

# Cooperative prey herding by the pelagic dolphin, *Stenella longirostris*

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Sonar techniques were used to quantitatively observe foraging predators and their prey simultaneously in three dimensions. Spinner dolphins foraged at night in highly coordinated groups of 16–28 individuals using strict four-dimensional patterns to increase prey density by up to 200 times. Herding exploited the prey's own avoidance behavior to achieve food densities not observed otherwise. Pairs of dolphins then took turns feeding within the aggregation that was created. Using a proxy estimate of feeding success, it is estimated that each dolphin working in concert has more access to prey than it would if feeding individually, despite the costs of participating in the group maneuvers, supporting the cooperation hypothesis. Evidence of a prey density threshold for feeding suggests that feedback from the environment may be enough to favor the evolution of cooperation. The remarkable degree of coordination shown by foraging spinner dolphins, the very strict geometry, tight timing, and orderly turn taking, indicates the advantage conferred by this strategy and the constraints placed upon it. The consistent appearance of this behavior suggests that it may be a critical strategy for energy acquisition by spinner dolphins in energy poor featureless environments in the tropical Pacific Ocean. © 2009 Acoustical Society of America.

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## I. INTRODUCTION

The pelagic ocean at low latitudes is low in available energy (Longhurst *et al.*, 1995), potentially making it difficult for large animals with high energetic needs to consume enough food to survive and reproduce. One solution to the challenge of finding and capturing dispersed food in this environment is to forage as a group. Searching together can increase a predator's prey detection rate, as shown in gulls (Gotmark *et al.*, 1986; Hoffman *et al.*, 1981) and dolphins (Norris and Prescott, 1961; Saayman *et al.*, 1973). Cooperation, collective action by a group of animals that increases each individual's fitness, in cormorants (Bartholomew, 1942), gulls (Gotmark *et al.*, 1986), and killer whales (Baird and Dill, 1996) increases their prey capture efficiency. Cooperative groups may also actively herd prey, increasing its density and decreasing its escape options. Increased densities of aquatic prey have been associated with groups of river otters (Serfass, 1995), various species of piscivorous marine fish (Hiatt and Brock, 1948; Partridge *et al.*, 1983; Schmitt and Strand, 1982), pelicans (Anderson, 1991; Goss, 1888), killer whales (Nottestad *et al.*, 2002; Similä and Ugarte, 1993), and dolphins (Gallo Reynoso, 1991; Würsig and Würsig, 1979).

Spinner dolphins (*Stenella longirostris*) are primarily pelagic animals that reside in the energy poor waters of the

subtropics. They feed at night on small prey including lanternfish, shrimp, and squid that are part of a deep-scattering layer (Norris and Dohl, 1980). Because of the small size of their prey (less than 0.002% of a spinner dolphin's mass), the prey's diel migration behavior, and their own energetic needs, spinner dolphins need to be efficient foragers, each consuming an estimated 1.25 prey items per minute throughout the night (Benoit-Bird, 2004). Spinner dolphins have been observed in groups while foraging (Benoit-Bird and Au, 2003b), which may play a role in maximizing their foraging efficiency. However, two-dimensional data collected in previous field studies of spinner dolphins do not address the behavior of groups of foraging spinner dolphins or their potential function. Dolphin feeding groups were organized, in agreement with predictions for cooperative foraging, encouraging further study.

Most aquatic animals forage beneath the ocean's surface, making it difficult to observe their behavior, particularly for nocturnal predators such as spinner dolphins. While group foraging has been observed in many aquatic species, their relative inaccessibility has made quantitative assessment of interactions between groups of predators and their prey difficult (Schmitt and Strand, 1982; Serfass, 1995; Similä and Ugarte, 1993). One way toward a better understanding of the behaviors and benefits of group foraging in aquatic animals is using data that allow us to place predators and prey in three-dimensional space over time. We used a multibeam echosounder capable of simultaneous high-resolution observations of predator and prey behavior be-

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neath the water's surface to observe the nocturnal behavior of spinner dolphins off the coast of Oahu, HI in three dimensions. We recorded the raw acoustic data from the sonar and used underwater acoustics techniques for analysis rather than analyzing the visual output of the sonar, as has been done in previous biological studies (Axelsen *et al.*, 2001; Nottestad and Axelsen, 1999; Ridoux *et al.*, 1997). This allowed us to quantify dolphin group size, foraging effort, and potential feeding opportunities while simultaneously measuring changes in prey density. Previous work on these animals has suggested that group foraging may be important; however, the short term behavior of dolphins could not be measured nor could the immediate effects of this behavior on prey distribution (Benoit-Bird and Au, 2003b), making it impossible to determine if cooperation could occur. Our goals in this study were to understand the benefits of group foraging and the mechanisms of prey aggregation to ultimately assess the potential importance of group foraging in predator survival.

## II. METHODS

### A. Survey design

To measure the distribution of spinner dolphins and the scattering layer that serves as their prey, two sites along the leeward coast of Oahu were surveyed with a 200 kHz Kongsberg-Simrad-Mesotech MS 2000 multibeam echosounder. The sonar provided three-dimensional information on the distribution of dolphins and their prey while the vessel was moving. This frequency was selected because of its high spatial resolution and its low likelihood of detection by a *Stenella* species. While an audiogram for *Stenella longirostris* is not available, the hearing of *Stenella coeruleoalba* shows a very steep roll-off in sensitivity, as is typical for mammals, above about 120 kHz (Kastelein *et al.*, 2003). This suggests that a *Stenella* sp. is unlikely to hear a 200 kHz signal with an approximately 7 kHz bandwidth.

Surveys were conducted between 2100 and 0300 h local time for ten nights in May and June of 2003. The moon was less than one-quarter illuminated during all sampling so the ambient light level was very low. Sampling was conducted around two areas known for the presence of dolphins, covering approximately 11 km surrounding Makua Bay and 10 km surrounding Kahe Point Beach, about half of the entire leeward (Waianae) coast of Oahu. Sampling was conducted along linear transects running primarily parallel to the shoreline at a vessel speed of approximately 1.5–2.0 m/s (3–4 kn) with occasional stops for other sampling (Benoit-Bird and Au, in press). These transects were located between 1.0 and 2.2 km from the shoreline, in water depths between 60 and 200 m. A total of 186 km was surveyed.

### B. Multibeam echosounder

The head of the 200 kHz multibeam echosounder was mounted off the starboard side of the vessel, approximately 0.5 m below the water's surface, at a 45° angle relative to the direction of travel and 30° up from the vertical plane perpendicular to the bottom. This permitted us to observe animals from the side, rather than having to drive directly over them,

limiting potential impacts of the survey on the dolphins. The multibeam system used a 150  $\mu$ s long outgoing pulse transmitted at a rate of 5.6 per second with a source level of 215 dB re 1  $\mu$ Pa. The system had a resolution of 0.22 m in the direction 30° from vertical, resulting in a true depth resolution of 0.19 m. The system had 120, 1.5° × 20° beams that overlapped by 0.25° in the narrower nearly across-track direction, providing an angular coverage of 120° with 1° resolution in this direction. Data were taken using the external imaging transducer of the sonar, thus forming a Mills Cross to provide the greatest spatial resolution, giving a received beam width of 1.5° in the direction 45° from along-track. The sonar system was set to cover a range of 65 m. In the geometry used, the instrument thus had a maximum range of 37.5 m from the vessel horizontally and 53 m vertically, giving a swath width of 113 m at the furthest point in its range. Further technical details about the sonar can be found in Cochrane *et al.* (2003).

The multibeam echosounder system was calibrated in the Applied Physics Laboratory, University of Washington seawater calibration facility using tungsten carbide spheres with diameters of 20 and 38.1 mm following the protocols established by Foote *et al.* (2005). The system showed a nearly linear gain function, stable performance, and beam patterns consistent with those predicted by the system geometry.

During field sampling, raw complex echo signals from each of the 80 elements of the multibeam echosounder were saved to hard disk with 12 bit digitization, resulting in a dynamic range of 72 dB. The data were beamformed with Chebyshev-type amplitude weighting and the amplitude and range of echoes in each beam were then extracted using a custom MATLAB program. The range versus azimuth data were transformed into a rectangular coordinate system where one axis is along the direction of travel, the second is across the direction of travel, and the third is the depth. To obtain three-dimensional information, six successive sonar returns, or about 1 s of data, were combined. All position data were corrected using coupled differential Global Positioning System (GPS) to eliminate the movement of the vessel. GPS readings were taken with each sonar signal at a rate of 5.6 per second. Correction for vessel pitch and roll could not be conducted; however, all sampling was conducted with sea states below Beaufort 2 (waves of less than 0.2 m, winds below 6 kn), often with completely glassy conditions, limiting undesirable vessel movement.

### C. Dolphin position analysis

The transformed, averaged, and position corrected data were used to identify large targets and to create isoscattering surfaces. Dolphins were identified from the data based on their unique set of acoustic scattering characteristics as identified by Benoit-Bird and Au (2003b), most notably, a very strong echo that is caused by their air filled lungs (Au, 1996) and possibly their nasal passages that is surrounded by remarkably low-amplitude echoes presumably by their blubber which is nearly impedance matched to seawater. Echoes from spinner dolphins identified during daylight surfacings

were taken nearly simultaneously with a calibrated 200 kHz echosounder (Simrad EK60) and the SM2000. Echoes from spinner dolphins SM2000 had values between  $-25.9$  and  $-28.2$  while the values measured with the EK60 were within  $0.3$  dB of  $-27.1$  dB. The SM2000 echoes showed more variance in their amplitude likely because of the increase in the variability in insonified angle relative to the narrow beam EK60. In both systems, the presumptive lung echo provided an extremely high target strength within this field of  $\sim -27$  dB echoes. The length of animals measured with the multibeam was consistent with the size for adult spinner dolphins in Hawaiian waters.

Other large targets, e.g., those with high target strengths and of measurable size with the multibeam's  $1.5^\circ$  resolution, were commonly observed along sampling transects. These targets were not consistent with the measured characteristics of known spinner dolphins and were never observed near targets consistent with spinner dolphins and thus were not considered in the analysis since sections of transects between dolphin observations were not utilized here. It is unlikely that similarly sized species of dolphins (e.g., the spotted dolphin *S. attenuata*) could be differentiated using the sonar. However, no other similarly sized species in this habitat are known to be foraging at depth at night and thus other species are not likely a large source of error.

Multiple echoes were simultaneously detected in multiple beams and range bins from a single spinner dolphin, so for the analysis of dolphin position, the single strongest echo from each animal was utilized, probably from its lungs, creating a standardized method of locating the animal in space and measuring distance between animals. However, all echoes matching the characteristics of an individual dolphin were utilized to estimate the length of each dolphin target by adding the width of the beam for each echo at the range it was detected together. The lengths of targets that were not perpendicular to the beam were corrected by estimating the angle of the target through differences in the range between adjacent beams and using basic trigonometric relationships to convert apparent to actual length.

The sonar system has a resolution of  $1.5^\circ$  in the azimuth direction and  $9.6$  cm in the range direction. To increase the resolution of measurement of animal spacing, information from six successive pings was used to calculate interanimal distances. Changes in spacing in this  $1$  s time period were assumed to be negligible. The movement of the sonar relative to the animals during this time, however, decreased the minimum interspacing distance that could be measured in all dimensions to approximately  $10$  cm.

Individual dolphins could not be tracked for extended periods using the multibeam echosounder because the echoes measured from each individual, while distinguishable in space, do not bear individual features that allow them to be identified from other similar echoes at a later time period. However, individual animals could be measured in several successive signals. The movement of each individual dolphin was measured by mapping the position of its strong dolphin air-passage echo in successive pings, permitting estimates of swimming speed to be made over short time intervals.

## D. Prey distribution analysis

After removal of large individually identified targets, volume scattering was thresholded at a value of  $-70$  dB. The scattering of the prey layer in each  $m^3$  within the sampling volume was then normalized to the overall average scattering per  $m^3$  for all observations of the scattering layer for statistical analysis. Spatial statistics (Benoit-Bird and Au, 2003c) were utilized to determine the location of significant changes in relative scattering in three-dimensional space. Each  $3$  dB  $m^{-3}$  change in scattering strength, representing a doubling in prey density [see Eq. (1)], was found to represent a significant difference

$$\Delta \text{prey density} = 10^{(\Delta \text{prey scattering strength}/10)} \quad (1)$$

Linear interpolation between points of the same relative scattering value created isodensity volumes in the prey field. The size of prey isodensity volumes and their location relative to dolphins could then be analyzed.

## III. RESULTS

We made 267 observations of groups of dolphins in the upper  $50$  m of the water column. Observation duration ranged from  $22$  to  $257$  s with a mean duration of  $123$  s. These observations are longer than expected based on the vessel speed for dolphins swimming in a random direction. Most of the observations of directionally swimming dolphins were of animals swimming along isobath, parallel to the transects, permitting longer observations when animals were swimming in the same direction as the vessel. The longest observations were only possible when the vessel happened to be making a turn about a group of animals and observed them from multiple angles. Indications of changes in behavior—e.g., increases in audible surfacing rate, bowriding, playing at the surface, and swimming around the boat—were noticed during a few times when the vessel was moving unpredictably for reasons unassociated with sampling. However, these types of behaviors were not detected during normal transect sampling, suggesting limited effects of the vessel or the instruments on the dolphins during sampling.

During night-time surveys, apparently foraging dolphins were found in groups in distinctive geometries, defined here as foraging stages. The split-beam echosounder, which could sample the entire water column throughout the study area, confirmed that the scattering layer in the sampling area did not extend past the  $50$  m vertical limit of the multibeam sonar. The depth of dolphins was always within the depth range of the detected scattering layer, except during brief surfacings, suggesting foraging activity. The depth of dolphins relative to the scattering layer is shown in Fig. 1. The results show that detected dolphin groups covered nearly the entire vertical range of the scattering layer, missing an average of  $1.5$  m at the top and  $3.5$  m at the bottom of the layer.

### A. Dolphin groups

Groups of dolphins ranged in size from  $16$  to  $28$  with a bimodal distribution (modes= $20, 24$ ). All 267 groups that we observed were comprised of distinct pairs of animals where one was ahead and slightly above the other dolphin in the

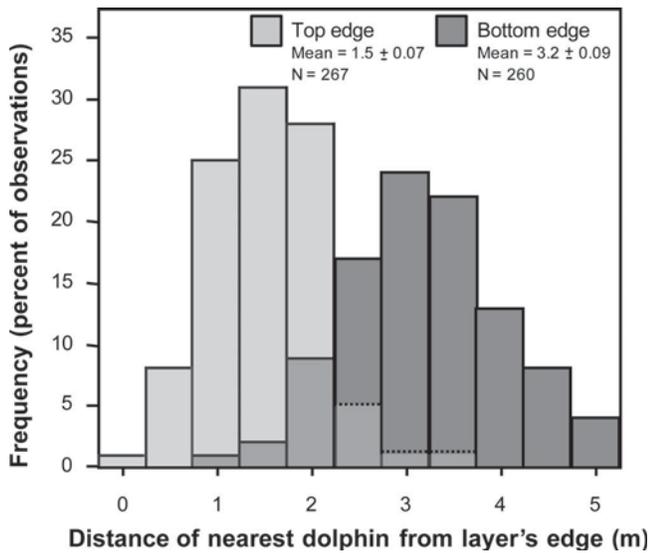


FIG. 1. Depth between the dolphin nearest the edge of the upper and lower edges of the scattering layer and the layer's edge. Foraging dolphins were within the scattering layer so dolphins were deeper than the upper edge of the layer and shallower than the lower edge.

pair (Fig. 2). Consequently, all foraging groups were made up of even numbers of dolphins. This is consistent with results from a previous study (Benoit-Bird and Au, 2003b) though measurements of animal spacing could not be mea-

sured from those results. Mean distances between individuals in the pair, corrected for a non-normal distribution using a square-root transformation, are  $0.91 \pm 0.02$  m (95% CI) in the  $X$ - $Y$  plane and  $1.1 \pm 0.01$  m (95% CI) in the  $Z$  plane. Repeated measures analyses of variance (ANOVAs) on transformed intrapair distance data showed no significant effect of the geometry of the group termed the foraging stage on intrapair distances ( $X$ - $Y$  plane: total  $N=163,589$ ,  $F_3 = 1.34$ , and  $p=0.38$ ,  $1-\beta=0.67$ ; depth ( $Z$ ): total  $N = 163,589$ ,  $dF=3$ ,  $F_3=1.08$ ,  $p=0.73$ , and  $1-\beta=0.77$ ).

An ANOVA revealed that group size varied significantly with the initial prey relative density defined as the density of prey measured just prior to the dolphins arrival at that location ( $F_{11}=23.11$ ,  $N=96$ , and  $p<0.001$ ). These estimates could only be made when the area was observed prior to the movement of a line of dolphins into the area, resulting in a limited sample size for these estimates. Group size tended to be larger when initial prey density was lower and smaller when prey density was higher. A regression showed that dolphin group size was predictably related to prey density (Fig. 3,  $r^2=0.40$ ,  $F=173.02$ , and  $P<0.001$ ). Dolphin group size was also significantly positively related to increases in variance in scattering strength, a measure of patchiness ( $r^2 = 0.54$ ,  $F=193.66$ , and  $P<0.001$ ). The smallest groups of 16 animals were in areas of the scattering layer with  $\sigma^2$  values of about 2000 while groups of 28 animals were in areas of

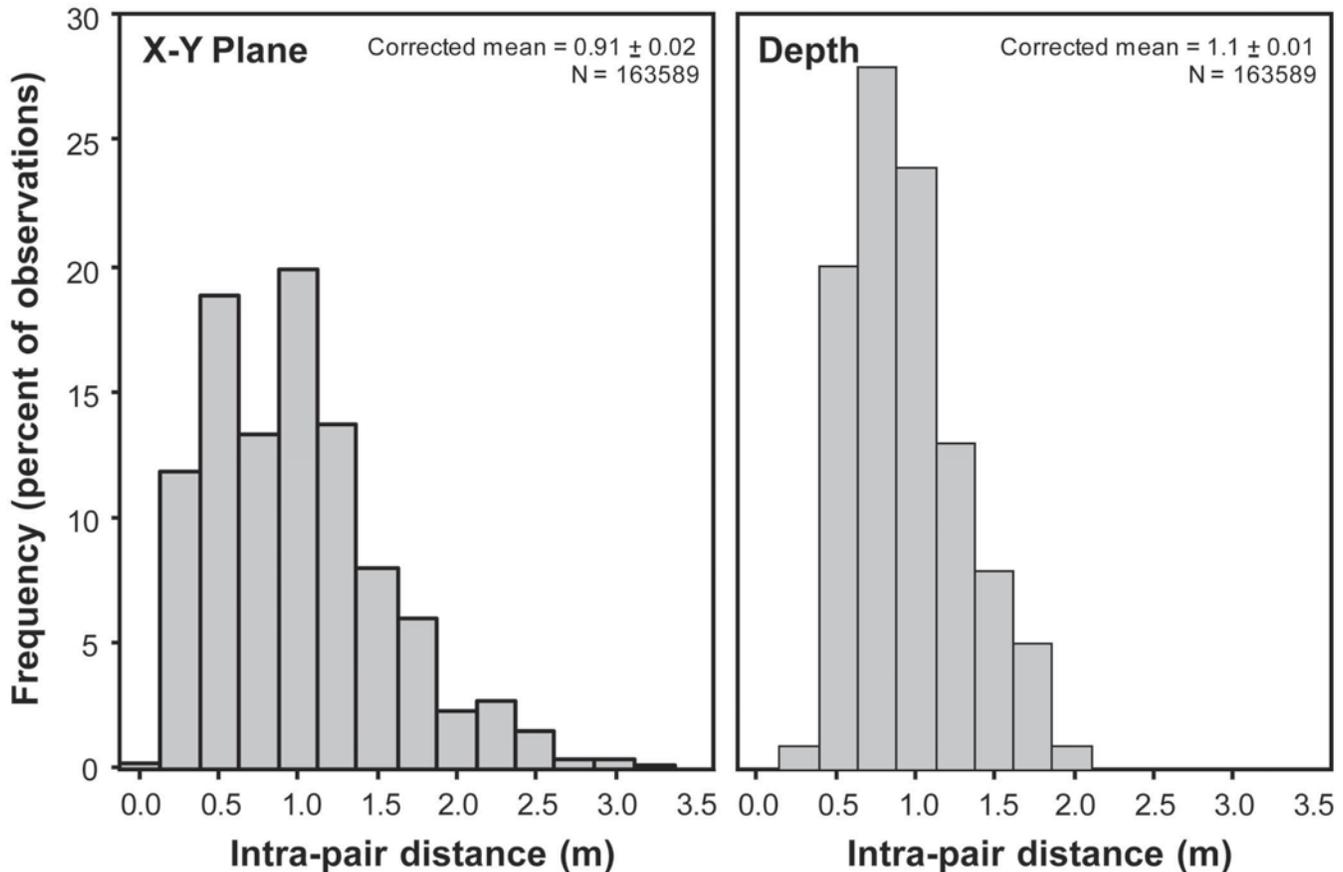


FIG. 2. Distance between individual dolphins within a pair in the  $X$ - $Y$  plane (left) and with depth (right). The mean value shown on each graph has been corrected using a square-root transformation of the data which produced a distribution not significantly different from normal. The corrected 95% confidence interval is also shown. Repeated measures ANOVAs on transformed data showed no significant effect of foraging stage on intrapair distances in either plane.

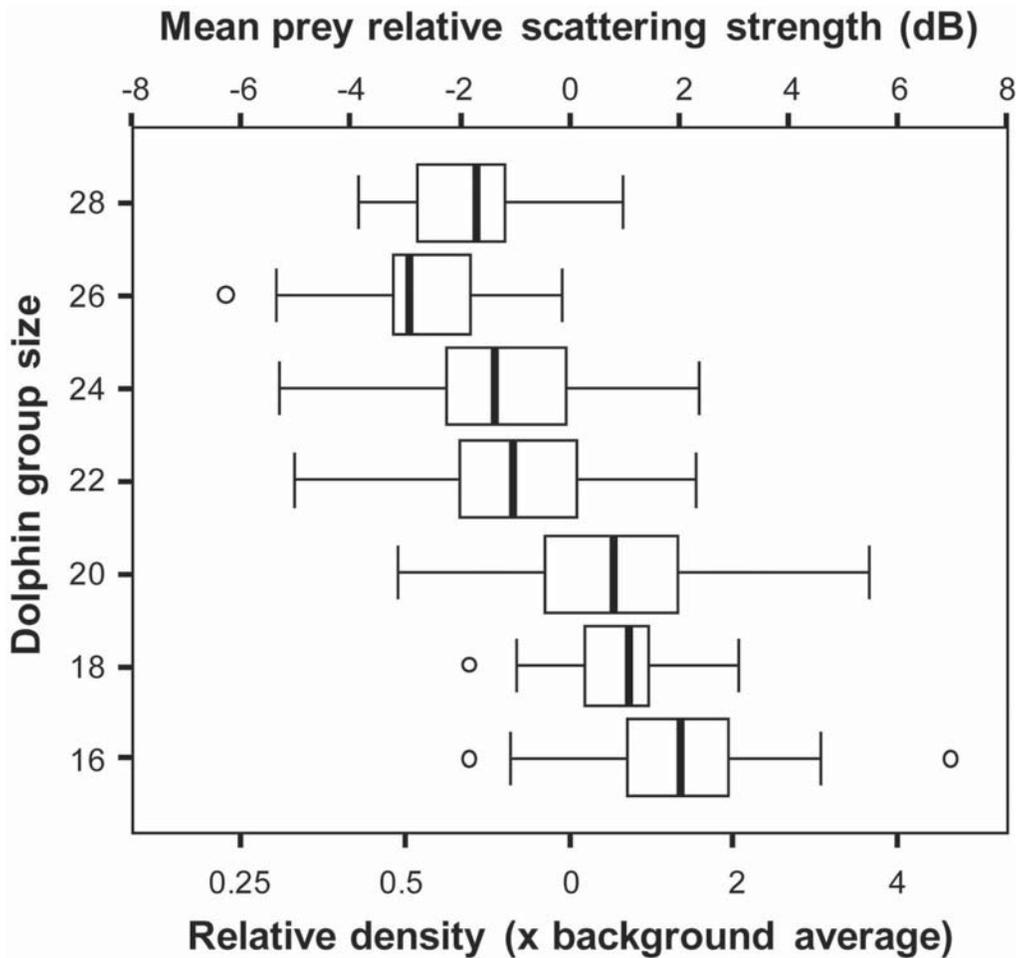


FIG. 3. Dolphin group size as a function of mean relative scattering of prey at the beginning of the observation. Black bars show the median, white boxes show one interquartile range, the error bars show the 95% confidence interval, and dots show outliers.

the scattering layer with  $\sigma^2$  values of just over 5000. While there was no affect of variance in scattering strength on interpair spacing with depth ( $r^2=0.06$ ,  $F=2.37$ , and  $P>0.05$ ), the average spacing in the  $XY$  plane between pairs of dolphins swimming in a circle was significantly affected by variance in scattering strength ( $r^2=0.40$ ,  $F=175.66$ , and  $P<0.001$ ). Spacing between animals decreased by up to 1.6 m as variance increased. However, prey relative scattering strength observed within the circle of dolphins, an estimate of the potential benefits of the behavior, did not vary significantly with dolphin group size ( $F_{11}=1.57$ ,  $N=267$ ,  $p>0.05$ , and  $1-\beta=0.76$ ).

### B. Foraging stages

There were four clear geometries or stages of foraging observed in spinner dolphins (Fig. 4). A brief summary will help follow the remaining results and the detailed methods of their determination. Animals were found to swim in a line running perpendicular to the shoreline, termed “wide line.” Next, the spacing between pairs in the line decreased dramatically while animals continued to swim forward. The animals in this line then formed a 28–40 m circle, closing the circle from offshore. The final stage of foraging before dolphins surfaced is termed “inside circle.” Pairs of dolphins at opposite sides of the circle moved inside the circle formed

by the other dolphins. In all foraging stages, dolphins were distributed over nearly the entire depth range of the scattering layer. Each pair of animals appeared to remain at a single depth through an entire foraging bout so that pairs are offset around the circle, forming a cylinder of prey as they repeatedly swim around it.

The beginning and end of foraging stages and their transitions were defined by changes in the geometry of foraging. The beginning of the transition from wide line to tight line was defined as the point when the mean interpair spacing decreased by 10% and the animals were determined to have achieved the tight line formation when the mean interpair spacing for all pairs was within 10% of the minimum of interpair spacing observed in that group later in the observation. The transition to circling from the tight line was determined to have begun when the distance between any two animals perpendicular to the plane of the line was greater than 7 m, slightly greater than the maximum interpair distance measured parallel to the line. The complete formation of the circle was determined as the point when the nearest-neighbor distance between pairs of animals in the group was less than 7 m. The transition to circling to moving inside the circle was defined as the point when the distance between any opposing pairs of animals in the circular formation, the radius of the circle, was 4 m less than the mean radius of the

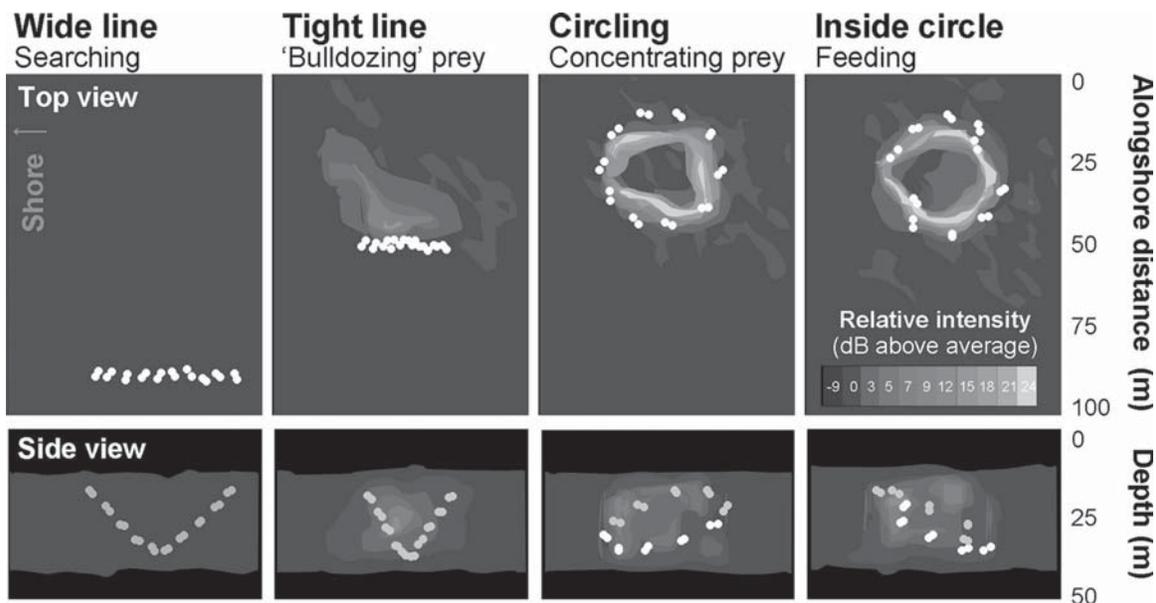


FIG. 4. Top and side view examples of dolphins in each of the four stages of foraging observed. For the top view, scattering was integrated through the entire water column for each square meter. For the side view, scattering was integrated for the 20 m immediately in front of the dolphin group. The relative scattering intensity of prey is indicated by grayscale. Prey density can be related to the scattering intensity with each 3 dB increase in scattering representing a doubling of prey density. The position of the air passage echoes from dolphins is shown as dots. In the side view, the dolphins behind the integration plane are shown as a darker shade.

circle comprised of all the other animals. The interpair spacing for animals clearly within each of the four defined stages is shown in Fig. 5.

Complete observations of entire foraging bouts could not be made from the data; however, estimates of stage duration and stage order could be made using data that contained complete foraging stages, defined as those that con-

tained at least some part of the stage before and after. Combining these data gives us an estimate of the order and duration a complete foraging bout. Figure 6 shows the mean duration of each foraging stage, the 95% confidence interval of the mean, and the number of times each stage was observed completely. Combining all the means gives us an estimate of the duration of a complete foraging bout of 4 min

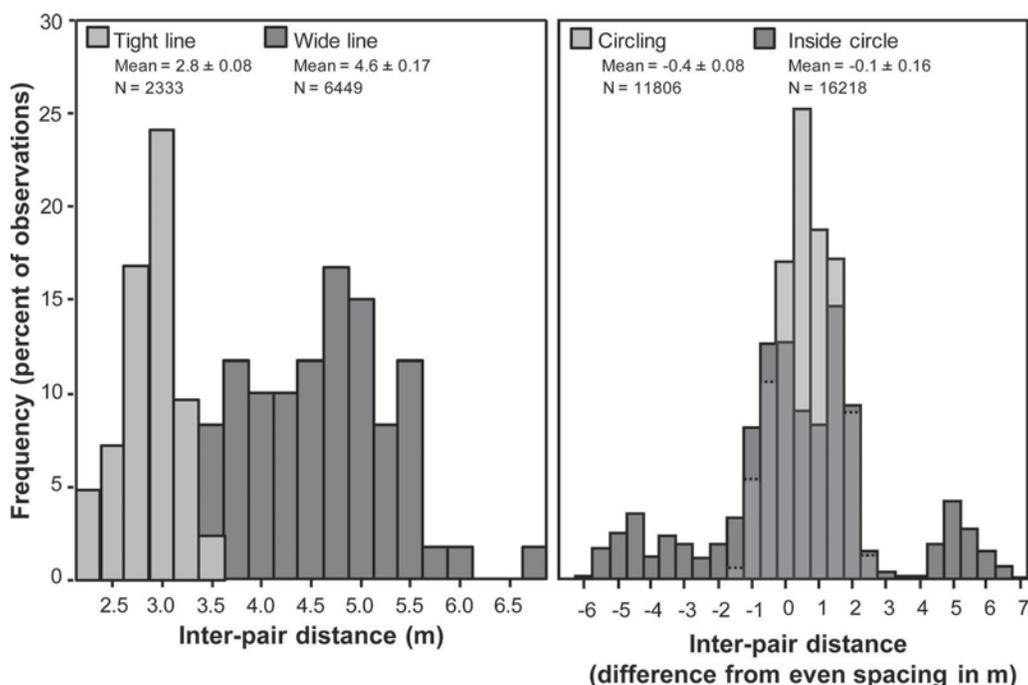


FIG. 5. (Left) Distance in the  $x$ - $y$  plane between pairs of dolphins in a foraging group for the first two foraging stages identified. The distances in line abreast swimming animals were consistent regardless of the size of the group. (Right) Distance in the  $x$ - $y$  plane between pairs of dolphins in a foraging group for the circling foraging stages. Because the distances are significantly affected by the size of the group, distances are shown as the difference between evenly spaced animals in each group, estimated by dividing the circle's diameter by the number of pairs of dolphins in the group, and the actual spacing. Note that the sample sizes represent the number of measurements between pairs, leading to a much greater sample size than the number of groups detected.

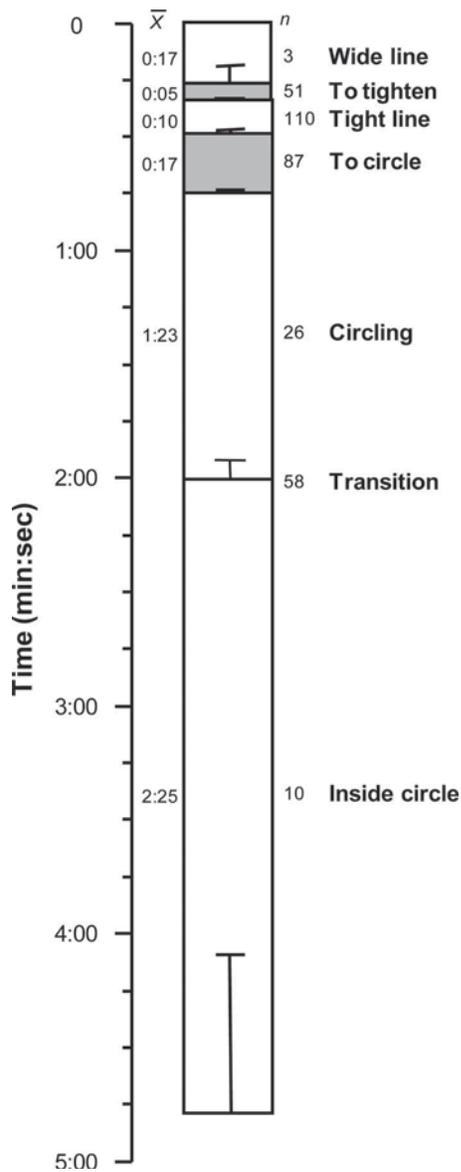


FIG. 6. Mean duration of each foraging stage with 95% confidence intervals indicated by the error bars. The number of complete observations for each stage is shown.

and 38 s with a total 95% CI for 1 min. The relatively high sample sizes of observed transition between stages, e.g., recording some part of the stage before and some part of the stage after, provide confidence in the interpreted order of behaviors and their consistency. No observations of targets consistent with the echo characteristics of spinner dolphins were made that moved between these stages in a different order from the proposed model of foraging.

There were significant differences in measured swimming speeds between the various defined foraging stages (Fig. 7, ANOVA  $F_3=267.96$ , and  $p < 0.0001$ ). There were no significant effects of time of night or group size on swimming speed ( $F_5=0.745$ ,  $P=0.59$ ;  $F_6=2.0$ , and  $P=0.08$ , respectively). A Dunnett's C *post hoc* comparison showed that swimming speed at each stage was significantly different from the speed of every other stage ( $p < 0.05$ ). The swimming speeds measured here compare well with the  $0.26\text{--}4.32\text{ m s}^{-1}$  estimates of bottlenose dolphins speeds

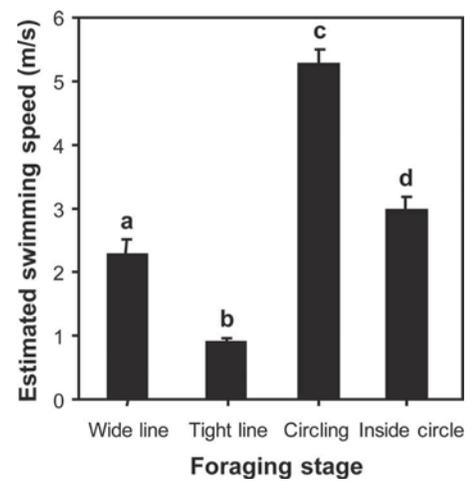


FIG. 7. Mean swimming speed measured from successive detections of dolphins is shown with 95% confidence intervals. An analysis of variance and *post hoc* tests revealed that the swimming speeds for each foraging stage were significantly different.

made from a video sonar (Ridoux *et al.*, 1997) with the highest speeds observed when animals were swimming in a circle before animals began to move into the circle when their swimming speed decreased by nearly half.

There were significant changes in prey relative scattering strength between and within foraging stages. An ANOVA showed that there was a significant effect of foraging stage on prey relative scattering strength ( $F_5=244.45$  and  $P < 0.0001$ ). *Post hoc* Dunnett's C comparisons showed that the prey relative scattering strength of each stage was significantly different from that of every other stage ( $P < 0.05$ ). Figure 8 shows prey relative scattering strength as a function of time within each foraging stage. Regression analyses were used to observe these changes. See Fig. 8 for all  $R^2$  and  $p$  values. There was no significant change in prey scattering while the dolphins were in their wide line, the transition from a line to a circle, or for the first 75 s when dolphins were inside the circle after which there was a significant decrease in prey scattering. There was a significant increase in prey relative scattering strength in the 5 m immediately in front of the dolphin group when the animals were tightening their line, were in the tight line, and were circling. Putting all the separate observations together, the foraging behavior observed correlates with an increase in the mean relative scattering intensity of 9.6 dB from the wide line until the end of circling, representing an increase in the prey density of about 11-fold. The maximum density of the scattering layer over this same observation period increases by an average of 60 times up to a maximum of approximately 200 times.

### C. Foraging stage possible functions

The role of each stage of foraging was investigated by simultaneously observing dolphin behavior and changes in the prey field. The mean relative scattering strength of prey as a function of distance from the dolphins is shown in Fig. 9. All of the observations shown were aligned using the time at which animals were first observed to tighten their line abreast formation. This figure only shows the 30 s surround-

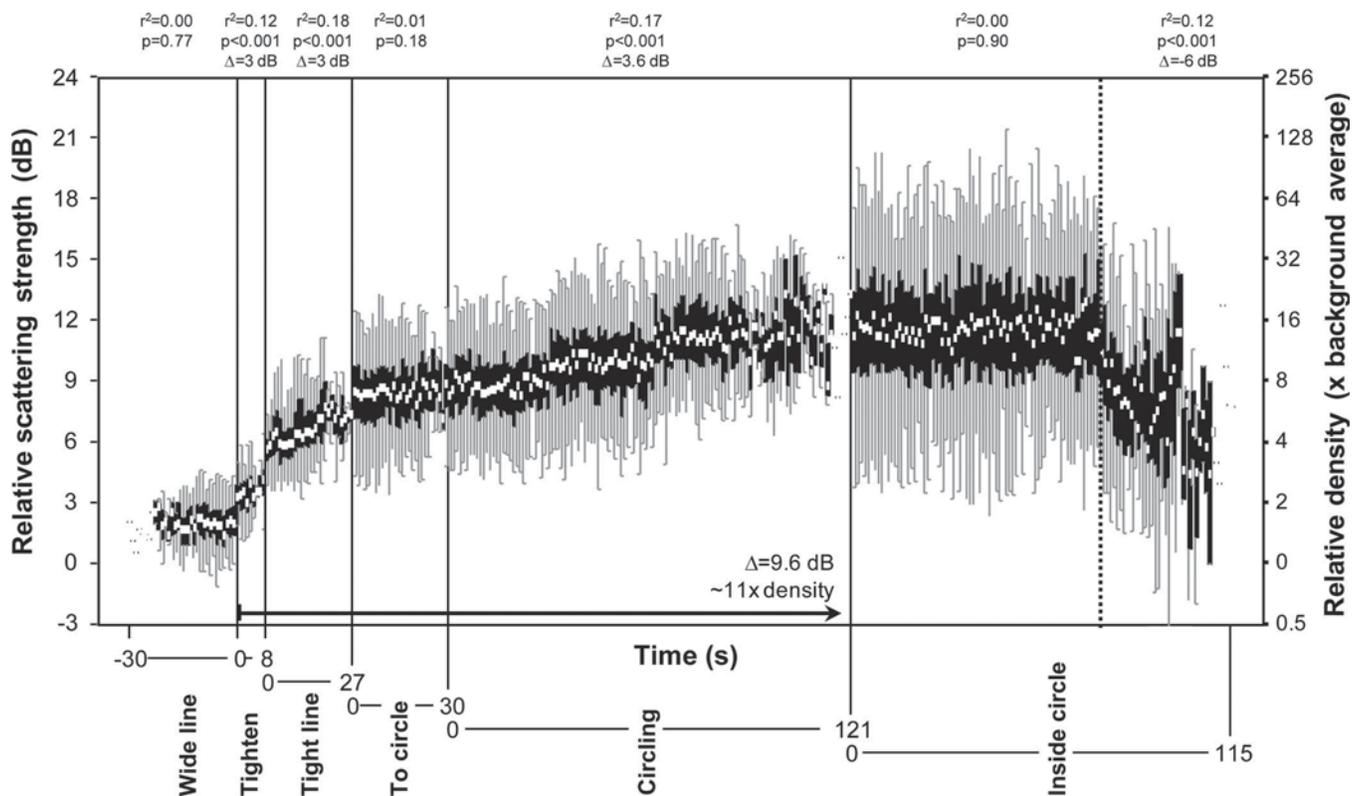


FIG. 8. Mean prey relative scattering strength per  $m^3$  for the 5 m in front of dolphins as a function of time in each foraging stage for all 267 observations. White bars show the median, black boxes show one interquartile range, and the error bars show the 95% confidence interval. Times with single samples are indicated by black points. The inside circle stage is broken up into two parts by a dotted line at 75 s into the behavior. Results of regression and  $F$ -tests for scattering strength within each foraging stage are shown at the top of the figure.

ing this event. While swimming in the wide line, dolphins appeared to approach an existing patch of increased scattering (shown in light gray) estimated to have a numerical density twice the average background prey density (Fig. 9, first row). This patch was observed up to 25 m ahead of the dolphins. When dolphins were observed to move to within 5 m of this patch, their interpair spacing began to decrease, with the final tight line formation achieved as they reach the edge of the patch (Fig. 9, second row). When groups of dolphins were coincident with the edge of this patch, the swimming speed of the dolphins was observed to decrease by about 60% (see Fig. 7), approximately matching the maximum sustained swimming speed for their prey (Reid, 1994; Sambilay, 1990). During this time, dolphins were also observed to swim in a sinusoidlike pattern, moving up and down by several meters. During this phase of foraging, the density of prey 1 m in front of the dolphins was measured to increase relative to the original patch (shown in dark gray), as the prey apparently tried to swim away from the dolphins, while the density immediately behind the dolphins was observed to decrease (Fig. 9, last two rows).

While the dolphins were observed to be circling, the density of the patch measured as an increase in volume scattering strength was measured to increase further by an average of another 2.5 times to about 11–12 times the background (Fig. 8). In addition, the distribution of prey was observed to change dramatically during this phase. Figure 10 shows the percent of peak prey scattering, or increased prey density, on the side of the circle from which the line of

dolphins approached from. There was a significant effect of time on this value ( $r^2=0.60$ ,  $F=7166.08$ , and  $p<0.001$ ). As the mean duration of the circling stage (1:23 min) is approached, the prey becomes close to evenly distributed on both sides of the circle even though the strong scattering or high prey density was initially on only one side of the circle. Figure 11 shows that the size of the circle is significantly affected by the size of the group ( $r^2=0.38$ ,  $F=165.30$ , and  $p<0.001$ ) with larger groups in larger diameter circles despite the fact that larger groups had significantly tighter spacing in the  $XY$  plane.

During the final stage of foraging observed, dolphins moved into the circle in sets of two pairs that were opposite or nearly opposite each other in the circle. The average number of movements into the circle calculated as the total number of observed movements into the circle divided by the number of pairs in the group was  $3.7$  per pair  $\pm 1.3$ . Individual pairs spent  $10.5 \pm 1.1$  s in the circle before falling back into their place in the circle. In all observations, the foraging that took place was very orderly with the pairs of dolphins immediately behind the initial pairs in the circle moving into the circle next and so on. The average number of movements into the circle by each pair of dolphins per foraging bout calculated as the total number of observed movements into the circle divided by the number of pairs in the group was not affected by group size (ANOVA  $N=154$ ,  $p>0.05$ , and  $1-\beta=0.69$ ) which means that more movements into the circle were conducted in larger groups. Unlike all the other foraging geometries, when dolphins were ob-

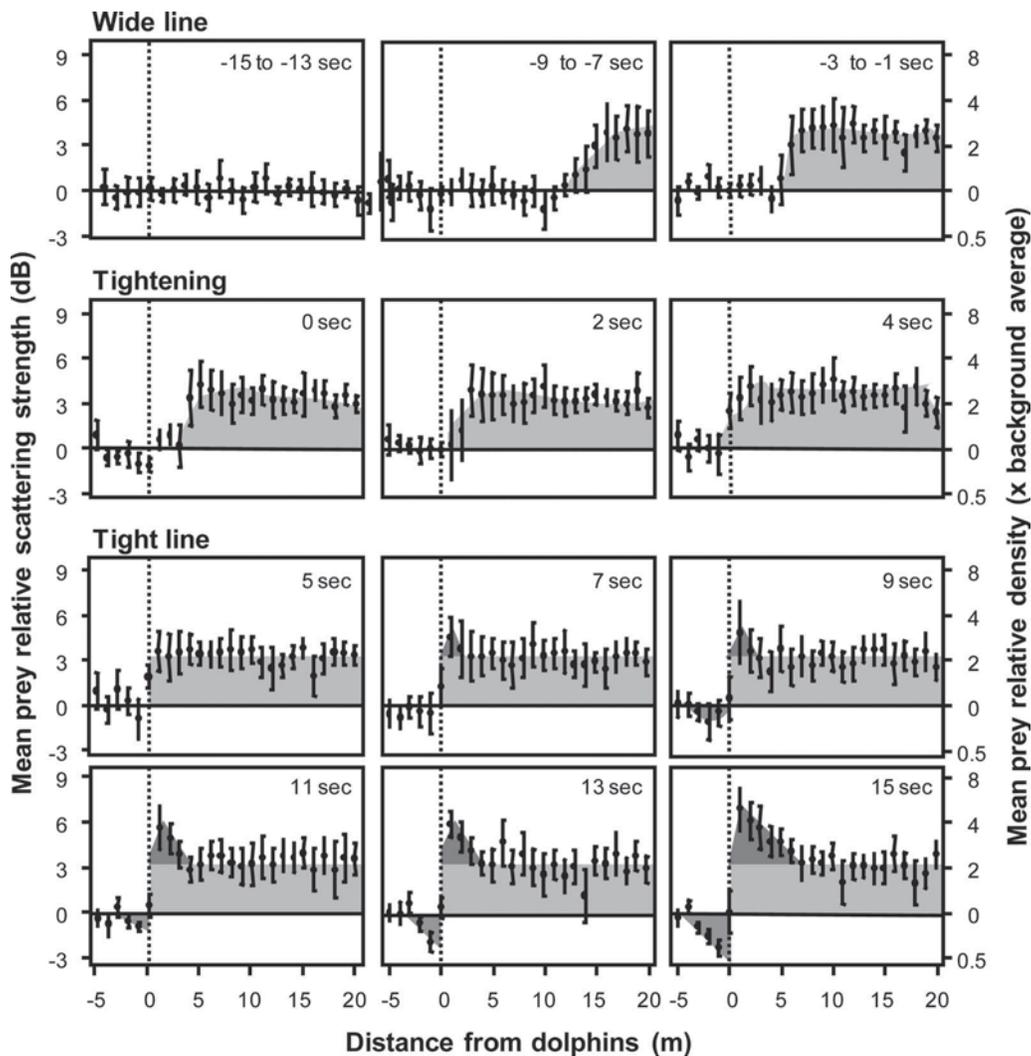


FIG. 9. Mean relative scattering strength of prey as a function of distance from dolphins at each time interval shown. Time zero for all observations was the first time that tightening of dolphins swimming line abreast was observed. Error bars represent the standard error of the mean. Light fill represents the density difference of an existing prey patch relative to the background prey density. Dark fill represents the prey density change hypothesized to have been caused by dolphins herding the prey.

served in the circle, no further increase in the prey density was observed (see Fig. 8), indicating a very different function for this foraging stage from the others. Figure 12 shows that dolphins moving into the circle were moving an average of 5.1 m into the circle, to the location where the prey has a relative scattering strength an average of 17.7 dB and up to 23.1 dB higher than the background scattering by the layer. That represents an average prey density increase of 60 times up to a maximum of 200 times over the average background prey density. Dolphins were strongly associated with the location of highest density of their prey while inside the circle. Near the edge of the circle of dolphins, volume scattering and thus estimated prey density were not significantly higher than the background. This was measured using a paired *t*-test comparing the average volume scattering near each pair of dolphins in the circle with the average volume scattering 5 m away from the pair toward the outside of the circle ( $N = 154$ ,  $p \gg 0.05$ , and  $1 - \beta = 0.99$ ).

#### IV. DISCUSSION

We present a model of spinner dolphin foraging based on observations of dolphins and their prey using a multibeam

echosounder. Four distinct geometries were consistently observed in the underwater nocturnal behavior of spinner dolphins feeding on a deep-scattering layer near the apex of its diel vertical migration. No single observation encompassed all stages because of limits in observation time from the moving vessel. To understand how these patterns fit into the overall foraging behavior of spinner dolphins, observations of transitions between these four stages were used to determine stage order and overall time course. Sample sizes of observations of these foraging stage transitions were relatively high (see Fig. 6); however, this approach is biased toward shorter foraging stages which can be seen in the sample sizes. Consistent progression in the foraging stage was observed throughout, suggesting that the model, presented as a time course in Fig. 6, is not often varied under the foraging conditions measured, validating further interpretation.

The model of dolphin foraging presented is a compilation of many observations that are assumed to be independent. We cannot know if individual dolphins were detected more than once in a single night since no method currently

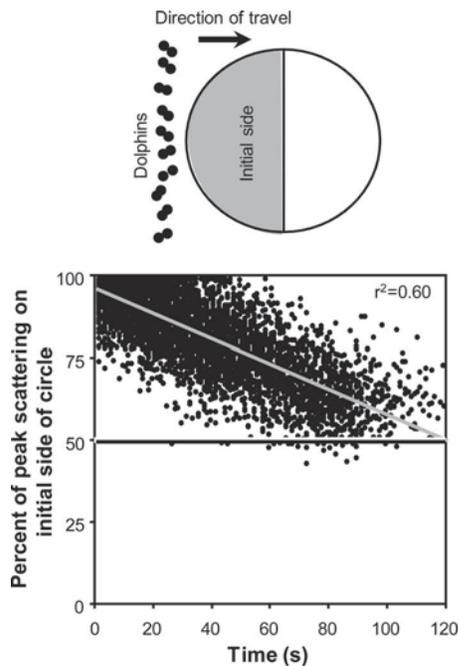


FIG. 10. The initial side of the dolphin foraging circle, the side from which the line of dolphins came from, is shown in the top panel. The percent of the volume of the foraging cylinder that had prey scattering within 6 dB of the maximum for that observation as a function of time from the inception of circling by the dolphins is shown in the bottom. The 50% line indicates the level where prey would be evenly distributed on both sides of the circle.

exists to identify individuals at night. However, using the best population estimates for spinner dolphins, we can estimate the population of spinner dolphins along the area we surveyed to be at least 120 and possibly up to 750 animals (Lammers, 2004; Mobley *et al.*, 2000). Given population estimates, our coverage of the area (~50%), and our average group sizes in the low to mid-20s, it is possible that 20 or more groups may have been present within the general area surveyed. Along individual parallel to shore transects, the number of groups sometimes reached an average of 4/km. During one 8 km long survey at a vessel speed of ~4 km (faster than the directional movement observed in the dolphins), 18 distinct groups of dolphins were detected. So

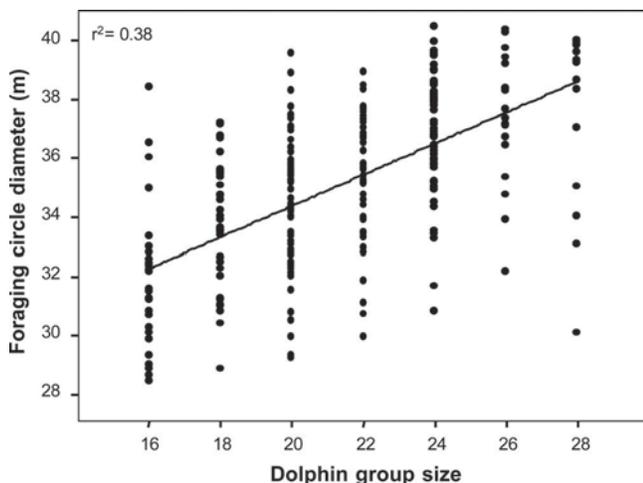


FIG. 11. Foraging circle diameter as a function of dolphin group size

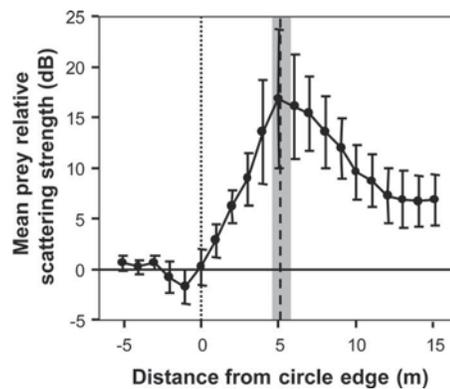


FIG. 12. Mean relative scattering strength of prey as a function of distance from the circle of dolphins. Positive values represent positions inside the circle and negative values represent positions outside the circle. Error bars represent the 95% confidence interval for the mean. The mean for the maximum movement of each pair of dolphins into the circle is shown by the dotted line near 5 m, along with gray bar representing the 95% confidence interval.

while it is possible that some groups may have been detected more than once over the course of a single night's survey, given the mean number of observations each night (~27), the likelihood of significant pseudoreplication is low.

Observations of individual foraging stages suggest that swimming in a wide line, tight line, and then a circle allowed dolphins to increase the density of their prey. Putting it all together, dolphins first found and approached an existing patch that was about twice the density of the background. Then, dolphins used their prey's own avoidance behavior to push it forward as they continued to swim, piling the prey up on itself like snow in front of a plow. Dolphins isolated this prey patch by encircling it. The final patch was, on average, 11–12 times higher in density than the background prey with a peak density that was an average of 60 times higher than the background. During the last observed stage of foraging, dolphins moved into the circle and appeared to actively feed. Inside the circle was where they most closely overlapped the maximum density regions in their prey while dolphins swimming at the edges of the circle did not experience prey densities that were significantly increased over the background. Presumably feeding dolphins moved into the circle with a high degree of coordination not only with their pair partners but also with other pairs. In all observations, two pairs were observed to move into the circle simultaneously from nearly opposite sides of the circle's perimeter. When these two pairs moved back to their places on the circle's edge, another two pairs of dolphins were observed to move into the circle from the next position behind them in the circle.

Group foraging can allow access to prey that would otherwise be difficult or unprofitable for the predator to find or consume alone. In terrestrial predators, this usually means obtaining access to hidden prey (Jones, 1999) or prey that are large relative to the predator (Estes and Duggins, 1995; MacDonald, 1983; Moehlman, 1986; Traniello, 1987). In pelagic aquatic predators, as in aerial predators (Brown *et al.*, 1991), cooperation most often involves finding or creating aggregations of small prey (Anderson, 1991; Bartholomew, 1942; Gallo Reynoso, 1991; Goss, 1888; Gotmark *et al.*, 1986;

Hiatt and Brock, 1948; Hoffman *et al.*, 1981; Norris and Prescott, 1961; Nottestad *et al.*, 2002; Partridge *et al.*, 1983; Saayman *et al.*, 1973; Schmitt and Strand, 1982; Serfass, 1995; Similä and Ugarte, 1993; Würsig and Würsig, 1979). Herding of prey seems to occur most often in markerless environments, like the midwater habitat of the prey of spinner dolphins, where prey do not naturally aggregate around other structures. Group foraging allows aquatic predators to exploit groups of small prey that would not be profitable prey if dispersed. However, unlike other species of marine animals that have been observed to herd prey (Evans, 1987; Gallo Reynoso, 1991; Serfass, 1995; Similä and Ugarte, 1993), spinner dolphins were not observed to bring their prey up to the surface or toward shore. They did not use these boundaries as walls against which to push their prey but rather swam continuously at relatively high speeds which appeared to create a barrier of predators to contain their prey. This makes the behavior difficult to observe and limits the amount of time that dolphins can maintain the patch before needing to surface to take a breath, about 5 min. Similar herding of prey at depth in other marine species has yet to be observed.

Comparing groups of foraging dolphins, we found that the dolphin group size was higher at lower background prey densities. However, the density at which dolphins began to move inside the circle was not affected by background density or group size. This suggests a threshold of prey density at which feeding becomes profitable. A possible threshold mechanism may be the cessation of avoidance of dolphins by masses of prey at the high densities herded prey reach after the circling behavior. This lack of avoidance, observed by measuring the volume scattering 5 m inside the circle of dolphins before and after the movement of dolphins into the circle, could be a result of decreased space for each individual prey. Estimates of the density of micronekton made with a calibrated sonar system in both this and previous studies reached  $1800 \text{ m}^{-3}$  (Benoit-Bird and Au, 2003a; Benoit-Bird and Au, 2004). This would put the prey, which average 7.5 cm in length (Benoit-Bird and Au, 2006), about 8 cm apart. Because these fish are not observed to swim in a polarized fashion (Benoit-Bird and Au, 2006; Reid, 1994), these densities would severely limit their flight distance, potentially causing great confusion of the prey while under attack. The increase in group size may be necessary to achieve the feeding threshold, whatever its mechanism of action, at lower prey densities.

The observations here lead to the question “is group foraging behavior in spinner dolphins cooperative?” Cooperation can be defined as an outcome that, despite potential individual costs, increases the fitness of the members of a group of two or more individuals, and whose achievement requires collective action (Dugatkin *et al.*, 1992). Coordination of movement, “collective action,” of the hunting dolphins is strongly supported by the data presented but that alone is not evidence of cooperation. For us to identify cooperation, we must measure the outcome of the behavior, a difficult task. So in this, as in most studies, we must rely on proxy measures. It was not possible to measure the prey capture success of individual dolphins. However, because

prey density is the factor affected by group behavior, we can use prey density, a measure of immediate prey availability as a proxy measure for feeding success. For the purposes of this discussion we will use a simple, one to one linear increase in foraging success with increasing density.

To assess cooperation, we must also estimate the costs of feeding in a group. Based on modeling of spinner dolphin energy needs (Benoit-Bird, 2004) and the density and size of the average patch, we estimate that the prey within at least some single patches of prey could feed the entire group of dolphins for a single day if they could exploit it effectively. Competition between individuals in the group is then not for the food itself but in time to feed. Group feeding reduces the time to feed because of the time it takes to create and maintain a dense prey patch, something we can estimate. Our observations suggest that, on average, each pair of dolphins is inside the circle where feeding is hypothesized to take place 3.7 times/foraging bout for an average of 10.5 s/movement within an average feeding bout of 4 min and 38 s. There is no evidence for significant variation in this time between different pairs of animals within the group. This means that individual dolphins are feeding about 14% of an average foraging bout. Short surfacing times detected in this study support the assumption that animals begin another foraging bout nearly immediately after a previous effort. So, we can use the value of 14% as an estimate of potential foraging time in which dolphins within groups are feeding. A solitary animal would potentially be able to feed 100% of foraging time.

Dolphins in groups experienced a mean prey density increase of about 5.5 times and an increase in maximum density of 30–100 times over the initially selected prey patch, something a solitary individual could also likely select. Looking at the mean density values, the prey capture success measured as density multiplied by access time was 0.75 times greater for animals in groups compared with those alone selecting natural patches in the environment. If maximum density is the important feature, then dolphins in groups could have feeding success rates of 4–14 times higher. Based on this assessment, animals feeding inside these highly dense dolphin-enhanced patches would indeed have higher per-capita feeding success than those attempting to forage alone but only in the high-density areas inside the circle of herding dolphins. The analysis supports the hypothesis that cooperation, rather than just coordinated foraging, occurs and suggests that feedback from the environment alone may be enough to discourage solitary foraging. It is important to note here that targets consistent with individual dolphins were not observed during the study.

The analysis presented supports a positive outcome of the observed collective action over solitary feeding, supporting the hypothesis that this behavior is cooperative. However, cooperation can only evolve if cheating is not a beneficial strategy. We made no observations of animals moving into the circle when it was not their “turn” to do so. No echoes consistent with dolphins were ever observed alone or in small groups. Targets consistent with dolphins were not observed engaging in behaviors that did not fit into the “foraging states” described here that would suggest stalking or

sneaking into a group nor were any observations made of animals spending significantly longer inside the circle than others. This suggests that cheating under the conditions of this study was absent or rare.

Our data show that spinner dolphins worked collectively to achieve densities of prey that did not occur in the habitat in the absence of this dolphin behavior, likely resulting in increased feeding success despite the individual costs of herding and maintaining a prey patch and other potential costs of social feeding. There was no evidence of cheating by animals either within groups or from outside groups. All of this, when considered together, strongly supports cooperative rather than simply group foraging. The remarkable degree of coordination shown by foraging spinner dolphins, the very strict geometry, tight timing, and orderly turn taking, indicates the advantage conferred by this strategy and the constraints placed upon it. The consistent appearance of this behavior shown here and indicated in previous studies (Benoit-Bird and Au, 2003b) suggests that it may be a critical strategy for energy acquisition in Hawaii by spinner dolphins. The number of pelagic species in which cooperative herding has been initially reported (Anderson, 1991; Axelsen *et al.*, 2001; Gallo Reynoso, 1991; Goss, 1888; Hiatt and Brock, 1948; Nottestad *et al.*, 2002; Partridge *et al.*, 1983; Schmitt and Strand, 1982; Serfass, 1995; Similä and Ugarte, 1993; Würsig and Würsig, 1979) suggests that prey herding may be an important strategy for food acquisition in energy poor relatively featureless environments like the tropical Pacific Ocean.

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