

SHORT-TERM EFFECTS OF BOAT TRAFFIC ON BOTTLENOSE DOLPHINS, *TURSIOPS* *TRUNCATUS*, IN SARASOTA BAY, FLORIDA

STEPHANIE M. NOWACEK
RANDALL S. WELLS

Chicago Zoological Society,
% Mote Marine Laboratory,
1600 Ken Thompson Parkway,
Sarasota, Florida 34236, U.S.A.
E-mail: stephanie@mote.org

ANDREW R. SOLOW
Woods Hole Oceanographic Institution,
45 Water Street,
Woods Hole, Massachusetts 02543, U.S.A.

ABSTRACT

Coastal cetaceans are subject to potential injury or disturbance from vessels. In Sarasota, Florida, where about 120 resident bottlenose dolphins, *Tursiops truncatus*, share the inshore waters with over 34,000 registered boats, disturbance potential is high. We assessed specific behavioral responses of individual dolphins to boat traffic. We conducted focal animal behavioral observations during opportunistic and experimental boat approaches involving 33 well-known identifiable individual bottlenose dolphins. Dolphins had longer interbreath intervals (IBI) during boat approaches compared to control periods (no boats within 100 m). Treatment IBI length was inversely correlated with distance to the nearest boat in opportunistic observations. During 58 experimental approaches to 18 individuals, a video system suspended from a tethered airship was used to observe subsurface responses of focal dolphins as boats under our control, operating at specified speeds, were directed near dolphins. Dolphins decreased interanimal distance, changed heading, and increased swimming speed significantly more often in response to an approaching vessel than during control periods. Probability of change for both interanimal distance and heading increased when dolphins were approached while in shallow water. Our findings provide additional support for the need to consider disturbance in management plans for cetacean conservation.

Key words: bottlenose dolphin, *Tursiops truncatus*, Florida, disturbance responses, boat, interbreath interval, conservation.

Wild animals are exposed to a variety of human activities. Although not all anthropogenic activities would be expected to have adverse impacts, motorized vehicles appear to have high disturbance potential for both marine and

terrestrial mammals. Since frequent exposure to motorized vehicles is now a part of life for many wild mammals, it is important to determine the impact of acoustic, visual, or physical contact on the survival or reproductive potential of individuals. Direct effects are relatively easy to identify, such as injuries to manatees (*Trichechus manatus*) or bottlenose dolphins from boat collisions (Wright *et al.* 1995, Wells and Scott 1997). Indirect effects are more difficult to evaluate. Research focusing primarily on deer, sheep, and elk has shown that animals tend to move away from the source of the disturbance (Freddy *et al.* 1986, Tyler 1991, Cassirer *et al.* 1992), shift use of their home range (Dorrance *et al.* 1975, Schultz and Bailey 1978, Cassirer *et al.* 1992), alter their behavior or activity (Richens and Lavigne 1978, Freddy *et al.* 1986), or alter their group interactions (Patterson 1988).

Similar studies have examined the impacts on some marine mammals, especially relative to human-generated noise (see Richardson 1995 for a review). Due to increased levels of boat traffic, marine animals are potentially subject to increased disturbances. Some odontocetes exhibit tolerance to watercraft, but apparent disturbance reactions have also been documented. Over a several-year period of increasing boat activity, beluga whale (*Delphinapterus leucas*) abundance declined in the St. Lawrence Estuary (Caron and Sergeant 1988). Spotted, spinner, and striped dolphins (*Stenella attenuata*, *S. longirostris*, *S. coeruleoalba*) changed their swimming track to avoid the path of an approaching vessel (Au and Perryman 1982). Killer whales, (*Orcinus orca*), observed in an area of increasing boat traffic off British Columbia, increased their swimming speed and left the area if more than one boat was present (Kruse 1991). Similar results were found with harbor porpoises, *Phocoena phocoena*, which tended to swim away from approaching vessels (Polacheck and Thorpe 1990). Harbor porpoises also show differential responses based on the size and behavior of the approaching vessel (Evans *et al.* 1993).

The use of coastal habitats by bottlenose dolphins exposes them to higher levels of human activities than many other cetaceans. Previous research has shown that boats can affect dolphin behavior. Specific responses include changes in dive length (Evans *et al.* 1992), surfacing patterns (Janik and Thompson 1996), and foraging habitat selection (Allen and Read 2000). In Sarasota Bay, Florida, short-term shifts in local habitat use have been observed during periods of heavy boat traffic (Wells 1993).

A first step toward evaluating the importance of cumulative small-scale or short-term disturbance responses to the longer-term survival or reproductive success of animals is defining the conditions leading to discernable responses. Previous research focused on behaviors that can be observed systematically from a shore station or the deck of a boat. Building on this preliminary research, we investigated the circumstances under which dolphins respond to approaches by boats, specifically looking for changes in focal animal respiration patterns, heading, swimming speed, and interanimal distance. Our research design included opportunistic observations of the surface behavior of focal dolphins relative to boats that passed or approached them and observations of

subsurface behavior relative to experimental approaches using remotely controlled overhead video recordings (Nowacek *et al.* 2001).

METHODS

The research was conducted in and near Sarasota Bay, Florida. The study area consists of a system of sheltered waterways and shallow bays, separated from the Gulf of Mexico by a series of barrier islands. Observations occurred throughout these inshore and nearshore Gulf of Mexico waters. This area is composed primarily of shallow water ranging from less than one meter over sandbars and seagrass meadows to about ten meters in passes communicating with the Gulf of Mexico. More than 34,000 vessels registered in Sarasota and Manatee Counties, plus an undetermined number of vessels brought by visitors, potentially operate in this study area.

The study animals are members of a resident community of bottlenose dolphins inhabiting Sarasota Bay. Research initiated in 1970 has provided data on age, sex, reproductive status, and genetic relationships, and opportunities to mark individuals for identification (Scott *et al.* 1990, Wells 1991). These data facilitated selection of focal animals for specific research questions. Non-calf male and female dolphins that were readily identifiable were selected for observation. Females with dependent calves were emphasized due to the potential for increased sensitivity or vulnerability to vessel disturbance (Wells and Scott 1997). These females were divided into two groups based on their maternal experience. "Experienced mothers" were those females that had successfully raised a calf to independence and "inexperienced mothers" were those that had not, including primiparous mothers. Independence was defined as the minimum age at which a calf typically left its mother and survived on its own (usually 3 yr; Wells *et al.* 1987), so mothers who had raised a calf to ≥ 3 yr of age were considered experienced.

Data collection for observations of opportunistic approaches—Data were collected from a 5.5-m Cobia® research vessel, with a 115-hp Yamaha® outboard engine. Upon sighting dolphins, location, group size, activity, heading, and environmental conditions were recorded. Whenever possible, individuals were identified in the field by dorsal fin features; photographs were also taken for photo-identification. The initial data collection period for each new sighting typically took at least 15 min. To standardize the collection of behavioral data, focal follows did not begin until at least 15 min after the first sighting of dolphins in the focal animal's group. Daily survey routes varied depending on weather and tide, decreasing the likelihood that the same dolphins would be found every day.

Observations were conducted using a combination of continuous and instantaneous point sampling (Altmann 1974). Instantaneous sampling is "a technique in which the observer records an individual's current activity at preselected moments in time." Continuous sampling is used in this paper to refer to Altmann's (1974) "sampling all occurrences of some behaviors." Behavioral observations were initiated when an appropriate (identifiable, known

age/sex) focal animal was identified. Follows ended as a result of three missed instantaneous point samples (>9 min without visual contact with focal animal) or inclement weather. For instantaneous point samples, a three-minute repeated countdown wristwatch indicated the times for data collection.

In Sarasota Bay, water opacity and low-viewing angle precluded continuous observations of underwater behaviors from the deck of the observation vessel; however, respiration data could be collected continuously for the focal animal. Each time the focal dolphin surfaced and took a breath, the time was recorded. If the focal dolphin surfaced too far from the observation boat or at an angle such that its dorsal fin was not recognizable then a break in the continuous data was recorded. Instantaneous point sampling was used to collect data about the boats in the nearby area (within 100 m of the focal dolphin). At three-minute intervals the total number of boats within 100 m of the focal dolphin was recorded. In addition, the speed, propulsion method, and distance of the closest boat to the focal animal were also recorded. "Nearest approach" times, the time when the distance between the focal animal and the nearest or approaching boat was at a minimum, were recorded continuously as boats passed the focal animal.

Data collection for experimental approaches—We conducted "experimental approaches" to focal animals using boats at specific speeds to elucidate responses not attainable from opportunistic observations. A 5.5-m Hobo® houseboat with a 90-hp Yamaha® outboard engine served as the observation platform for the experimental approaches. Continuous observations of the focal animal beneath the water surface were conducted using an overhead video observation system developed by Nowacek *et al.* (2001). The video operator on the observation vessel monitored the video signal in real-time to keep the focal dolphin within the frame thereby maintaining a continuous image of subsurface behaviors. Changes in heading, interanimal distance and swimming speed were identified from digital video segments. Nowacek *et al.* (2001) found that dolphins sometimes exhibit brief (<10 sec) avoidance behavior towards the airship's shadow; however, these occurrences are infrequent and responses are not consistent. To eliminate this bias, video segments in which the blimp shadow passed over the dolphins were not used.

For approach vessels, we used one of the most common types of boats found in the Sarasota Bay waters, a small outboard-powered vessel, and a boat type that has been increasing in popularity over the last few years, the jet-drive personal watercraft (PWC) (Burger and Leonard 2000). The outboard was a 5.8-m center console Mako® with a 115-hp two-stroke Yamaha® outboard engine; the PWC was a Yamaha WaveRunner III®. Each boat type performed different type approaches (Table 1). Approach types were selected to represent those that dolphins are exposed to on a daily basis in Sarasota Bay. While the approaches mimicked those of the general boating public, continuous monitoring from the overhead perspective and radio and visual communications between the observation and approach vessels minimized the risks to the dolphins.

Behavioral data collection during experimental approaches was identical to

Table 1. Approach speeds (mph) and headings for each of two vessel types used for experimental approaches.

Vessel type	Treatment					
	Fast		Slow		Erratic	
	Speed	Heading	Speed	Heading	Speed	Heading
Personal watercraft	35	constant	15	constant	variable	variable
Small outboard	31	constant	9	constant	na	na

the opportunistic data collection with the addition of water depth, which was recorded after the trial at the actual location of the nearest approach. The designated approach boat first took up station, idling, 100 m from the focal dolphin about 180° relative to the dolphin's heading (head-on). When the approach vessel operator could visually confirm the location and heading of the focal animal, they were told *via* VHF radio to begin their approach. The approach vessel maintained its heading throughout the approach, completing the trial when the boat was about 100 m past the dolphin. The start and end times of the approach were recorded. It was not possible to test the effects of both speed and relative heading; therefore, our experimental approaches were conducted as head-on approaches only. Dolphins can react to acoustic stimuli at great distances, so could react to the acceleration of the approach boat as it began its approach. To minimize this potential bias, when scoring video segments of the approaches, we watched for changes in behavior only at the nearest approach time, not over the entire length of the approach.

Data analyses—Summary statistics were performed using Microsoft Excel®, Statistica® 5.0, and Systat® 7.0. Significance for all statistical tests was set at $P = 0.05$.

Respiration patterns for both opportunistic and experimental datasets were analyzed because of their demonstrated utility in other cetacean-disturbance studies (e.g., Richardson 1995). Analyses were performed on interbreath intervals (IBI), which are defined as the time between breaths. IBI were categorized using passing/approaching boats' nearest approach times. "Treatment IBI" were those recorded when the distance between the approaching boat and the dolphin was at a minimum, *i.e.*, nearest approach times. These treatment IBI were compared with "control IBI" which were recorded when there were no boats within 100 m of the focal dolphin and there had been no boats within 100 m of the focal animals for five minutes before or after the IBI. Five minutes was chosen as the length of time to account for the longest possible dives made by bottlenose dolphins in Sarasota (4 min 25 sec, Irvine *et al.* 1981).

Because these observations include multiple sequences of dive durations for the same animal, two issues arise. The first is whether there is dependence among successive IBI. We tested for lag-one serial correlation in the 16 control sequences of length greater than 30 IBI. Of these, only one sequence exhibited significant lag-one correlation at the 0.05 level. Even for this sequence, the

estimated lag-one correlation was only 0.36. On the basis of these results, we concluded that the sequences could be treated as serially independent. The second issue is accounting for individual variation of focal animal responses with unequal sample sizes per animal. We controlled for this by using the focal animal as the sampling unit in each analysis (Aebischer *et al.* 1993).

IBI data from opportunistic and experimental data collection periods were combined for analyses. Data were normalized using a log-transformation. An unbalanced two-way analysis of variance (ANOVA) using IBI type and focal animal as factors was used to compare treatment to control IBI (Miller 1986). The high level of individual variability in respiratory patterns (Würsig and Lynn 1996) makes it difficult to elucidate clear patterns of response. We categorized focal dolphins based on sex and reproductive status (12 males, 10 females without dependent calf, 8 inexperienced mothers, and 6 experienced mothers) and then used another two-way ANOVA with IBI type and animal class as factors to see if differential response occurred by class. Age and body size were not used for analyses as only non-calf dolphins were used for analyses and current body size measurements were not available for all focal dolphins. Estimated body size was unlikely to be meaningful due to high size-at-age variation in all age classes (Read *et al.* 1993).

For both periods of data collection (opportunistic and experimental), observations were made from an outboard vessel. The observation boat was a consistent presence during focal follows and, in theory, should affect all follows similarly. We used the distance between the observation vessel and the focal animal as a factor to test whether this, in fact, was true. A large unbalanced ANCOVA was used to test the effects of two covariants (distance between the focal animal and both the observation vessel and the approaching vessel) and three factors (focal animal, approaching boat speed, and propulsion type) on IBI length (Sokal and Rohlf 1981). Only 27 dolphins were included in this analysis due to incomplete data sets.

Two sets of video segments from experimental data were used for analyses. The first set were the actual approach segments, each usually lasting about 15 sec. The second set included randomly selected control segments, also lasting about 15 sec. Video recordings were categorized based on quality; the ability to continuously track behaviors of the focal animal was imperative, so segments in which the focal animal was not continuously viewable were considered "poor" and were not included in analyses. Segments were watched twice by two observers and scored using either "change" or "no change" for each of three behavioral categories: swimming speed, heading, and interanimal distance (when more than one animal was in the subgroup). If observers disagreed, the segment was watched a third time and if still no agreement could be reached the data from that approach were not used. Quantitative measures of amount of change (for example, number of degrees of heading change) were not possible. Fluke strokes could be counted and were used to determine qualitative changes in swimming speed. The approaching boat maintained a constant heading throughout the approach, providing a ruler to detect change in heading by the focal dolphin. Lastly, interanimal distance could be mea-

sured. Changes in the zoom and orientation of the camera could complicate analyses; therefore, if either of these changed drastically during a segment, the data were not used.

Analyses for the experimental approach data were tiered. The first question asked whether there was a difference in the frequency of "change" *vs.* "no change" in swimming speed, heading, and interanimal distance during treatment as compared to control intervals. We used a test for an additive effect (due to treatment) at the logistic scale, allowing for heterogeneity between individuals (McCullagh and Nelder 1989). Subsequent analyses focused on determining under which specific conditions change occurred, *i.e.*, different water depths, approach boat type, speed, and distance. Although we were interested in addressing the question of water depth with respect to the observations of opportunistic approaches, our data collection methodology did not allow it because depth was recorded at the observation boat, not where the dolphin was swimming.

A generalized linear model (GLM) using a binary distribution with a logit link function was used to compare frequencies of "change" *vs.* "no change" under different approach conditions (water depth, boat approach speed, boat type, approach distance). The individual animal was not considered an independent categorical factor in the model for two reasons. First, the experimental design was such that most dolphins were approached only once under each set of conditions making it impossible to test for individual variation. Secondly, test results from comparing treatment *vs.* control segments showed that individuals responded the same way.

RESULTS

Surface behavioral responses: Interbreath intervals—IBI were recorded during both opportunistic and experimental data collection periods (collected data are summarized in Table 2). Both IBI type and focal animal yielded significant results (2-way ANOVA: focal animal $F_{31, 4049} = 8.2253$, $P < 0.001$; IBI type $F_{1, 4049} = 294.9153$, $P < 0.001$). Treatment IBI were significantly longer than control IBI. The interaction term between IBI type and focal animal was not significant ($P = 0.209$). In the same two-way ANOVA, animal class was used instead of focal animal and again significant results were found for each factor (2-way ANOVA: animal class $F_{3, 4061} = 6.5857$, $P < 0.001$; IBI type $F_{1, 4061} = 257.2336$, $P < 0.001$). The interaction term was not significant ($P = 0.617$); all classes of dolphins responded in the same way (Fig. 1). Tukey's HSD test showed males were not significantly different than any other class of animals, but both females without dependent calves and inexperienced mothers were significantly different than experienced mothers ($P = 0.029$ and $P < 0.0001$, respectively) with experienced mothers having the longest treatment IBI of any class of dolphins.

Treatment IBI length varied with the distance between the approaching boat and the focal animal such that closer approaches yielded longer IBI (ANCOVA: $F_{1, 366} = 7.267$, $P < 0.01$; Fig. 2). Focal animal as a factor was also

Table 2. Data collection details.

	Opportunistic	Experimental
Number of dolphins followed	33	18 ^a
Dates	1 July–30 October 1997; 12–19 May 1998	10 June–7 July 1998
Follow length:		
Mean (min)	72	46
SD	48	32
<i>n</i>	83	26
Instantaneous point samples	3,302	434
Interbreath intervals	11,250	1,920
Total vessel approaches	1,008	138
Usable vessel approaches	510	58
Control segments		642

^a 12 of these dolphins were also followed during opportunistic observations.

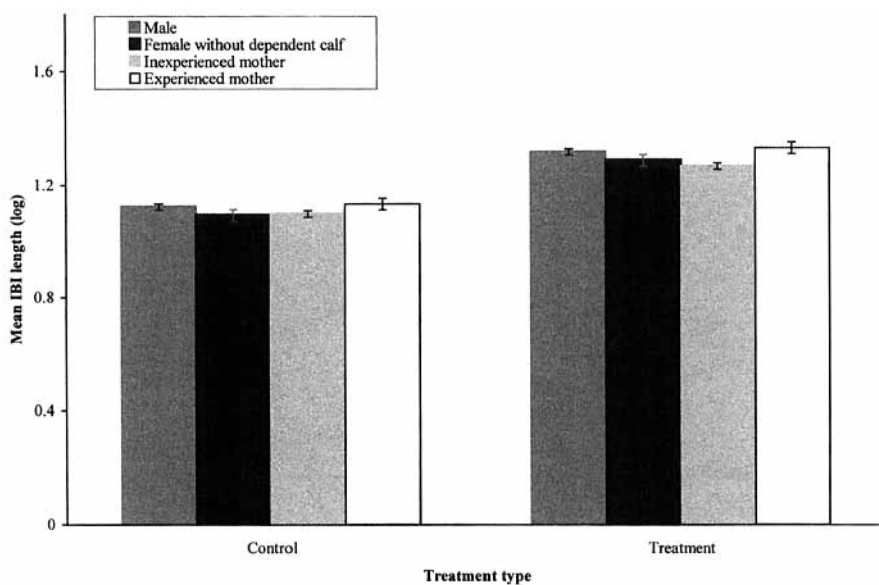


Figure 1. Treatment and control mean (log-transformed) IBI length by animal class. Error bars show standard error.

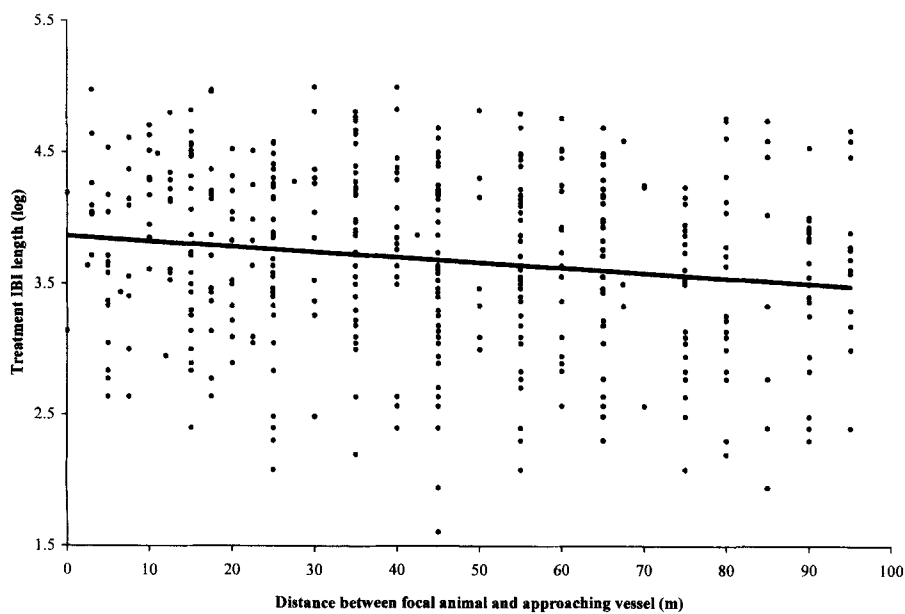


Figure 2. Treatment IBI lengths at various approach distances. Distance was a significant covariant in ANCOVA analyses as demonstrated by simplified linear trend line shown.

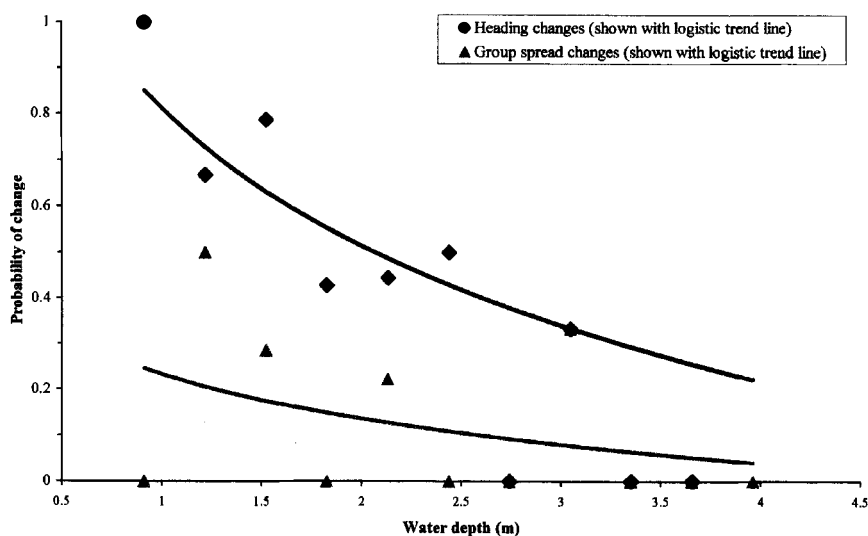


Figure 3. Changes in subsurface behaviors with respect to water depth, GLM results simplified for graphical representation.

significant ($F_{26, 366} = 2.003$, $P < 0.005$). Distance between the observation vessel and the focal animal, approaching boat speed, and propulsion type did not have significant effects on IBI length ($P = 0.723$, $P = 0.102$, $P = 0.537$, respectively). No interaction terms were significant.

Subsurface behavioral responses: Interanimal distance, swimming speed, and heading—Significantly more changes in each behavior were found during treatment segments than during control segments ($P < 0.001$ for each behavior: heading, interanimal distance, and swimming speed). Additionally, the estimates of change for each individual were (1) consistently >0 , indicating that the effect of treatment is to increase the probability of change; and (2) similar to each other for each of the three behaviors, indicating that the assumption of a common effect at the logistic scale is good. Of the treatment segments that demonstrated changes in behavior, 77% of changes in interanimal distance consisted of a decrease in distance; 94% of swimming speed changes were increases, and all heading changes involved dolphins altering course to move away from the path of the approaching boat.

Treatment segments were then compared to determine which factors caused differences in behavioral responses. Significantly more changes in heading and interanimal distance were found with respect to water depth (GLM: (heading) $df = 1$, $\chi^2 = 7.239$, $P < 0.01$; (interanimal distance) $df = 1$, $\chi^2 = 5.596$, $P < 0.05$; Fig. 3), approach boat type (GLM: (heading) $df = 1$, $\chi^2 = 5.972$, $P < 0.05$; (interanimal distance) $df = 1$, $\chi^2 = 10.3444$, $P < 0.005$; Fig. 4) and speed (GLM: (heading) $df = 2$, $\chi^2 = 10.329$, $P < 0.01$; (interanimal distance) $df = 2$, $\chi^2 = 6.579$, $P < 0.05$; Fig. 4). Distance to the approach vessel was not a significant factor for either behavior; no interaction terms were significant either. The rate of change for swimming speed did not change

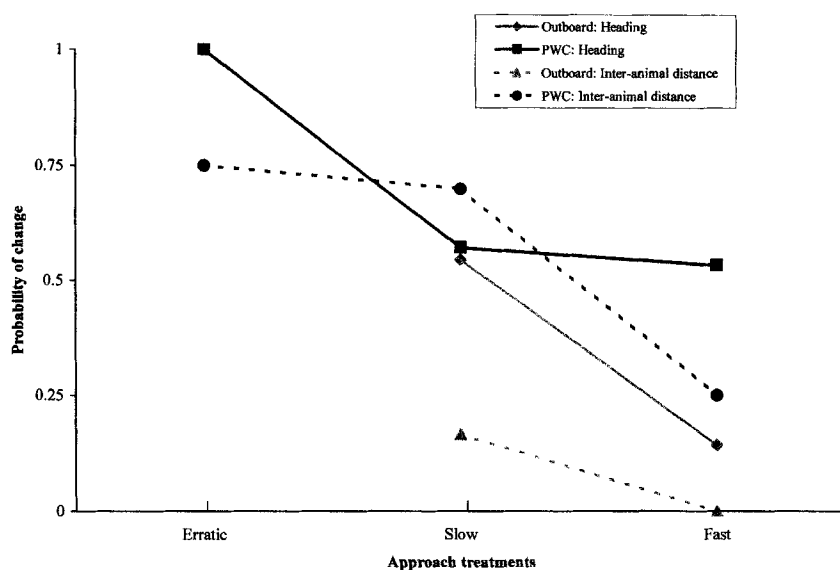


Figure 4. Probability of change in heading and interanimal distance during approaches by an outboard and a PWC at various speeds. Speed significantly impacted change in both behaviors as found in GLM analyses.

significantly with varying conditions (boat type, speed, water depth, or distance to approach vessel).

DISCUSSION

The effects of boat disturbance on individual dolphin behavior—Individual dolphins, as well as classes of dolphins, responded to vessel approaches in the same way, exhibiting longer IBI than when no boats were present. Experienced mothers were significantly different in their IBI lengths than both inexperienced mothers and females without dependent calves (Fig. 1). IBI length for experienced mothers was longer than that for any other class of dolphins. Lack of experience is hypothesized to be a possible reason for lower calf survivorship reported for primiparous mothers. It is possible that one of the learned behaviors for experienced mothers is boat avoidance. Longer IBI during boat approaches means less time when boats are nearby at the surface effectively decreasing the probability of being struck by a vessel. Wells and Scott (1997) showed that compromised dolphins are more likely than other classes of dolphins to be struck by boats, especially during periods of heavy boat traffic. A dependent calf could hinder maneuverability for its mother thereby increasing the vulnerability of both mother and calf.

Closer boat approaches yield significantly longer treatment IBI (Fig. 2). Acevedo (1991) reported that boats had to pass dolphins within 5 m of the dolphin's location to elicit a diving response. Our results show that significant changes in dive duration can occur when a boat passes much farther away.

Dolphins can detect and localize acoustic stimuli at varying distances dependent on source level and environment. Perhaps dolphins use acoustic cues to gauge the distance to the approaching boat and, based on that knowledge, plan their dives accordingly. Although acoustic measures were not a part of this project, these could be important in further elucidating the impact of boat traffic on dolphins. While we were not able to find any significant change in the length of IBI related to the proximity of the observation vessel to the focal animal, it is important to acknowledge that the observation vessel was present during all approaches so changes in IBI length cannot be attributed entirely to the approaching vessel. In fact, our experimental design actually tested the impact of multiple boats nearby the focal animal.

Our findings of changes in interanimal distance, heading, and swimming speed in response to vessel approaches are consistent with reports by others. Most previous observations, however, were of surface behaviors only (Irvine *et al.* 1981, Au and Perryman 1982, Acevedo 1991, Evans *et al.* 1992, Bejder *et al.* 1999). Using the overhead video observation system, we were able to monitor subsurface behaviors and obtain a more accurate and detailed record of the animals' responses to vessels. These continuous observations showed that dolphins are making quick, and sometimes subtle, changes in heading, swimming speed, and/or interanimal distance. These changes occur rapidly and are unlikely to be observed at their actual frequency of occurrence by examining surface behaviors alone.

The effect of specific factors in differentiating subsurface behavioral responses— Figure 4 shows two causes of disturbance; the first is duration of exposure. We observed more heading and interanimal distance changes during slow approaches. Janik and Thompson (1996) noted that dolphins were more likely to change their respiratory patterns in response to a dolphin-watching boat than to other types of boat traffic. Dolphin-watching boats "behaved" differently from other types of vessels by remaining in the channel for longer periods of time and usually following the animals (Janik and Thompson 1996). Our findings indicate that duration of exposure alone could be a predictor for impact on dolphin behavior. The second probable cause of disturbance is the rate of change by the source disturbance. Erratic approaches caused far more changes in heading and interanimal distance than either slow or fast approaches. Erratic approaches mimicked typical PWC use patterns in Sarasota Bay. Richardson *et al.* (1985) indicated that differential reactions occur based on the type of disturbance. Bowhead whales were more likely to respond to rapidly changing situations than to ongoing disturbances (Richardson *et al.* 1985). The type and/or operation of watercraft acts as either a rapidly changing disturbance or an ongoing disturbance based on factors such as the frequency of turns or the likelihood of changing engine speed. It is likely that PWC elicit more changes in behavior due to their unpredictability.

Changes in behavior were more likely to occur in response to a PWC than to an outboard at slow and fast speeds as well (Fig. 4). According to Evans *et al.* (1992), "jet-skis" are not acoustically detectable at the same distances as are other types of watercraft. If dolphins are unable to detect jet propelled

vessels until they are relatively close, then they would not be afforded the same opportunity to adjust their behavior in anticipation of the boat approach as they might for a noisier vessel. Again, lack of predictability translates into greater disturbance and possibly danger potential. If watercraft are not loud enough to be detected or localized at reasonable distances then the likelihood of collisions between marine mammals and boats increases. Future research should examine the acoustic component of boat traffic by looking at the received noise levels for individual animals from various boat types, and the transmission characteristics of these sounds through various common habitat types.

Water depth appears to be a confounding factor. Personal watercraft, along with the increasingly popular "flats boats," and airboats, are able to travel in extremely shallow water (less than 1 m), enabling them to invade waters traditionally considered inaccessible to most forms of watercraft (Burger 1998, Burger and Leonard 2000). A significantly higher frequency of heading and interanimal distance changes occurred during experimental approaches while dolphins were in shallow water. Sound propagation in shallow water is poor compared to that in deep water, so dolphins may not be able to detect or localize approaching vessels at the same distances as possible while in deeper waters. Wells (1993) reported that, before the increased use of shallow draft vessels, dolphins were likely to move out of channels and into shallow water during periods of heavy boat traffic. Shallow waters are typically used for feeding and calf rearing, probably in part because they are relatively undisturbed; it appears that dolphins may also have been using shallow waters as havens from boat traffic. If those shallow, protected waters are no longer safe feeding or nursery areas because personal watercraft, airboats, and flats boats can travel in them, then a dolphin's ability to sustain itself, avoid boat traffic, or a mother's ability to safely rear her calf could be compromised. Future research should address the effect of increased shallow-draft vessel usage on dolphin habitat use. For example, increased management of boat traffic may be warranted in shallow-water habitats shared by both bottlenose dolphins and the endangered Florida manatee, a species for which 25% of mortalities are ascribed to boat collisions (Ackerman *et al.* 1995).

The resident community of bottlenose dolphins in Sarasota Bay, Florida, co-exists with a high level of boat traffic with an average of six minutes between vessel approaches (within 100 m) during daylight hours. Despite dolphins' long-term exposure to boat traffic, short-term behavioral responses were documented. The behavioral changes that we observed appear to be reasonably straightforward short-term responses to the immediate threats posed by vessel approaches. Longer IBI keep the dolphins away from the surface, below the physical threat imposed by the vessels. Changes in heading and swimming speed move the dolphins out of the vessel's path in shallow water where vertical escape is not possible. Coalescence of subgroups may improve the ability of the animals to coordinate movements through visual or physical contact; this may be especially important if vessel noise masks communication sounds.

The long-term or cumulative effects of vessel disturbance remain to be determined.

Except in a few cases where longitudinal studies are ongoing, information on the long-term effects of vessels on the survival and reproduction of coastal bottlenose dolphins is difficult to collect, and even more difficult to distinguish from the effects of other anthropogenic and natural factors. In spite of these limitations, it seems clear from the results of this and other studies that vessel traffic can result in "harassment" as defined under the U.S. Marine Mammal Protection Act of 1972 (as modified in 1994):

"[Harassment is defined as] . . . any act of pursuit, torment, or annoyance which (i) has the potential to injure a marine mammal or marine mammal stock in the wild; or (ii) has the potential to disturb a marine mammal stock in the wild by causing disruption of behavioral patterns, including, but not limited to, migration, breathing, nursing, breeding, feeding, or sheltering." (Baur *et al.* 1999)

As a documented form of harassment, it seems that vessel disturbance warrants increased attention in the development of management plans for bottlenose dolphins, both to increase immediate protection of the animals, and to refine our understanding of the effects of vessel traffic on this and similar species.

ACKNOWLEDGMENTS

This project was made possible through the dedicated efforts of a large team of individuals. We would like to thank Kristi Fazioli, Kara Buckstaff, Colleen Corrigan, Allison Evanchik, Sue Hofmann, Kristen Lorentzen, Dirk Neumann, Doug Nowacek, Edward Owen, Jennifer Sands, Anna Sellas, Julie Smathers, Caryn Owen, and others who assisted with the fieldwork. We would also like to thank Colin Simpfendorfer for his statistical advice. Mote Marine Laboratory, Dolphin Biology Research Institute, the Florida Marine Research Institute, and Woods Hole Oceanographic Institution provided crucial logistical support. Fieldwork was conducted under General Authorization No. 522-1435 issued by the National Marine Fisheries Service. Funding support for field work and analyses was graciously provided by the Disney Wildlife Conservation Fund, the Chicago Zoological Society, the Henry Foundation, Don and Lee Hamilton, the Earl and Ethyl B. Myers Oceanographic Trust, the University of California Santa Cruz Ocean Sciences Department, and the Steven E. Smathers Needy-Graduate-Student Fund. Earlier drafts of this manuscript were improved through the much appreciated and insightful comments of Dan Costa, Terrie Williams, Amy Samuels, Kim Urian, Sue Hofmann, Martha Holland, Doug Nowacek, Kim Bassos-Hull, Caryn Owen, and two anonymous reviewers.

LITERATURE CITED

- ACEVEDO, A. 1991. Interactions between boats and bottlenose dolphins, *Tursiops truncatus*, in the entrance to Ensenada de La Paz, Mexico. *Aquatic Mammals* 17:120–124.
- ACKERMAN, B. B., S. D. WRIGHT, R. K. BONDE, D. K. ODELL AND D. J. BANOWETZ. 1995. Trends and patterns in mortality of manatees in Florida, 1974–1992. Pages 223–258 in T. J. O'Shea, B. B. Ackerman and H. F. Percival, eds. *Population biology of the Florida manatee*. National Biological Service Information and Technology Report 1.

- AEBISCHER, N. J., P. A. ROBERTSON AND R. E. KENWARD. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74:1312–1324.
- ALLEN, M. C., AND A. J. READ. 2000. Habitat selection of foraging bottlenose dolphins in relation to boat density near Clearwater, Florida. *Marine Mammal Science* 16: 815–824.
- ALTMANN, J. 1974. Observational study of behavior: Sampling methods. *Behaviour* 49: 227–265.
- AU, D., AND W. PERRYMAN. 1982. Movement and speed of dolphin schools responding to an approaching ship. *Fishery Bulletin*, U.S. 80:371–379.
- BAUR, D. C., M. J. BEAN AND M. L. GOSLINER. 1999. U.S. laws governing marine mammal conservation. Pages 48–86 in J. R. Twiss and R. R. Reeves, eds. *Conservation and management of marine mammals*. Smithsonian Institution Press, Washington, DC.
- BEJDER, L., S. M. DAWSON AND J. A. HARRAWAY. 1999. Responses by Hector's dolphins to boats and swimmers in Porpoise Bay, New Zealand. *Marine Mammal Science* 15:738–750.
- BURGER, J. 1998. Effects of motorboats and personal watercraft on flight behavior over a colony of common terns. *The Condor* 100:528–534.
- BURGER, J., AND J. LEONARD. 2000. Conflict resolution in coastal waters: The case of personal watercraft. *Marine Policy* 24:61–67.
- CARON, L. M. J., AND D. E. SERGEANT. 1988. Yearly variation in the frequency of passage of beluga whales (*Delphinapterus leucas*) at the mouth of the Saguenay River, Quebec, over the past decade. *Naturaliste Canadien* 115:111–116.
- CASSIRER, E. F., D. J. FREDDY AND E. D. ABLES. 1992. Elk responses to disturbance by cross-country skiers in Yellowstone National Park. *Wildlife Society Bulletin* 20: 375–381.
- DORRANCE, M. J., P. J. SAVAGE AND D. E. HUFF. 1975. Effects of snowmobiles on white-tailed deer. *Journal of Wildlife Management* 39:563–569.
- EVANS, P. G. H., P. J. CANWELL AND E. J. LEWIS. 1992. An experimental study of the effects of pleasure craft noise upon bottle-nosed dolphins in Cardigan Bay, West Wales. Pages 43–46 in P. G. H. Evans, eds. *European research on cetaceans*. European Cetacean Society, Cambridge.
- EVANS, P. G. H., Q. CARSON, P. FISHER, W. JORDAN, R. LIMER AND I. REES. 1993. A study of the reactions of harbour porpoises to various boats in the coastal waters of southeast Shetland. Pages 60–64 in P. G. H. Evans, eds. *European research on cetaceans*. European Cetacean Society, Cambridge.
- FREDDY, D. J., W. M. BRONAUGH AND M. C. FOWLER. 1986. Responses of mule deer to disturbance by persons afoot and snowmobiles. *Wildlife Society Bulletin* 14: 63–68.
- IRVINE, A. B., M. D. SCOTT, R. S. WELLS AND J. H. KAUFMANN. 1981. Movements and activities of the Atlantic bottlenose dolphin, *Tursiops truncatus*, near Sarasota, Florida. *Fishery Bulletin*, U.S. 79:671–688.
- JANIK, V. M., AND P. M. THOMPSON. 1996. Changes in surfacing patterns of bottlenose dolphins in response to boat traffic. *Marine Mammal Science* 12:597–602.
- KRUSE, S. 1991. The interactions between killer whales and boats in Johnstone Strait, B.C. Pages 149–159 in K. S. Norris and K. Pryor, eds. *Dolphin societies: Discoveries and puzzles*. University of California Press, Berkeley, CA.
- MCCULLAGH, P., AND J. NELDER. 1989. *Generalized linear models*. Chapman and Hall, London.
- MILLER, R. G. 1986. *Beyond ANOVA, basics of applied statistics*. Wiley, New York, NY.
- NOWACEK, D. P., P. L. TYACK, AND R. S. WELLS. 2001. A platform for continuous behavioral and acoustic observation of free-ranging marine mammals: Overhead video combined with underwater audio. *Marine Mammal Science* 17:191–199.

- PATTERSON, I. J. P. 1988. Response of Apennine chamois to human disturbance. *Zeitschrift für Säugetierkunde* 53:245–252.
- POLACHECK, T., AND L. THORPE. 1990. The swimming direction of harbor porpoise in relationship to a survey vessel. Report of the International Whaling Commission 40:463–470.
- READ, A. J., R. S. WELLS, A. A. HOHN AND M. D. SCOTT. 1993. Patterns of growth in wild bottlenose dolphins, *Tursiops truncatus*. *Journal of Zoology*, London 231: 107–123.
- RICHARDSON, W. J. 1995. Documented disturbance reactions. Pages 241–576 in W. J. Richardson, C. R. Greene, C. I. Malme and D. L. Thomson, eds. *Marine mammals and noise*. Academic Press, San Diego, CA.
- RICHARDSON, W. J., M. A. FRAKER, B. WÜRSIG AND R. S. WELLS. 1985. Behaviour of bowhead whales *Balaena mysticetus* summering in the Beaufort Sea: Reactions to industrial activities. *Biological Conservation* 32:195–230.
- RICHEMS, V. B., AND G. R. LAVIGNE. 1978. Response of white-tailed deer to snowmobiles and snowmobile trails in Maine. *The Canadian Field-Naturalist* 92:334–344.
- SCHULTZ, R. D., AND J. A. BAILEY. 1978. Responses of national park elk to human activity. *Journal of Wildlife Management* 42:91–100.
- SCOTT, M. D., R. S. WELLS AND A. B. IRVINE. 1990. A long-term study of bottlenose dolphins on the west coast of Florida. Pages 235–244 in S. Leatherwood and R. R. Reeves, eds. *The bottlenose dolphin*. Academic Press, San Diego, CA.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry*. W. H. Freeman and Company, San Francisco, CA.
- TYLER, N. J. C. 1991. Short-term behavioural responses of Svalbard reindeer *Rangifer tarandus platyrhynchus* to direct provocation by a snowmobile. *Biological Conservation* 56:179–194.
- WELLS, R. S. 1991. The role of long-term study in understanding the social structure of a bottlenose dolphin community. Pages 199–225 in K. Pryor and K. S. Norris, eds. *Dolphin societies: Discoveries and puzzles*. University of California Press, Berkeley, CA.
- WELLS, R. S. 1993. The marine mammals of Sarasota Bay. Pages 9.1–9.23 in P. Roat, C. Cicciolella, H. Smith and D. Tomasko, eds. *Sarasota Bay: 1992 Framework for Action*. Published by the Sarasota National Estuary Program, 5333 N. Tamiami Trail, Sarasota, FL.
- WELLS, R. S., AND M. D. SCOTT. 1997. Seasonal incidence of boat strikes on bottlenose dolphins near Sarasota, Florida. *Marine Mammal Science* 13:475–480.
- WELLS, R. S., M. D. SCOTT AND A. B. IRVINE. 1987. The social structure of free-ranging bottlenose dolphins. Pages 247–303 in H. H. Genoways, ed. *Current mammalogy*. Plenum Press, New York, NY.
- WRIGHT, S. D., B. B. ACKERMAN, R. K. BONDE, C. A. BECK AND D. J. BANOWETZ. 1995. Analysis of watercraft-related mortality of manatees in Florida, 1979–1991. Pages 259–268 in T. J. O'Shea, B. B. Ackerman and H. F. Percival, eds. *Population biology of the Florida manatee*. National Biological Service Information and Technology Report 1.
- WÜRSIG, B., AND S. K. LYNN. 1996. Movements, site fidelity, and respiration patterns of bottlenose dolphins on the central Texas coast. NOAA Technical Memorandum to Contract No. NMFS-SEFSC-383.

Received: 9 November 1999
Accepted: 31 December 2000