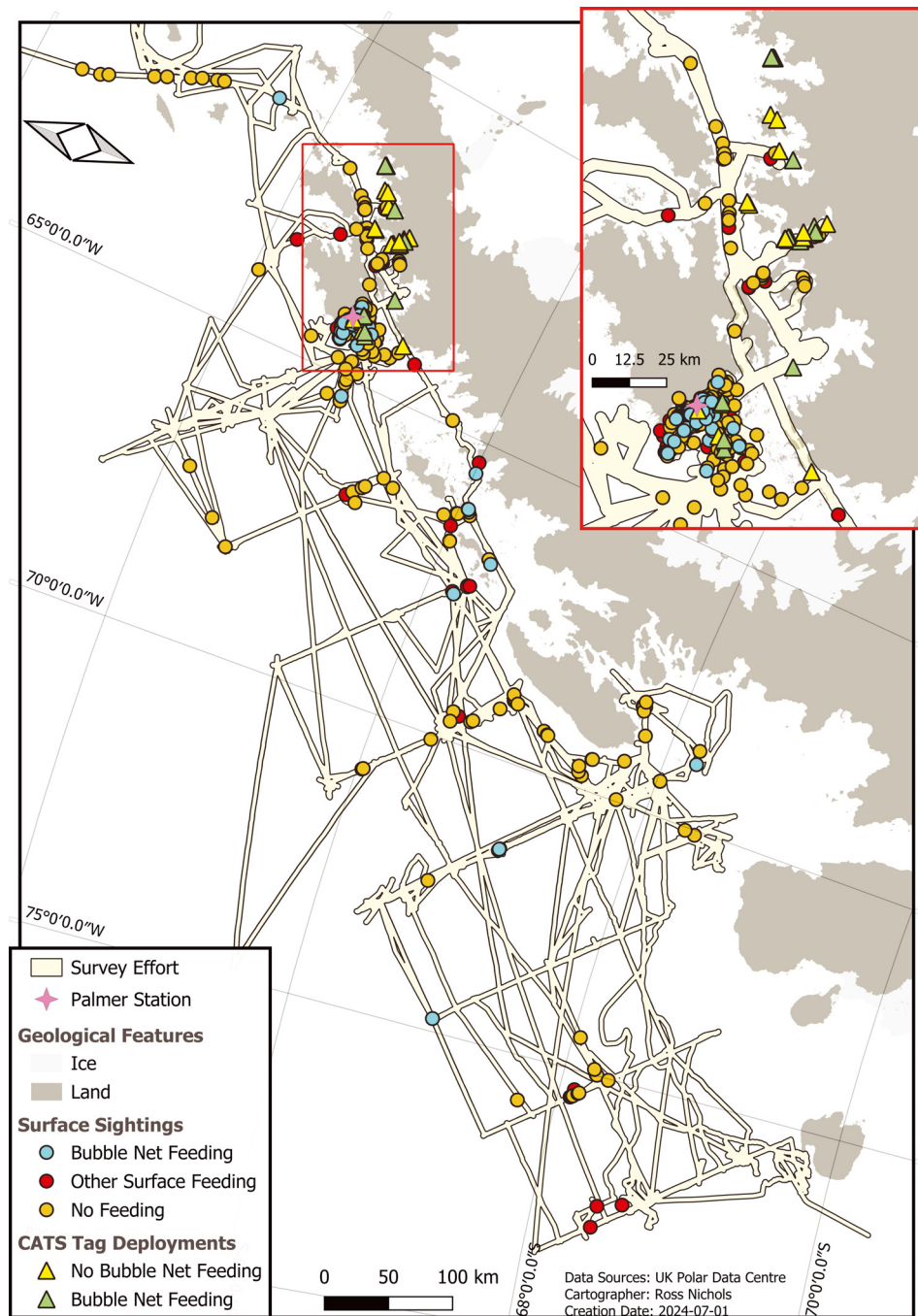


Fig. 1. Study area and locations of humpback whale bubble net observations from both sightings observations and tag deployments

Single individuals made up a larger proportion of non-BNF sightings (29.3%) compared to BNF sightings (6.0%) (Fig. 5). Pairs had the most comparable proportions (40.8 vs. 37.3%, respectively), while groups of 3 or more represented a larger proportion of BNF sightings (56.6%) compared to other feeding strategies (30.0%).

3.3. Temporal patterns

3.3.1. Sightings data

There was a clear seasonal pattern in the use of BNF that skewed towards the beginning of the foraging season (Kruskal-Wallis $\chi^2 = 8.60$, $p = 0.014$; Fig. 6).

Table 1. Summary of bubble-net feeding (BNF) sightings by humpback whales across the study period represented as both counts and proportions. Note that foraging sightings here do not include deep feeding

Year	Total sightings	Foraging sightings	BNF sightings	% Foraging of total	% BNF of foraging	% BNF of total
2015	92	17	12	18.5	70.6	13.0
2016	85	27	6	31.8	22.2	7.1
2017	109	30	8	27.5	26.7	7.3
2018	133	56	5	42.1	8.9	3.8
2019	360	123	24	34.2	19.5	6.7
2020	228	93	18	40.8	19.4	7.9
2023	101	30	13	29.7	43.3	12.9
Total	1108	378	86	34.1	22.0	7.8

Table 2. Summary of individual humpback whales observed across the study period represented as both counts and proportions. These include all foraging sightings and bubble-net feeding (BNF) sightings. Note that the total number of unique individuals will not be the sum of the unique individuals in each year, as some individuals were resighted in multiple years

Year	Unique/total individuals	Unique/total foraging	Unique/total BNF	% Total BNF of foraging	% Total BNF of total
2015	144/188	48/50	40/41	82.0	21.8
2016	101/161	43/62	11/11	17.7	6.8
2017	190/233	76/88	30/32	36.4	13.7
2018	202/252	92/102	12/12	11.8	4.8
2019	346/791	212/308	63/80	26.0	10.1
2020	244/454	146/219	37/53	24.2	11.7
2023	142/189	69/81	37/42	51.9	22.2
Total	1363/2268	682/910	227/271	29.8	11.9

Table 3. Summary of bubble-net feeding (BNF) presence across humpback whale tag deployments. Proportion of BNF deployments are out of total deployments that could be analyzed. Proportion of BNF lunge are out of total foraging lunges detected. All lunges were defined as any lunge detected from tag sensor data; note that these do not include lunges identified by video footage or BNF events with no detected lunge

Year	Total deployments	BNF deployments	Video hours	Total foraging lunges	BNF lunges
2015	1	0 (0%)	2.6	4	0 (0%)
2016	1	1 (100%)	7.3	281	105 (37.4%)
2017	4	0 (0%)	9.5	19	0 (0%)
2018	10	6 (60%)	57.8	1572	148 (9.4%)
2019	5	2 (40%)	16.6	32	0 (0%)
2020	5	2 (40%)	20.6	136	32 (23.5%)
Total	26	12 (46%)	114.5	2045	285 (13.9%)

While OSF occurred in every month of the season (December–April), BNF was only observed in January–March. BNF significantly decreased in occurrence from January–February (Dunn test: $Z = -2.93$, $p = 0.003$) but did not significantly change

from February–March (Dunn test: $Z = 0.689$, $p = 0.681$). In contrast, non-BNF did not significantly change across months (Kruskal-Wallis $\chi^2 = 8.06$, $p = 0.089$), although the sightings did decrease from January–April in a trend towards significance.

Sightings of BNF were significantly lower than OSF in January (Kruskal-Wallis $\chi^2 = 4.36$, $p = 0.034$) and February (Kruskal-Wallis $\chi^2 = 13.3$, $p < 0.001$), but not in March (Kruskal-Wallis $\chi^2 = 0.041$, $p = 0.839$). However, the difference in February had a much stronger significance. This was further supported by the effect size of month on sightings occurrences, which was moderate in January ($\epsilon^2 = 0.082$) but strong in February ($\epsilon^2 = 0.403$).

3.3.2. Tag data

Seasonal patterns identified in the sightings data were essentially corroborated by the tag data (Fig. 7). BNF and non-BNF (OSF and deep feeding combined) hourly feeding rates were highest in January and declined over the season. While neither of these declining trends was significant, both trended closely towards significance (BNF Kruskal-Wallis $\chi^2 = 5.478$, $p = 0.065$; non-BNF: Kruskal-Wallis $\chi^2 = 5.94$, $p = 0.052$). There were significant differences in all lunge depths between all months (Kruskal-Wallis $\chi^2 = 55.94$, $p < 0.0001$), with lunge depths becoming progressively deeper from January through March. BNF lunge depths were also significantly different between all months (Kruskal-Wallis $\chi^2 = 70.35$, $p < 0.0001$). However, contrary to the overall trend, BNF lunges While OSF occurred in every month of the season (December–April), BNF was only observed in January–March. BNF significantly decreased in occurrence from

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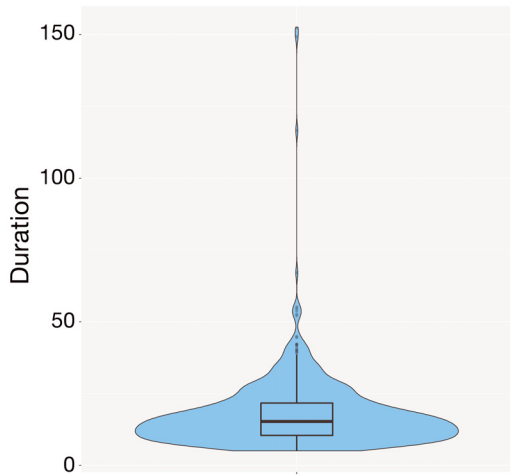


Fig. 2. Duration (seconds) of bubble events detected from tag video footage of humpback whales. Bar: median; box: 1st–3rd quartiles (IQR); whiskers: min./max. values within $1.5 \times$ IQR; dots: outliers

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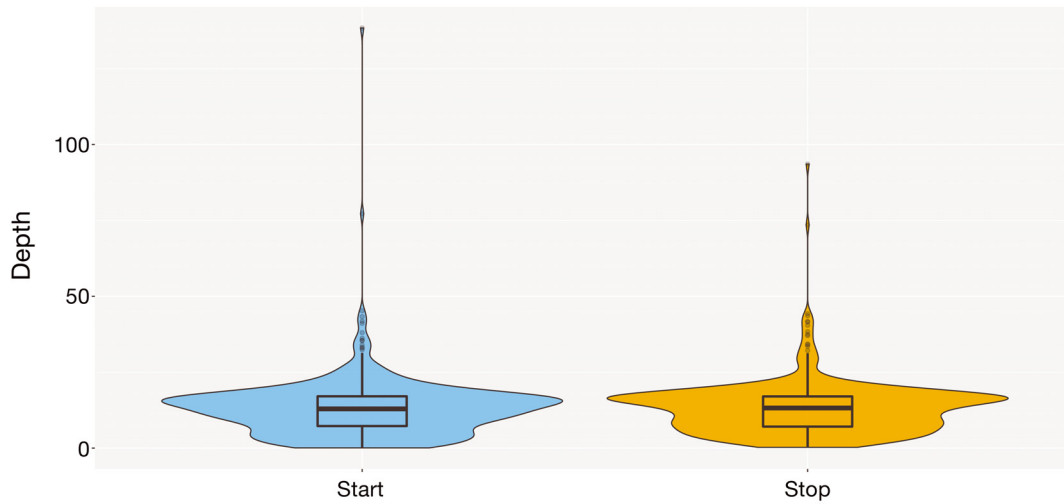


Fig. 3. Start and stop depths (m) of each bubble event detected from tag video footage of humpback whales. Boxplots as in Fig. 2

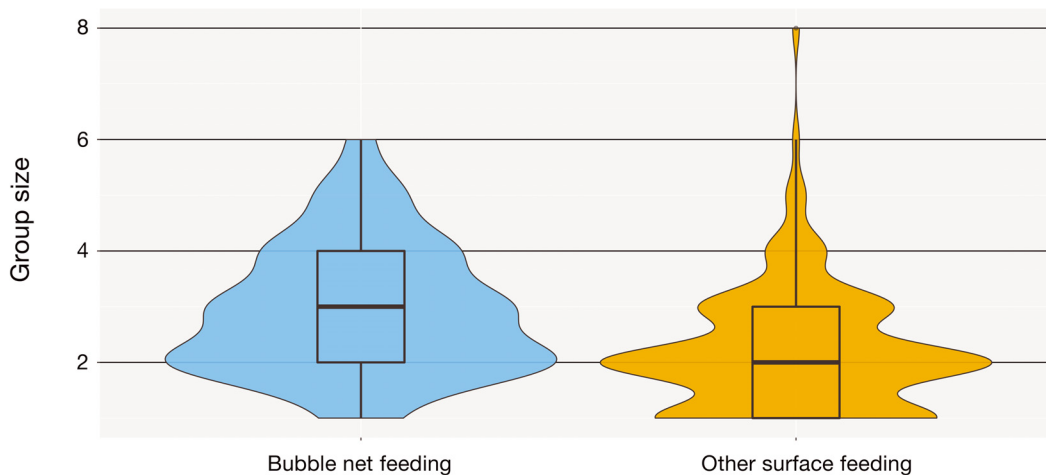


Fig. 4. Humpback whale group size for each foraging tactic: bubble-net feeding (blue) and other surface feeding strategies (orange). Boxplots as in Fig. 2

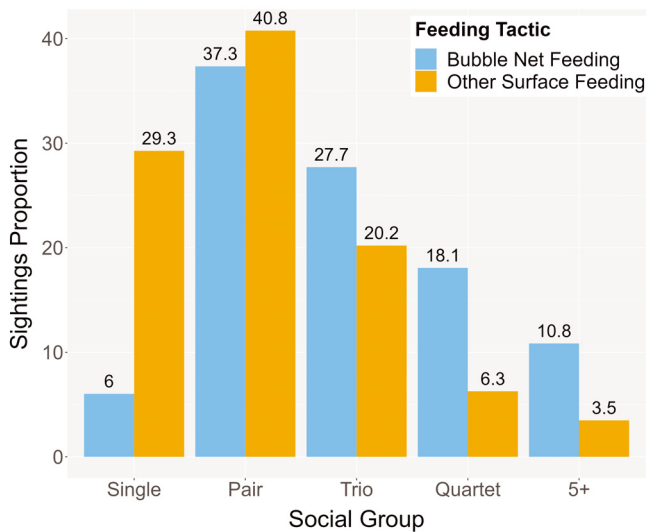


Fig. 5. Proportion of humpback whale sightings by group size for each foraging tactic: bubble-net feeding (BNF) (blue) and other surface feeding strategies (orange). Each proportion is relative to the feeding strategy (i.e. proportions shown for BNF are out of total BNF sightings)

hourly feeding rates were highest in January and declined over the season. While neither of these declining trends was significant, both trended closely towards significance (BNF Kruskal-Wallis $\chi^2 = 5.478$, $p = 0.065$; non-BNF: Kruskal-Wallis $\chi^2 = 5.94$, $p = 0.052$). There were significant differences in all lunge depths between all months (Kruskal-Wallis $\chi^2 = 55.94$, $p < 0.0001$), with lunge depths becoming progressively deeper from January through March. BNF

lunge depths were also significantly different between all months (Kruskal-Wallis $\chi^2 = 70.35$, $p < 0.0001$). However, contrary to the overall trend, BNF lunges became shallower from January to March. OSF lunge depths showed no significant differences between months (Kruskal-Wallis $\chi^2 = 3.2$, $p = 0.201$). Deep feeding lunges were significantly different between all months (Kruskal-Wallis $\chi^2 = 102.14$, $p < 0.0001$), with lunges becoming deeper from January to March. As with the sightings data, feeding rates were significantly lower in BNF compared to non-BNF strategy rates (Kruskal-Wallis $\chi^2 = 2.97$, $p = 0.003$). When feeding rates were examined across months, both January and February also had differences that trended towards significance (January, Kruskal-Wallis $\chi^2 = 3.43$, $p = 0.064$; February, Kruskal-Wallis $\chi^2 = 3.65$, $p = 0.056$), while March was not significant (Kruskal-Wallis $\chi^2 = 2.931$, $p = 0.129$).

4. DISCUSSION

4.1. Use and description of BNF

BNF was observed in every year of study across the 2 research platforms (sightings and tags). Neither the frequency of BNF observations nor the proportion of observed individuals engaged in BNF increased over the study period, and across both platforms it was used less frequently than other feeding strategies. Together, these results suggest that while it is not the primary tactic used, BNF has become an established

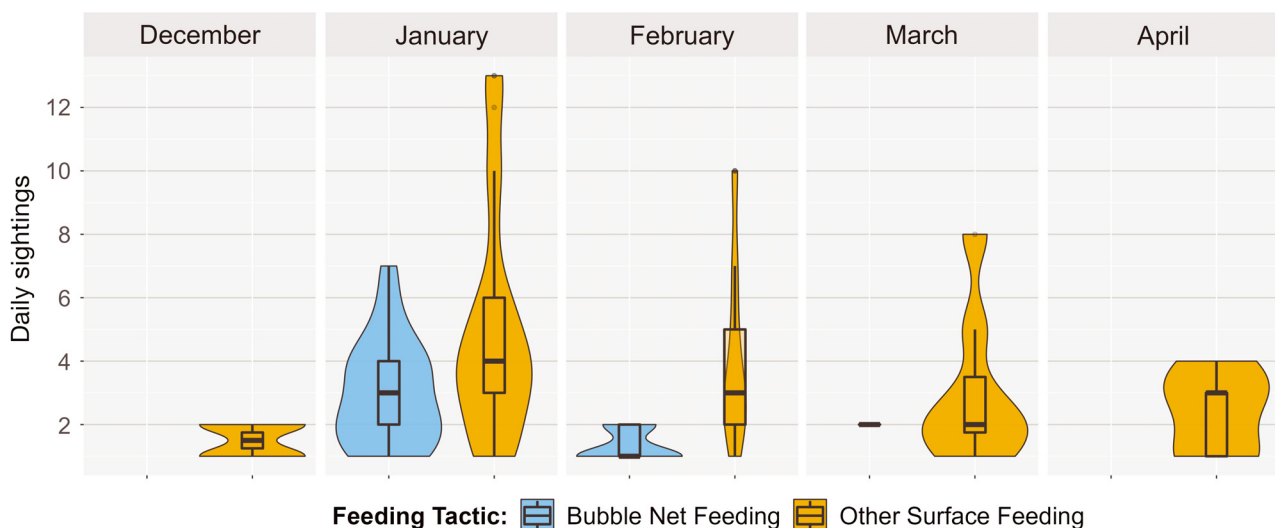


Fig. 6. Daily sightings, pooled across all years, of humpback whale bubble-net feeding (blue) and other surface feeding strategies (orange) separated by month. Note that December is shown prior to January to reflect the timing of the foraging season, which is December to April. Boxplots as in Fig. 2

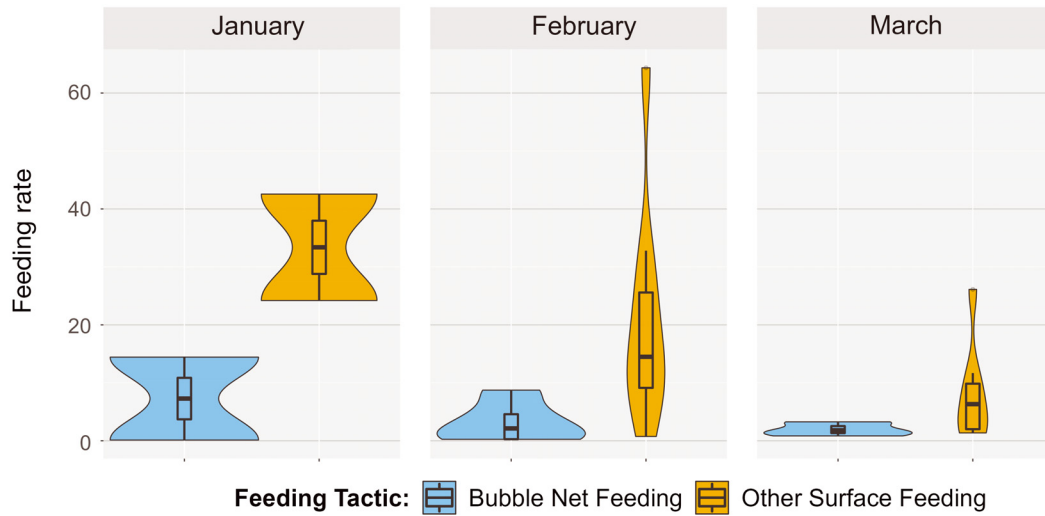


Fig. 7. Hourly feeding rates from tag deployments, pooled across all years, of humpback whale bubble-net feeding (blue) and other non-bubble-net feeding strategies (orange) separated by month. Boxplots as in Fig. 2

part of the WAP population's foraging strategy repertoire. This is not unusual, as humpback whales are known for their plasticity in foraging strategies within a single population (Jurasz & Jurasz 1979, McMillan et al. 2019, Mastick et al. 2022). Northern Hemisphere populations similarly use BNF as only one of multiple tactics, but BNF seems to have been established in these populations for much longer (Jurasz & Jurasz 1979, Allen et al. 2013). BNF was primarily a shallow depth strategy, with 95% of bubble events occurring at a depth of less than 25 m. This follows studies that have found a similar depth threshold in other populations (Sharpe 2002, Wiley et al. 2011) and it is thought to be due to a limitation of how bubbles disperse over depth (Wiley et al. 2011). Such consistency across hemispheres and populations indicates that it is likely to be a fundamental part of the strategy. However, an interesting outlying bubble event occurred at ~77 m, although there was no corresponding lunge detected with it. This suggests that BNF is at least attempted at much greater depths.

The WAP version of BNF appears to be comparatively simple in its current execution (Wiley et al. 2011, Allen et al. 2013): there do not appear to be additional components such as lobtails, and it is unclear to what degree there is explicit cooperation or role specialization. In contrast, BNF in both the Gulf of Maine and Gulf of Alaska often involves coordination among multiple individuals (Jurasz & Jurasz 1979, Sharpe 2002, Mastick et al. 2022). There are several possible explanations for this difference. One possibility is that these Northern Hemisphere populations have innovated the technique in the substan-

tially longer time they appear to have been using it, while the WAP population is still in the earlier stages of learning. This could be due to the outsized impact of commercial whaling in the Southern Hemisphere, which saw a take of 200 000 whales in the 20th century compared to ~34 000 whales in the Northern Hemisphere over the same period (Rocha et al. 2015). Severe population declines or removal of key demographics have been shown to erode social and cultural knowledge in animal species (McComb et al. 2001, Crates et al. 2021). An increased loss of cultural foraging tactics could have resulted in the Northern Hemisphere 'relearning' BNF much earlier, thus giving those populations more time to innovate and evolve the tactic. This could also explain the lack of diversity in tactics seen in the Southern Hemisphere compared to the Northern Hemisphere.

Behaviors also frequently develop and evolve over time as individuals make improvements or adapt to changing conditions. For example, when the herring stock crashed in the western North Atlantic in the late 1970s, a novel innovation emerged known as 'lobtail feeding', whereby individuals incorporated a surface tail-slap to their bubble feeding (Weinrich et al. 1992, Allen et al. 2013). A second hypothesis is that Northern Hemisphere populations feed on a much wider variety of prey species, many of which are schooling fish (Jurasz & Jurasz 1979, Hain et al. 1982, Kirchner et al. 2018). As krill are smaller with differing swarming behaviors, perhaps a more complex version of a bubble net is not needed as it might be for larger prey that are more mobile and could escape or avoid predation more easily. Thus, rather than preventing

escape, the purpose of BNF on krill is likely to increase prey density through horizontal and vertical compression against the surface of the water and the surrounding bubbles. Finally, a third possibility is that there is coordination in the WAP population that simply has not been captured by this study. This could be addressed by a targeted study of BNF groups using animal-borne tags, following similar studies in other populations (Wiley et al. 2011, Parks et al. 2014, Mastick et al. 2022). More broadly, cross-hemisphere comparisons of BNF would allow for direct comparison of bubble-net structures and the influence of intrinsic or extrinsic variables specific to those populations.

4.2. Seasonal patterns

Our surface observations show that while OSF skewed towards the first half of the foraging season, the use of BNF skewed more strongly towards the earlier part of the foraging season than OSF. This corroborates previous work on the seasonality of feeding in the WAP (Nichols et al. 2022). Nichols et al. (2022) found increased shallow-depth foraging in the early portions of the summer feeding period (January–February), which shifted to deeper feeding at lower rates in the latter part of the season (March–June). They also found that foraging shifted from occurring during all hours in the early season to exclusively at night in the later season. The proposed drivers are thought to be a shift in prey availability as krill become less concentrated at the surface later in the summer and into fall, showing a much stronger diel vertical migration pattern that relates to available light and nutrients associated with primary production (Cresswell et al. 2009). Our sightings results would support this as a driver of seasonal foraging behavior, given that BNF appears to be a tactic exclusive to shallow foraging. Krill swarms are also less dense in the earlier summer months than later in the year (Nichol 2006), which would make a foraging technique such as BNF that increases prey density (and therefore foraging efficiency) more effective at that stage of the season. Light availability may also play a role if the shallow nature of BNF is partly due to the tactic requiring a visual component. Previous work in the Gulf of Maine on the timing of when bubble nets are produced showed that they exclusively occur during daylight periods (Friedlaender et al. 2009). Environmental variables seem to drive BNF, suggesting dependence on factors impacting prey behavior. This could explain why BNF prevalence drops

off earlier in the season compared to OSF strategies. Direct studies modeling the use of specific foraging strategies with environmental factors, particularly those that fluctuate across a season, would provide insight into what drives strategy selection and potentially the broader impacts of changing ecosystem conditions.

Similar temporal trends were seen in the tag data, with BNF rates being highest in January and declining throughout the season. While not significant, these results did trend towards significance, which suggests support for the patterns observed in our sightings results. Furthermore, a previous study examined an expanded version of the tagging dataset used here and found clear seasonal trends in overall feeding rates that support declining feeding as the season progresses (Nichols et al. 2022). This same study also corroborates our seasonal trend of overall lunges becoming significantly deeper as whales shift from surface strategies to deep feeding. Interestingly, BNF lunges became significantly shallower over the season while OSF lunges showed no changes. If krill do aggregate more densely in the later summer months, perhaps BNF does not need to be as deep to effectively corral the prey. The shift away from BNF would also suggest that bubble nets become less necessary as krill aggregations become denser and deeper.

Our study was limited to tags that were equipped with cameras, as that is currently the most reliable means of detecting bubble netting from tag sensor data alone. Additionally, the use of detected lunges as a proxy for BNF was likely to be a conservative estimate of BNF lunges due to the presence of undetected lunges in the video analysis. We feel that together, these factors make the tagging dataset unable to accurately parse the seasonality of the behavior. However, when combined with both the significant sightings patterns and the seasonality found in past studies, a future study using tagging data with a larger sample size and a more reliable means of detecting bubble-net lunges is warranted, as we feel it would be likely to support our findings more fully.

Despite the demonstrated drop-off in BNF after January, 75% of the BNF tag deployments occurred in February or March. This indicates that at least for some individuals, BNF remains a worthwhile tactic to employ later into the season even after conditions are no longer optimum. One possibility is that krill availability in the surface waters may not always diminish as substantially over the course of a season. Individuals may therefore find BNF sufficiently effective to prefer it over other tactics. Such individual preference for specific strategies occurs in other humpback

whale populations (Allen et al. 2013, Kosma et al. 2019, McMillan et al. 2019, Wray et al. 2021). While the use of lobtail feeding, a BNF variation in the Gulf of Maine, is largely driven by sand lance abundance, it was still observed in low sand lance years (Allen et al. 2013). In other species, foraging preferences can be so strong that it is actually detrimental to the population (Allen 2019). Resident killer whales in British Columbia have a cultural preference for the endangered Chinook salmon — a preference which is leading to population declines as they seem to refuse other prey options (Williams et al. 2011). In the Kitimat Fjord System of British Columbia, BNF played a strong role in humpback whale social structure and mediation between individuals based on their preference for the strategy (Wray et al. 2021). Given the strong role that social learning and culture is likely to play in humpback whale foraging ecology, individual tactic preference is likely to contribute to the fine-scale use of BNF and should be accounted for in future studies.

4.3. Group size

The clear preference for using BNF in larger groups is consistent with Northern Hemisphere populations. Similar trends were found in a Canadian Pacific foraging population, where BNF occurred in significantly larger groups than other feeding strategies (Wray et al. 2021). BNF is also consistently documented as a group strategy in the Gulf of Maine and Gulf of Alaska, with most group sizes comparable to our population (1–8 individuals; D'Vincent et al. 1985, Mastick et al. 2022), although the specific relationship with group size relative to other strategies has not been quantified in these populations (Jurasz & Jurasz 1979, Mastick et al. 2022). This is also consistent with the limited observations we have of its use in the Southern Hemisphere, as BNF was documented in 'super-groups' of 20+ individuals within the Tasmanian Sea (Pirotta et al. 2021). However, BNF is not exclusively a group strategy. Single individuals did account for ~8% of BNF sightings in the WAP, suggesting that it can be done alone. BNF in the Gulf of Maine has also been consistently documented in single individuals, making up ~35% of BNF observations in a 10 yr tagging study (Mastick et al. 2022). Incorporating the impact of group size into cross-population comparisons would help determine how consistent its role is and how it interacts with other variables such as prey type.

One possible driver for the increased group sizes seen in BNF both here and in other populations may

relate to foraging effort and efficiency. There are multiple aspects of BNF that make it a more energy-intensive tactic: (1) it requires a series of exhalations to form the bubble net, (2) it requires turning in a relatively tight configuration, and (3) it takes longer to complete as a multi-step behavior than a typical single lunge (i.e. Ware et al. 2011). Additionally, the angular movement likely reduces speed, reducing the total drag force necessary in the expansion of their gular pouch during a lunge and thus potentially reducing total engulfment volume. In line with optimal foraging theory, it would follow that BNF would only be employed in situations where the benefits of the strategy outweigh the costs to the individual. One possibility is that a larger group size reduces the energetic costs to each individual within the group. Mastick et al. (2022) found that individual exertion appeared to decrease with increasing group size during BNF. The advantages of collaborative efforts would make a complex tactic like BNF more worthwhile in groups. In the case of the WAP specifically, the focus on krill as a primary prey target rather than schooling fish could be why single BNF was so rarely seen compared to other populations (Mastick et al. 2022). Perhaps the effort is only worthwhile with at least one other individual participating. Furthermore, once prey shifts to deeper waters as krill tend to do in the later summer months, BNF may no longer be worth the additional energy required even in larger groups. This could help to explain the apparent preference for using BNF in the earlier foraging season, in combination with the abiotic factors of light availability and the physical depth restrictions on bubble dispersal.

4.4. Emergence of BNF

The potential dependence of BNF on environmental factors such as prey distribution and density could point to the reason for its emergence in the Southern Hemisphere over the last several decades. While Antarctic krill availability shows high degrees of inter-annual variability, stock distributions in the South Atlantic and adjacent areas of the Southern Ocean have declined at their northern limits since the mid-1970s (Atkinson et al. 2019). This has been coupled with a southward shift in distribution farther down the WAP. These shifts could have contributed to the emergence of BNF as a behavioral adjustment to less concentrated prey availability, particularly given that BNF appears to be a tactic specific to better corralling more dispersed prey. Mean krill body length also appears to have increased over time due to a lack of juvenile

recruitment, further improving the conditions suitable for BNF as bubble nets may be more effective on larger prey that might be less likely to escape between bubble blasts. Such changes to the food base are likely to have population-level consequences for predators. In this case, these shifts in krill abundance influence the reproductive rates of the WAP humpback whales (Pallin et al. 2023). Furthermore, individual behavioral changes are proposed to be one of the first and earliest indicators of population stressors (Cerini et al. 2023). For example, the emergence of the novel lobtail feeding tactic in the Gulf of Maine population was a response to the stressor of a crash in a key prey species. The appearance and spread of BNF as a novel foraging tactic within the WAP could be similar behavioral indicator of the increasing stress that climate change is putting on the WAP area, which is one of the fastest warming Antarctic regions. This reinforces the need to examine the occurrence of BNF with respect to environmental variables.

The ability to adapt to environmental shifts through innovating and learning effective foraging strategies may contribute to population recoveries such as the one seen in the study population. The WAP population has doubled from ~6000 to ~12000 individuals between 2006 and 2020 (Félix et al. 2021), indicating that it is recovering effectively from commercial whaling along with the global humpback whale population (Bettridge et al. 2015, Noad et al. 2019). The broad behavioral plasticity that humpback whales exhibit, particularly in regard to foraging, may be part of the reason for this global rebound. Population size is thought to influence the appearance and subsequent spread of innovations (Chimento et al. 2021), with some studies linking larger populations to increased innovation in both humans (Derex et al. 2013, Bromham et al. 2015) and animals (Ashton et al. 2019, Chimento et al. 2021). Additionally, socially learned knowledge and innovations are key to the ecology of many species and thus play a role in their ability to grow and thrive (Brakes et al. 2019, 2021). Humpback whales demonstrate a clear relationship between social associations and foraging tactics and innovations, with strong evidence that some foraging innovations are socially transmitted (Sharpe 2002, Allen et al. 2013, Parks et al. 2014, McMillan et al. 2019, Wray et al. 2021). The implications of foraging diversification need to be considered in the management of a successfully recovering population such as the WAP, as well as how behavioral diversification and population growth interact with shifting environments. For example, the WAP exhibits relatively high pregnancy rates that fluctuate with krill availability

(Pallin et al. 2023). This suggests that the population's ability to grow is tied to its ability to effectively respond to these fluctuations in prey. Understanding the dynamic between behavioral innovation, population dynamics, and environmental conditions will improve the effectiveness of how the foraging ecology of top krill predators is interpreted in the context of the increasing changes seen in the Antarctic.

Data archive. All datasets generated during and/or analyzed are available at Dryad (<https://doi.org/10.5061/dryad.zkh1893js>). Please seek prior written permission from A.S.F. and J.A.A. to reuse data in any form except to confirm the study results.

Acknowledgements. Funding for this work was provided by the National Science Foundation Office of Polar Programs (Postdoctoral Fellowship 2218949 and Grants 1643877, ANT-07-39483, 1250208, and 1440435), the Palmer Long-Term Ecological Research Program (Grants 1440435 and 2026045), the Winifred Violet Scott Trust, the National Geographic Society (NGS-909906R-21), the Marine Mammal Commission, World Wide Fund for Nature—Australia (WWF—Australia), The International Whaling Commission's Southern Ocean Research Partnership (P0710, 0711-02), the US Biological Adaptations to Environmental Change in Antarctica, the Scientific Committee of Antarctic Research (SCAR). All work was conducted under National Marine Fisheries Services permits (14809, 23095), Antarctic Conservation Act permits (2015-011, 2020-016), and Institutional Animal Care and Use Committee protocols (4513 and 4943 approved by Oregon State University; Friea1706, Friea2004, and Frie2305dn approved by the University of California Santa Cruz). We are grateful to all field team members who helped collect data throughout the field seasons. We thank the crew and marine technicians of the ARSV 'Laurence M Gould', RVIB 'Nathaniel B Palmer', and all the Antarctic Support Staff at Palmer Station for their efforts. We thank the editor and 2 anonymous reviewers for their constructive feedback to the manuscript.

LITERATURE CITED

- ✦ Acevedo J, Plana J, Aguayo-Lobo A, Pastene LA (2011) Surface feeding behavior of humpback whales in the Magellan Strait. *Rev Biol Mar Oceanogr* 46:483–490
- ✦ Allen JA (2019) Community through culture: from insects to whales: how social learning and culture manifest across diverse animal communities. *BioEssays* 41:1900060
- ✦ Allen J, Weinrich M, Hoppitt W, Rendell L (2013) Network-based diffusion analysis reveals cultural transmission of lobtail feeding in humpback whales. *Science* 340:485–488
- ✦ Allen AN, Goldbogen JA, Friedlaender AS, Calambokidis J (2016) Development of an automated method of detecting stereotyped feeding events in multisensor data from tagged rorqual whales. *Ecol Evol* 6:7522–7535
- ✦ Ashton BJ, Thornton A, Ridley AR (2019) Larger group sizes facilitate the emergence and spread of innovations in a group-living bird. *Anim Behav* 158:1–7
- ✦ Atkinson A, Hill SL, Pakhomov EA, Siegel V and others (2019) Krill (*Euphausia superba*) distribution contracts southward during rapid regional warming. *Nat Clim Chang* 9:142–147

- Baldwin R, Collins T, Minton G, Willson A, Corkeron P (2011) Arabian Sea humpback whales 2011 update: resights, bubble feeding and hotspots. Document SC/54/O4 presented to the Scientific Committee of the International Whaling Commission
- Beekman M, Lew JB (2008) Foraging in honeybees — When does it pay to dance? *Behav Ecol* 19:255–261
- Bettridge SOM, Baker CS, Barlow J, Clapham P and others (2015) Status review of the humpback whale (*Megaptera novaeangliae*) under the Endangered Species Act. NOAA Tech Memo NMFS-SWFSC-540
- Brakes P, Dall SR, Aplin LM, Bearhop S and others (2019) Animal cultures matter for conservation. *Science* 363: 1032–1034
- Brakes P, Carroll EL, Dall SR, Keith SA and others (2021) A deepening understanding of animal culture suggests lessons for conservation. *Proc R Soc B* 288:20202718
- Bromham L, Hua X, Fitzpatrick TG, Greenhill SJ (2015) Rate of language evolution is affected by population size. *Proc Natl Acad Sci USA* 112:2097–2102
- Cade DE, Friedlaender AS, Calambokidis J, Goldbogen JA (2016) Kinematic diversity in orqual whale feeding mechanisms. *Curr Biol* 26:2617–2624
- Cade DE, Seakamela SM, Findlay KP, Fukunaga J and others (2021) Predator-scale spatial analysis of intra-patch prey distribution reveals the energetic drivers of orqual whale super-group formation. *Funct Ecol* 35:894–908
- Cade DE, Kahane-Rapport SR, Wallis B, Goldbogen JA, Friedlaender AS (2022) Evidence for size-selective predation by Antarctic humpback whales. *Front Mar Sci* 9: 747788
- Calhoun AJ, Hayden BY (2015) The foraging brain. *Curr Opin Behav Sci* 5:24–31
- Cerini F, Childs DZ, Clements CF (2023) A predictive timeline of wildlife population collapse. *Nat Ecol Evol* 7:320–331
- Cheeseman T, Southerland K, Park J, Olio M and others (2022) Advanced image recognition: a fully automated, high-accuracy photo-identification matching system for humpback whales. *Mamm Biol* 102:915–929
- Chimento M, Alarcon-Nieto G, Aplin LM (2021) Population turnover facilitates cultural selection for efficiency in birds. *Curr Biol* 31:2477–2483.e3
- Crates R, Langmore N, Ranjard L, Stojanovic D, Rayner L, Ingwersen D, Heinsohn R (2021) Loss of vocal culture and fitness costs in a critically endangered songbird. *Proc R Soc B* 288:20210225
- Cresswell KA, Tarling GA, Thorpe SE, Burrows MT, Wiedemann J, Mangel M (2009) Diel vertical migration of Antarctic krill (*Euphausia superba*) is flexible during advection across the Scotia Sea. *J Plankton Res* 31:1265–1281
- D’Vincent CG, Nilson RM, Hanna RE (1985) Vocalization and coordinated feeding behavior of the humpback whale in southeastern Alaska. *Sci Rep Whales Res Inst* 36:41–47
- Daura-Jorge FG, Cantor M, Ingram SN, Lusseau D, Simões-Lopes PC (2012) The structure of a bottlenose dolphin society is coupled to a unique foraging cooperation with artisanal fishermen. *Biol Lett* 8:702–705
- Derex M, Beugin MP, Godelle B, Raymond M (2013) Experimental evidence for the influence of group size on cultural complexity. *Nature* 503:389–391
- Félix F, Acevedo J, Aguayo-Lobo A, Ávila IC and others (2021) Humpback whale breeding Stock G: updated population estimate based on photo-ID matches between breeding and feeding areas. Document SC/68C/ASI/02 presented at the International Whaling Commission Scientific Committee Meeting
- Findlay R, Gennari E, Cantor M, Tittensor DP (2016) How solitary are white sharks: Social interactions or just spatial proximity? *Behav Ecol Sociobiol* 70:1735–1744
- Findlay KP, Seakamela SM, Meÿer MA, Kirkman SP and others (2017) Humpback whale ‘super-groups’—a novel low-latitude feeding behaviour of Southern Hemisphere humpback whales (*Megaptera novaeangliae*) in the Benguela Upwelling System. *PLOS ONE* 12:e0172002
- Finley LA, Nicol S, MacMillan DL (2003) The effectiveness of a bubble curtain for preventing physical damage to Antarctic krill in captivity. *Mar Freshwat Behav Physiol* 36: 285–293
- Fonseca ML, Ramírez-Pinzón MA, McNeil KN, Guevara M and others (2022) Dietary preferences and feeding strategies of Colombian highland woolly monkeys. *Sci Rep* 12:14364
- Freedman D, Diaconis P (1981) On the histogram as a density estimator: L_2 theory. *Z Wahrscheinlichkeitstheor Verwandte Geb* 57:453–476
- Friard O, Gamba M, Fitzjohn R (2016) BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods Ecol Evol* 7: 1325–1330
- Friedlaender AS, Hazen EL, Nowacek DP, Halpin PN and others (2009) Diel changes in humpback whale *Megaptera novaeangliae* feeding behavior in response to sand lance *Ammodytes* spp. behavior and distribution. *Mar Ecol Prog Ser* 395:91–100
- Friedlaender AS, Tyson RB, Stimpert AK, Read AJ, Nowacek DP (2013) Extreme diel variation in the feeding behavior of humpback whales along the western Antarctic Peninsula during autumn. *Mar Ecol Prog Ser* 494:281–289
- Friedlaender AS, Johnston DW, Tyson RB, Kaltenberg A and others (2016) Multiple-stage decisions in a marine central-place forager. *R Soc Open Sci* 3:160043
- Goldbogen JA, Cade DE, Boersma AT, Calambokidis J and others (2017) Using digital tags with integrated video and inertial sensors to study moving morphology and associated function in large aquatic vertebrates. *Anat Rec (Hoboken)* 300:1935–1941
- Hain J, Carter G, Kraus S, Mayo C, Winn H (1982) Feeding behavior of the humpback whale, *Megaptera novaeangliae*, in the western North Atlantic. *Fish Bull* 80:259–268
- Jenks GF (1967) The data model concept in statistical mapping. *Int Yearb Cartogr* 7:186–190
- Jha S, Kremen C (2013) Resource diversity and landscape-level homogeneity drive native bee foraging. *Proc Natl Acad Sci USA* 110:555–558
- Jurasz CM, Jurasz VP (1979) Feeding modes of the humpback whale, *Megaptera novaeangliae*, in Southeast Alaska. *Sci Rep Whales Res Inst* 31:69–83
- Kahane-Rapport SR, Savoca MS, Cade DE, Segre PS and others (2020) Lunge filter feeding biomechanics constrain orqual foraging ecology across scale. *J Exp Biol* 223:jeb224196
- Katona S, Whitehead H (1981) Identifying humpback whales using their natural markings. *Polar Rec (Gr Brit)* 20: 439–444
- Kirchner T, Wiley DN, Hazen EL, Parks SE, Torres LG, Friedlaender AS (2018) Hierarchical foraging movement of humpback whales relative to the structure of their prey. *Mar Ecol Prog Ser* 607:237–250
- Kosma MM, Werth AJ, Szabo AR, Straley JM (2019) Pectoral

- herding: an innovative tactic for humpback whale foraging. *R Soc Open Sci* 6:191104
- ✦ Kruskal WH, Wallis WA (1952) Use of ranks in one-criterion variance analysis. *J Am Stat Assoc* 47:583–621
- ✦ Krützen M, Mann J, Heithaus MR, Connor RC, Bejder L, Sherwin WB (2005) Cultural transmission of tool use in bottlenose dolphins. *Proc Natl Acad Sci USA* 102:8939–8943
- Levene H (1960) Robust tests for equality of variances. In: Olkin I, Ghurye SG, Hoefding W, Madow WG, Mann HB (eds) *Contributions to probability and statistics: essays in honor of Harold Hotelling*. Stanford University Press, Palo Alto, CA, p 278–292
- ✦ Mastick NC, Wiley D, Cade DE, Ware C, Parks SE, Friedlaender AS (2022) The effect of group size on individual behavior of bubble-net feeding humpback whales in the southern Gulf of Maine. *Mar Mamm Sci* 38:959–974
- ✦ McComb K, Moss C, Durant SM, Baker L, Sayialel S (2001) Matriarchs as repositories of social knowledge in African elephants. *Science* 292:491–494
- ✦ McMillan CJ, Towers JR, Hilderger J (2019) The innovation and diffusion of 'trap-feeding,' a novel humpback whale foraging strategy. *Mar Mamm Sci* 35:779–796
- ✦ Methion S, Díaz López B (2019) Individual foraging variation drives social organization in bottlenose dolphins. *Behav Ecol* 31:97–106
- ✦ Nichol S (2006) Krill, currents, and sea ice: *Euphausia superba* and its changing environment. *Bioscience* 56:111–120
- ✦ Nichols RC, Cade DE, Kahane-Rapport S, Goldbogen J and others (2022) Intra-seasonal variation in feeding rates and diel foraging behaviour in a seasonally fasting mammal, the humpback whale. *R Soc Open Sci* 9:211674
- ✦ Nicol S, Worby A, Leaper R (2008) Changes in the Antarctic sea ice ecosystem: potential effects on krill and baleen whales. *Mar Freshw Res* 59:361–382
- NOAA (2016) Endangered and threatened species; identification of 14 distinct population segments of the humpback whale (*Megaptera novaeangliae*) and revision of species-wide listing. *Fed Regist* 81:62260–62320
- ✦ Noad MJ, Kniest E, Dunlop RA (2019) Boom to bust? Implications for the continued rapid growth of the eastern Australian humpback whale population despite recovery. *Popul Ecol* 61:198–209
- ✦ Owen K, Jenner KCS, Jenner MNM, McCauley RD, Andrews RD (2019) Water temperature correlates with baleen whale foraging behaviour at multiple scales in the Antarctic. *Mar Freshw Res* 70:19–32
- ✦ Pallin LJ, Kellar NM, Steel D, Botero-Acosta N and others (2023) A surplus no more? Variation in krill availability impacts reproductive rates of Antarctic baleen whales. *Glob Change Biol* 29:2108–2121
- Palsboll P, Larsen F, Sigurd-Hansen E (1991) Sampling of skin biopsies from free-ranging large cetaceans at West Greenland: development of biopsy tips and new designs of bolts. *Rep Int Whal Comm Spec Issue* 13:71–79
- ✦ Parks SE, Cusano DA, Stimpert AK, Weinrich MT, Friedlaender AS, Wiley DN (2014) Evidence for acoustic communication among bottom foraging humpback whales. *Sci Rep* 4:7508
- ✦ Pirota V, Owen K, Donnelly D, Brasier MJ, Harcourt R (2021) First evidence of bubble-net feeding and the formation of 'super-groups' by the east Australian population of humpback whales during their southward migration. *Aquat Conserv* 31:2412–2419
- R Core Team (2021) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Rea LM, Parker RA (2014) *Designing and conducting survey research: a comprehensive guide*. John Wiley & Sons, Hoboken, NJ
- ✦ Riekkola L, Andrews-Goff V, Friedlaender A, Constantine R, Zerbini AN (2019) Environmental drivers of humpback whale foraging behavior in the remote Southern Ocean. *J Exp Mar Biol Ecol* 517:1–12
- ✦ Rocha RC Jr, Clapham PJ, Ivashchenko Y (2015) Emptying the oceans: a summary of industrial whaling catches in the 20th century. *Mar Fish Rev* 76:37–48
- ✦ Rutz C, Hunt GR, St Clair JJ (2018) Corvid technologies: How do New Caledonian crows get their tool designs? *Curr Biol* 28:R1109–R1111
- ✦ Shapiro SS, Wilk MB, Chen HJ (1968) A comparative study of various tests for normality. *J Am Stat Assoc* 63:1343–1372
- Sharpe FA (2002) Social foraging of the southeast Alaskan humpback whale, *Megaptera novaeangliae*. PhD thesis, Simon Fraser University, Burnaby
- ✦ Stephens DW, Brown JS, Ydenberg RC (2008) *Foraging: behavior and ecology*. University of Chicago Press, Chicago, IL
- ✦ Sharpe F, Dill L (1997) The behavior of Pacific herring schools in response to artificial humpback whale bubbles. *Can J Zool* 75:725–730
- ✦ Stevick PT, Berrow SD, Bérubé M, Bouveret L and others (2016) There and back again: multiple and return exchange of humpback whales between breeding habitats separated by an ocean basin. *J Mar Biol Assoc UK* 96: 885–890
- Tomczak M, Tomczak E (2014) The need to report effect size estimates revisited. An overview of some recommended measures of effect size. *Trends Sport Sci* 1:19–25
- ✦ Tuomainen U, Candolin U (2011) Behavioural responses to human-induced environmental change. *Biol Rev Camb Philos Soc* 86:640–657
- ✦ Villegas-Amtmann S, Costa DP, Tremblay Y, Salazar S, Aurioles-Gamboa D (2008) Multiple foraging strategies in a marine apex predator, the Galapagos sea lion *Zalophus wollebaeki*. *Mar Ecol Prog Ser* 363:299–309
- ✦ Ware C, Friedlaender AS, Nowacek DP (2011) Shallow and deep lunge feeding of humpback whales in fjords of the West Antarctic Peninsula. *Mar Mamm Sci* 27:587–605
- ✦ Ware C, Wiley DN, Friedlaender AS, Weinrich M and others (2014) Bottom side-roll feeding by humpback whales (*Megaptera novaeangliae*) in the southern Gulf of Maine, USA. *Mar Mamm Sci* 30:494–511
- ✦ Weinrich MT, Schilling MR, Belt CR (1992) Evidence for acquisition of a novel feeding behaviour: lobtail feeding in humpback whales, *Megaptera novaeangliae*. *Anim Behav* 44:1059–1072
- ✦ Wiley D, Ware C, Bocconcelli A, Cholewiak D, Friedlaender A, Thompson M, Weinrich M (2011) Underwater components of humpback whale bubble-net feeding behaviour. *Behaviour* 148:575–602
- ✦ Williams R, Krkošek M, Ashe E, Branch TA and others (2011) Competing conservation objectives for predators and prey: estimating killer whale prey requirements for Chinook salmon. *PLOS ONE* 6:e26738
- ✦ Wray J, Keen E, O'Mahony EN (2021) Social survival: humpback whales (*Megaptera novaeangliae*) use social structure to partition ecological niches within proposed critical habitat. *PLOS ONE* 16:e0245409