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ARTICLE

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The effect of group size on individual behavior of bubble-net feeding humpback whales in the southern Gulf of Maine

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Abstract

In many species, group foraging is a strategy used to increase the efficiency of individuals to find and exploit patchy prey. Humpback whales (*Megaptera novaeangliae*) are one of the few baleen whale species reported to use coordinated foraging strategies. One of these behaviors, bubble-net feeding, has been observed in several populations, though the behaviors of individuals within these groups are largely unknown. This study used multisensor kinematic tag data from 26 whales foraging in the Southern Gulf of Maine to analyze individual bubble-net feeding behaviors. Linear mixed effects models were used to test if there were differences in individual whales' dive behaviors across group size. The results indicate that individuals performed consistent bubble-net feeding behaviors regardless of the size of their foraging group, except when using one specific foraging behavior, the upward spiral. Overall complexity of foraging dives, based on the three-dimensional movements of the dive, decreased with increasing group size when group members used upward spirals. This may indicate that in larger groups, participants in coordinated feeding events need to move less and expend less energy to corral prey. This study provides new insights into the effects of group size on individual behavior and group coordination in humpback whales.

KEYWORDS
bubble-net, group foraging, humpback whale, individual feeding roles, *Megaptera novaeangliae*

1 | INTRODUCTION

Using group coordination to herd and capture prey, hereafter referred to as group foraging, offers a suite of advantages that enhance fitness for individuals and thus may play a significant role in the evolution of collective behavior. The potential evolutionary advantages of foraging in groups includes increased detection of and protection from predators, increased detection of patchy or scarce food, increased ability to defend resources, and as we focus on in this paper, improved prey capture ability (Clark & Mangel, 1986). For group foraging to be advantageous, there needs to be a combination of a dependence on food sources that are difficult to exploit individually, and a prevalence of food sharing to maximize energy gain from a resource (Alexander, 1974). Although many species regularly forage in groups, the nature of the group foraging relationship is differentiated by the behaviors at the individual level. Both terrestrial and marine species across trophic levels have adopted coordinated foraging behaviors (Beauchamp, 2014). As the marine environment is three-dimensional, prey have more directions in which to escape predation, and complex prey movements may facilitate more complex predator maneuvers.

Humpback whales (*Megaptera novaeangliae)* are unique among baleen whales in that individuals frequently demonstrate coordinated feeding behaviors that likely increase prey capture rates while minimizing prey disturbance (Weinrich & Kuhlberg, 1991). In bubble-net feeding, individuals or groups of whales dive beneath an aggregation of prey and release a stream of bubbles through their nares in a circular pattern around the prey (Hain et al., 1982; Jurasz & Jurasz, 1979; Leighton et al., 2004; Wiley et al., 2011). The bubbles act as a boundary, confining and concentrating the prey before engulfment (Hain et al., 1982; Jurasz & Jurasz, 1979; Sharpe & Dill, 1997). This behavior has been recorded in Southeast Alaska, the Gulf of Maine, the Magellan Strait, and the Antarctic Peninsula (Acevedo et al., 2011; Hain et al., 1982; Jurasz & Jurasz, 1979; Mastick, 2016; Pirotta et al., 2021). Though there have been many recorded visual observations of bubble-net feeding from the surface, little is known about the coordination between participants involved in this foraging strategy. Wiley et al. (2011) described the variability in behaviors of individuals participating in bubble-net feeding groups. Our study is the first to examine how individual behaviors differ within groups of varying group sizes.

Individual behaviors are likely influenced by the size of the group in other contexts (Pulliam & Caraco, 1984), therefore group size may also affect the behaviors of individuals in a group feeding setting (Smith, 1982). Additionally, in cooperative group herding behaviors, members sometimes adopt different roles, known as a division of labor; this has been observed in lions (*Panthera leo*) and common bottlenose dolphins (*Tursiops truncatus*) (Gazda et al., 2005; Stander, 1992). If bubble-net feeding was cooperative through a division of labor, we would expect similar role partitioning; previous research has hypothesized that one individual blows the bubbles while others have auxiliary roles (Wiley et al., 2011). Alternatively, some group foraging events are known to be motivated by scrounging relationships, in which some participants herd while others do little work and benefit from the others' labor (Beauchamp, 2014). In this study, we examined if and how the behavior of individuals changes as group size increased by examining the behavior of individuals across multiple group sizes both qualitatively (categorical dive type) and quantitatively (dive metrics). We used motion-sensor tag data to determine dive types and measure the components of individual dive behavior during bubble-net dives, to test the following hypotheses regarding individual roles based on diving behavior during bubble-net feeding events: (1) individual feeding behavior is stable, (2) whales behave differently in different sized feeding groups, and (3) whales in the same feeding group adopt different behaviors. We use this information to assess the likelihood and prevalence of different roles within a feeding group.

2 | METHODS

2.1 | Data collection

2.1.1 | Study site

Data came from whales tagged around Stellwagen Bank National Marine Sanctuary in the Southern Gulf of Maine in the Northwest Atlantic Ocean (42°27′07.45″N, 70°20′10.52″W). Tagging took place in June and July over 7 years between 2006 and 2016 as part of a collaborative long-term humpback whale monitoring project. The whales in this population are well-studied and the sex, age, and matrilineal relationships for many of the individuals are known by the Center for Coastal Studies, which curates a catalog of the individual whales.

2.1.2 | Tagging

We used minimally invasive, tri-axial motion-sensor archival tags designed to measure the three-dimensional movement patterns of cetaceans underwater throughout this study. We used three types of suction cup tags: DTAGs (Johnson & Tyack, 2003), Acousonde (Burgess, 2009; Greeneridge Sciences, Santa Barbara, CA), and CATS (Cade et al., 2016; Customized Animal Tracking Solutions, Moffat Beach, Australia) tags. DTAG accelerometers and magnetometers were sampled at 50 Hz, while Acousondes were sampled at 10 Hz. CATS tags accelerometers, magnetometers, and gyroscopes were sampled at 50 Hz in 2015 and in 2016 accelerometers were sampled at 400 Hz.

Whales were tagged between foraging dives during bubble-net feeding bouts. Generally, only one tag was deployed at a time, though there were instances in which multiple animals in a feeding group were tagged concurrently. The tagging process has been described previously by Wiley et al. (2011) and resulted in a variety of responses, ranging from no response to short-term disturbance that typically lasted 0–4 min (Wiley et al., 2011).

2.1.3 | Focal follows

We conducted focal animal follows on all the tagged whales by recording time, location, behavioral state, and associations with other whales at each surfacing, using standardized behavioral descriptions. Associations were defined as whales within two body lengths undergoing coordinated behavior (Weinrich, 1991). We assumed that individuals were feeding in a coordinated manner because they were feeding within two body length of one another, synchronizing their dives, and moving in the same direction (Baker, 1985; Mobley & Herman, 1985; Whitehead, 1983). This information was used to determine when individuals were engaged in bubble-net feeding and their corresponding group sizes. Any behaviors that incorporated bubbles in a foraging setting were included for analysis. Whales were photo-identified using standard techniques (e.g., Mizroch et al., 1990), allowing for identification of whales that were tagged on multiple occasions to compare behaviors across tagging events (Ware et al., 2014; Weinrich, 1991; Weinrich & Kulhberg, 1991). Follows continued as long as conditions allowed or until the tag fell off, at which point the tag was retrieved and data were downloaded for analysis.

2.2 | Data analysis

Tag data were first imported into Matlab v2014a using custom scripts (Cade et al., 2021) to correct for the orientation of the tag on the whale, to calculate animal orientation, and to down sample data to 10 or 5 Hz. Data were then further down sampled to 1.25 or 1 Hz using a Hamming filter during the import to TrackPlot, a software package that was designed specifically for studying the underwater kinematic patterns of whales using continuous motion and orientation data (Ware et al., 2006). TrackPlot processes the components of the tag data into a pseudo-track, or three-dimensional computerized replication, based on dead-reckoning from the sensor data of the animal's movement to provide a visual interface for identifying and analyzing kinematic patterns (Crain et al., 2012; Friedlaender et al., 2016; Ware et al., 2014).

Any dives occurring in the first 4 min after tag deployment were removed, as whales typically react to tagging for at most 4 min (Wiley et al., 2011). Feeding events with calves present were also excluded from analysis, as calf presence may influence the mother's behavior and affect the group size. The dive patterns observed in the track were used to broadly categorize feeding behavior into what we refer to as "dive types." We categorized bubble-net behaviors based on definitions in Wiley et al. (2011) into two main categories: double-loops and upward spirals. When bubble-nets did not conform to one of these categories, we categorized the dive based on the pattern of the track, including the number of surfacings, the shape of the net, and the orientation of the whale. These additional dive types we derived were upward lunges, half-spirals, single loops, and hybrids of a double-loop and upward spiral. Dive type descriptions are included in Figure 1.

Sensor data associated with each bubble-net feeding dive (including change in pitch, roll, and heading, and the change in depth in meters for each time step [0.8–1 s]) were extracted from TrackPlot, from the initial descent until the return to the surface following the feeding event. All dives contained a single engulfment event, but some feeding events contained multiple surfacings before a lunge as part of the prey-herding strategy; for these events we defined the dive as the point of initial descent to the point of terminal surfacing. For each bubble-net feeding dive, we calculated seven response variables for statistical analysis: (1) total azimuthal heading change in degrees (the sum of all absolute heading changes), (2) total change in depth in meters (the total distance dived over the course of a feeding dive, including in some instances multiple surfacings as previously described [the sum of all absolute depth changes]), (3) total change in pitch [the sum of all pitch changes], (4) total change in roll [the sum of all roll changes],

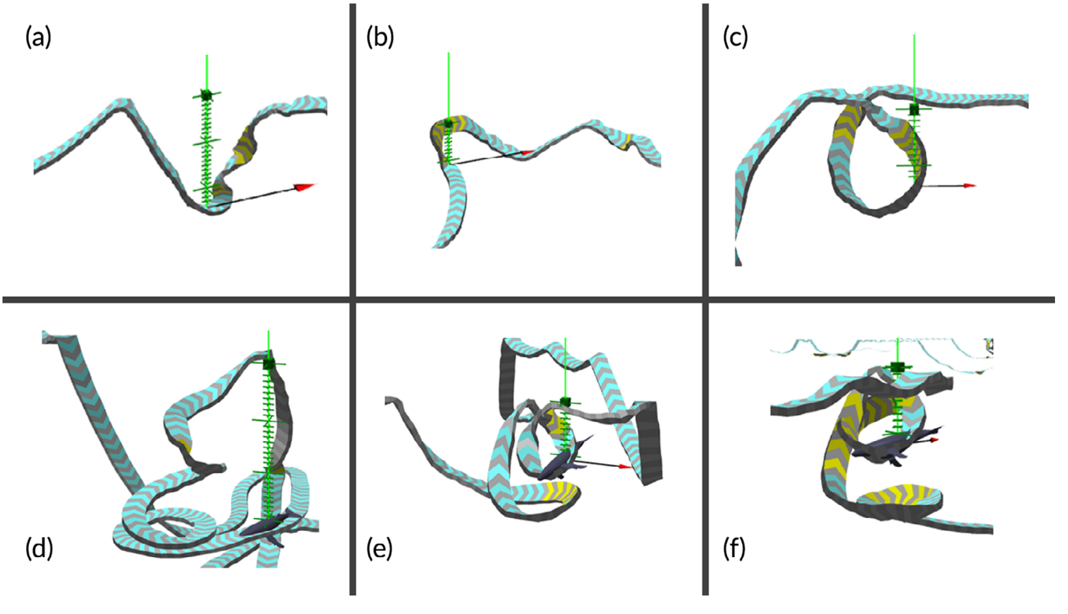

FIGURE 1 The different dive types as observed in TrackPlot. (a) an upward lunge without any clear bubble-net pattern; (b) a half spiral, a 180° turn towards the surface, (c) a single loop, a sharp downward dive into a 360° turn back towards the surface (d) an upward spiral, 360° horizontally oriented rotations from depth towards the surface (e) a double-loop, two consecutive feeding loops at the surface, and (f) an upward spiral into a double-loop, which can include several upward rotations prior to surfacing and subsequent loop.

(5) maximum depth, (6) duration in seconds, and (7) fluke frequency in fluke strokes per second. As some whales were tagged more than once, whale identity and group size were used as explanatory variables to compare the dynamics of feeding dives across the population. In total, 9 males, 15 females, and 2 individuals of unknown sex were tagged across 32 tagging events, though because all tagged whales were mature adults, we did not incorporate demographic data into our model.

The tag data allow for the calculation of angular accelerations in the whale's movement, giving an indication of the fluking pattern of the animal. Fluke stroke frequency is correlated with heart rate in other marine mammals (Kooyman & Ponganis, 1998), and thus can be used as a metric of effort or energetic cost. We counted the number of fluke strokes each animal made during each bubble-net dive through visual identification in TrackPlot, ignoring any angular accelerations not clearly identifiable as fluke strokes, and divided the total fluke stroke by dive duration. We used the resulting frequency of fluke strokes per second as a dive variable, which was used as a relative estimate of exertion and a means of comparing among the individuals and group sizes (Davis & Williams, 2012; Williams et al., 2004).

The seven response variables were not necessarily independent; therefore, we used a principal component analysis (PCA) to determine if there was a subset of variables that, in concert, accounted for most of the variability in the data (Friedlaender et al., 2016; Goldbogen et al., 2013). PCAs were conducted using *prcomp* in the statistical package of the open-source software R (v. 3.3.0; R Core Team, 2013). The data were scaled to have unit variance and centered using the *prcomp* package in running the PCA. The resulting principal component or components were used for all further statistical analyses, referred to as “dive metrics” for simplicity. This PCA method has been used to analyze the dives of other species, including blue whales, by Goldbogen et al. (2013) and Friedlaender et al. (2016). Each of the principal components described a statistically independent characteristic of the animal's movement.

The qualitative dive types and quantitative dive metrics were used to determine if tagged whales change behaviors as a function of group size during bubble-net feeding. If an individual exhibited a statistically significant difference in the principal components of their dive behavior across group sizes, this reflected a change in the overall movement or “complexity” of their behavior. Complexity was defined by the three-dimensional aspects of the dive which indicate deviation of the whale from a straight-line path; a dive with higher complexity consisted of higher values of azimuthal change in heading, change in pitch, and change in roll, represented by the principal component or components.

2.2.1 | The stability of individual dive behavior and the influence of group size

To determine whether individuals changed their dive pattern over the tagging duration, we calculated the frequency of each individual's observed dive types. To determine whether group size influences an individual whale's feeding behavior, we used tag data from individuals observed feeding in at least two different group sizes for at least three feeding dives, a criterion used for all further analysis. We then performed a linear mixed effects model that compared the dive metrics (principal components) across group size to determine if there was a relationship with group size and dive metrics for each individual. Group size was treated as a continuous variable and treated as a fixed effect, and both whale identity and the interaction of whale identity and group size were treated as random effects. To test whether dive type influenced the relationship between dive metrics and group size, we separated the data into subsets according to dive type and ran a linear mixed effects model across each to determine if there was a correlation with group size in each respective dive category.

2.2.2 | The variability of behaviors in a feeding group

On five occasions there were multiple whales tagged concurrently within a feeding group. To test whether there are differences in dive metrics and dive types between individuals feeding together in a group, we used focal follow data to determine when the tagged whales were feeding together, then matched the times of those events with the tag data for each whale. To qualitatively describe the differences in these group's dive behaviors, we located each groups' synchronous dive using time stamps in TrackPlot and compared the individuals' dive types over the course of the association. We categorized each dive during the association to determine if there was any switching in dive types across the synchronous dives. We split the groups that were larger than two individuals into pairs to perform pairwise comparisons and grouped the individuals' dive data by the group's dive, labeled by a number. We used paired t-tests, linked by pair's dive number, to determine if there was a difference in the mean principal component dive metrics across participants, inferring differences in the overall complexity of the participants' movements.

3 | RESULTS

In total, 32 tags were deployed on 26 individual whales (15 mature females, 9 mature males, and 2 individuals of unknown sex). There were 691 observations of bubble-nets with at least one tagged individual in a group, and group sizes ranged from 1 to 8 individuals (Figure 2). There were six individuals tagged multiple times, two of which were tagged across multiple years, with a total of 280 dives (Table 1). Five groups contained multiple tagged whales, with a total of 70 synchronous dives.

3.1 | Principal component analysis

The principal component analysis showed that the first two components accounted for 77.2% of the variation in the data (Table 2). Based on the eigenvalues of each raw variable, the first principal component mainly describes the variance in (1) change in depth of the dive, (2) total pitch, (3) duration, and (4) total change in azimuth. The second

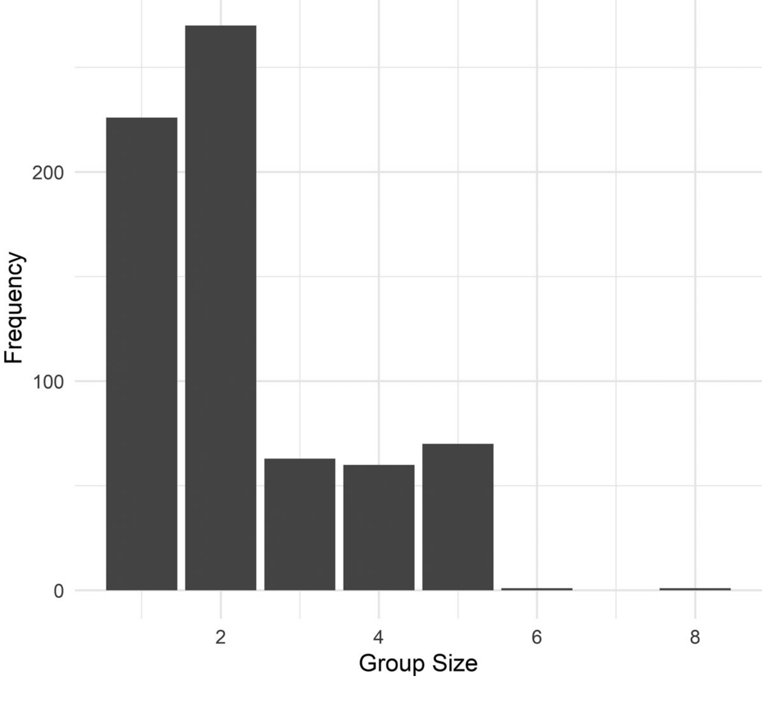

FIGURE 2 The distribution of group sizes in which tagged whales were observed bubble-net feeding.

TABLE 1 Demographic and tagging data for each tagged whale. In the age class column, "M" refers to a mature adult. "U" refers to unknown, when the whale's exact age or the whale itself is unknown. Group sizes are fluid, thus are represented by a range of sizes, and dive types are described in Figure 1. Superscripts (a, b) represent the same whale across years.

Tag #	Sex	Age class	Exact age	No. feeding events	Group sizes	Dive types
mn189b_06, mn192a_06	F	M	9	44	2–3	loops, double loops, and hybrids
mn195b_06	M	M	U	33	2–3	spirals
mn192b_06[a]	F	M	13	14	3	half spirals, spirals
mn188a_06	M	M	U	33	2–3	loops, double loops
mn188b_06	F	M	U	27	2	none, half spirals, spirals, loops, double loops
mn189c_06	F	M	U	21	1	loops, double loops
mn199a_07	M	M	16	5	3	spirals
mn197c_07	F	M	U	17	2–4	loops, double loops
mn197b_07	M	M	7	4	1–4	none, spirals, loops
mn202a_07	M	M	5	12	1–2	spirals
mn198c_07	M	M	5	11	2	spirals
mn184b_08[a]	F	M	17	43	1–3	none, half spirals, spirals, loops, double loops
mn196b_08	M	M	23	2	2	loops
mn192a_08, mn184a_08	F	M	6	130	1–2	loops, double loops
mn189a_08	M	M	U	1	3	spirals
mn196a_08	F	M	18	33	2–3	loops
mn182a_08	F	M	U	37	1–3	none, loops, spirals, double loops
mn184c_08	F	M	U	43	1–3	none, loops, spirals, double loops
mn209b_09, mn211a_09	M	M	5	4	1	hybrids
mn211b_09	F	M	14	9	2	spirals
mn209a_09	F	M	U	4	1	spirals
mn173a_12[b]	F	M	U	15	1–3	spirals
mn176b_12	F	M	U	21	2–4	none, spirals
mn173a_15[b]	F	M	U	56	4–5	spirals, loops
mn173b_15	U	M	U	32	2, 5	none, spirals
mn173c_15	F	M	18	49	3–5	half spirals, spirals
mn169b_16	U	U	U	7	2	double loops
mn169c_16	F	M	U	7	2	half spirals, spirals

principal component mainly describes the variance in (1) fluke frequency, (2) total roll, and (3) maximum depth. Because the first two components accounted for such a high percentage of the variability, we used the two principal components, referred to as PC1 and PC2, and generally as "dive metrics." Based on the most heavily weighted variables in PC1, we interpret a change in this component to be more heavily correlated with the length of time and distance dived in the feeding dive. As PC2 was more heavily weighted by dive depth and fluke frequency, we interpret a change in PC2 to be more heavily correlated with a whale's exertion in a dive. An *increase* in PC1 and a *decrease* in PC2 reflect negative trends in the raw independent variables. While the variables were relatively evenly weighted across PC1 and PC2, we decided it was important to include all movement variables available from the tag rather than depending on fluke frequency and maximum depth alone. Both principal components reflect a change in what we refer to as "dive complexity."

TABLE 2 Principal component analysis results. The loadings of each variable in the principal component analysis, and the variance explained by each component. PC1 accounts for 61.35% of the variance in the data, and PC2 accounts for another 15.84% of the data.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Σ Δ Azim	**0.15018**	**0.17222**	0.09630	0.07288	0.24813	0.25328	0.07174
Σ Δ Pitch	**0.16360**	**0.09711**	0.06690	0.18631	0.02114	0.18153	0.30771
Σ Δ Roll	**0.11467**	**0.21203**	0.01844	0.34343	0.09974	0.06643	0.00525
Σ Δ Depth	**0.17211**	**0.06107**	0.09236	0.05584	0.10707	0.23515	0.30487
Duration	**0.16343**	**0.04644**	0.02999	0.10034	0.36864	0.16286	0.09322
Maximum depth	**0.13111**	**0.18450**	0.31993	0.10497	0.12052	0.09798	0.18136
Fluke frequency	**0.10490**	**0.22664**	0.37607	0.13623	0.03476	0.00277	0.03586
Eigenvalues							
Variance	**4.294**	**1.109**	0.571	0.538	0.267	0.144	0.077
% of variance	**61.349**	**15.841**	8.157	7.688	3.820	2.051	1.094
Cumulative % of variance	**61.349**	**77.190**	85.347	93.035	96.855	98.906	100

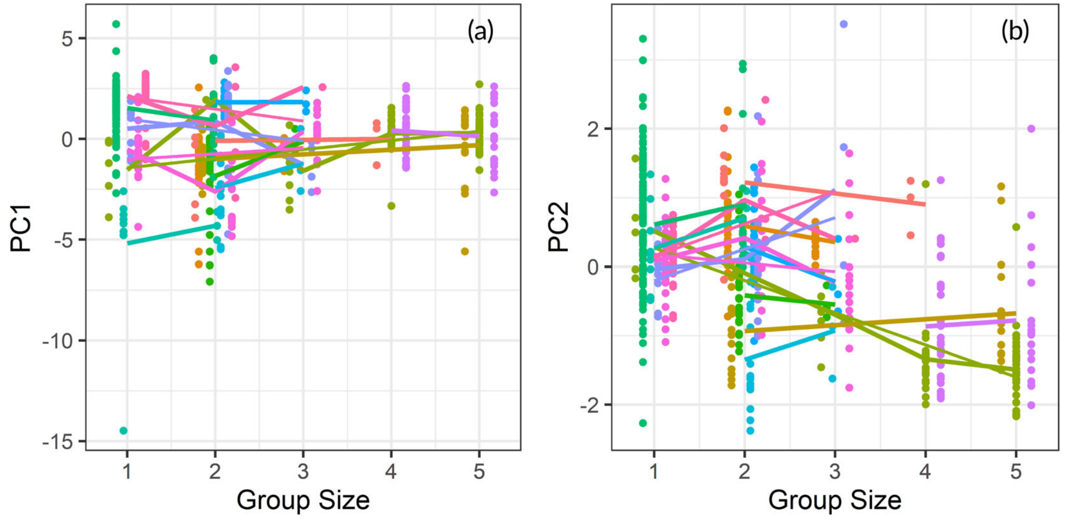

FIGURE 3 The relationship between group size and PC1 (a) and PC2 (b) for each individual in the southern Gulf of Maine population. PC2 mainly describes the variance in fluking frequency, roll, and maximum depth. Each color represents a different animal, and lines connecting points indicate the trend of the relationship between PC2 and group size within a certain individual. There is an overall negative trend with group size and PC2 ($F_{1,12} = 5.808$, $p = .033$).

3.2 | The stability of individual dive behavior and the influence of group size

Most (88.5%) of the whales performed one specific dive type for a majority of their dives. 15.4% of whales performed double-loops for a majority of their dives, 50% performed upward spirals, 19.2% performed single loops, 11.5% used hybrids, and none of the whales used upward lunges or half-spirals for a majority of their dives. Some

TABLE 3 ANOVA results for the effect of group size on principal components. Listed are the *p*-values of the ANOVA interpreting the results of linear models on PC1 and PC2 for whales observed feeding in that group size three or more times, respectively. The degrees of freedom indicate the number of tagged individuals observed in a certain group size (no. whales) and the total number of feeding dives in each group size (no. obs.).

Group size	PC1 *p*-value	PC2 *p*-value	No. whales	No. obs.
1	**<2.2e−16**	**7.98e−14**	8	213
2	**<2.2e−16**	**<2.2e−16**	15	241
3	**3.91e−07**	**.006583**	7	43
4	.7565	**4.99E−06**	2	51
5	.2739	**2.31E−05**	2	65

TABLE 4 The groups of whales tagged synchronously. The number of dives refers to the numbers of synchronous bubble-net dives in which both whales were tagged. The group size is the number participating in that foraging group.

	Tagged members of the group	Number of dives	Total group size
Group A	Mn192a_06	12	3
	Mn192b_06		
Group B	Mn169b_16	7	2
	Mn169c_16		
Group C_1	Mn173a_15	16	5
	Mn173b_15		
	Mn173c_15		
Group C_2	Mn173a_15	24	4
	Mn173c_15		

TABLE 5 Results of paired *t*-tests between individuals feeding together. A significant *p*-value (in bold) supports the alternative hypothesis that the true difference in means for the pair is not equal to 0.

	p	*df*
Group A		
PC1	**.000364**	11
PC2	**.01866**	11
Group B		
PC1	**.000595**	6
PC2	**3.19E−05**	6
mn173a_15 & mn173b_15		
PC1	.09822	17
PC2	**.000513**	17
mn173a_15 & mn173c_15		
PC1	.6293	40
PC2	**1.52E−05**	40
mn173b_15 & mn173c_15		
PC1	.3025	15
PC2	.8029	15

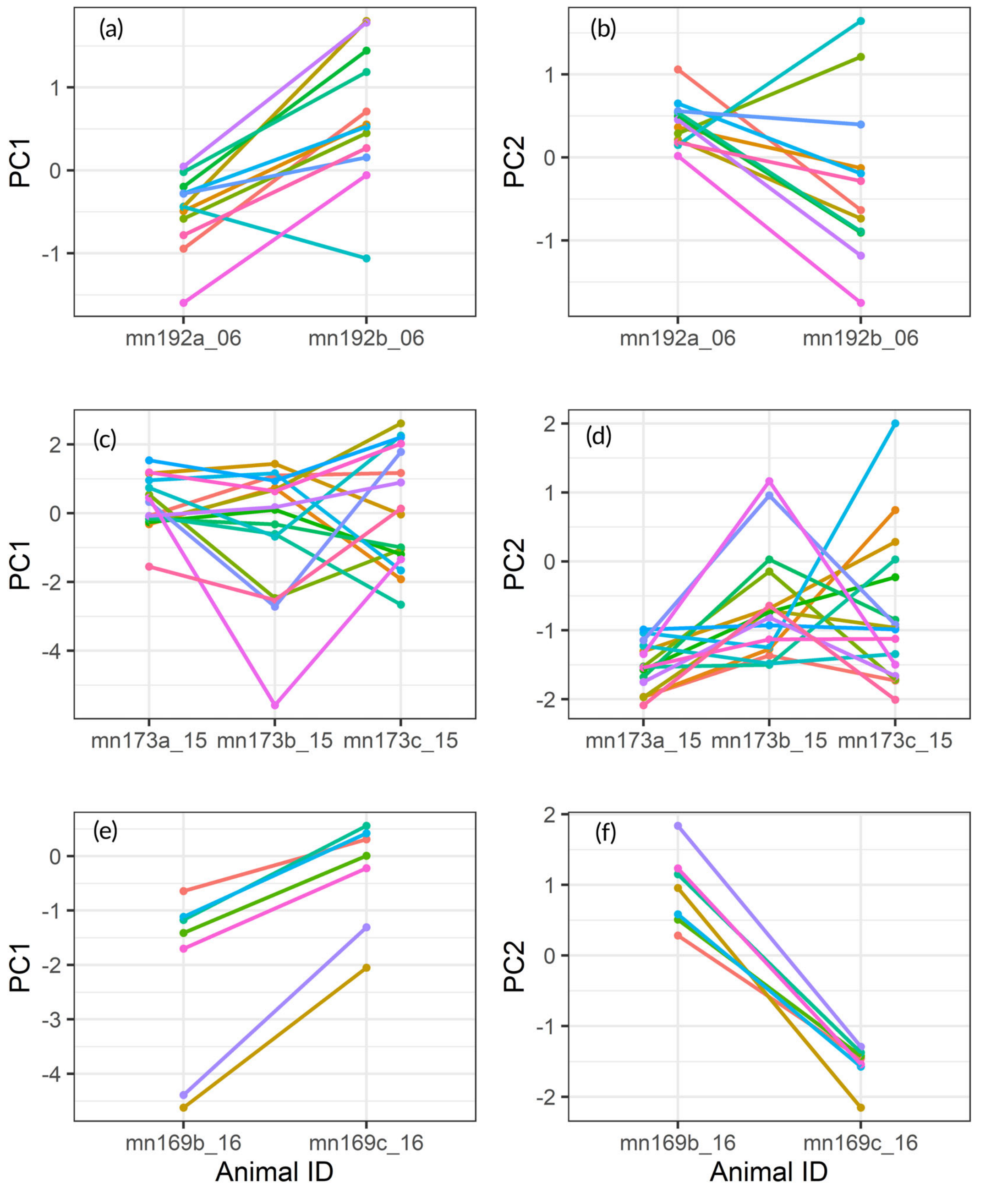

FIGURE 4 Each pair's dive variables plotted together. The lines connecting points are colored based on paired dive number; the lines indicate what the whales were doing during the same synchronous dive. Mn192a_06 and mn192b_06 (a and b) and mn169b_16 and mn169c_16 (e and f) showed significant differences in their dive behaviors. Mn173a_15, mn173b_15, and mn173c_15 (c and d) exhibited no difference in PC1 dive metrics between the three whales (c), but there was a significant difference in PC2 (d).

whales (11.5%) showed more plasticity, performing several dive types at similar frequencies. Double-loops and hybrids were seen in smaller groups of 1–3 and 1–2 individuals, respectively. Upward spirals, upward lunges, half spirals, and single-loops were observed for all group sizes.

For the linear mixed effects model across group sizes and dive types for the 13 individuals, there was no evidence to support the hypothesis that there is an effect of group size on PC1 ($F_{1,12} = 1.505$, $p = .243$). The model provided evidence to support that there is a significant negative effect of group size on PC2 ($F_{1,12} = 5.808$, $p = .033$; Figure 3), suggesting that increasing group size decreases exertion but not dive length. We excluded groups of 6 and 8 because there was only one tagged individual in each group size (Figure 2). For group sizes of 1, 2, and 3, both the PC1 and PC2 variables were significantly different across individuals observed in each respective group size, suggesting variability in dive duration and exertion across individuals (Table 3). For group sizes of 4 and 5, which had smaller sample sizes (Figure 2), the dives were significantly different in PC2, indicating variability in exertion. Only a single feeding type, the upward spiral behavior, showed a correlation between group size and both PC1 ($p = .012$) and PC2 ($p = .022$), suggesting increasing group size changes the dive behavior of participants.

3.3 | The variability of behavior in a feeding group

Tagged individuals feeding within the same group showed statistically different dive behaviors from each other. Two of the five deployments in which there was more than one tagged individual in the same feeding group only had 1–2 dives recorded synchronously, which was insufficient for comparison and not included in this analysis. In two of the remaining three instances, two individuals in a feeding group were tagged together, groups A and B (Table 4). In the third instance, three whales were tagged feeding together, but one of the whales left the group (groups C_1 and C_2). Group A was joined by one untagged whale to make up a group of 3, Group B were a group of 2, Group C_1 was part of a group of 5, and Group C_2 a group of 4.

The paired *t*-test revealed that the means of each dive metric differed for Group A or B (Table 5). Group C_1 and C_2, split into pairs for *t*-tests, had different results. We found no significant difference in the mean PC1s, and the mean PC2 was only significantly different than the other two whales for one of the whales (mn173a_15). The relationships between the individuals in all three groups are represented in Figure 4.

Both Group A and B had one tagged member that performed double-loop dives in 100% of the recorded synchronous dives, while the other tagged animal performed other types of dives (upward lunges, half spirals, upward spirals, and loops). All tagged members in Group C_1 and C_2 performed upward spiral behaviors in most of their synchronous dives.

4 | DISCUSSION

Using a combination of motion-sensing tag data and individual sighting histories, we found that individual bubble-net feeding humpback whales show consistency in their dive behavior independent of group size, providing evidence for individual variation in behavior within feeding groups. Additionally, there appears to be role differentiation within feeding groups depending on the type of bubble-net behavior collectively being performed. Specifically, in two separate pairs performing double-loop bubble-nets, one member consistently performed double-loops, while the other associated whale performed less complex dive behavior suggestive of herding. This may indicate that double-looping is a feeding behavior that can be performed with multiple active members taking on different roles, providing preliminary support for a division of labor. In other groups consisting of three whales, all of which were tagged (C_1 and C_2), each whale performed kinematically similar upward spirals on the same dives. This suggests that the three whales performed similar dive behaviors in the bubble-net feeding event, which may indicate that individuals participating in group upward spiral behavior use more similar dive patterns to the other participants than those observed foraging using double-loops. However, more samples of concurrently tagged whales would be necessary to provide more support.

Based on the data from whales tagged concurrently, it is possible that individual preference for certain dive behaviors impacts the size and collective behavior of the group, or that prey patch size influences group size. For instance, double-loops are active and require substantial maneuvering and herding on the part of the individual (Wiley et al., 2011). The behavior involves two shallow, consecutive loops with a lobtail at the surface in between, which may result in a relatively small concentration of prey. As we observed repeated associations between active participants—or whales performing some type of herding behavior—and double-looping individuals (12 coordinated dives in Group A, 7 in Group B), it is possible that an additional herder is useful, though other participants may not need to perform as complicated of herding techniques. These groups were also comparatively small (2–3 individuals), which could indicate that the number of whales that can successfully share the catch is limited. Therefore, double-loop behaviors might only facilitate the capture of smaller prey patches, and perhaps could be used as an indicator of relative prey patch size in an environment. Alternatively, upward spirals appear to be a relatively flexible behavior, with the number of spirals, the diameter, and the speed all varying between feeding events and individuals. We observed in all 40 of the dives recorded for groups of four to five individuals (C_1 and C_2) that multiple individuals in a group were performing upward spirals. This leads us to postulate that the number of whales feeding in a group may limit the amount of movement of each individual by restricting the space accessible for each whale within the bubble-net, or it may limit the amount of movement necessary to herd the prey. Alternatively, the size and orientation of the prey patch may limit the inclusion of additional participants. Hazen et al. (2009) found that surface feeding humpbacks in this region target relatively large, vertically distributed schools of sand lance (*Ammodytes americanus* and *A. dubius*), but there may be variability in patch size and characteristics targeted by different sized groups. As larger group sizes are seen less often on this foraging ground, it is likely prey patch size (and possibly increased scrounging events) that limits large group formation. This variability in behavior may be indicative of changing roles within a group dependent on group size, as supported by the changing dive behaviors in large groups performing upward spirals. While individual preference for dive types might drive the formation of groups and limit group size, the size and composition of the prey patch targeted likely plays a role as well.

Our results suggest a decrease in exertion by each whale with increasing group size during bubble-net feeding, as evidenced by the decrease in PC2 with increasing group size, indicating that there is a reduction of effort in larger groups. While both PC1 and PC2 were used to describe complexity, the PC2 was weighted by the fluke frequency variable, roll, change in azimuth, and depth. Because fluking frequency can be used as a metric of effort (Kooyman & Ponganis, 1998) and turning requires more energy relative to the straight path (Wilson et al., 2013), this might indicate a decrease in exertion with increasing group size and a subsequent energetic benefit to feeding in a group. Feeding in a larger group decreases the energy expended by the individual, potentially increasing the net energetic benefit of group foraging, or counteracting the decrease in intake resulting from competition within the group (Beauchamp, 2014; Packer & Ruttan, 1988). However, as we observed, not all groups were large. Variability in group sizes may represent different solutions to procuring food in variable environments, as group sizes tend to increase with food quality as well as the patchiness of its distribution (Pulliam & Caraco, 1984). However, due to the underlying impacts of intergroup competition, as well as potential scrounging, the observed group size might not represent the optimal situation for individual fitness (Clark & Mangel, 1986). The additional benefits of group foraging, such as increased search ability, reach a maximum more quickly in larger groups. In large groups, individuals end up overlapping in search areas, making the additional members a detriment to the fitness of the group (Pulliam & Caraco, 1984).

We found no significant relationship between group size and the other dive metrics (PC1), suggesting there may be stability in other components of dive behavior like dive length with increasing group size, while exertion (PC2) decreased with group size in all animals tagged in multiple group sizes. Only whales within the subset of individuals using upward spirals showed a significant trend between group size and both dive metrics (PC1 and PC2), which indicates that the tagged animals performing coordinated upward spirals decreased the length and the energetics of their dives, which we describe together as “complexity,” with increasing group size. This suggests that upward spirals might be the most mutually beneficial strategy, as there are fewer observations of more complicated behaviors in larger groups and a reduced complexity of dives with group size.

We can assume, given its ubiquity, that group feeding is effective and that it increases the net energy gain of the participants by reducing the amount of work performed by each individual to find and exploit prey, increasing the amount of prey captured, or both. A more comprehensive understanding of these changes in foraging behavior requires information on prey patches targeted by the whales bubble-net feeding in different group sizes to test if larger groups target larger prey patches. Additionally, understanding if consumption rates increase commensurate with these changes in group size and patch quality is necessary. While much is known about sand lance in the Gulf of Maine, little information exists on their schooling behavior. As noted earlier, bubble net feeding humpbacks are known to target large, vertically distributed prey aggregations at the surface (Hazen et al., 2009) but how this relates to the general schooling behavior of sand lance is unknown. Foraging behavior is known to be highly plastic due to the mobile nature of sand lance prey patches (Kirchner et al., 2018). Therefore, the optimal feeding strategy and group size needed to exploit certain types of patches may be spatially and temporally variable. Incorporating spatial prey data and comparing it to the different dive types being used may provide more information about the environmental context of different dive strategies.

While we reported basic demography data, incorporating more detailed information on individuals may provide more information about the relationship between age, sex, and feeding strategy. The whales tagged in this study were all mature, but future research should target a wider demographic range to investigate how these different behaviors are developed. Using social information about these populations may provide more evidence for group size, associate, and feeding type preferences among individuals in the populations that can aid in testing the hypothesis for cooperation in this, and other, species. Some individuals in the southern Gulf of Maine are known to move between feeding groups, potentially scrounging. There are also individuals that are known to form stable associations within this population (Weinrich, 1991), which allows for more cooperative or behavioral complexity than the behaviors adopted by individuals that form more fluid associations. It is certainly possible that both cooperation and scrounging are occurring on the same foraging ground. Incorporating social data in an analysis of a greater sample of the population may indicate whether scrounging or cooperation are the rules in coordinated feeding in the southern Gulf of Maine. Additionally, while our study provides insight into variability of behaviors in a feeding group, incorporating information on which individuals are blowing bubbles would provide useful information in determining roles within foraging groups, and whether a division of labor occurs.

4.1 | Conclusion

Our findings support the hypothesis that in the southern Gulf of Maine, individual humpback whales show a preference for certain bubble-net feeding dive types, and group size influences the exertion required to perform that behavior. The dive types that individuals use showed some stability across group sizes, suggesting specialization in certain bubble-net feeding behaviors, which could influence the composition of the feeding group and the behaviors of other individuals, especially if different roles are adopted within a group. The diversity of dive types and metrics observed within group sizes provides further evidence for the variability of bubble-net feeding strategies adopted in this population, especially in smaller group sizes. There was evidence to suggest a decrease in exertion with increasing group size, indicating less exertion on the part of the individual when participating in larger groups. The decrease in dive complexity observed with increasing group size in animals using upward spirals indicates that upward spirals may be a behaviorally plastic group and mutually beneficial foraging strategy. By tagging whales feeding together, we were able to show that whales within a feeding group perform different behaviors, providing preliminary support for a division of labor. Future studies should investigate whether this amounts to role specialization on the Southern Gulf of Maine foraging ground.

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AUTHOR CONTRIBUTIONS

Natalie Claire Mastick: Conceptualization; data curation; formal analysis; investigation; methodology; visualization; writing – original draft; writing – review and editing. **David Wiley:** Conceptualization; data curation; methodology; project administration; resources; supervision. **Dave Cade:** Conceptualization; data curation; methodology; software; validation; writing – review and editing. **Colin Ware:** Conceptualization; software; writing – review and editing. **Susan Parks:** Conceptualization; project administration; resources; writing – review and editing. **Ari Friedlaender:** Conceptualization; funding acquisition; project administration; resources; supervision; validation; writing – review and editing.

COMPLIANCE WITH ETHICS STANDARDS

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