

## The bottlenose dolphin *Tursiops truncatus* foraging around a fish farm : Effects of prey abundance on dolphins ' behavior

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**Abstract** The extent to which prey abundance influences both bottlenose dolphin foraging behavior and group size in the presence of human activities has not previously been studied. The primary aim of this study was to identify and quantify how wild bottlenose dolphins respond , individually and as groups , to the relative abundance of prey around a fish farm. Detailed views of dolphins ' behavior were obtained by focal following individual animals whilst simultaneously collecting surface and underwater behavioral data . A total of 2150 dive intervals were analyzed , corresponding to 342 focal samples , lasting over 34 hours. Bottlenose dolphins remained submerged for a mean duration of 46.4 seconds and a maximum of 249 seconds. This study provides the first quantified data on bottlenose dolphin diving behavior in a marine fin-fish farm area. This study 's results indicate that within a fish farm area used intensively by bottlenose dolphins for feeding , dolphins did not modify dive duration. Additionally , underwater observations confirmed that dolphins find it easier to exploit a concentrated food source and it appears that hunting tactic and not group size plays an important role during feeding activities. Thus , bottlenose dolphins appear capable of modifying their hunting tactics according to the abundance of prey. When top predators display behavioral responses to activities not directed at them , the task of studying all possible effects of human activities can become even more challenging [ *Current Zoology* 55 ( 4 ) : 243 – 248 , 2009 ].

**Key words** Bottlenose dolphin , *Tursiops truncatus* , Diving behavior , Foraging behavior , Prey abundance , Human activities , Hunting tactics , Aquaculture

Two major resources vital to a mammal 's survival are air and food. There have been previous efforts to explore the trade offs between these two essential resources for marine mammals by relating foraging with dive duration of free ranging animals ( Costa et al. , 1989 , Baird and Dill 1995 , Boyd et al. , 1995 , Harcourt et al. , 2001 , Acevedo-Gutierrez et al. , 2002 , Díaz López et al. , 2008 ) , but with mixed success. However , changes in free ranging bottlenose dolphin *Tursiops truncatus* dive behavior have been linked to both prey distribution and abundance ( Acevedo-Gutierrez and Parker , 2000 ) , with long dives often associated with foraging behavior ( Bearzi et al. , 1999 , Díaz López et al. , 2008 ). Dive duration rather than the level of activity appears to dictate many of the physiological responses of diving bottlenose dolphins ( Williams et al. , 1999 ). Furthermore , bottlenose dolphins , like other marine mammals , must balance the metabolic demands of activity with the conservation of oxygen stores ( Castellini et al. , 1985 ; Williams et al. , 1999 ).

For many species , the behavior that individuals exhibit within different habitats clearly indicates the ecological function that those areas provide ( Hastie et al. , 2004 ). Throughout the world marine fin-fish farms have been introduced into environments that have natural resident fish eating predators such as marine mammals. It is well known that wild fish are strongly attracted to floating cages as they provide structure and resources

through unused feed that falls through cages ( Dempster et al. , 2004 ; Díaz López , 2006 ; Díaz López et al. , 2005 ). However , marine aquaculture and its effects on marine species remains a controversial topic and interactions of bottlenose dolphins with fin-fish farms have caused concern amongst industrial stakeholders and conservationists alike ( Díaz López and Shirai , 2008 ) likely because few data on foraging and dive behavior of dolphins around fish farms exists.

This study focuses on the north-eastern coast of Sardinia Island ( Italy ) where fin-fish aquaculture has been linked with direct and indirect changes in the distribution and behavior of bottlenose dolphins ( Díaz López , 2006 ; Díaz López and Shirai , 2007 ; Díaz López et al. , 2005 ). A total of 32 photo-identified adult bottlenose dolphins were observed hunting both schooling and solitary prey around a fish farm area , using both cooperative and individual feeding tactics ( Díaz López and Shirai , 2007 ). This feeding around a fish farm is comparable with strategies used in association with trawlers and gillnets , which allow for an increased rate of feeding while decreasing the energy expenditure necessary for foraging ( Fertl and Leatherwood , 1997 , Díaz López 2006 ). However , there are currently no direct data on the diving and sub-surface foraging behavior for this species in this particular habitat , limiting our understanding of their habitat use and foraging behavior. The primary aim of this study was to identify and quantify

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how wild bottlenose dolphins respond, individually and as groups, to the relative abundance of prey near a fish farm.

## 1 Study area and Methods

### 1.1 Study area

Field work was conducted from January 2005 to March 2007 in a 12000 m<sup>2</sup> area around a marine fin-fish farm with caged sea-bass *Dicentrarchus labrax*, gilthead sea bream *Sparus auratus*, and shi drum *Umbrina cirrosa*, on the north-eastern coast of Sardinia (40°59.98' N 9° 37.09' E), Italy (Fig.1). The fin-fish farm consisted of 21 floating cages which attracted dolphin prey species such common grey mullet *Mugil cephalus*, bogue *Boops boops*, salema *Salpa sarpa*, garfish *Belone belone* and pilchard *Sardina pilchardus* (Díaz López, 2006). The floating cages were grouped into three rows of seven cages. Each floating cage was constructed of nylon mesh netting and was 22 m in diameter and 15 m deep. The cages were situated approximately 200 meters from the shore, with a minimum depth of 18 meters and a maximum depth 26 meters. The sea bottom in the study area was characterized by mostly mud with scattered areas of rock and sand.

### 1.2 Field Procedure

Detailed views of dolphins' behavior were obtained by focal following individual animals whilst simultaneously collecting surface and underwater behavioral data. To ensure that all behaviors were visible across the study area, samples were only collected when the sea-state was

less than 4 (Douglas sea force scale) and in clear conditions with no precipitation.

### 1.3 Duration of dives and surface behavior

The primary data set incorporates all information recorded regarding surface behavior and the duration of dives.

To minimize the effect of our presence on dolphin behavior data were collected from a 14 m fish farm boat when the engine was off during normal daily farmed fish feeding operations and whilst the boat remained in the same position for at least 90 minutes at a time. These operations were carried out between 0800 and 1900 h year round. At least two experienced observers were stationed on a 4-m high observation deck and used both the naked eye and 10 × 50 binoculars to observe dolphin behavior during daylight hours. Dolphins were typically within 10 to 50 meters of the boat during data collection and the boat was present in the area before the dolphins' arrival.

Throughout this study, I use the term "diving" to refer to information on dive duration during subsurface foraging behavior (reviewed in Hooker and Baird, 2001). Data collection involved timing, to the nearest second, the dive intervals of dolphins using a stopwatch. Dive intervals were defined as the elapsed time between two breaths. While recording dive intervals we collected data on dolphins' pre-dive back arching behavior (Díaz López et al., 2008). During sightings involving the presence of two or more identified dolphins I chose at random one focal individual.

Dolphins' pre-dive back arching behavior were

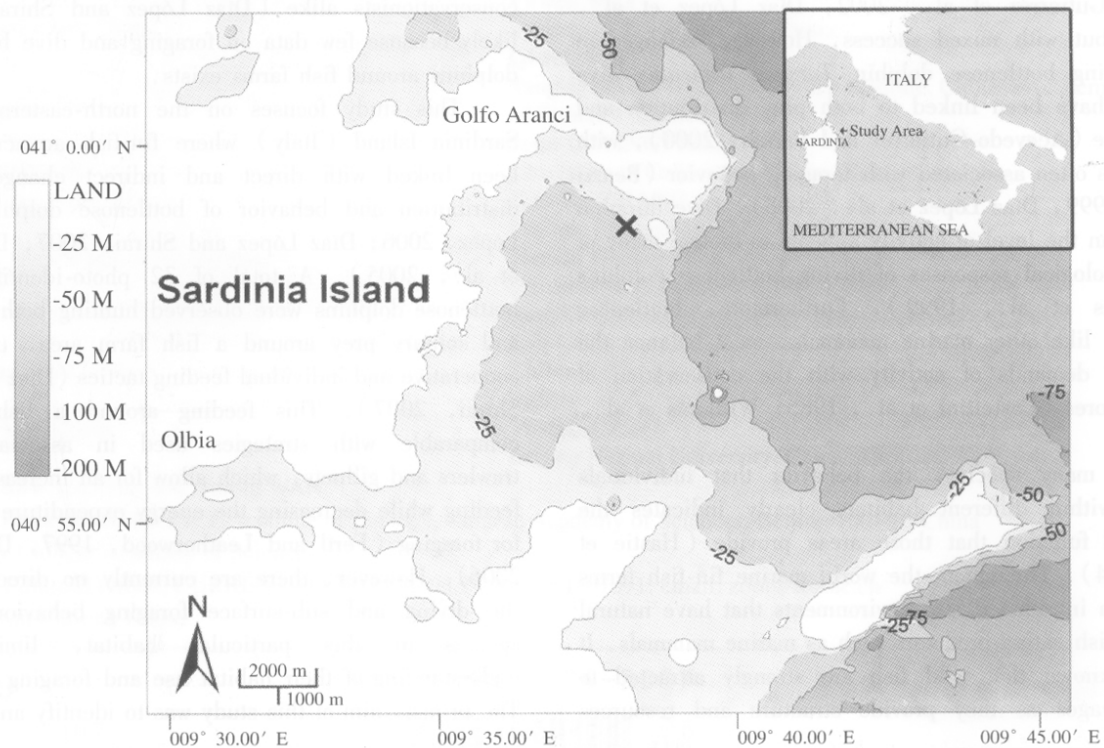


Fig.1 Map of the north-eastern coast of Sardinia (Italy), showing the location of the marine fin-fish farm

defined by Shane ( 1990 ) as : “ regular dive ” ( only the blowhole , part of the back , and the dorsal fin are exposed ); “ tail-stock dive ” ( the dolphin arches its back and exposes its peduncle but not its flukes ); and “ flukes-up dive ” ( the dolphin arches its back and exposes its flukes as it dives ).

In each encounter , focal individuals were identified in situ based on natural marks , nicks , scars , or unique skin pigmentations on the dorsal fin and surrounding area ( Würsig and Jefferson , 1990 ). Photographs and video recordings were also used to document and verify visible surface activities . Underwater observations aided in identification and sex determination . Sex was determined by direct observation of the genital region . Males were identified by a gap between the uro-genital slit and the anus , lack of mammary slits , or observation of an erection . Females were identified by observation of mammary slits .

#### 1.4 Underwater behavior and fish abundance

After photographing dorsal fins from the surface , one observer entered the water with snorkel gear to photograph animals underwater , observe their behavior , determine their sex , and estimate fish abundance . Since dolphins are habituated to the presence of divers due to daily underwater maintenance checks in the fish farm area I can be fairly confident I was able to obtain underwater observations of dolphin activities without directly influencing their behavior .

Dolphins in association observed during underwater encounters were defined as “ subgroups ” ( Díaz López , 2006 ). Every encounter continued until the subgroup was lost ( a subgroup was considered lost after 3 min without an underwater observation ) ( Díaz López , 2006 ).

Dolphins use a variety of different foraging tactics around fish farms ( described by Díaz López , 2006 ). To categorize each foraging tactic the start time , subgroup size , underwater dolphin behavior , depth and GPS location were recorded during snorkeling with a carbon pencil and underwater slate .

Estimates of fish abundance were made during snorkeling with 5 minutes visual counts that covered a 7875 m<sup>3</sup> volume of water around a fin-fish farm cage where the dolphin was feeding ( 15 m wide × 15 m deep × 35 m long ).

To minimize the effects of the underwater observer on the dolphins ' behavior two criteria were adopted : ( 1 ) dive intervals were not recorded whilst the underwater observer was in the water making the 5 minutes visual counts and ( 2 ) samples were collected when the observer remained in the same position for at least 10 minutes at a time . Adopting these criteria means that measures of prey abundance and dive duration were not recorded at the exact same time , but I believe prey abundance was likely the same immediately following and preceding the recording of dive durations .

#### 1.5 Data processing and statistical analysis

The duration of a follow can influence the overall mean dive time for that sample . It is expected that the correlation between the two will decrease as sample time increases . Partial correlations were calculated between the sampling period and mean dive interval in order to determine threshold where the correlation was no longer significant ( Williams et al . , 2002 ). All focal samples beneath the threshold were discarded .

I pooled dive samples within each category of dive defined by the three pre-dive back arching behaviors . The range and overall mean dive time was obtained from these data in order to avoid influence by the frequency of pre-dive back arching behaviors during a sample ( Díaz López et al . , 2008 ). This technique measures the duration of the dives while presenting a perspective on the surfacing behavior , rather than solely the dive duration .

A common problem of behavioral studies has been the pooling effect , where multiple measurements on the same individual or group are considered independent of each other ( Hurbert , 1984 ). In order to avoid the potential for pseudoreplication and lack of independence arising from repeated sampling of individual dolphins , median scores were calculated for each individual dolphin in each feeding tactic and category of dive and used as individual raw data for the comparisons . Medians were considered the appropriate measure of central tendency for subsequent analyses because of the lack of normal distributions in the variables measured ( Zar , 1999 ).

I used generalized linear mixed models ( GLMMs ) to investigate the variables related to dive duration . GLMMs are useful for fitting linear relationships with non-Gaussian data distributions ( McCullagh and Nelder , 1989 ). The analysis was blocked for individual dolphin , pre-dive back arching behavior , subgroup size , underwater feeding tactic , and fish abundance . Individual dolphin , feeding tactic , subgroup size , fish abundance and pre-dive back arching behavior were treated as random variables . Dive time was considered as response variable for the analysis . One of the most frequent difficulties when performing a GLMM analysis is the issue of multicollinearity where two or more of the independent variables are highly correlated . However , the correlation coefficient matrix with independent variables indicated correlations below 0.25 , and as such it is unlikely this analysis suffers from issues concerning multicollinearity . To follow the assumptions of the GLMM ( normality , homogeneity of variance and normality of residuals and linearity ) the response variable was Log<sub>10</sub> transformed , and the residuals were examined . If the GLMM showed significant inequality of the means , a Tukey 's post-hoc contrast was performed .

Discriminant analysis was performed to explore the differences between the observed hunting tactics . For the purposes of this study , discriminant analysis was used in

a descriptive sense for revealing major differences between these tactics. The larger the standardized coefficients for each variable in each discriminant function, the greater the contribution of the respective variable to the discrimination between groups. To follow the assumptions of the discriminant analysis the predictors were  $\text{Log}_{10}$  transformed, and the residuals were examined. Equality of the means of the groups was tested by a multivariate analogue to the t test, called Hotelling's T-squared, and a  $P$  value for this test was given.

All the statistical tests and mathematical analysis were performed with MINITAB<sup>®</sup> and PAST (Hammer et al., 2001) software packages, and Microsoft Excel<sup>®</sup>. Statistical significance was tested at the  $P < 0.05$  level. The data are presented as means  $\pm SE$ .

## 2 Results

Between January 2005 and January 2008, 296 hours over 285 separate days were spent observing wild bottlenose dolphins feeding around the fish farm. Data were collected from 11 different identified adult bottlenose dolphins. Of these, sex was known for 9 dolphins (5 males and 4 females).

### 2.1 Duration of dives and surface behavior

Follow length and dive duration were significantly correlated (Spearman's rho correlation  $r = 0.16$ ,  $P = 0.03$ ,  $n = 406$ ) up until 73 seconds in length. As such, only follow samples greater than 73 seconds in length were used for the remaining analysis and sixty four short samples were therefore discarded (remaining samples: Spearman's rho correlation  $r = 0.16$ ,  $P = 0.07$ ,  $n =$

342). A total of 2700 dive intervals were analyzed, corresponding to 342 samples lasting over 34 hours. These focal samples had a mean duration of  $277 \pm 29$  seconds.

The bottlenose dolphins feeding around the fin-fish farm cages displayed dive intervals ranging between 2 and 249 seconds in length (mean =  $46.4 \pm 2.5$  seconds).

The GLMM model (Table 1) explained 74.6% of the variability of length of dives and indicated that fish abundance did not significantly predict the duration of bottlenose dolphin dives during feeding activities ( $F_{14,7} = 0.97$ ,  $P = 0.47$ ). Likewise, neither individual nor group size were significant predictors of the duration of dives. The only significant predictor of the duration of dives was the pre-dive back arching behavior ( $F_{2,4} = 13.97$ ,  $P = 0.009$ ). This relationship allows an objective discrimination between two different types of diving behavior (Table 2).

**Table 1 Results of the GLMM model for bottlenose dolphin dive duration during foraging activities**

| Linear term                | df | Adj SS <sup>a</sup> | F     | P     | Overall deviance explained |
|----------------------------|----|---------------------|-------|-------|----------------------------|
| Individual                 | 10 | 0.12                | 1.38  | 0.32  |                            |
| Subgroup size              | 3  | 0.17                | 3.93  | 0.06  |                            |
| Hunting tactic             | 1  | 0.02                | 0.87  | 0.38  | 74.6%                      |
| Dive back arching behavior | 2  | 1.14                | 25.86 | 0.00* |                            |
| Fish abundance             | 74 | 0.01                | 0.21  | 0.64  |                            |

<sup>a</sup> Adj SS (Adjusted sums of squares), the additional sums of squares determined by adding each particular term to the model given the other terms are already in the model; Asterisk indicates significance level.

**Table 2 Results of the Tukey's post-hoc contrast comparing pre-dive back arching behaviors to all others**

| Pre-dive back arching behaviors | Regular dives            | Tail-stock dives         | Flukes-up dives          |
|---------------------------------|--------------------------|--------------------------|--------------------------|
| Regular dives                   |                          | $t = 3.41$ , $P = 0.02$  | $t = -7.02$ , $P < 0.01$ |
| Tail-stock dives                | $t = 3.41$ , $P = 0.02$  |                          | $t = -1.22$ , $P = 0.47$ |
| Flukes-up dives                 | $t = -7.02$ , $P < 0.01$ | $t = -1.22$ , $P = 0.47$ |                          |

### 2.2 Underwater behavior and fish abundance

The total time spent underwater in the presence of dolphins was 34 hours, with mean encounter duration of  $7 \pm 4.3$  minutes. Solitary and groups of dolphins fed around the fish farm cages at bottom depths of 1 – 23 m (mean =  $6.1 \pm 0.3$  m). Abundance of fish around the fin-fish farm cages varied between 8 and 400 fish per visual count (mean =  $82.5 \pm 4$ ). The largest percentage was formed by bogue (64%) and common grey mullets (23%), other species included Mediterranean horse mackerel *Trachurus mediterraneus* (6%), salpa (4%), pilchard (2%) and garfish (1%).

During the current study, bottlenose dolphins employed two different hunting tactics:

1) "Encircling cage", which was observed in 53.5% of underwater observations. Dolphins were

observed in a tight group form (< 1 body length between dolphins) or solitary, swimming around a floating fish farm cage, facing in various directions and oriented toward the floating cage where they had driven isolated fish. Just before reaching the cage, the dolphin would suddenly make hairpin turns on their side to catch the disoriented fish. Burst-pulsed sounds were audible when dolphins captured the prey and as the dolphin lifted its head, a small fish (10 – 15 cm) was sometimes visible in its mouth. Subgroup size during this hunting strategy ranged from singletons to subgroups of three dolphins and showed a median group size of two (mean =  $1.6 \pm 0.06$ ).

2) "Carousel swim", which was observed in 46.5% of underwater observations, consisted of dolphins surrounding wild fish schools forcing fish to swim in a concentrated ball. The dolphins swam in circles around

the fish , gradually tightening the school whilst one individual would dart against the school to catch fish. Fish visible in the immediate vicinity may have been disoriented out of the school. At this point , echolocation clicks were audible in the water. Subgroup size during this hunting strategy ranged from singletons to subgroups of four dolphins and showed a median group size of two ( mean =  $1.9 \pm 0.07$  ).

Discriminant analysis indicated that the hunting tactics were indeed significantly different from one another ( Hotelling 's T-squared ,  $P < 0.0001$  ), attributed to differences in fish abundance. The resulting function with dive duration , subgroup size , depth and fish abundance was established as the largest proportion correct 80.4% of

the dolphins ' hunting tactics ( Table 3 ). As shown in the table 4 , the discriminant analysis correctly identified 269 of 342 hunting tactics , though the probability of correctly classifying an " Encircling cage " was lower ( 136/183 or 74.4% ) than was the probability of correctly classifying a " Carousel swim " ( 133/159 or 83.6% ). The variable that displayed the strongest discriminant power in the model was the fish abundance , when this variable was excluded there were not significant differences ( Hotelling 's T-squared ,  $P = 0.14$  ), and the percentage of correctly predicted classifications decreased drastically ( 56.3% of the " Encircling cage " and 56.0% of the " Carousel swim " ).

**Table 3 Comparisons between hunting tactics , with four variables in the model ( dive duration , subgroup size , depth and fish abundance )**

| Hunting tactics     | n   | Dive duration ( s ) | Subgroup size  | Depth ( m )    | Fish abundance    |
|---------------------|-----|---------------------|----------------|----------------|-------------------|
| " Encircling cage " | 183 | $46.8 \pm 3.2$      | $1.6 \pm 0.06$ | $6.32 \pm 0.4$ | $47.27 \pm 4.3^a$ |
| " Carousel swim "   | 159 | $46.06 \pm 3.4$     | $1.9 \pm 0.07$ | $5.91 \pm 0.4$ | $111.6 \pm 5.7^b$ |

The number of samples within each hunting tactic is represented by N. Means  $\pm$  standard errors ( SE ) are given for all measured variables. Depths are given in meters. Different superscripts in the same column indicate significant difference. Equality of the means of the groups was tested by Hotelling 's T-squared with a  $P < 0.001$ .

**Table 4 Classification success of the discriminant analysis for the two hunting tactics , with four variables in the model ( dive duration , subgroup size , depth and fish abundance )**

| Hunting tactics     | TOTAL | Correctly identified | Percent correct |
|---------------------|-------|----------------------|-----------------|
| " Encircling cage " | 183   | 136                  | 74.4%           |
| " Carousel swim "   | 159   | 133                  | 83.6%           |
| <i>TOTAL</i>        | 342   | 269                  | 80.4%           |

The number and percentage of tactics correctly classified are displayed.

### 3 Discussion

This study provides the first quantified data on bottlenose dolphin diving behavior in a marine fin-fish farm area. These results indicate that within a fish farm area used intensively by bottlenose dolphins for feeding , dolphins did not modify dive duration with changes in prey abundance , which may indicate they did not modify time spent searching prey. However , underwater observations confirmed that dolphins find it easier to exploit this concentrated food source and it appears that hunting tactic and not group size plays an important role during feeding activities. Thus , bottlenose dolphins appear capable of modifying their hunting tactics according to the abundance of prey.

#### 3.1 Length of dives

Bottlenose dolphins remained submerged a mean duration of 46.4 seconds and a maximum of 249 seconds , suggesting that most dives by bottlenose dolphins during this study are likely within the aerobic dive limit ( ADL ) predicted for adult bottlenose dolphins swimming faster than 2 m/s ( 252 seconds ) by Yazdi et al. ( 1999 ).

Shorter duration dives observed during foraging in an area of concentrated prey , compared with longer dives , most probably permit greater flexibility in speed and swimming mode due to lower relative impact on oxygen stores ( Williams et al. , 1996 ).

The two observed hunting tactics were mainly characterized by sudden , fast upward movements and interrupted patterns of gliding. These feeding tactics could take advantage of changes in pressure and buoyancy with depth and provide chances for conserving limited oxygen stores during submergence ( Williams et al. , 1999 ).

The existence of a relationship between the length of dives and the different pre-dive back arching behaviors was coherent with results of previous studies ( Shane , 1990 ; Díaz López et al. , 2008 ). This view is supported by the relationships observed between ( 1 ) " regular-dives " and shorter dives , and ( 2 ) " tail-stock " and " flukes-up dives " with longer dives ( Shane , 1990 ; Díaz López et al. , 2008 ).

#### 3.2 Hunting tactics

My findings show that hunting tactics play an important role during foraging. Thus , bottlenose dolphins appear capable of various tactics with the abundance of prey influencing what type of tactic is exhibited.

In the current study , dolphins were seen to feed both cooperatively and individually on wild fish in the fish farm area. The foraging tactics I have documented could be predicted by the game theory ( Smith , 1982 , 1984 ) and the related concept of the evolutionarily stable strategies ( Parker , 1984 ). Bottlenose dolphins could maximize their foraging efficiency , and presumably overall fitness ,

by foraging individually or in small groups. Thus, the tactic denominated “Encircling cage” (Díaz López, 2006) was typically observed when prey were in small clumps and widely dispersed that may be rapidly consumed by the first dolphin to reach them. Otherwise, during the cooperative tactic called “Carousel swim” (Bel’kovich et al., 1991), characterized by dolphins surrounding bigger fish schools, individuals could receive by-product benefits by coordinating their behaviors.

In summary, this study represents some insights into understanding free ranging wild bottlenose dolphins’ feeding behavior. Dolphins may change hunting tactics as prey abundance change but how rapidly this occurs is unclear. However, they do not appear to concurrently modify their dive duration, and likely the time spent searching for prey. When top predators display behavioral responses to activities not directed at them, the task of studying all possible effects of human activities can become even more challenging. Further work should focus on elucidating how different levels of food intake induce social and behavioral changes in marine top predators.

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