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ORIGINAL ARTICLE

Evidence of sociality and group foraging in Antarctic minke whales (*Balaenoptera bonaerensis*)

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Abstract

Top krill predators such as the Antarctic minke whale (AMW) serve a vital role within the fragile Antarctic sea-ice ecosystem. They are an abundant krill specialist, but their ecological role in the Antarctic remains poorly understood due to their cryptic behavior and remote habitat. It is therefore crucial to develop a baseline understanding of their basic social and foraging ecology. This study uses animal-borne camera tags to quantitatively explore these critical ecological aspects. Twenty-eight tags were deployed on AMW between 2018 and 2019 in Andvord and Paradise Bays around the Western Antarctic Peninsula. Tag data were analyzed with respect to diving, foraging, and social behavior. Results suggest the presence of loose fission-fusion sociality, with individuals forming short-term associations in 60.6% of cases including both foraging and non-foraging contexts. Socializing was significantly more common for larger individuals and resulted in a significant decrease in foraging rates for both shallow (<30 m) and deep (>30 m) dives. There were 12 instances of simultaneously tagged individuals that associated with one another in pairs or trios, displaying synchronized spatial movement and diving behavior. These data illustrated the use of group foraging strategies, with high incidence of synchronized foraging dives (67.5% of associated dives) and lunges (64% of associated lunges). Our results provide clear baseline information on AMW sociality and group foraging, which will help direct future studies for more targeted work. This study will improve our ability to understand the relationship between Antarctic species and their environment as climate change continues to alter the ecosystem landscape.

Significance

Baseline information on sociality is thus key to understanding broader species ecology, which is especially important for keystone species. Our study is the first to directly provide these foundational insights for AMW, a common krill predator in the Antarctic sea-ice ecosystem. Individuals displayed short-term associations in a fission-fusion social structure similar to other baleen whale species, and socializing was associated with both larger individuals and lower foraging rates. In simultaneous tag deployments, tagged individuals frequently associated with one another and displayed synchronized diving and foraging behavior. Our results suggest that sociality may be more important to minke whale ecology than previously thought. These results provide necessary baseline information for more targeted ecological questions, such as the benefit of group foraging or how such precise synchrony might be coordinated.

Keywords Behavioral ecology · Sociality · Group foraging · Foraging strategy · Biologging · Antarctic minke whales

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Introduction

Changing ecosystem conditions are often reflected in the ecology, behavior, or physiology of both keystone species and their predators. Due to this link, a number of Antarctic krill (*Euphausia superba*) predators serve as sentinel species for the Antarctic sea-ice ecosystem (CCAMLR 2004). Krill are a keystone Antarctic species, heavily reliant on sea ice conditions and cover, and thus their abundance is particularly vulnerable to the impacts of a warming climate (Nicol et al. 2008). For example, Southern Hemisphere humpback whales (*Megaptera novaeangliae*) show a strong correlation between body condition and key Antarctic climate indices due to their high-fidelity krill diet (Bengtson Nash et al. 2018). It is therefore important to have strong baseline understandings of predator ecology to better identify shifts in the ecosystem and the potential drivers behind those shifts (Bengtson Nash et al. 2018; Groß et al. 2020). The foraging behaviors of Antarctic minke whales (AMW, *Balaenoptera bonaerensis*), a key predator of Antarctic krill, and their relationship to both krill abundance and environmental conditions are becoming better studied (Friedlaender et al. 2014; Lee et al. 2017; Cade et al. 2023). However, there is still a dearth of studies regarding their social behavior and how it relates to their foraging ecology. The drivers of these processes are fundamental to species ecology, as they influence key population processes such as fitness (Lemonnier et al. 2022), genetics (Archie et al. 2008), and ecosystem dynamics (He et al. 2019). Theoretical models suggest that animals group together when the benefits of social living (e.g., decreased predation risk) outweigh the costs (e.g., resource sharing, increase in disease transmission) (Alexander 1974; Silk et al. 2017). For example, group size is often larger when food is more abundant and of higher quality (see Hanya and Chapman (2013) and Macdonald and Johnson (2015) for reviews). As the sea-ice ecosystem shifts due to climate change (Turner et al. 2005; Stammerjohn et al. 2008; Kusahara 2016), it is crucial to better understand these interdependent relationships through baseline knowledge (Bengtson Nash et al. 2018) and thus improve our ability to utilize sentinel species.

Social behavior in baleen whale species such as minke whales has been historically difficult to study for a variety of logistical reasons. In addition to the inherent difficulties of studying many marine species that are often far-ranging and only spend a portion of their time at the surface, most baleen whales appear to lack the strong and more long-term social bonds that are often seen in toothed whale species such as killer whales (*Orcinus orca*), sperm whales (*Physeter macrocephalus*), or bottlenose dolphins (*Tursiops spp.*) (Mann et al. 2000). Instead, they tend to demonstrate short-term associations with unrelated individuals in a loose fission-fusion structure (Clapham 1993; Alves et al. 2010). Large aggregations can sometimes occur (Landino et al. 1994; Findlay et al. 2017; Cade et al. 2021a; Herr et al. 2022), but these are typically associated with resource availability such as prey or mate access. Long-term stable associations have been documented in some species such as humpback whales (Weinrich 1991; Ramp et al. 2010), but detection of these relationships require multi-year studies in populations where individuals can be identified and re-sighted with consistency (Weinrich 1991; Ramp et al. 2010). Historically, studies have been limited to sightings data and photo-identification to examine social structure. Recent technological advances on these studies, such as the animal-borne camera tags employed here, allow for the inclusion of the rare and essential data on underwater behavior. It is only through such advances that progress has been made regarding the direct study of sociality in baleen whale species (Alves et al. 2010; Cade et al. 2021a, c; Casey et al. 2022; Mastick et al. 2022). The application of these advancements strongly positions our study to make novel contributions to the understanding of AMW association and social behavior.

Foraging is one of the main instances where baleen whales are known to associate (Landino et al. 1994; Mann et al. 2000; Sharpe 2002; Kot et al. 2014; Allen 2019) making them a valuable study species for the relationship between sociality and foraging ecology. This more commonly manifests in the form of aggregations around available prey, feeding near one another rather than explicitly coordinating. However, cooperative strategies have been documented in a select few species including bubble-net feeding in humpback whales (Sharpe 2002; Wiley et al. 2011), cooperative lateral lunging in Eden's whales (*Balaenoptera edeni edeni*) (Chen et al. 2023), and synchronized feeding dives in bowhead whales (*Balaena mysticetus*) (Moore et al. 2010). Animal borne tagging advancements are now allowing for a further exploration of the extent and role of coordination through simultaneous tagging events (Ware et al. 2014; Cioffi et al. 2021; Mastick et al. 2022). For example, tagging studies on humpback whales have shown coordination with conspecifics for multiple strategies such as bottom (Parks et al. 2014) or bubble-net feeding (Mastick et al. 2022). In cetaceans such as Cuvier's beaked whales (*Ziphius cavirostis*) which are highly cryptic, extended synchronized foraging dives have been recorded in simultaneously tagged individuals (Cioffi et al. 2021). AMW have been documented foraging in small groups (Friedlaender et al. 2014; Risch et al. 2014; Casey et al. 2022), suggesting that a social component is at least partially present in their foraging behavior. This is further supported by recent documentation of a call, the *rumble*, which occurs during foraging and thus may be utilized for group foraging (Casey et al. 2022). Baleen whales have been observed in large aggregations when prey densities are high (Cade et al. 2021a), and it is thought that aggregation formation may be socially mediated (Cade et al. 2021c). When feeding on fish, whales may also benefit directly from coordinated herding of otherwise disparate prey (Sharpe 2002), or the decreased energy required to feed when in a group (Mastick et al. 2022).

Among baleen whales, AMW social structure is particularly understudied due to their cryptic nature, short surface intervals, and the inaccessibility of their polar habitat. Despite their comparatively high abundance (Risch et al. 2019), what is known suggests that social bonds are not particularly strong (Casey et al. 2022). They are rarely found in large aggregations as sometimes seen in the larger rorqual species, though groups of up to 40 have been documented (Friedlaender et al. 2014; Risch et al. 2014). Instead, they seem to be primarily solitary or found in small groups of 2–6 that do not seem to associate for extended periods of time (Casey et al. 2022). Spatial sex-segregation has been found in both common minke whales (*Balaenoptera acutorostrata*) (Laidre et al. 2009) and AMW of East Antarctica (Horwood 1989), suggesting that socializing may have a sex-based component. While sex ratios of our AMW study population on the western Antarctic Peninsula do not significantly differ from parity, a possible skew towards females has been suggested (Pallin et al. 2022). Acoustics studies have found seasonality and diel patterns in the use of certain minke vocalizations, suggesting possible social functions such as social contact (Edds-Walton 2000) or reproduction (Casey et al. 2022). Furthermore, recent work by Casey et al. (2022) identified a newly described call, the *growl*, that predominantly occurred (~70% of call records) in the presence of close conspecifics. Growls occurred in both foraging and non-foraging situations, suggesting intentional social contact independent of active foraging.

The aim of this study was to provide baseline information on AMW sociality in a feeding ground context using data collected from animal-borne tags which captured video footage, underwater behavior metrics, and 3-dimensional movements. Our specific objectives were to (1) determine if there was a relationship between group size and foraging efforts (in the form of feeding rates) and (2) provide a detailed description of movement, behavior, and foraging effort for simultaneously tagged individuals during bouts of social association. Based on the common occurrence of short-term associations in other baleen whale species, we hypothesized that similar sociality would be present in foraging AMW. We further hypothesized that some degree of social or group foraging would be utilized, given previous documentation of foraging aggregations and the recent evidence of a possible foraging acoustic signal. Together, these will provide a more comprehensive understanding of the role that sociality may play in AMW foraging ecology.

Methods

Data collection and processing

Field work consisted of 24 total field days occurring in February and March of 2018 and 2019 aboard the ARSV Laurence M Gould. Tagging work was conducted from inflatable boats launched from the *Gould*, a 4.8 m aluminum-hulled SOLAS and a 5 m Zodiac Mark. A 6 m carbon-fiber pole was used to deploy suction cup attached video and inertial measurement unit (IMU) tags manufactured by Customized Animal Tracking Solutions (CATS) (Cade et al. 2016; Goldbogen et al. 2017a). Tags were equipped with tri-axial accelerometers and integrated video cameras (1290 × 720 or 1920 × 1080 resolution). A total of 28 deployments on 24 unique individual AMW were used for this study: 6 deployments on 6 unique individuals in 2018, and 22 deployments on 18 unique individuals in 2019 (4 individuals were tagged twice). 19 of these animals were with conspecifics at the time of tag deployment, while 9 animals were solitary. All deployments were in Andvord Bay and Paradise Bay, both of which are on the western side of the Antarctic Peninsula (Fig. 1). Blind data recording was not possible as our study involved focal animals in the field.

To determine spatial movements of each tagged whale, 2-dimensional animal "pseudotracks" were created by integrating animal speed and heading, then distributing accumulated error along the tracks between known locations, following previous studies (Cade et al. 2021c). Known location data included tag on and off locations, locations taken from animal resights, and the GPS on the tag, all of which were then corrected for topographical features (Wilson et al. 2007; Linsky et al. 2020; Cade et al. 2021b). Tag accelerometers for all deployments were sampled at 400 Hz, magnetometers and gyroscopes at 50 Hz, and pressure, light, temperature and GPS at 10 Hz. All data were decimated to 10 Hz, tag orientation on the animal was corrected for, and animal orientation (pitch, roll, heading) was calculated using custom-written scripts in Matlab 2014a (following Cade et al. (2021c). Animal speed for all deployments was determined using the amplitude of tag vibrations (Cade et al. 2018), and the animal's spatial positions for the duration of each deployment were mapped using pseudotracks. Diel period (Day vs. Night) was determined from the angular sun position at a given location and time using the Matlab package "Sunrise Sunset". Body lengths for animals were reported previously (Cade et al. 2023) and in that study were either directly measured via UAS photogrammetry or

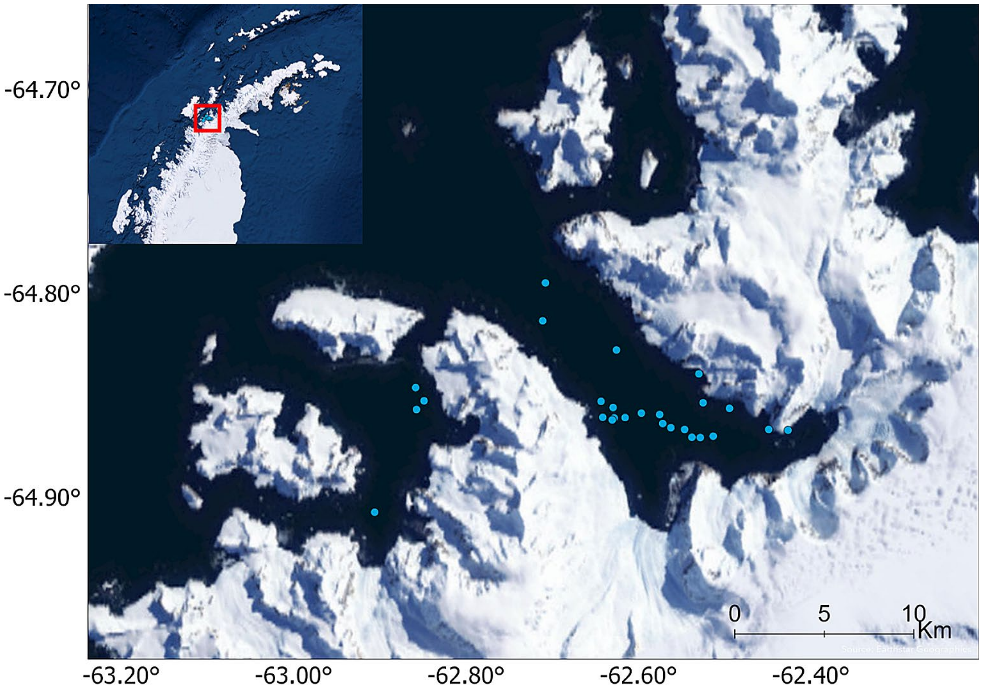

Fig. 1 A map of the study area within the Western Antarctic Peninsula. Blue dots indicate tag deployment locations

estimated from allometric regression on the calculated distance travelled during engulfment (see Cade et al. 2023 for full methodology details).

The highly stereotyped lunge feeding on krill (Goldbogen et al. 2006; Cade et al. 2016) allows for individual lunge feeding events to be identified from the tag records. These events, defined as the rapid engulfment of a mouthful of prey-laden water followed by subsequent filtration, were identified by stereotyped maneuvers, typified by acceleration followed by rapid deceleration (Cade et al. 2016; Kahane-Rapport et al. 2020) as the whale is slowed from the engulfed water mass (Potvin et al. 2020). Feeding rate (as lunges/hr) was calculated for every dive with at least one lunge feeding event. Feeding rate was calculated over 10-minute time bins by counting the number of lunges from 5 min before to 5 min after the midpoint of the dive. These values were then converted into lunges per hour by multiplying this rate by 6. Dives were defined as an individual beginning at the surface, descending to at least five meters, and returning to the surface. Foraging dives were defined as any dive that included at least one detected lunge. A ‘dive record’ is all data associated with a single dive (as defined above) such as depth, duration, social status, and foraging status (see raw data in Dryad for complete list of all variables). ‘Dive time’ is defined as the total duration of a single dive, measured in seconds.

Social data

Social audit data previously published in Casey et al. (2022) were calculated using the video footage obtained from each CATS tag. Expert observers used BORIS auditing software (Friard et al. 2016) to count the number of conspecifics in direct view of the camera frame, indicating close proximity of the tagged individual while moving in the same direction. This proximity and coordination allowed us to consider these individuals to be associates following previous studies using both sightings (Baker and Herman 1984; Clapham 1993; Ramp et al. 2010) and camera tags (Casey et al. 2022). Social data could only be obtained during daylight hours and at shallow enough depths that visual confirmation of conspecifics could be reliably determined in the video footage. This varied throughout the season with weather conditions and seasonal sun angles, but images typically became too dark to use with light levels under 20 lx. Horizontal field of view was approximately 95 degrees, while vertical field of view was approximately 54 degrees. Due to these limitations in the camera field of view, the number of conspecifics per dive event was broadly categorized into two social states: alone and group. “Alone” was defined as the absence of any conspecifics in the field of view. “Group” was defined as the presence of a one or more conspecifics in the field of view.

To determine if social state have a relationship with foraging efforts, the lunge rates were compared between social states in two distinct bins: shallow dives (< 30 m) and deep dives (> 30 m). This separation reflects that AMW typically exhibit significantly higher foraging efforts in shallow dives compared to deep dives (Cade et al. 2023). Data containing both social audit and lunge rate values were tested for normality using the Shapiro-Wilk Test (Shapiro et al. 1968) and variance was tested using the Levene’s Test (Levene

1961). As these data were found to be neither normally distributed nor having equal variance, comparisons were therefore made using the non-parametric Kruskal-Wallis test (Kruskal and Wallis 1952). The size of social state's effect on lunge rate was quantified with the Epsilon-squared Test, which is used for non-parametric tests such as the Kruskal-Wallis (Tomczak and Tomczak 2014). It uses the following formula:

$$\in^2_{KW} = H \times \frac{n+1}{n^2-1}$$

where H is the test statistic (here, the Kruskal-Wallis Chi-squared statistic), and n is the total sample size. Values range from 0 to 1 to indicate the strength of the effect, where 0-0.01 = 'negligible', 0.01–0.04 = 'weak', 0.04–0.16 = 'moderate', 0.16–0.36 = 'relatively strong', 0.36–0.64 = 'strong', and 0.64-1.0 = 'very strong' (Rea and Parker 2014; Tomczak and Tomczak 2014).

Association data

Of the 28 tag deployments, there were 15 simultaneous deployments from 15 unique individuals, allowing for an examination of the movement and behavior of associated individuals. Two of these deployments were from March 2018 and 13 were from March 2019. Tags were identified as simultaneous based on date and time stamps on the tag records. Social associations were determined based on closely synchronized movements and motion patterns, as determined by the pseudotracks which were animated using ArcGIS Pro. Pseudotracks are made from integrating samples at 10 Hz, each with an unknown error in heading and speed. Since tracks do not account for current velocities, positional error can accumulate rapidly. However, pseudotracks are highly accurate representations of animal movements over short time scales because relative movement is measured directly from the tag's sensors. Therefore, coordinated motion between tags was the primary determiner of association during simultaneous tags. Each instance in which simultaneously tagged individuals were associated with one another was labelled as a separate "Association Event" (see Table 1). When group composition changed (i.e., a third tagged individual joined an associated pair or two tagged individuals separated for a period and then joined back together), it was labelled as a new Association Event. Online Resource 14 provides the animation showing the pseudotracks of both animals in Association Events E and F (with a period in which they separate), which illustrates the clear coordinated movements of each individual during the association events and the lack of synchrony during the period of separation. Tag records provided depth and time stamps for each dive recorded. Acceleration records also provided the timing of each lunge (Goldbogen et al. 2017b). The degree of synchronization of both dives and lunges for associated individuals was determined through pairwise comparisons of group members, allowing us to calculate the difference in the nearest neighbor timestamps between all group members, following Cioffi et al. (2021). Dive records of associated individuals were considered synchronized if dives began within 30 s of one another. Lunge events were considered synchronized if they occurred within 5 s of one another, as minke lunges take approximately 15 s to complete (Cade et al. in review) and our lunge timing data records the point at which the mouth opens. Absolute value of the timing differences was used as a proxy for how closely synchronized the individual behaviors were.

Results

Social audits

Of the 13,049 dive records, 3,456 contained social aufditing data where the presence and number of conspecifics could be assessed using tag video footage (summary in Table 2). Minkes associated with conspecifics in the majority (60.6%) of socially audited dive records (Fig. 1). Individuals also frequently switched between social states; of the 25 deployments with social data available, the vast majority (95.6%) exhibited both social states, with only one individual recorded alone without any conspecifics observed (Table 2). Socializing occurred during both foraging and non-foraging contexts (Fig. 2), indicating that it is not restricted to certain behavioral states. Socializing also appeared to interact with body size, as animals with conspecifics were significantly larger compared to those alone (Fig. 3, Kruskal-Wallis: Chi-squared = 149.96, $p < 0.001$). Overall effect size of body size on social state was weak (Epsilon-squared = 0.0434).

Foraging efforts as reflected by lunging rate were significantly higher for individuals who were alone versus those with conspecifics in both shallow (< 30 m, Kruskal-Wallis: Chi-squared = 48.448, $p < 0.05$) and deep dives (> 30 m, Kruskal-Wallis: Chi-squared = 26.822, $p < 0.05$), as shown in Fig. 4. The effect size of social state on lunging rate was shown to be moderate (Epsilon-squared = 0.06 for both shallow and deep dives). There were 8 individuals that were found in both social states during shallow dives and 15 individuals found in both social states during deep dives. The changes to their feeding rates skewed towards increasing with group size. A majority of individuals increased feeding rate with group size for both shallow (87.5%) and deep (66.7%).

Table 1 Association Event information. Mean dive and lunge differences are reported as absolute values

Association Events	Group Size	Start	Duration (hh: mm)	Mean Dive Dif. (s)	Mean Lunge Dif. (s)	Whale IDs	Total Dives	Foraging Dives	Lunge Counts	Deep Dives	Shallow Dives	Day Dives	Night Dives
A	**2**	**6/03/2018 17:55**	**0:23**	**6**	**2**	**bb180304-45**	14	21.4%	30	21.4%	78.6%	100.0%	0.0%
						bb180305-42b	10	20.0%	19	20.0%	80.0%	100.0%	0.0%
B	**2**	**25/02/2019 16:46**	**1:01**	**13**	**24**	**bb190224-48**	39	12.8%	13	15.4%	84.6%	100.0%	0.0%
						bb190224-52	46	10.9%	24	10.9%	89.1%	100.0%	0.0%
C	**2**	**26/02/2019 11:05**	**7:05**	**11**	**4**	**bb190225-54**	210	77.1%	376	10.0%	90.0%	100.0%	0.0%
						bb190225-55	238	73.9%	412	7.6%	92.4%	100.0%	0.0%
D	**3**	**27/02/2019 19:37**	**0:42**	**16**	**9**	**bb190226-48**	25	52.0%	36	8.0%	92.0%	100.0%	0.0%
						bb190226-51	32	56.3%	44	6.3%	93.8%	100.0%	0.0%
						bb190226-53	33	60.6%	37	6.1%	93.9%	100.0%	0.0%
E	**2**	**27/02/2019 20:30**	**4:58**	**16**	**5**	**bb190226-48**	250	56.4%	504	0.0%	100.0%	5.2%	84.4%
						bb190226-51	259	57.9%	566	0.0%	100.0%	6.6%	80.3%
F	**2**	**28/02/2019 9:32**	**7:30**	**12**	**6**	**bb190226-48**	199	27.6%	439	29.1%	70.9%	100.0%	0.0%
						bb190226-51	204	27.0%	431	28.4%	71.6%	100.0%	0.0%
G	**2**	**3/03/2019 17:12**	**0:24**	**17**	**1**	**bb190302-48**	12	25.0%	8	8.3%	91.7%	100.0%	0.0%
						bb190302-52	11	9.1%	6	9.1%	90.9%	100.0%	0.0%
H	**3**	**3/03/2019 17:39**	**1:53**	**14**	**3**	**bb190302-48**	45	31.1%	103	37.8%	62.2%	100.0%	0.0%
						bb190302-52	31	48.4%	118	54.8%	45.2%	100.0%	0.0%
						bb190302-53	39	30.8%	90	35.9%	64.1%	100.0%	0.0%
I	**2**	**3/03/2019 19:40**	**12:09**	**17**	**3**	**bb190302-52**	293	78.2%	950	12.6%	87.4%	7.5%	85.7%
						bb190302-53	389	55.5%	853	11.1%	88.9%	9.5%	84.3%
J	**2**	**5/03/2019 14:12**	**1:55**	**14**	**8**	**bb190304-45**	75	13.3%	67	14.7%	85.3%	100.0%	0.0%
						bb190304-51	65	13.8%	50	15.4%	84.6%	100.0%	0.0%
K	**2**	**5/03/2019 10:11**	**2:51**	**23**	**13**	**bb190304-51**	88	6.8%	19	11.4%	88.6%	100.0%	0.0%
						bb190304-57	65	9.2%	18	16.9%	83.1%	100.0%	0.0%
L	**2**	**5/03/2019 16:13**	**2:03**	**21**	**12**	**bb190304-51**	66	9.1%	44	9.1%	90.9%	100.0%	0.0%
						bb190304-57	39	20.5%	53	20.5%	79.5%	100.0%	0.0%

Table 2 A summary Table of deployments with social auditing data. Total dive records and total lunges are counts, while all other dive record columns are proportions out of the tag's total dive records

Deployment ID	Individual Unique ID	Duration (hh: mm)	Total Dive Records	Alone	Group	Foraging Dives	Total Lunges	Deep Dives	Shallow Dives	Day Dives	Night Dives
bb180227-45	bb180227-45	06:07	208	5.8%	94.2%	43.8%	201	7.7%	92.3%	79.8%	17.8%
bb180228-42	bb180228-42	05:44	185	66.5%	33.5%	37.8%	206	15.1%	84.9%	69.7%	15.1%
bb180304-40	bb180304-40	09:25	191	30.4%	69.6%	57.6%	443	52.9%	47.1%	84.8%	5.8%
bb180304-42	bb180304-42	02:03	66	12.1%	87.9%	13.6%	34	15.2%	84.8%	100.0%	0.0%
bb180304-45	bb180304-45	07:19	222	32.0%	68.0%	16.7%	305	21.2%	78.8%	89.2%	3.6%
bb180305-42b	bb180305-42b	06:54	234	33.8%	66.2%	8.5%	154	11.5%	88.5%	70.5%	16.7%
bb190224-48	bb190224-48	00:44	39	5.1%	94.9%	12.8%	13	15.4%	84.6%	100.0%	0.0%
bb190224-52	bb190224-52	05:26	306	77.1%	22.9%	30.4%	291	11.4%	88.6%	73.9%	14.7%
bb190225-54	bb190225-54	05:08	196	3.1%	96.9%	79.1%	346	7.1%	92.9%	100.0%	0.0%
bb190225-55	bb190225-55	05:01	214	31.3%	68.7%	74.8%	360	5.1%	94.9%	100.0%	0.0%
bb190225-57	bb190225-57	04:39	132	100.0%	0.0%	89.4%	379	33.3%	66.7%	87.9%	0.0%
bb190226-48	bb190226-48	03:48	130	7.7%	92.3%	37.7%	167	8.5%	91.5%	41.5%	40.0%
bb190226-51	bb190226-51	02:31	132	57.6%	42.4%	17.4%	55	3.0%	97.0%	37.9%	55.3%
bb190226-53	bb190226-53	02:10	99	27.3%	72.7%	33.3%	85	14.1%	85.9%	90.9%	0.0%
bb190226-56	bb190226-56	05:15	194	67.0%	33.0%	21.1%	125	11.3%	88.7%	62.9%	34.0%
bb190228-52	bb190228-52	02:35	68	47.1%	52.9%	4.4%	19	11.8%	88.2%	100.0%	0.0%
bb190228-55b	bb190228-55b	04:06	128	93.8%	6.3%	26.6%	221	27.3%	72.7%	96.9%	0.0%
bb190302-48	bb190302-48	02:00	64	3.1%	96.9%	25.0%	103	25.0%	75.0%	100.0%	0.0%
bb190302-52	bb190302-52	04:08	94	8.5%	91.5%	41.5%	280	44.7%	55.3%	87.2%	6.4%
bb190302-53	bb190228-52	02:41	78	6.4%	93.6%	32.1%	164	33.3%	66.7%	78.2%	16.7%
bb190304-45	bb190304-45	02:51	86	80.2%	19.8%	10.5%	79	17.4%	82.6%	100.0%	0.0%
bb190304-51	bb190304-51	02:11	79	0.0%	100.0%	6.3%	18	11.4%	88.6%	100.0%	0.0%
bb190304-57	bb190304-57	03:43	80	10.0%	90.0%	22.5%	84	30.0%	70.0%	100.0%	0.0%
bb190306-52	bb190228-55b	01:59	125	12.0%	88.0%	56.0%	173	9.6%	90.4%	93.6%	0.0%
bb190309-52	bb190309-52	05:04	106	61.3%	38.7%	31.1%	283	34.0%	66.0%	100.0%	0.0%

Synchronized behavior

There were 7,127 dive records during the simultaneous tagging of at least two individuals. Of these, 2,777 dive records reflected individuals associating with one another based on coordinated pseudotrack movements and dive records (see Online Resource 14). These could be broken down into 12 distinct association events (labelled A-L), made up of 10 pairs and two groups of three (Table 1). A total of 15 unique individuals were captured during these association events, with 7 individuals involved in more than one event. Associations were only defined here based on the coordination of tagged individuals rather than social audit data, to maintain a focus on verifiably synchronized behavior. Associations between individuals were more common during foraging dives compared to non-foraging dives (67.5% foraging dive time). Association events lasted an average of 3.58 h (range = 0.39 to 12.2 h). Multiple events involved the same individuals whose group composition changed through splitting up and rejoining later or through the splitting off and/or joining of a third individual with a pair. There were 7 individuals involved in association events with available sex data (4 males, 3 females). These individuals were involved in 4 associations (Events B, G, H, I) – of these, one was all male (Event I) and the other three (Events B, G, H) were mixed-sex. See Table 1 for full details of association events.

Synchronized behavior was clearly indicated in spatial movement, diving behavior, and lunging efforts (see Online Resources 2–13 for dive and lunge profiles of each association event). Of the dives recorded during association events, the majority (78.3%) were synchronized within 30 s of one another. Dive profiles illustrate that close synchrony was reflected in both diving depths and durations. This was the case regardless of whether foraging was taking place, suggesting that social associations are not solely for any potential or perceived foraging benefit. There was an average of 15 s difference (range 6–23 s) in the dive timings (i.e., the beginning of a dive record) between associated individuals, indicating the high degree of synchrony occurring with respect to dive behavior. Synchronized lunges (i.e., lunges within 5 s of each other) made up 64% of the individual lunges recorded during association events. These synchronized lunge events occurred more often during deep dives of greater than 30 m (59.5%). This suggests that actual lunging events during foraging dives are not as highly synchronized as the dives themselves.

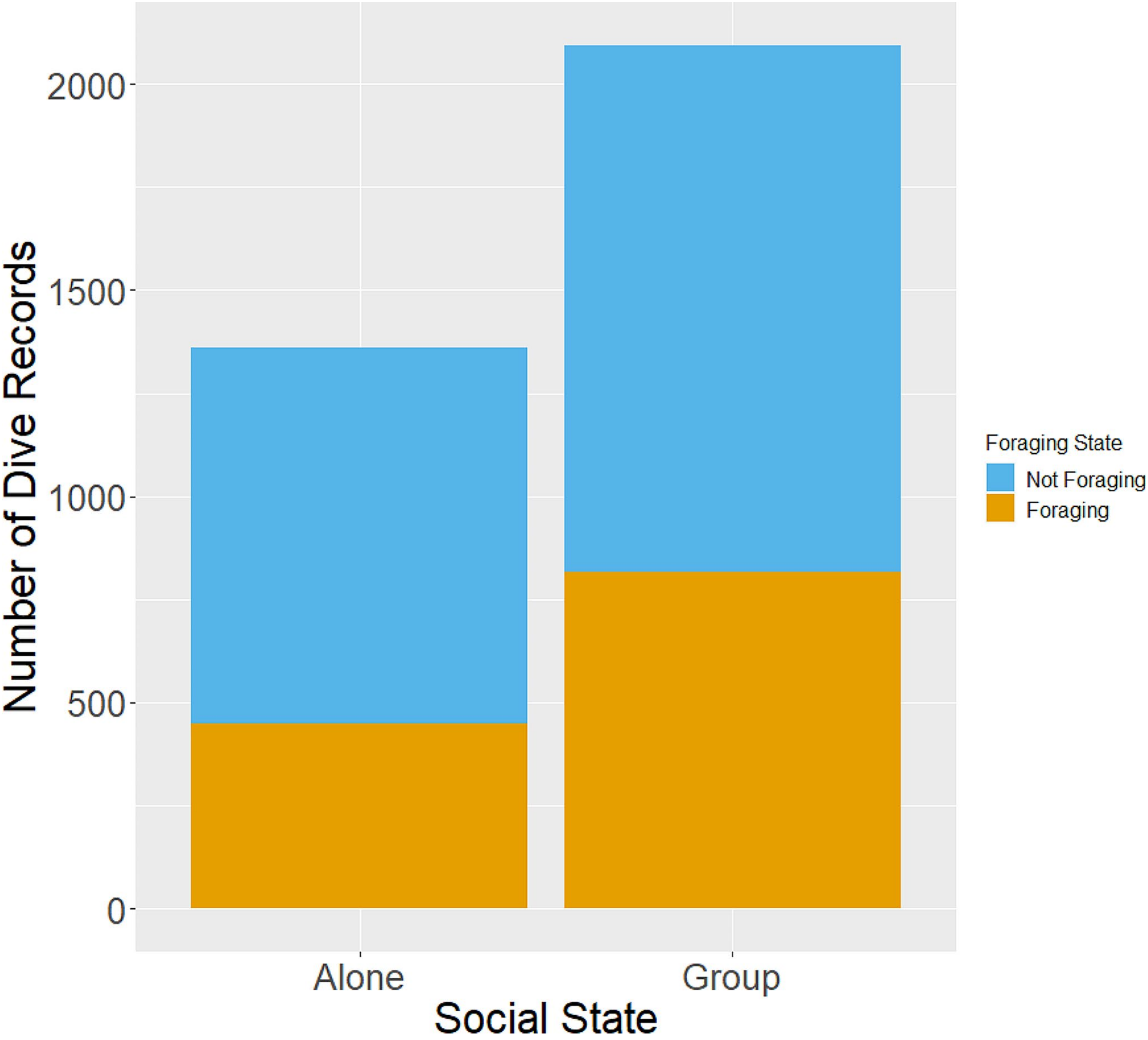

Fig. 2 Count of social auditing dive records for each social state (Alone and Group) and foraging state (Foraging and Not Foraging)

Behavioral and foraging synchrony was largely maintained over the duration of the association periods, even in instances where individuals split up for several hours and rejoined one another later. Association Events E and F provide a strong example of this (Fig. 5). In Association Event E (Fig. 5a), the two individuals were associated for nearly five hours at night, during which they maintained shallow dives (mean depths of 9.5 m) and foraged at high rates (mean rates 110–120). After splitting for about eight hours, they joined each other again for 7.5 h during the day in Association Event F (Fig. 5b). During this second event, they mirrored behavioral shifts to deeper dives (mean depths of 41–45 m) and lower foraging rates (mean rates of 57–59).

Discussion

This work represents one of the only studies into the social behavior and social structure of AMW, which otherwise remains poorly studied. We provide clear evidence of regular social associations in AMW, including synchrony between individuals in both diving and foraging lunges. Our results suggest socializing does occur in both foraging and non-foraging contexts. These are foundational insights into the sociality and social foraging behaviors of AMW.

Our results suggest that minke whale sociality follows a loose fission-fusion structure, similar to what has been shown in other rorqual species (Clapham 1993; Ramp et al. 2010). 96% of all individuals with social audit data were recorded

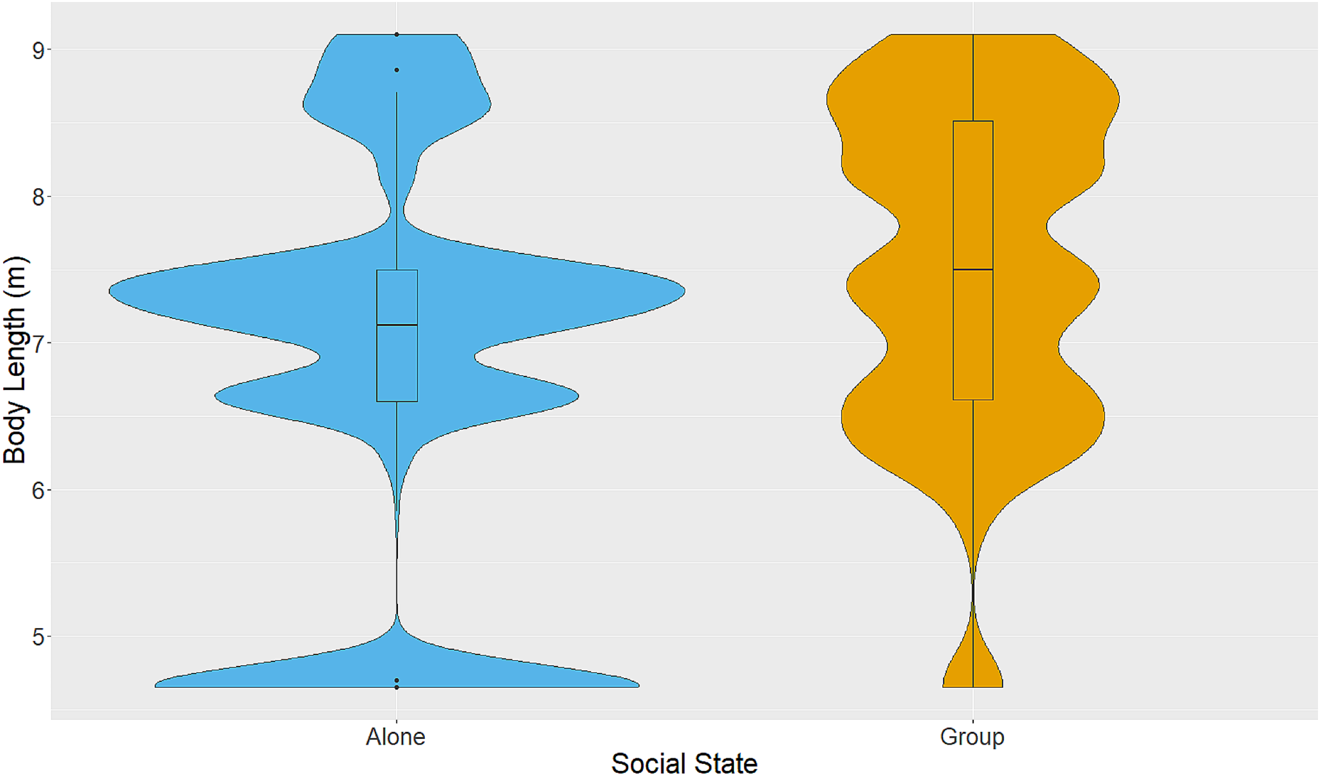

Fig. 3 Body length (m) for each social state (Alone and Group). Box-and-whisker plots in the center of each violin graph denote the data median (horizontal bar in the center of the box), the box denotes the first to third quartile of the data, and the whiskers on each end indicate the minimum and maximum values

in multiple social states, switching frequently. The simultaneous tagging data further supports fission-fusion structure, showing frequent changes in group composition and a preference for short-term associations (average of ~3.5 h). While long-term associations cannot be ruled out, future studies to explore this will require a combination of reliable individual identifications and association matrix data. These results are consistent with recent acoustic behavioral studies into AMW (Casey et al. 2022), which also suggest the presence of fission-fusion structure. However, social individuals may be easier to tag as they may be less likely to respond to an approaching boat and are easier to find/locate than single animals. This may have led to individuals in groups being tagged more often (68% of deployments), though not exclusively. Future studies using observational data that includes a more equitable representation of solitary individuals will provide clarity of the extent of social interactions.

Although social associations did not occur exclusively in foraging states, there is strong evidence that foraging often has a social component. Half of recorded social associations occurred during foraging dives. Furthermore, synchronized dives with foraging activity were twice as common as synchronized non-foraging dives. Synchronized lunging within 5 s made up approximately 65% of the lunges recorded during association events, and occurred in all 12 association events. These results suggest intentional coordination of foraging efforts to varied extents. The evidence of group foraging is consistent with previous work done on minke whale foraging behavior. Observations have previously been recorded of group foraging, including groups of two to six and aggregations of up to forty (Friedlaender et al. 2014; Casey et al. 2022). Recent work by Casey et al. (2022) found two specific calls associated with group foraging, *growls* and *rumbles*, and suggest that they might serve as contact calls. Together with our results, this strongly points towards the type of social foraging that would be consistent with other rorqual species' use of contact calls during foraging to coordinate foraging behavior. For example, humpback whales use acoustic calls in coordinated strategies such as paired bottom feeding (Ware et al. 2014). The coordinated foraging observed in this study would be consistent with the use of contact calls to coordinate synchrony. However, the foraging dive synchrony observed does not indicate the presence of role specialization in group foraging strategies. Instead, lunges were only synchronized in 65% of all cases. It is therefore less likely that minkes use complex group feeding strategies as seen in species like humpback whales, but instead employ simpler coordinated lunging as observed in species like fin and blue whales (Kot et al. 2014).

Fig. 4 Feeding rate for each social state (Alone and Group), separated into shallow dives (< 30 m) and deep dives (> 30 m). Box-and-whisker plots in the center of each violin graph denote the data median (horizontal bar in the center of the box), the box denotes the first to third quartile of the data, and the whiskers on each end indicate the minimum and maximum values

Larger individuals were significantly more likely to be found in groups, suggesting that body size and/or age class influences socializing. Estimates suggest that adult AMW are ~8 m in length (Pallin et al. 2022) and whaling data suggests that they are weaned at 4.5–5.5 m (Cade et al. 2023). Body length means for groups (7.5 m) were closer to the adult range than the means for solitary individuals (6.9 m). This suggests the possibility that younger individuals such as juveniles were more likely to be alone. This is consistent with what is known of other baleen whale species – humpback whale juveniles appear to associated less than adults (Ramp et al. 2010; Garrigue and Derville 2022). However, age class is still difficult to confidently quantify in AMW and thus this is only one possibility. Epigenetic aging of biopsy samples paired with body length measurements would provide stronger evidence for the relationship between age class and social behavior. While the presence of several mixed-sex association groups does not support sex segregation in socializing, the sample size ($n = 7$) is too small to assess this aspect appropriately and thus should not rule it out. Another possibility is that socializing provides benefits such as predator protection or improved foraging efficiency. The only known predators of AMW are killer whales, which are also found around the Western Antarctic Peninsula (Fearnbach et al. 2019). If smaller individuals are more susceptible to predation, it could lead to a bias of larger animals in groups. Our results also indicate significantly lower feeding rates in individuals found in groups. As these animals tended to be larger, this corresponds well with previous studies showing lower feeding rates in larger individuals. Larger and healthier animals may prefer to group together if groups allow for increased efficiency and reduced foraging efforts.

The high prevalence of synchronized foraging dives suggests that there is a degree of coordination involved in the group foraging observed, and individuals typically remained synchronized for multiple foraging sessions. Furthermore, synchronized lunges skewed towards deep (> 30 m) foraging dives compared to shallow ones (< 30 m). Several hypotheses could explain these results. Coordinated foraging could serve to improve foraging efficiency by lowering energy expenditure, possibly as a strategic compensation for the reduced daytime foraging efforts that minkes typically exhibit due to shifts in prey to deeper depths. However, several factors make unclear how substantial any benefit of group foraging may be on a broader ecological level. These include the moderate effect of social state on feeding rate, the trend of specific individuals to increase feeding rate when joining groups, and the pre-established link between body size and feeding rate. To determine the impact of

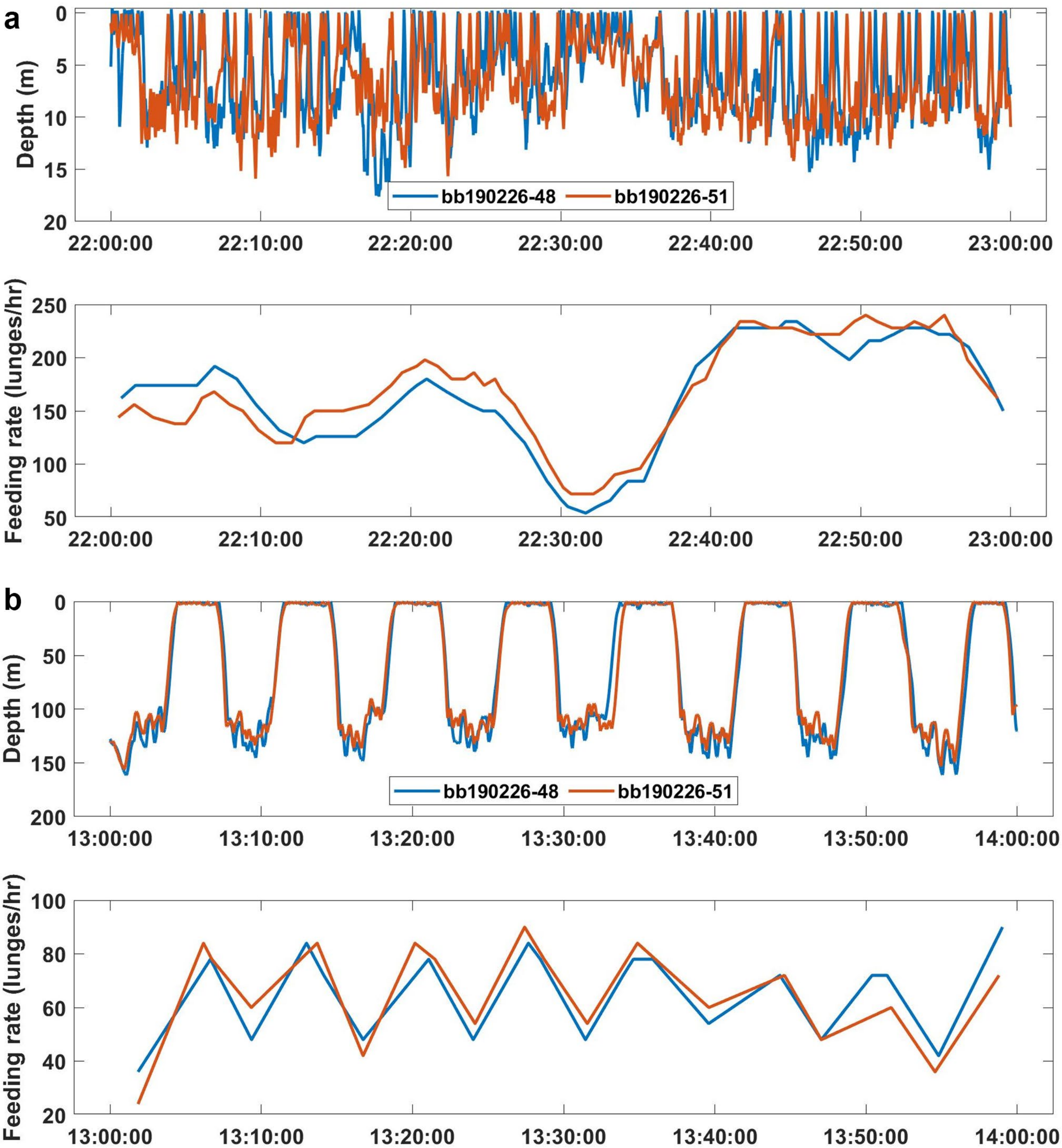

Fig. 5 One-hour dive and lunge profile subsets for simultaneous tag deployments during. (**a**) Association Event E which occurred at night and (**b**) Association Event F which occurred during the day, with local datetime on the x-axis, depth in meters (top) and feeding rate (bottom) on the y-axis. The two individuals are indicated by colour. Note that Y-axes are not consistent across profiles. Complete set of dive and lunge profiles are in the supplementary information (Online Resources 2–13)

group foraging on efficiency and how it interacts with body size, future studies should compare (1) prey patch size and density and (2) prey consumption mass between single individuals and groups.

Conclusions

The key foundational knowledge of this study is needed to better understand the foraging and social ecology of AMW as a species with a clear link between its sociality and prey presence and availability. We provide clear evidence of fission-fusion sociality and the use of social foraging techniques in this species. Our results show that Antarctic minkes whales form short-term associations, have significantly lower foraging rates in groups, and frequently undertake synchronized foraging dives. Our study provides baseline ecological information through novel insights into AMW social behavior and group foraging dynamics. As climate change alters the sea-ice ecosystem of the Antarctic Peninsula, it is vital that we fill gaps in what is known about the relationship between the Antarctic environment and the species with which it is inextricably linked.

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Data availability All datasets generated during and/or analysed during this study are attached as Supplemental Material (Allen et al. 2023 – BES Raw Data Final.xlsx) in the form of an Excel spreadsheet. Please seek prior written permission from ASF to reuse data in any form except to confirm the study results.

Declarations

Ethics approval All work was conducted under National Marine Fisheries Services permits (#23095 and 16111), and Antarctic Conservation Act permits 2020-016, as well as institutional animal care protocols approved by the University of California Santa Cruz (Friea2004a). All applicable international, national, and institutional guidelines for the use of animals were followed.

Competing interests There are no competing interests among any of the authors.

References

Alexander RD (1974) The evolution of social behavior. Annu Rev Ecol Syst 5:325–383

Allen JA (2019) Community through culture: from insects to whales: how social learning and culture manifest across diverse animal communities. BioEssays 41:1900060

Alves F, Dinis A, CASCao I, Freitas L (2010) Bryde's whale (*Balaenoptera brydei*) stable associations and dive profiles: new insights into foraging behavior. Mar Mammal Sci 26:202–212

Archie EA, Maldonado JE, Hollister-Smith JA, Poole JH, Moss CJ, Fleischer RC, Alberts SC (2008) Fine-scale population genetic structure in a fission–fusion society. Mol Ecol 17:2666–2679

Baker CS, Herman LM (1984) Aggressive behavior between humpback whales (*Megaptera novaeangliae*) wintering in hawaiian waters. Can J Zool 62:1922–1937

Bengtson Nash SM, Castrillon J, Eisenmann P, Fry B, Shuker JD, Cropp RA, Dawson A, Bignert A, Bohlin-Nizzetto P, Waugh CA (2018) Signals from the south; humpback whales carry messages of Antarctic sea-ice ecosystem variability. Global Change Biol 24:1500–1510

Cade DE, Friedlaender AS, Calambokidis J, Goldbogen JA (2016) Kinematic diversity in rorqual whale feeding mechanisms. Curr Biol 26:2617–2624

Cade DE, Barr KR, Calambokidis J, Friedlaender AS, Goldbogen JA (2018) Determining forward speed from accelerometer jiggle in aquatic environments. J Exp Biol 221:jeb170449

Cade DE, Fahlbusch JA, Oestreich WK, Ryan J, Calambokidis J, Findlay KP, Friedlaender AS, Hazen EL, Seakamela SM, Goldbogen JA (2021a) Social exploitation of extensive, ephemeral, environmentally controlled prey patches by supergroups of rorqual whales. Anim Behav 182:251–266

Cade DE, Gough WT, Czapanskiy MF, Fahlbusch JA, Kahane-Rapport SR, Linsky JM, Nichols RC, Oestreich WK, Wisniewska DM, Friedlaender AS (2021b) Tools for integrating inertial sensor data with video bio-loggers, including estimation of animal orientation, motion, and position. Anim Biotelemetry 9:34

Cade DE, Seakamela SM, Findlay KP, Fukunaga J, Kahane-Rapport SR, Warren JD, Calambokidis J, Fahlbusch JA, Friedlaender AS, Hazen EL (2021c) Predator-scale spatial analysis of intra-patch prey distribution reveals the energetic drivers of rorqual whale super-group formation. Funct Ecol 35:894–908

Cade DE, Kahane-Rapport SR, Gough WT, Bierlich KC, Linsky JMJ, Calambokidis J, Johnston DW, Goldbogen JA, Friedlaender AS (2023) Minke whale feeding rate limitations suggest constraints on the minimum body size for engulfment filtration feeding. Nat Ecol Evol 7:535–546

Casey C, Weindorf S, Levy E, Linsky J, Cade D, Goldbogen J, Nowacek D, Friedlaender A (2022) Acoustic signalling and behaviour of Antarctic minke whales (*Balaenoptera bonaerensis*). R Soc Open Sci 9:211557

CCAMLR (2004) CCAMLR Ecosystem Monitoring Program: standard methods. CCAMLR Hobart, Australia

Chen B, Wu C, Ballance LT, Fertl D, Jiang H, Qiao Y, Du Z, Zhang Y, Yang F, Yang G (2023) Cooperative feeding and foraging lateralization by Eden's whales off southern China. Mar Mammal Sci 39:200–219

Cioffi WR, Quick NJ, Foley HJ, Waples DM, Swaim ZT, Shearer JM, Webster DL, Friedlaender AS, Southall BL, Baird RW (2021) Adult male Cuvier's beaked whales (*Ziphius cavirostris*) engage in prolonged bouts of synchronous diving. Mar Mammal Sci 37:1085–1100

Clapham PJ (1993) Social organization of humpback whales on a North Atlantic feeding ground. In: Boyd IL (ed) Marine Mammals: Advances in Behavioural and Population Biology: The Proceedings of a Symposium held at The Zoological Society of London on 9th and 10th April 1992. Oxford University Press, Oxford, pp 131–145

Edds-Walton PL (2000) Vocalizations of minke whales Balaenoptera acutorostrata in the St. Lawrence Estuary. Bioacoustics 11:31–50

Fearnbach H, Durban JW, Ellifrit DK, Pitman RL (2019) Abundance of type A killer whales (*Orcinus orca*) in the coastal waters off the western Antarctic Peninsula. Polar Biol 42:1477–1488

Findlay KP, Seakamela SM, Meÿer MA, Kirkman SP, Barendse J, Cade DE, Hurwitz D, Kennedy AS, Kotze PG, McCue SA (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

Friard O, Gamba M, Fitzjohn R (2016) BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. Method Ecol Evol 7:1325–1330

Friedlaender A, Goldbogen J, Nowacek D, Read A, Johnston D, Gales N (2014) Feeding rates and under-ice foraging strategies of the smallest lunge filter feeder, the Antarctic minke whale (*Balaenoptera bonaerensis*). J Exp Biol 217:2851–2854

Garrigue C, Derville S (2022) Behavioral responses of humpback whales to biopsy sampling on a breeding ground: the influence of age-class, reproductive status, social context, and repeated sampling. Mar Mammal Sci 38:102–117

Goldbogen JA, Calambokidis J, Shadwick RE, Oleson EM, McDonald MA, Hildebrand JA (2006) Kinematics of foraging dives and lunge-feeding in fin whales. J Exp Biol 209:1231–1244

Goldbogen J, Cade D, Boersma A, Calambokidis J, Kahane-Rapport S, Segre P, Stimpert A, Friedlaender A (2017a) Using digital tags with integrated video and inertial sensors to study moving morphology and associated function in large aquatic vertebrates. Anat Rec 300:1935–1941

Goldbogen J, Cade D, Calambokidis J, Friedlaender A, Potvin J, Segre P, Werth A (2017b) How baleen whales feed: the biomechanics of engulfment and filtration. Annu Rev Mar Sci 9:367–386

Groß J, Virtue P, Nichols PD, Eisenmann P, Waugh CA, Bengtson Nash S (2020) Interannual variability in the lipid and fatty acid profiles of east Australia-migrating humpback whales (*Megaptera novaeangliae*) across a 10-year timeline. Sci Rep 10:18274

Hanya G, Chapman CA (2013) Linking feeding ecology and population abundance: a review of food resource limitation on primates. Ecol Res 28:183–190

He P, Maldonado-Chaparro AA, Farine DR (2019) The role of habitat configuration in shaping social structure: a gap in studies of animal social complexity. Behav Ecol Sociobiol 73:9

Herr H, Viquerat S, Devas F, Lees A, Wells L, Gregory B, Giffords T, Beecham D, Meyer B (2022) Return of large fin whale feeding aggregations to historical whaling grounds in the Southern Ocean. Sci Rep 12:9458

Horwood JW (1989) Biology and exploitation of the minke whale. CRC, Boca Raton

Kahane-Rapport S, Savoca M, Cade D, Segre P, Bierlich K, Calambokidis J, Dale J, Fahlbusch J, Friedlaender A, Johnston D (2020) Lunge filter feeding biomechanics constrain rorqual foraging ecology across scale. J Exp Biol 223:jeb224196

Kot BW, Sears R, Zbinden D, Borda E, Gordon MS (2014) Rorqual whale (Balaenopteridae) surface lunge-feeding behaviors: standardized classification, repertoire diversity, and evolutionary analyses. Mar Mammal Sci 30:1335–1357

Kruskal WH, Wallis WA (1952) Use of ranks in one-criterion variance analysis. J Am Stat Assoc 47:583–621

Kusahara K (2016) Cryosphere: warming ocean erodes ice sheets. Nat Clim Change 6:22

Laidre KL, Heagerty PJ, Heide-Jørgensen MP, Witting L, Simon M (2009) Sexual segregation of common minke whales (Balaenoptera acutorostrata) in Greenland, and the influence of sea temperature on the sex ratio of catches. ICES J Mar Sci 66:2253–2266

Landino S, Treacy S, Zerwick S, Dunlap J (1994) A large aggregation of bowhead whales (Balaena mysticetus) feeding near Point Barrow, Alaska, in late October 1992. Arctic:232–235

Lee JF, Friedlaender AS, Oliver MJ, DeLiberty TL (2017) Behavior of satellite-tracked Antarctic minke whales (Balaenoptera bonaerensis) in relation to environmental factors around the western Antarctic Peninsula. Anim Biotelemetry 5:23

Lemonnier C, Bize P, Boonstra R, Dobson FS, Criscuolo F, Viblanc VA (2022) Effects of the social environment on vertebrate fitness and health in nature: moving beyond the stress axis. Horm Behav 145:105232

Levene H (1961) Robust tests for equality of variances. In: Olkin I, Ghurye SG, Hoeffding W, Madow WG, Mann HB (eds) Contributions to Probability and statistics: essays in honor of Harold Hotelling. Stanford University Press, Palo Alto, CA, pp 279–292

Linsky JM, Wilson N, Cade DE, Goldbogen JA, Johnston DW, Friedlaender AS (2020) The scale of the whale: using video-tag data to evaluate sea-surface ice concentration from the perspective of individual Antarctic minke whales. Anim Biotelemetry 8:31

Macdonald DW, Johnson DDP (2015) Patchwork planet: the resource dispersion hypothesis, society, and the ecology of life. J Zool 295:75–107

Mann J, Connor RC, Tyack PL, Whitehead H (2000) Cetacean societies: field studies of dolphins and whales. University of Chicago Press, Chicago

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 Mammal Sci 38:959–974

Moore SE, George JC, Sheffield G, Bacon J, Ashjian CJ (2010) Bowhead whale distribution and feeding near Barrow, Alaska, in late summer 2005–06. Arctic 63:195–205

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

Pallin L, Bierlich K, Durban J, Fearnbach H, Savenko O, Baker C, Bell E, Double M, de la Mare W, Goldbogen J (2022) Demography of an ice-obligate mysticete in a region of rapid environmental change. R Soc Open Sci 9:220724

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

Potvin J, Cade DE, Werth AJ, Shadwick RE, Goldbogen JA (2020) A perfectly inelastic collision: bulk prey engulfment by baleen whales and dynamical implications for the world's largest cetaceans. Am J Phys 88:851–863

Ramp C, Hagen W, Palsbøll P, Bérubé M, Sears R (2010) Age-related multi-year associations in female humpback whales (*Megaptera novaeangliae*). Behav Ecol Sociobiol 64:1563–1576

Rea LM, Parker RA (2014) Designing and conducting survey research: a comprehensive guide. Wiley, Hoboken

Risch D, Gales NJ, Gedamke J, Kindermann L, Nowacek DP, Read AJ, Siebert U, Van Opzeeland IC, Van Parijs SM, Friedlaender AS (2014) Mysterious bio-duck sound attributed to the Antarctic minke whale (Balaenoptera bonaerensis). Biol Lett 10:20140175

Risch D, Norris T, Curnock M, Friedlaender A (2019) Common and Antarctic minke whales: conservation status and future research directions. Front Mar Sci 6:247

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 novaengliae. PhD Thesis, Simon Fraser University

Silk MJ, Croft DP, Delahay RJ, Hodgson DJ, Boots M, Weber N, McDonald RA (2017) Using social network measures in wildlife disease ecology, epidemiology, and management. Bioscience 67:245–257

Stammerjohn SE, Martinson D, Smith R, Yuan X, Rind D (2008) Trends in Antarctic annual sea ice retreat and advance and their relation to El Niño–Southern Oscillation and Southern Annular Mode variability. J Phys Res 108:C03S90

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

Turner J, Colwell SR, Marshall GJ, Lachlan-Cope TA, Carleton AM, Jones PD, Lagun V, Reid PA, Iagovkina S (2005) Antarctic climate change during the last 50 years. Int J Clim 25:279–294

Ware C, Wiley DN, Friedlaender AS, Weinrich M, Hazen EL, Bocconcelli A, Parks SE, Stimpert AK, Thompson MA, Abernathy K (2014) Bottom side-roll feeding by humpback whales (*Megaptera novaeangliae*) in the southern Gulf of Maine, USA. Mar Mammal Sci 30:494–511

Weinrich MT (1991) Stable social associations among humpback whales (*Megaptera novaeangliae*) in the southern Gulf of Maine. Can J Zool 69:3012–3019

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

Wilson RP, Liebsch N, Davies IM, Quintana F, Weimerskirch H, Storch S, Lucke K, Siebert U, Zankl S, Müller G (2007) All at sea with animal tracks; methodological and analytical solutions for the resolution of movement. Deep Sea Res Pt II 54:193–210

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