

# Bottlenose dolphin communication during a role-specialized group foraging task

Rebecca A. Hamilton<sup>a,f,\*</sup>, Stefanie K. Gazda<sup>b</sup>, Stephanie L. King<sup>c</sup>, Josefin Starkhammar<sup>d</sup>, Richard C. Connor<sup>e,f</sup>

<sup>a</sup> School of Health Sciences, University of Manchester, Manchester, UK

<sup>b</sup> Department of Biology, University of Florida, FL, USA

<sup>c</sup> School of Biological Sciences, University of Bristol, Bristol BS8 1TQ, UK

<sup>d</sup> Department of Biomedical Engineering, Lund University, Lund, Sweden

<sup>e</sup> Institute of Environment, Florida International University, FL, USA

<sup>f</sup> Department of Biology, University of Massachusetts Dartmouth, MA, USA

## ARTICLE INFO

### Keywords:

Communication  
Role specialization  
Driver-barrier feeding  
Cetaceans  
Bottlenose dolphins  
Division of labor

## ABSTRACT

A division of labor with role specialization is defined as individuals specializing in a subtask during repetitions of a group task. While this behavior is ubiquitous among humans, there are only four candidates found among non-eusocial mammals: lions, mice, chimpanzees, and bottlenose dolphins. Bottlenose dolphins in the Cedar Keys, Florida, engage in role specialized “driver-barrier feeding”, where a “driver” dolphin herds mullet towards “barrier” dolphins. Thus trapped, the mullet leap out of the water where the dolphins catch them in air. To investigate whether dolphins use acoustic cues or signals to coordinate this behavior, vocalizations were recorded before and during driver-barrier feeding. Results of fine-scale audio and video analysis during 81 events by 7 different driver individuals suggest that barrier animals coordinate movements during these events by cueing on the driver’s echolocation. Analysis of dolphin whistle occurrence before driving events versus another foraging technique, which does not involve role specialization, revealed significantly higher whistle production immediately prior to driver-barrier events. Possible whistle functions include signaling motivation, recruiting individuals to participate, and/or behavioral coordination. While the use of cues and signals is common in humans completing role-specialized tasks, this is the first study to investigate the use of vocalizations in the coordination of a role-specialized behavior in a non-human mammal.

## 1. Introduction

Individuals that perform different subtasks to complete a team task partake in a “division of labor” (Anderson and Franks, 2001). Division of labor with role specialization (DLRS), in which individuals maintain the same role throughout multiple iterations of the team task, is ubiquitous in both humans and eusocial animals, but is notably limited in other species. The first documented example of a DLRS behavior in non-eusocial mammals was in African lionesses (*Panthera leo*), who specialize in the role of “wing” or “center” while hunting (Stander, 1992). The Steppe mouse (*Mus spicilegus*) uses role specialization while cooperatively building mounds, with different individuals collecting certain types of building materials (Hurtado et al., 2013). Chimpanzees

(*Pan troglodytes*) have been suggested to engage in role specialization in a foraging context (Boesch, 2002), although these claims have been challenged (Gilby et al., 2015; Gilby and Connor, 2010). In addition, decades after the initial suggestion that role specialization is present in bubble-net feeding humpback whales (*Megaptera novaeangliae*), confirmation is still lacking (D’Vincent et al., 1985; Wiley et al., 2011). To date, the common bottlenose dolphin (*Tursiops truncatus*) is the only marine mammal confirmed to engage in a DLRS behavior. This behavior is known as “driver-barrier” feeding (Gazda et al., 2005).

Driver-barrier feeding is performed by a subset (<10%) of a resident population (379 ± 48 individuals (SD), Gazda unpublished data) of common bottlenose dolphins in the shallow coastal waters near the Cedar Keys, Florida (Gazda et al., 2005; Gazda, 2016). One “driver”

\* Corresponding author at: School of Health Sciences, University of Manchester, Manchester, UK.

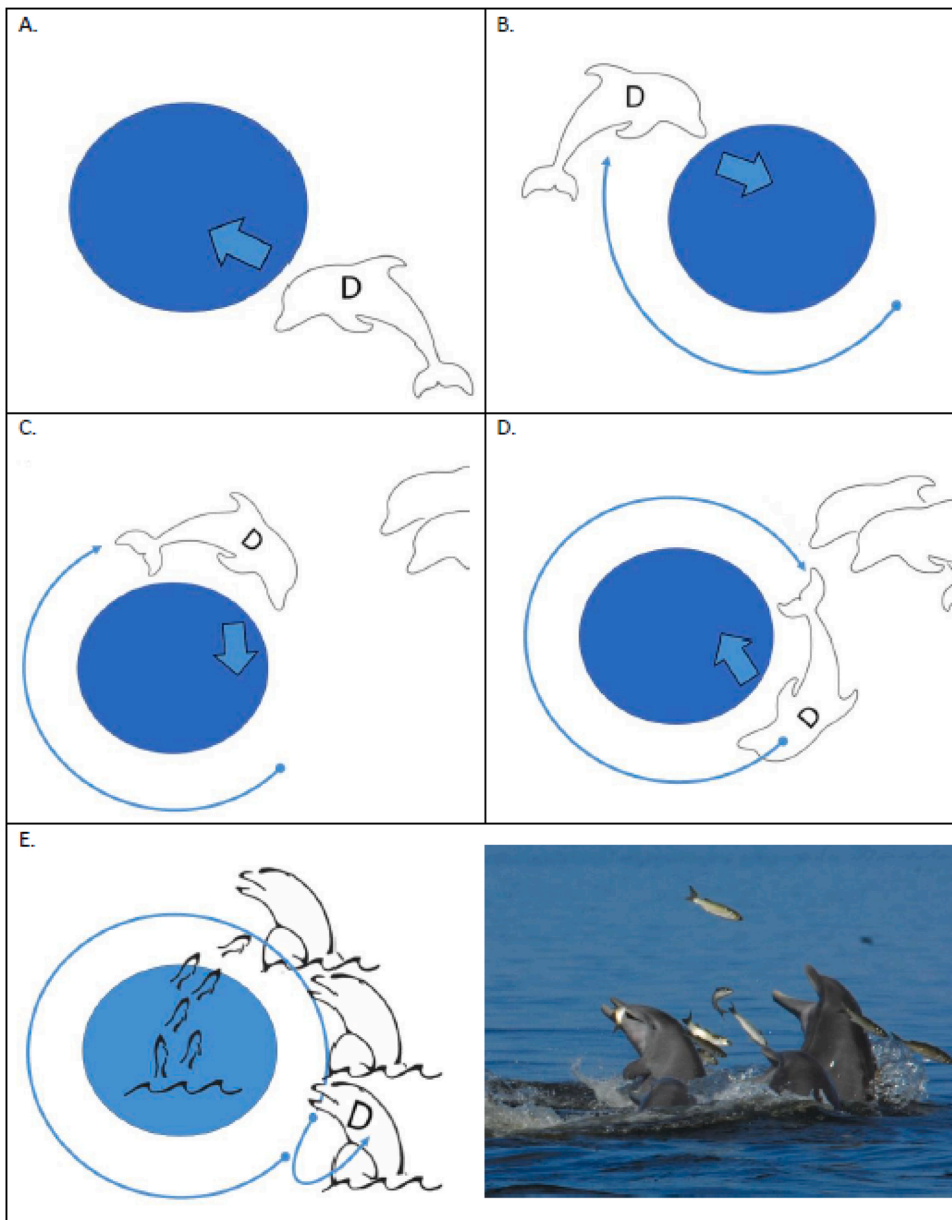
E-mail address: [rebecca.hamilton-5@postgrad.manchester.ac.uk](mailto:rebecca.hamilton-5@postgrad.manchester.ac.uk) (R.A. Hamilton).

<sup>1</sup> ORCID: 0000-0002-0739-3746

dolphin initiates the behavior by herding a school of mullet (*Mugil spp.*), which can be done singly but is most often performed in the presence of “barrier” dolphins (126 of 145 (86.9%) driver-barrier events with identified drivers documented by Gazda et al. (2005)). The barrier dolphins line up, likely blocking the escape of the fish. The fish leap out of the water after the completion of driving, when all the participating dolphins raise their heads to catch them in mid-air (Gazda et al., 2005) (Fig. 1). Driver-barrier events have been documented previously to last an average of 19.9 s (range: 11 – 28 s), involve a typical group size of three individuals (range: 1 – 6 individuals), and with an average of 13 fish jumping per event (Gazda et al., 2005). Driver and barrier individuals specialize in their roles and are rarely seen switching (Gazda et al., 2005). Currently, there are a total of 14 known active driver dolphins in the population and 20 identified barriers, however the true number of barriers is thought to be higher as not all barrier individuals can be identified during foraging events as their dorsal fins often stay below the surface. The ontogeny of the behavior is currently unknown, including how age and sex may impact these roles.

For such cooperative foraging tactics to be favored, it is expected that

the behavior must provide a higher payoff for participating individuals, on average, than foraging alone (Connor, 2010). For example, in cooperatively hunting lionesses, hunting success of groups increased when individuals performed their preferred roles (Stander, 1992). Measuring the success of different driver-barrier groups revealed that while drivers and barriers had no significant difference in catch rates, there was a significantly higher number of “incomplete” events when drivers performed the behavior without any barrier participants (Gazda, 2016). An incomplete event is defined as any time the driver dolphin initiated a driving circle but then abandoned the effort before completing driving, and no fish jumped (Gazda, 2016). Additionally, a higher number of barrier participants further decreased the number of incomplete events, increasing overall success rates and thereby providing a benefit to all participants (Gazda, 2016). These data suggest that driver-barrier behavior is a cooperative by-product mutualism, where participants obtain benefits as a by-product of the selfish behavior of others (Connor, 1995). This is supported by the fact that in Gazda et al. (2005), no avoidance behavior of conspecifics by driver individuals has been observed, which would be expected if drivers were more successful on



**Fig. 1. Diagram showing the steps of driver-barrier feeding from a birds-eye perspective.** The blue circle indicates the location of the targeted school of mullet. The arrow within the circle indicates the direction the mullet will move as a result of the dolphin’s positioning. A) Driver individual initiates the driving circle. B) During driving, the driver moves in a rapid clockwise circle. C) As driving occurs, the barrier individuals are oriented towards the driver and move closer. D) As the driver nears the completion of the driving circle, the barrier animals move in behind the driver. E) At the completion of the driving circle, fish leap out of the water, where barrier and driver animals raise their heads to catch the fish in midair.

their own. In fact, the behavior normally occurs in bouts, with the driver and barrier individuals travelling closely in a group between events (average of four to five minutes between events noted by Gazda et al. (2005)).

For groups to succeed when foraging cooperatively, individuals need to coordinate their behavior in space and time, for which they may rely on cues or signals. Cues are passive information an animal collects from the environment or other individuals, while signals are adapted to affect the behavior of a receiver (Bradbury and Vehrencamp, 2011). The use of both cues and signals is common during cooperative tasks in humans and other animals (Böckler et al., 2016; Melis and Semmann, 2010). For example, it has been shown in multiple experiments that humans will automatically track cues from other individuals when performing specialized roles (Atmaca et al., 2011; Böckler et al., 2012), using signals to indicate intentions when tasks require temporal or spatial coordination between individuals (Goebl and Palmer, 2009; Van der Wel et al., 2011). Chimpanzees use visual signals to coordinate behavior in cooperative tasks that require a division of labor (Bullinger et al., 2011; Melis and Tomasello, 2019). Common bottlenose dolphins can use vocal signals to facilitate the successful execution of coordinated, cooperative actions (King et al., 2021), and spinner dolphins (*Stenella longirostris*) appear to use echolocation cues to coordinate the herding of schooling fish (Benoit-Bird and Au, 2009). However, these cooperative tasks do not include role specialization as seen in driver-barrier feeding.

Among role-specializing non-eusocial mammals, lionesses are thought to coordinate using visual cues about the location of prey relative to other hunters, while there is no evidence that mound-building mice use communication to facilitate DLRS (Hurtado et al., 2013; Stander, 1992). Therefore, evidence of signal use in DLRS behavior in non-eusocial mammals is notably lacking. In this study, focal follows were conducted to investigate how bottlenose dolphins coordinate their behavior during driver-barrier feeding. Dolphin species rely primarily on sound for communication, since vision is limited underwater, and sound travels further and faster than in air (Urlick, 1983; Tyack, 1998). Since the shallow waters in the Cedar Keys area (frequently less than 1 m in depth) are also often extremely murky, it can be assumed that dolphins participating in driver-barrier feeding rely on acoustic cues or signals to coordinate their behavior.

Bottlenose dolphin acoustic communication can be broadly divided into clicks and whistles. Clicks are generally broadband, meaning they cover a wide range of frequencies, but are very short in duration (50–80 $\mu$ s in *Tursiops* spp. (Au, 1993)). Clicks serve two different functions: (i) trains of clicks form the basis for a biological sonar system (Norris et al., 1967); and (ii) a wide range of modified clicks are used in social communication (Overstrom, 1983; Connor and Smolker, 1996; Moore et al., 2020). Whistles, which are signals used for communication between individuals, are narrow-band and frequency-modulated. The best-studied whistles to date are signature whistles, which are individually distinctive signals that encode identity information in the frequency modulation pattern of the whistle independently of general voice features (Janik et al., 2006; Sayigh et al., 1999, 2017).

Here, detailed behavioral and acoustic analysis was used to determine whether dolphins rely on acoustic cues and/or acoustic signals (namely clicks or whistles) to coordinate their behavior during driver-barrier feeding. Clicks, being echolocation in this case, were parsimoniously interpreted as being cues since echolocation is used to sense the surroundings and has not been shown to be used as intentional communication between individuals. Furthermore, to determine whether the use of acoustic signals (i.e., intentional communication with the purpose of affecting the behavior of a conspecific) in this context is likely associated with individuals coordinating their behavior, the presence of whistles was compared between animals engaged in driver-barrier feeding and another specialized foraging technique, “bottom-grubbing”, conducted in the same habitat area as driver-barrier feeding. Bottom-grubbing is characterized by large splashing induced by tail stroking at the surface of the water as the dolphin’s head is oriented

toward the substrate, and is often performed by multiple animals in the same social group, but without coordination or role specialization.

## 2. Methods

### 2.1. Data collection

Data collection methods, described below, closely followed those described in Gazda et al. (2005) and Gazda (2016), occurring in inshore areas (within 2 km of land) along approximately 35 km of coastline directly south of the Cedar Keys, Florida. This area is mostly shallow seagrass beds and oyster bars among small islands and inlets with an average depth of 1 m.

Boat-based surveys were conducted from May to August 2018 and June to July 2019. The dorsal fins of individuals were photographed with a Nikon D300 camera with a 400 mm Nikkormat zoom lens. Individuals were identified using standard photo-ID procedures for this species, based on unique characteristics of the dorsal fin (Würsig and Würsig, 1977). Individuals identified as driver-barrier participants during previous research (Gazda et al., 2005; Gazda, 2016) were encountered along with individuals newly discovered performing the behavior during this study.

Focal follows, lasting a minimum of 30 min, were carried out on driver individuals. A distance of 10–200 m from the focal animal was maintained at all times. Several opportunistic follows were also conducted using the same methods on animals engaged in shallow water bottom-grubbing.

Underwater sounds were recorded using a towed hydrophone array (similar to Quick et al., 2008), with four HTI-96 Min series hydrophones (flat frequency response: 0.002–30 kHz  $\pm$  1 dB; sensitivity including pre-amplification:  $-173$  dB re 1 V/ $\mu$ Pa) deployed off the four corners of the boat (approx. 5 m x 1.5 m) and kept 0.5 m or 0.25 m below the water’s surface, depending on available depth. Recordings were made on a Tascam DR 680MKII multitrack recorder at a sampling rate of 96 kHz. On a synchronized spoken track, observed behaviors, estimated distance, and bearing of animals relative to the center of the boat (with the vessel’s bow being 0°) were recorded continuously. Whenever possible, the boat engine was turned off to reduce background noise on recordings. Concurrent synchronized video was captured using a handheld video camera (Sony Handycam HDR-SR11).

The beginning of driver-barrier events was defined as the moment the driver individual started driving. This was characterized by rapid swimming in a clockwise circular direction at or just below the surface, with some events starting with the driver slapping their tail on the water’s surface (Gazda et al., 2005). Both continuous still photos and video were taken until the end of the event, defined as the moment the heads of all participating animals were back below the surface of the water (i.e., after they had raised their heads above the water’s surface to catch the leaping mullet, see Fig. 1). The number of participants in an event was determined by analysis of photographs and video. Identity of the driver and whether any participants caught a fish above water was also recorded. The start of bottom-grubbing events was considered to be when at least one animal in the group initiated fluke thrusts at the water’s surface. During bottom-grubbing, hand-held video and still photos were taken to confirm the number and identity of participants. In all groups in which bottom-grubbing foraging was observed, all animals in the group participated in bottom-grubbing.

Driver-barrier feeding events were classified as “incomplete” or “complete”, with complete events being further classified as “unsuccessful” or “successful”. Incomplete events were those in which driving was started but subsequently stopped before completing the driving circle. Complete events were those in which driving circles were complete and participants raised their heads above water to catch fish (Gazda et al., 2005), see Fig. 1. Complete events were considered unsuccessful if it was confirmed no participants caught any fish in air, or successful if at least one participant was confirmed to have caught a fish

(Gazda, 2016). It is possible that some fish catches, unobservable to us, occurred underwater at the end of events.

All audio recordings were visualized as spectrograms (FFT length 1024, Blackmann-Harris window) in Adobe Audition v6.0 (Adobe Systems). The start time of all events were annotated on recordings using information from recorded video and voice-notes. To investigate the use of vocalizations during driver-barrier events, clips of audio during the driving stage of events were isolated for analysis under the condition that the event occurred within 200 m of the research vessel, the boat engine was off, and dolphin vocalizations were clearly visible on the spectrogram over background noise.

### 2.1.1. Data analysis: echolocation

Echolocation was present in all audio clips extracted during the driving phase of driver-barrier events. The driving phase was defined as the initiation of the foraging event by the driver until the driver individual put their head above water. The drivers were always the last to raise their heads and we did not observe any cases when barrier individuals lowered their heads before drivers raised theirs. The driving phase, and the corresponding audio clips, had an average duration of 7.15 s (range = 1 – 19 s, SD = 3.99 s). A custom written MATLAB-based click group separation (CGS) algorithm was used to determine the maximum number of echolocating animals in an audio clip. This method was originally described in Starkhammar et al. (2011), and improved upon in Hamilton et al. (2021). This algorithm assigns clicks in each audio clip to click groups, which can be used as a proxy to estimate the maximum number of animals echolocating. The algorithm compares several properties of each click with preceding clicks: peak-to-peak amplitude, inter-click interval (ICI), and spectral correlation. The algorithm was found to produce accurate results in data taken from the same field site as used in this study, characterized by a shallow depth profile and high levels of natural background noise (Hamilton et al., 2021). In testing the updated version of the CGS algorithm, recordings of animals completing solo driving events were used as clips known to contain the echolocation of only one animal (“solo clips”). Artificial merging of these solo clips was used to create clips known to contain interrupting and/or overlapping echolocation of exactly two and three individuals (“2 merged” and “3 merged”, respectively). In all clips, the algorithm never underestimated the number of echolocating animals, showing that the output from this method can be used to confidently estimate the maximum number of echolocating animals on a recording (Hamilton et al., 2021). See Table S1 for full details of the clips used to test the algorithm and Table S2 for user-set parameter values used on this data.

The analysis of echolocation click groups was complemented by a fine-scale comparison of slow-motion video and audio in order to determine whether drivers or barriers produced the detected echolocation click groups. Audio and video were synced to the 100th of a second in Adobe Audition by aligning the audio of a standardized non-biological noise recorded on both the voice-notes channel and on the audio of the video camera. The mean time difference between the driver individual raising their head above water and the time in the audio clips of that event at which echolocation stopped on the spectrogram was calculated. The same calculation was made with the timing of the drivers lowering their head back below the water’s surface at the end of events versus the time at which echolocation started again on the spectrogram. Drivers always raise their heads out of the water last, so when they are raising their head, barrier participants already have their heads above the surface, but the order of heads going back below water at the end of the event is random.

### 2.1.2. Data analysis: whistles

Examination of social signal use first involved visually scanning spectrograms for whistles that occurred during the driving phase of driver-barrier feeding events (N = 81 events). To examine the production of whistles immediately prior to the start of both driver-barrier and bottom-grubbing events, a separate set of recordings were included in

analysis. These recordings were of the 30 s before the start of the relevant foraging events and were included in the analysis if there was no engine noise and the animals were within 100 m of the hydrophone array (N = 35 driver-barrier events, N = 21 bottom-grubbing events). All whistles within these clips were found by visual scanning and marking of spectrograms in Adobe Audition. To increase certainty that whistles analyzed were related to foraging events, all whistles produced at the same time as bouts of intense social behavior between animals (indicated by body-to-body contact or socio-sexual behavior) as captured on video and/or voice-notes were disregarded.

### 2.1.3. Statistical analysis

All statistical tests were conducted in R v.3.5.2 (R Core Team, 2017). In order to estimate the number of echolocating animals during driver-barrier events, the results from the click train separation program were compared with those from the three comparison datasets (solo, 2 merged, and 3 merged; from Hamilton et al., 2021). A generalized linear model (glm using lme4 package in R; Mächler et al., 2015) with a Poisson family was built with the number of click trains detected as the response variable and the recording type as a minimal predictor variable in order to compare algorithm output from echolocation during driver-barrier events versus the previously analyzed clips.

To determine whether whistle occurrence in the 30 s prior to driver-barrier versus bottom-grubbing events differed, a binomial generalized linear model was built (glm using lme4 package in R; Mächler et al., 2015) with whistle occurrence (absence = 0 and presence = 1) as the response variable. The model predictor was foraging type as a nominal variable (driver-barrier or bottom-grubbing). Since the animals performing bottom-grubbing were different individuals than those recorded during driver-barrier events, comparison was limited to groups in the same size range (2 or 3 individuals). It is known that larger group sizes lead to an increased likelihood of whistles (Quick and Janik, 2008); therefore, despite the limited range in group size, group size was included as an offset in this model.

In determining the effect of whistle rates on driver-barrier event outcome, a generalized linear model with binomial family was built with number of whistles in the 30 s prior to driving as the explanatory variable, event success (unsuccessful or successful) was a nominal response variable, and group size was included as an offset. For all models, ANOVA (stats package in R) was used to compare the full model to a null model that only included the intercept. A threshold of 0.05 was used to determine significance. Diagnostic plots for all significant models confirmed no violations of model assumptions. Full model outputs are provided in Online Resource 1.

## 2.2. Results

During 29 focal follows, which lasted between 30 min and 5.5 h, more than 300 driver-barrier events were observed. Of those events, acoustic data were recorded during 268 complete events and 26 incomplete events. Group size averaged 4.1 (range: 1–12) and involved 14 different driver individuals. Acoustic data were also collected from 60 bottom-grubbing events. Group size averaged 2.4 (range: 2 – 3) and involved 9 different bottom-grubbing individuals. Only two animals were recorded participating in both foraging types.

A total of 81 of 268 clips during the driving stage of complete group driver-barrier events recorded from at least seven different drivers met the criteria for inclusion in our analysis (within 200 m of the boat and hydrophone array, with boat engine off and dolphin vocalizations visible on the spectrogram over background noise). These events occurred at an average distance of 56.9m from the boat and hydrophone array, with all but one event taking place within 100 m (range 10–130 m, SD: 23.7 m). The positioning of the animals relative to the boat was not controlled for nor consistent, thereby it can be assumed there was no bias in the acoustic recordings due to relative positions of certain animals. The data included 64 events with confirmed driver ID

and 17 of unconfirmed driver ID, and 9 of the 81 events (11%) were completed by a driver alone (“solo”) while the rest (89%) involved group sizes of 2–12 individuals. A subsample of 32 driving events by six different drivers had continuous video and audio.

2.2.1. Echolocation

For all analyzed audio clips during non-solo complete driver-barrier events (“group clips”, N = 72), there was a mean of 1.49 click groups detected (SD: 0.90, range: 1–5). For recordings of solo complete events (N = 9), known to contain the echolocation of a single animal, there was a mean of 1.67 click groups detected (SD: 0.71, range: 1–3). For 2 merged and 3 merged clips (from Hamilton et al., 2021), there was a mean of 3.15 (SD: 1.23, range: 2–6) and 3.92 (SD: 1.07, range: 3–5) click groups detected, respectively. Statistical analysis revealed significant differences in the number of click groups detected between all recording types except for solo vs. group clips and 2 merged vs. 3 merged (group versus solo, glm: estimate = -0.1100, z = -0.400, P = 0.6892; group versus 2 merged, glm: estimate: 0.74606, z = 4.802, P < 0.001; group versus 3 merged, glm: estimate: 0.964, z = 5.608, P < 0.001; solo versus 2 merged, glm: estimate = 0.6366, z = 2.216, P = 0.0267; solo versus 3 merged: estimate = 0.854, z = 2.881, P < 0.05; 2 merged versus 3 merged, glm: estimate = 0.2178, z = 1.130, P = 0.258. Fig. 2, Table S2a, S2b). The output of the algorithm from the group clips closely matched the output of clips known to contain echolocation by only one animal, and was mostly of a single click group, strongly suggesting that the group clips also contain echolocation only of one animal. Additionally, the CGS algorithm never underestimated the number of echolocating animals in the 2 merged or 3 merged clips.

Comparison of video and audio at the end of driving revealed that the mean time difference between driver individuals raising their heads out of the water and echolocation no longer being detected was 0.16 s (range: 0–0.62), suggesting that driver individuals were responsible for the echolocation recorded before raising their head above water. Group sizes for the events where video was available (N = 32) averaged 3.6 individuals (range: 2–5). For 30 of the 32 events, echolocation was also detected as participating animals lowered their heads at the end of events. The mean difference in timing of this echolocation starting with

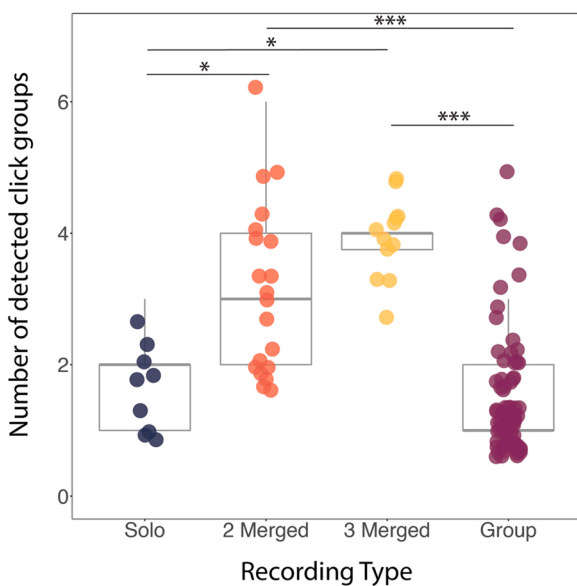


Fig. 2. Number of click groups detected in comparison data sets of solo (N = 9), 2 merged (N = 20), and 3 merged (N = 12) clips compared to clips from group events (N = 72). Each jittered dot represents a single data recording event. Asterisks indicate significant differences between group recordings and comparison datasets (\*p < 0.05, \*\*\*p < 0.001). Solo, 2 merged, and 3 merged data from Hamilton et al. (2021).

the time the driver individual’s head re-entered the water was 2.22 s (range: 0.7–8.13). In 17 of these events, it was noted that the time at which echolocation started was closer to when a barrier animal, rather than the driver, placed its head underwater. This suggests any individual may have been echolocating as they submerged their heads at the end of events.

2.2.2. Whistles

During the driving stage of driver-barrier feeding events, whistles only occurred in 7.4% of recordings (N = 6 of 81). In two-thirds of these cases, the whistles occurred in a sequence (i.e., same whistle type produced repeatedly) both before and during the time participants had their heads above water, with no noticeable change in volume and no audible whistles in air. Therefore, the source animal for these whistles was determined to be a non-participant. In particular, in 4 of the 6 events the group included an associated calf that was very likely the producer of the whistles since the calf remained near the group but did not actively participate in the foraging activity. One other notable case of repeated whistle use during active driver-barrier foraging occurred when an identified barrier individual was rushing in from some distance towards the group as an active event was underway.

When comparing whistles produced in the 30 s before the driving stage of driver-barrier events (N = 35) and in the 30 s before bottom-grubbing events (N = 21) for comparable group sizes (2–3 individuals), there was a significantly higher likelihood of whistles occurring before driver-barrier events than before bottom-grubbing (glm: z = 3.699, p < 0.001; Fig. 3; Table S3). Only one of 21 (0.05%) bottom-grubbing events was preceded by whistles, versus 25 of 35 (71.4%) driver-barrier events. When investigating whistle rate in the 30 s before driver-barrier events for all group sizes i.e., not restricted to group sizes of 2–3 individuals (N = 43), there were more whistles associated with successful events (N = 23, mean = 2.35 whistles, range = 0–6) than unsuccessful events (N = 20, mean = 1.25 whistles, range = 0–5), although this trend was not significant (glm: z = 1.713, p = 0.0867, effect size (odds ratio) = 1.428; Tables S4). Full whistle data are provided in Table S5.

Despite recording with equipment and protocols that are standard for dolphin communication studies (Quick and Janik, 2008; King et al., 2019), the current data set of recorded whistles associated with driver-barrier feeding did not include a high enough proportion of whistles with sufficiently high signal to noise ratio (SNR) to allow for

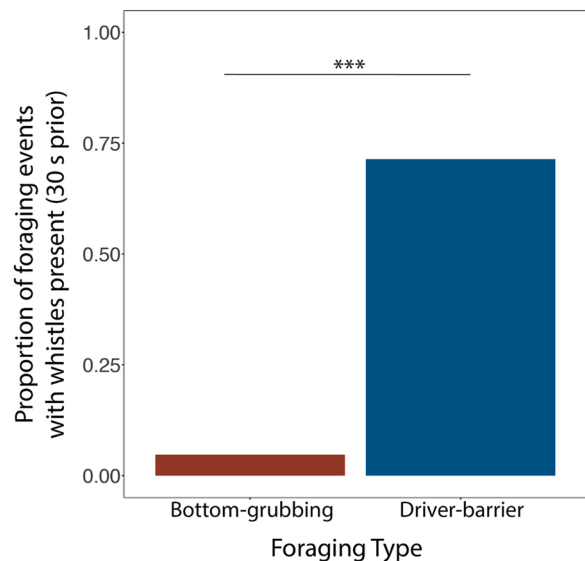


Fig. 3. The proportion of bottom-grubbing (N = 21) versus driver-barrier (N = 35) foraging events that contained whistles in the 30 s prior. Asterisks indicate significant difference (\*\*p < 0.01, \*\*\*p < 0.001).

more in-depth analysis of whistle use, including localization. This is due both to the naturally noisy habitat of the area, as well as the shallow depth, meaning that sounds associated with both the bottom and surface (i.e. snapping shrimp, wave action) were of significant volume on recordings. Most whistles were not of a sufficient SNR for their contours to be clearly visible, and therefore they were unable to be used in either human or neural network pattern analysis. Thus, it was not possible to extract whistle contours in order to determine potential signature whistles of participants, or to determine if there were whistles of similar contour shape associated with driver-barrier behavior between groups containing different individuals.

### 2.3. Discussion

Our results suggest that only one individual echolocates during role-specialized driver-barrier feeding events in bottlenose dolphins, at least the vast majority of the time. With few exceptions, the number of detected click groups during group driver-barrier events closely matched the number of detected click groups during solo driving events and differed significantly from merged clips known to contain the echolocation of two or three animals. Five of the 72 group driver-barrier event clips generated CGS algorithm outputs of 4 or 5 click trains (Fig. 2), which was higher than the output seen in the small sample of solo driving clips. This result could still be generated from a clip in which only one animal is echolocating if that animal, for example, momentarily turns their head off-axis from the hydrophone so that echolocation fades, or the individual may momentarily stop echolocating and then start a new click train. The same typical echolocation pattern was recorded during both solo events and group events, suggesting that the driver individual is the one echolocating. This was supported by video analysis showing that the timing of driver individuals raising their heads above water corresponded with the timing of echolocation fading on the underwater recordings. After events, however, it appears that any individual may echolocate.

To achieve coordination of the behavior in space and time, groups of animals conducting driver-barrier feeding must rely on cues or signals. In the shallow, coastal environment in which driver-barrier behavior is observed, underwater visibility is often poor, making reliance on visual cues unlikely, particularly as animals may be up to 20 m apart at the onset of a driver-barrier event. There was a notable lack of whistle production during the driving phase. Thus, the only cue evident that barrier animals could use to coordinate their movements relative to the driver was the driver's echolocation.

Barrier animals may be directly detecting the outgoing echolocation to gain information about the relative position and movement of the driver individual and/or using reflected echolocation signals to detect the location and movement of the prey. Both mechanisms would fit with the echoic eavesdropping hypothesis, in which individuals gain information via echolocation clicks produced by a conspecific (Gregg et al., 2007). Studies on captive animals have shown that they possess the ability to eavesdrop on conspecifics, but observations of this behavior in free-swimming dolphins are sparse and unconfirmed (Gregg et al., 2007; Götz et al., 2006; Xitco and Roitblat, 1996).

A study of recorded inter-click intervals of spinner dolphins suggests that individuals use echolocation to determine the relative positions of conspecifics to coordinate shifts between discrete stages of feeding on schooling fish (Benoit-Bird and Au, 2009). It is improbable that the echolocation of drivers during driver-barrier feeding primarily serves to track barrier animals since driving individuals also echolocate during solo events. Additionally, driving usually happens in less than 30 s and in one complete movement, thereby providing driver individuals little to no opportunity to adjust their positioning relative to barriers after initiating the behavior (Gazda et al., 2005). Instead, the barrier animals appear to be responsible for correctly positioning themselves relative to the driver. This aligns with studies on humans completing group tasks when individual sub-tasks vary in complexity; those performing less

demanding sub-tasks make more effort to coordinate than those performing more difficult sub-tasks (Vesper et al., 2011).

The second objective of this study was to determine if social signal use changed in association with driver-barrier feeding. Whistles were more likely to be produced in the 30 s leading up to driver-barrier events versus a foraging tactic that is neither cooperative nor role-specialized (i.e. bottom-grubbing), suggesting these vocalizations are associated with driver-barrier behavior. There are several possible hypotheses for associated whistle use, including signaling motivation (Ridgway et al., 2014; Rehn et al., 2011), recruiting conspecifics (King and Janik, 2015), or behavioral coordination (King et al., 2021). Food-related calls that recruit new individuals to a foraging area are seen across many species (Clay et al., 2012). In some cases, such as group foraging cliff swallows, increasing group size may increase foraging success for participants (Brown et al., 1991). A few species of cetaceans, including bottlenose dolphins, have been shown to produce food-associated calls (Janik, 2000; King and Janik, 2015; Parks et al., 2014; Deecke et al., 2011). In the present case, the driver is more successful if barrier dolphins are present (Gazda, 2016), thus, recruiting barrier dolphins prior to the driving event would certainly benefit the driver individual. If the whistles associated with driver-barrier behavior function to recruit conspecifics, these calls could serve to increase by-product benefits associated with more participants (Connor, 1986; Gazda, 2016).

It remains to be determined if the whistles associated with driver-barrier behavior may be context-specific or possibly contain additional information. For example, signature whistles are known to promote group cohesion (Janik and Sayigh, 2013), and maintaining close spatial proximity to the driver leading up to driver-barrier events would be beneficial given that the behavior requires the participating animals to converge upon a small area in a short amount of time. Since driving is only performed by a small number of individuals in the population, barriers have an interest in identifying driver individuals with whom to maintain close contact, which could be facilitated by signature whistle recognition. Future studies, with more acoustic recordings available, should aim to determine the signature whistles of both driver and barrier participants in order to determine which individuals in the group may be responsible for whistles produced in this context. Additionally, whistle types that are shared between groups of different individuals may indicate a foraging-specific social call type (King and Janik, 2015).

It is also possible that whistle rates, rather than referential whistles, convey information to recruit individuals and/or coordinate actions within groups. Hyenas use the same whoop call across contexts, with increased call rate associated with the presence of lions, leading to the recruitment of more group members (Gersick et al., 2015). Similarly, it has been suggested that bottlenose dolphins may use an increased rate of whistling to recruit others to foraging groups (Acevedo-Gutiérrez and Stienessen, 2004). Recent work with dolphins under human care has also shown that increased whistle use facilitates behavioral coordination and leads to significantly more successful trials in a cooperative task (King et al., 2021). Given that the higher whistle rates associated with successful events rather than unsuccessful events was not significant (effect size = 1.428;  $P = 0.09$ ), it should be cautioned that more data collection is required to confirm the causation of these higher whistle rates (whistle rates may be associated with increased fish number, or more whistles may facilitate the recruitment of more barrier individuals, for example).

To summarize, our analysis suggests that only the driver individual echolocates during driver-barrier events, and that barrier animals likely use the driver's echolocation, either directly or indirectly, as a cue to coordinate their movement and timing. While the specific use of whistles in this context remains speculative, evidence suggests that free-swimming dolphins rely on echoic eavesdropping in this role-specialized group foraging task. Our study sheds important new light on the use of vocalizations in facilitating role-specialized behavior in bottlenose dolphins and is the first study demonstrating the use of vocal cues to coordinate a DLRS behavior outside of humans.

## Funding

Funding was provided by National Geographic Society, US (grant number EC-329R-18) and a Louis M. Herman Research Scholarship via The Society for Marine Mammalogy, US. Funding was also provided by generous private donations to the Cedar Key Dolphin Project Inc. (501 (c)(3) US registered charity).

## Ethics approval

All research was conducted under National Marine Fisheries Science Scientific Research Permits 14450/21938 and strictly adhered to the laws of the United States of America.

## Declarations

NA.

## Availability of data and material

All data generated or analyzed during this study are included in this published article and its supplementary information files.

## Acknowledgments

This work was supported by research grants from National Geographic Society and the Louis M. Herman Research Scholarship via The Society for Marine Mammalogy. Funding was also provided by generous donors to the Cedar Key Dolphin Project Inc. Fieldwork would not have been possible without many dedicated field assistants and volunteers. We would also like to thank the reviewers of this article for providing clear and helpful feedback to improve this manuscript.

## Author contributions

RAH, SKG, SLK, and RCC conceived and designed the study. RAH and SKG secured funding and collected the data. RAH conducted the analysis. JS provided and edited code used in echolocation analysis. SLK provided statistical analysis advice. All authors edited the manuscript, provided review, and gave approval for submission.

## Code availability

Custom code used in this study may be made available upon reasonable request.

## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.beproc.2022.104691](https://doi.org/10.1016/j.beproc.2022.104691).

## References

Acevedo-Gutiérrez, A., Stienessen, S.C., 2004. Bottlenose dolphins (*Tursiops truncatus*) increase number of whistles when feeding. *Aquat. Mamm.* 30, 357–362.

Anderson, C., Franks, N.R., 2001. Teams in animal societies. *Behav. Ecol.* 12, 534–540.

Atmaca, S., Sebanz, N., Knoblich, G., 2011. The joint flanker effect: sharing tasks with real and imagined co-actors. *Exp. Brain Res.* 211, 371–385.

Au, W.W., 1993. Characteristics of Dolphin Sonar Signals. *The sonar of dolphins*. Springer, New York, NY, pp. 115–139.

Benoit-Bird, K.J., Au, W.W., 2009. Cooperative prey herding by the pelagic dolphin, *Stenella longirostris*. *J. Acoust. Soc. Am.* 125, 125–137.

Böckler, A., Knoblich, G., Sebanz, N., 2012. Effects of a coactor's focus of attention on task performance. *J. Exp. Psychol.: Hum. Percept. Perform.* 38, 1404.

Böckler, A., Wilkinson, A., Huber, L., Sebanz, N., 2016. Social coordination: from ants to apes. *Wiley Handb. Evolut. Neurosci.* 478–494.

Boesch, C., 2002. Cooperative hunting roles among Tai chimpanzees. *Hum. Nat.* 13, 27–46.

Bradbury, J.W., Vehrencamp, S.L., 2011. Principles of Animal Communication, second ed. Sinauer Associates, Sunderland, MA, US.

Brown, C.R., Brown, M.B., Shaffer, M.L., 1991. Food-sharing signals among socially foraging cliff swallows. *Anim. Behav.* 42, 551–564.

Bullinger, A.F., Wyman, E., Melis, A.P., Tomasello, M., 2011. Coordination of chimpanzees (*Pan troglodytes*) in a stag hunt game. *Int. J. Prima* 32, 1296–1310.

Clay, Z., Smith, C.L., Blumstein, D.T., 2012. Food-associated vocalizations in mammals and birds: what do these calls really mean? *Anim. Behav.* 83, 323–330.

Connor, R.C., 1986. Pseudo-reciprocity: investing in mutualism. *Anim. Behav.* 34, 1562–1566.

Connor, R.C., 1995. The benefits of mutualism: a conceptual framework. *Biol. Rev.* 70, 427–457.

R Core Team, 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria (URL). (<https://www.R-project.org/>).

Connor, R.C., 2010. Cooperation beyond the dyad: on simple models and a complex society. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365, 2687–2697.

Connor, R.C., Smolker, R.A., 1996. 'Pop' goes the dolphin: a vocalization male bottlenose dolphins produce during consortships. *Behavior* 133, 643–662.

D'Vincent, C.G., Nilson, R.M., Hanna, R.E., 1985. Vocalization and coordinated feeding behavior of the humpback whale in southeastern Alaska. *Sci. Rep. Whales Res. Inst.* 36, 41–47.

Deecke, V.B., Nykänen, M., Foote, A.D., Janik, V.M., 2011. Vocal behavior and feeding ecology of killer whales (*Orcinus orca*) around Shetland, UK. *Aquat. Biol.* 13, 79–88.

Gazda, S.K., 2016. Driver-barrier feeding behavior in bottlenose dolphins (*Tursiops truncatus*): New insights from a longitudinal study. *Mar. Mamm. Sci.* 32, 1152–1160.

Gazda, S.K., Connor, R.C., Edgar, R.K., Cox, F., 2005. A division of labor with role specialization in group-hunting bottlenose dolphins (*Tursiops truncatus*) off Cedar Key, Florida. *Proc. R. Soc. B: Biol. Sci.* 272, 135–140.

Gersick, A.S., Cheney, D.L., Schneider, J.M., Seyfarth, R.M., Holekamp, K.E., 2015. Long-distance communication facilitates cooperation among wild spotted hyaenas, *Crocuta crocuta*. *Anim. Behav.* 103, 107–116.

Gilby, I.C., Connor, R.C., 2010. The Role Of Intelligence In Group Hunting: Are Chimpanzees Different From Other Social Predators. University of Chicago Press, Chicago, IL, pp. 220–233.

Gilby, I.C., Machanda, Z.P., Mjungu, D.C., Rosen, J., Muller, M.N., Pusey, A.E., Wrangham, R.W., 2015. 'Impact hunters' catalyse cooperative hunting in two wild chimpanzee communities. *Philos. Trans. R. Soc. B: Biol. Sci.* 370, 20150005.

Goebel, W., Palmer, C., 2009. Synchronization of timing and motion among performing musicians. *Music Percept.* 26, 427–438.

Götz, T., Verfuss, U.K., Schnitzler, H., 2006. 'Eavesdropping' in wild rough-toothed dolphins (*Steno bredanensis*)? *Biol. Lett.* 2, 5–7.

Gregg, J.D., Dudzinski, K.M., Smith, H.V., 2007. Do dolphins eavesdrop on the echolocation signals of conspecifics? *Int. J. Comp. Psychol.* 20, 65–88.

Hamilton, R.A., Starkhammar, J., Gazda, S.K., Connor, R.C., 2021. Separating overlapping echolocation: An updated method for estimating the number of echolocating animals in high background noise levels. *J. Acoust. Soc. Am.* 150, 709–717.

Hurtado, M.J., Fénéron, R., Gouat, P., 2013. Specialization in building tasks in the mound-building mouse, *Mus spicilegus*. *Anim. Behav.* 85, 1153–1160.

Janik, V.M., Sayigh, L.S., 2013. Communication in bottlenose dolphins: 50 years of signature whistle research. *J. Comp. Physiol. A* 199, 479–489.

Janik, V.M., Sayigh, L.S., Wells, R.S., 2006. Signature whistle shape conveys identity information to bottlenose dolphins. *Proc. Natl. Acad. Sci.* 103, 8293–8297.

Janik V.M. (2000) Food-related bray calls in wild bottlenose dolphins (*Tursiops truncatus*). *Proceedings of the Royal Society of London Series B: Biological Sciences* 267:923–927.

King, S.L., Janik, V.M., 2015. Come dine with me: food-associated social signalling in wild bottlenose dolphins (*Tursiops truncatus*). *Anim. Cogn.* 18 (4), 969–974.

King, S.L., Allen, S.J., Krützen, M., Connor, R.C., 2019. Vocal behaviour of allied male dolphins during cooperative mate guarding. *Anim. Cogn.* 22 (6), 991–1000.

King, S.L., Guarino, E., Donegan, K., McMullen, C., Jaakkola, K., 2021. Evidence that bottlenose dolphins can communicate with vocal signals to solve a cooperative task. *R. Soc. Open Sci.* 8, 202073.

Mächler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using lme4. *J. Stat. Softw.* 67 (1), 1–48.

Melis, A.P., Semmann, D., 2010. How is human cooperation different? *Philos. Trans. R. Soc. B: Biol. Sci.* 365, 2663–2674.

Melis, A.P., Tomasello, M., 2019. Chimpanzees (*Pan troglodytes*) coordinate by communicating in a collaborative problem-solving task. *Proc. R. Soc. B* 286, 20190408.

Moore, B.L., Connor, R.C., Allen, S.J., Krützen, M., King, S.L., 2020. Acoustic coordination by allied male dolphins in a cooperative context. *Proc. R. Soc. Lond.: Biol. Sci.* 287 (1924), 20192944.

Norris, K.S., Evans, W., Turner, R., 1967. Echolocation in an Atlantic bottlenose porpoise during discrimination. In: Busnel, R.G. (Ed.), *Animal Sonar Systems, Biology and Bionics*. Laboratoire de Physiologie Acoustique, Jouy-en-Josas 78, France.

Overstrom, N.A., 1983. Association between burst-pulse sounds and aggressive behavior in captive Atlantic bottlenose dolphins (*Tursiops truncatus*). *Zoo. Biol.* 2, 93–103.

Parks, S.E., Cusano, D.A., Stimpert, A.K., Weinrich, M.T., Friedlaender, A.S., Wiley, D.N., 2014. Evidence for acoustic communication among bottom foraging humpback whales. *Sci. Rep.* 4, 7508.

Quick, N.J., Janik, V.M., 2008. Whistle rates of wild bottlenose dolphins (*Tursiops truncatus*): Influences of group size and behavior. *J. Comp. Psychol.* 122, 305.

Quick, N.J., Rendell, L.E., Janik, V.M., 2008. A mobile acoustic localization system for the study of free-ranging dolphins during focal follows. *Mar. Mamm. Sci.* 24, 979–989.

- Rehn, N., Filatova, O.A., Durban, J.W., Foote, A.D., 2011. Cross-cultural and cross-ecotype production of a killer whale 'excitement' call suggests universality. *Naturwissenschaften* 98, 1–6.
- Ridgway, S., Moore, P., Carder, D., Romano, T., 2014. Forward shift of feeding buzz components of dolphins and belugas during associative learning reveals a likely connection to reward expectation, pleasure and brain dopamine activation. *J. Exp. Biol.* 217, 2910–2919.
- Sayigh, L.S., Wells, R.S., Janik, V.M., 2017. What's in a voice? Dolphins do not use voice cues for individual recognition. *Anim. Cogn.* 20, 1067–1079.
- Sayigh, L.S., Tyack, P.L., Wells, R.S., Solow, A.R., Scott, M.D., Irvine, A., 1999. Individual recognition in wild bottlenose dolphins: a field test using playback experiments. *Anim. Behav.* 57, 41–50.
- Stander, P.E., 1992. Cooperative hunting in lions: the role of the individual. *Behav. Ecol. Socio* 29, 445–454.
- Starkhammar, J., Nilsson, J., Amundin, M., Kuczaj, S.A., Almqvist, M., Persson, H.W., 2011. Separating overlapping click trains originating from multiple individuals in echolocation recordings. *J. Acoust. Soc. Am.* 129, 458–466.
- Tyack, P.L., 1998. Acoustic Communication Under the Sea. In: Hopp, S.L., Owren, M.J., Evans, C.S. (Eds.), *Animal Acoustic Communication*. Springer, Berlin, Heidelberg.
- Urick, R.J., 1983. *Principles of Underwater Sound*, third ed. Peninsula Publishing, Los Altos, California.
- Van der Wel, R.P.R.D., Knoblich, G., Sebanz, N., 2011. Let the force be with us: dyads exploit haptic coupling for coordination. *J. Exp. Psychol.: Hum. Percept. Perform.* 37, 1420.
- Vesper, C., Van der Wel, R.P.R.D., Knoblich, G., Sebanz, N., 2011. Making oneself predictable: Reduced temporal variability facilitates joint action coordination. *Exp. Brain Res.* 211, 517–530.
- Wiley, D., Ware, C., Bocconcelli, A., Cholewiak, D., Friedlaender, A., Thompson, M., Weinrich, M., 2011. Underwater components of humpback whale bubble-net feeding behavior. *Behavior* 148, 575–602.
- Würsig, B., Würsig, M., 1977. The photographic determination of group size, composition, and stability of coastal porpoises (*Tursiops truncatus*). *Science* 198 (4318), 755–756.
- Xitco, M.J., Roitblat, H.L., 1996. Object recognition through eavesdropping: Passive echolocation in bottlenose dolphins. *Anim. Learn Behav.* 24, 355–365.