

EFFECTS OF WATERCRAFT NOISE ON THE ACOUSTIC BEHAVIOR OF BOTTLENOSE DOLPHINS, *TURSIOPS TRUNCATUS*, IN SARASOTA BAY, FLORIDA

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ABSTRACT

Watercraft may provide the greatest source of anthropogenic noise for bottlenose dolphins living in coastal waters. A resident community of about 140 individuals near Sarasota, Florida, are exposed to a vessel passing within 100 m approximately every six minutes during daylight hours. I investigated the circumstances under which watercraft traffic may impact the acoustic behavior of this community, specifically looking for short-term changes in whistle frequency range, duration, and rate of production. To analyze whistles and received watercraft noise levels, acoustic recordings were made using two hydrophones towed from an observation vessel during focal animal follows of 14 individual dolphins. The duration and frequency range of signature whistles did not change significantly relative to vessel approaches. However, dolphins whistled significantly more often at the onset of approaches compared to during and after vessel approaches. Whistle rate was also significantly greater at the onset of a vessel approach than when no vessels were present. Increased whistle repetition as watercraft approach may simply reflect heightened arousal, an increased motivation for animals to come closer together, with whistles functioning to promote reunions. It may also be an effective way to compensate for signal masking, maintaining communication in a noisy environment.

Key words: bottlenose dolphin, *Tursiops truncatus*, acoustic communication, whistles, disturbance response, watercraft, received level, conservation.

In recent years, motorized transportation and recreational activities have been steadily increasing both in terrestrial and aquatic environments. These activities bring humans and wildlife into greater contact, either directly through physical presence, or indirectly through increased anthropogenic noise. Cars and snowmobiles can elicit strong disturbance responses from terrestrial animals. White-tailed deer change the use of their home range and alter their activity in

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response to snowmobiles (Dorrance *et al.* 1975, Richens and Lavigne 1978). Grassland birds exhibit disturbance behavior by leaving breeding sites near roadways in response to automobile traffic (Reijnen *et al.* 1996).

Studies in the marine environment have shown similar disturbance reactions by cetaceans. Evidence suggests that motorized watercraft elicit avoidance behavior by cetaceans. Most behavioral reactions included increased swimming speed (Au and Perryman 1982, Kruse 1991, S. M. Nowacek *et al.* 2001), longer dive durations (Janik and Thompson 1996, S. M. Nowacek *et al.* 2001), heading changes (Au and Perryman 1982, S. M. Nowacek *et al.* 2001), decreased interanimal distance (Bejder *et al.* 1999, S. M. Nowacek *et al.* 2001), and increased breathing synchrony (Hastie *et al.* 2003).

Of particular importance in both environments are the effects of these activities not only on animal movements and energetics, but on acoustic communication as well. In terrestrial animals, studies have shown changes in vocal behavior such as call amplitude modulation (*e.g.*, zebra finches, *Taeniopygia guttata*, Cynx *et al.* 1998, and macaques, *Macaca spp.*, Sinnott *et al.* 1975) and frequency range shifts (white-lipped frogs, *Leptodactylus albilabris*, Lopez *et al.* 1988) in order to compensate for the presence of noise, particularly if it overlaps with the frequency band of species-typical vocalizations.

Concern has arisen that anthropogenic sounds introduced into the marine environment could have deleterious effects on cetacean acoustic communication (Payne and Webb 1971). Elevated background noise levels from man-made sources may prevent detection of other sounds important to cetaceans, such as calls from conspecifics and echolocation clicks (Erbe and Farmer 1998, Erbe *et al.* 1999, for review see Richardson *et al.* 1995). In coastal waters, recreational watercraft provide perhaps the greatest source of anthropogenic noise. Energy of boat noise ranges between 0.1 and 10 kHz. This range overlaps that of dolphin whistles (4–20 kHz), an important mode of communication among individuals. Recent studies indicate that the direction and type of acoustic behavioral responses are variable among species, but typical responses may enhance signal detectability and group cohesion in a noisy environment (*e.g.*, frequency range shifts, changes in call types and rates, Lesage *et al.* 1999; changes in call rates, Scarpaci *et al.* 2000, Van Parijs and Corkeron 2001).

Previous studies have shown that bottlenose dolphins in Sarasota Bay, Florida are occasionally the victims of collisions with watercraft (Wells and Scott 1997) and respond to approaches by boats through changes in swimming and diving behavior (S. M. Nowacek *et al.* 2001). However, direct relationships between watercraft noise and acoustic behavior of these dolphins have not been investigated. I investigated the circumstances under which watercraft approaches may impact the acoustic behavior of this resident community of dolphins. Short-term changes in whistle structure and production were studied, specifically looking for changes in frequency range and duration of signature whistles, and in overall whistle rate in response to opportunistic vessel approaches. Signature whistles are described as unique rising and falling patterns of frequency modulation, distinctive by individual (Caldwell *et al.* 1990). The contour can be repeated any number of times in each whistle and these repetitive elements are called loops. Most commonly, signature whistles span a frequency range of 4–20 kHz and last about 1 sec (Caldwell *et al.* 1990). A major function of signature whistles is to announce the location of individuals within a group and this can be useful in facilitating group cohesion. Both temporal changes in whistle duration and rate and shifts in whistle frequency range can

increase the likelihood that a whistle is heard during periods of elevated background noise, such as watercraft approaches.

METHODS

Study Site

The study site consists of a series of barrier islands and their associated waters paralleling the western central Florida coastline of Sarasota and Manatee counties, creating a system of sheltered channels and shallow bays, the largest of which is Sarasota Bay. This shallow bay ranges in depth from <1 m over grass flats to about 10 m in the passes that connect the bay to the Gulf of Mexico. This study area is used by watercraft for recreational and commercial purposes. In 2002 41,558 recreational watercraft were registered in Sarasota and Manatee counties combined (Florida Fish and Wildlife Conservation Commission, unpublished), accounting for 95% of total registered vessels (the other 5% being commercial vessels). This number does not include the many watercraft brought to the area by visitors. Watercraft documented during my study varied in size (approximately 3–30 m) and propulsion systems (inboard, outboard, and jet-drive).

These vessels move through the home range of a long-term resident community of approximately 140 dolphins, whose behavior and ecology has been studied extensively since 1970 (Wells 1991, 2003). Due to the high level of watercraft traffic in the study area, these dolphins are exposed to a vessel passing within 100 m approximately every 6 min during daylight hours (S. M. Nowacek *et al.* 2001). Females with dependent calves were selected for this study because they represent the most vulnerable segment of the community from the boat risk perspective (Wells and Scott 1997). Notably, two of the focal mothers had survived collision with a boat, bearing scars from their injuries. In Sarasota Bay, mothers range in age from 6 yr to more than 50 yr. Calves typically accompany their mothers for the first 3–6 yr of their lives.

Underwater Acoustic Recording System

Data were collected from a 6-m center-console Mako equipped with a 4-stroke, 100-hp Yamaha outboard engine. Acoustic recordings were obtained using a 2-hydrophone “hammerhead” system similar in design to one described by Sayigh *et al.* (1993). The hydrophones were designed by High Tech Inc. (model HTI-96-MIN, sensitivity: -170 dB re $1\text{V}/\mu\text{Pa}$, frequency response: 2 Hz–30 kHz \pm 1 dB). Weighted hydrophone cables were fed through a PVC tube set across the boat’s bow (hydrophone separation was 3.2 m), and connected to a Tascam DA-P1 digital audio tape recorder (frequency response: 20 Hz–20 kHz \pm 0.5 dB, sampling rate: 48 kHz). Acoustic recordings were collected continuously during focal animal behavioral observations, and monitored about every 3 min *via* headphones for quality assurance.

Data Collection for Dolphin Surface Behavior

Focal animal behavioral observations (Altmann 1974, Mann 1999, for cetaceans) were conducted on the mother of mother-calf pairs (Table 1A). Mothers with calves

Table 1. Data collection and processing summary.

Variable	
A. Summary of focal follow and vessel approach data.	
Number of dolphins followed	14
Number of focal follows	69
Focal follow hours (min)	80.82 (4, 849)
Mean follow hours (min)/dolphin	5.77 (346)
Total vessel approaches	1,233
Vessel approaches (including PWCs) suitable for SNR ^a	220
Subset of vessel approaches (including PWCs) used for SNR	50
B. Summary of whistle data.	
Frequency and duration analyses:	
Total number of best quality whistles	1,576
Usable whistles for analyses ^b	756 (48%)
Individuals with usable whistles ^c	19
Usable whistles scored without vessel(s)	445
Usable whistles scored with vessel(s) ^d	309
Rate analysis:	
Control segments ^e	93
Vessel approach segments (single + multiple):	
Onset segments	53
During segments	96
After segments	56

^a Suitable approaches for SNR (signal-to-noise ratio) processing were those in which the dolphin surfaced between the observation boat and the approaching vessel. PWC = personal, jet-propelled watercraft.

^b Of the best quality whistles, 70% of whistles were matched to signature whistles of known individuals, however, 48% were matched to signature whistles of known animals having >10 whistles each and these were considered usable for analysis.

^c Among the 19 individuals with usable whistles, 7 were of the 14 focal dolphins while the remaining whistles came from their calves or other group associates.

^d "With vessels" included whistles from single and multiple approach segments.

^e Segments were 3-min intervals for control periods, 1-min intervals for "onset" and "after," and variable length samples (based on exposure time) for "during" approaches.

of one or two years of age (known from monitoring individually identifiable mothers, Wells 2003) were chosen as focal subjects ($n = 14$). Surface behavioral data were recorded at 3-min instantaneous time points (instantaneous point sampling technique, Altmann 1974). These data were collected at the first surfacing of the focal dolphin after the time point. Follows lasted up to 2 h, unless visual contact with the focal dolphin was lost and three consecutive point samples (>9 min) were missed. During follows, the observation vessel consistently maneuvered at slow speeds (≤ 9 km/h), typically at a distance of 20 m from the group; the engine remaining on throughout the follow. Data recorded for the focal dolphin included: GPS location of the observation vessel (latitude and longitude), group membership (dolphin identification noted when known, otherwise subsequently verified through photographs), group size (a group including dolphins within an estimated 100-m radius of the focal animal), and dolphin activity.

Altmann's (1974) method of continuous sampling described as "sampling all occurrences of some behaviors" was used to collect positional data for all dolphins in the group relative to the hydrophones. These data were collected to allow whistles to be localized, based on the position of the whistler to the two hydrophones, in turn assigning identification to the whistler. The data recorded at every surfacing by any animal within the group were: time of surfacing (for asynchronous large, group surfacings the time of the first individual to surface was used), ID of the surfacing dolphin(s), an indication of whether the dolphin(s) surfaced closest to the right or left hydrophone, position of the surfacing relative to the hydrophone (forward, back or aside), and habitat type of location in which the dolphin(s) surfaced. Habitat characterizations of shallow, channel, bay, pass, sand, and edge were based on water depth and bottom type as per Waples (1995). Generally, shallow habitats, such as sand and shallow, are characterized by sand bars and grass flats and a water depth of 1.8 m at mean low tide. Deeper habitats, including channels, bays, and passes, are defined by depths greater than 1.8 m at mean low tide.

Data Collection for Watercraft Activity

Watercraft activity data were collected continuously as vessels came within a 400-m radius of the focal dolphin. Laser rangefinders were used to obtain distances to watercraft. The maximum distance measurable using these rangefinders over water and in varying lighting conditions was 400 m. The data collected as vessels reached their nearest approach to the focal dolphin were: time of nearest approach defined as the time at which the minimum distance between the focal animal and the approaching vessel was reached, distance from the observation vessel to the approaching vessel (used as an estimate for the distance between the approaching vessel and the focal dolphin), watercraft speed (defined as idling: slow with minimum or no wake, plowing: moderate speed with large wake and bow "pushing" through water, planing: fast speed with most of the boat riding on top of the water, or underway: variable speed, used for larger displacement vessels that move through the water rather than plane) and size, propulsion type, habitat type through which the watercraft passed, number of other watercraft within a 400-m radius of the focal dolphin, and focal dolphin position relative to the approaching watercraft and the observation platform. Position was noted because it formed the basis for a criterion used later in estimating received watercraft noise level (RL), and was recorded only if the animal surfaced during the approach, as water clarity was not sufficient to allow us to keep track of the animal below the surface.

Acoustic Analyses

All audible whistles and vessel approaches were viewed as spectrograms (FFT size: 512, Hamming window) using Cool Edit Pro 1.2 (Syntrillium Software Corporation, Phoenix, AZ) and saved for analyses.

Using the two-hydrophone "hammerhead system" did not allow me to localize the whistler, as I had hoped, due to the small separation between the hydrophones. This separation was not great enough for me to detect differences in signal arrival times. Therefore, I was not able to make positive signature whistle identifications using field data alone. However, signature whistles recorded during temporary capture-release projects have been archived, making the signature whistles of the

focal animals, and often other animals in the group, available. Using this signature whistle database, which is maintained by Laela Sayigh at the University of North Carolina-Wilmington, I was able to identify 1,103 (or 70%) of 1,576 whistles as signature whistles. Of these whistles, 48% (756) were matched to signature whistles of known animals having >10 whistles each and these were considered usable for analyses. There were 19 animals with usable whistles and 7 were of the 14 focal dolphins while the remaining whistles came from their calves or other group associates.

Signature whistle matches were made by visually comparing spectrograms of whistles (Sayigh *et al.* 1990) recorded from temporarily restrained animals to the free-ranging dolphins in the follows. These comparisons were made using the contour of the fundamental frequency of the whistles. Signature whistles of restrained wild bottlenose dolphins are well known from several studies conducted on the Sarasota Bay community (*e.g.*, Sayigh *et al.* 1990, 1995, 1998). Recent studies have shown that free-swimming dolphins produce the same whistle repertoire as when they are temporarily restrained. Many of these animals also produced their signature whistles under both conditions (Watwood *et al.*, in review).

Mimicry of whistles has been reported in captive and free-ranging bottlenose dolphins (Tyack 1986, Janik 2000). In the Sarasota Bay community, signature whistle similarities have been documented for paired males (Watwood 2003, Watwood *et al.* 2004). Therefore, it is possible that instances in which I identified an individual's signature whistle could actually represent another dolphin producing that individual's whistle, and there was no means by which to tell a copy of a whistle apart from the original for this study. Consequently, if changes are seen in whistle parameters, such as range, duration, and rate, then it could indicate that (1) an individual is changing its whistle parameters or (2) that different individuals vary in how they use this whistle in response to watercraft. Even though I could not identify which explanation was correct, this would still indicate an acoustic reaction with respect to a vessel.

Signature Whistle Frequency Range and Duration

I matched whistles of dolphins present during follows to signature whistles recorded from the same dolphin during restraint. This allowed me to analyze changes in signature whistle frequency range and whistle duration as a function of exposure to vessels (Table 1B). Matlab 5.3 (Mathworks, Natick, MA) was used to generate values for minimum and maximum frequency and duration from the already created spectrograms of individual whistles. Prior to analysis of whistle frequency range and duration, all whistles were categorized as produced either: (1) when no watercraft were within 400 m, (2) when only one vessel was within 400 m (single approach), or (3) when one or more watercraft were within 400 m (multiple approach). Each categorization also included the observation/recording boat, so any potential effect of the observation boat's engine should be consistent across categories. Whistles were considered to have occurred during vessel approaches when they were produced within 1 min before or 1 min after the closest approach time of a vessel or vessels. This criterion was used instead of a minimum RL criterion, for example, because it was necessary to account for the presence of motorized watercraft (based on closest approach times recorded in the field) even if they were not audible over our engine noise (*e.g.*, idling boats). The majority of

watercraft were within audible range during this 2-min period. Generally, sound levels gradually increased up to the point of closest approach and planing boats with various propulsion types produced broadband noise with energy spread continuously over a range of frequencies. The dominant broadband components are caused primarily by propeller cavitation and flow noise (Richardson *et al.* 1995), and can potentially mask more of the dolphin whistle frequency range than a narrower band source. On a few occasions watercraft (*e.g.*, large, underway vessels) were audible for longer durations and whistles occurring during these approaches were considered “during vessel approach” even though the ± 1 -min criterion was exceeded. The maximum distance that watercraft were audible was approximately 400 m, although this was only true for larger, planing boats. Typically, idling boats and jet-propelled personal watercraft (PWC) were not audible at appreciable distance from the observation vessel. Watercraft traveling at speeds between 9 and 75 km/h (5 and 40 mph) can cover distances between 150 and 1,235 m in 1 min. If there were no watercraft either audible or with closest approach times that overlapped within 1 min of a whistle, then the whistle was considered to occur in the absence of vessels.

Data were non-normally distributed even after log-transformation, however normality probability plots of within-group residuals for the non-transformed data revealed only slight departures from normal (as skewness) for all parameters tested. All plots of means *vs.* variances revealed that variances did not increase with means indicating that the two were not correlated. All parametric statistical tests were performed using Statistica 6.0 (Statsoft, Tulsa, OK) and the level of significance was set at $P = 0.05$.

Analysis of variance tests were performed for frequency range and duration of signature whistles because the F statistic is robust against violations of heterogeneity of variances, and the effect of skewness can be ignored (Box and Andersen 1955, Lindman 1974). Two-way, factorial ANOVAs were performed to determine if level of vessel presence (scored as no vessel, single vessel, or multiple vessels) and individual dolphin had an effect on signature whistle frequency range and duration.

Whistle Rate

Analyses were also conducted to determine if vessel approaches affected the rate of whistle production. For the samples with vessels, the minute before the vessel was audible (to the author), the duration of the vessel's presence (defined and measured by audibility), and the minute after the vessel was no longer audible were analyzed (Table 1B). For each of these conditions (before, during, and after), the number of all whistles, not just signature whistles, was counted. The number of whistles during the presence of a vessel was divided by the total number of minutes that the vessel was present, providing an estimate for the number of whistles occurring per minute. All conditions were divided by the number of dolphins present (recorded at 3-min intervals during the focal follows) to remove the effect of group size on the number of whistles. In this manner, whistle rates were calculated as the total number of whistles per dolphin per minute for single and multiple vessel approaches. A repeated-measures ANOVA was used to consider the influence of time (defined as before, during, and after approaches) on whistle rate for both approach types.

I used the following procedure to select a control "no vessel" period to match with each vessel present period. To determine the appropriate time interval to use for samples without watercraft, the average duration was calculated for single and multiple approaches combined. Since the mean approach duration of 1.25 min (\pm SD 48 sec) varied considerably, two standard deviations were added to provide a more realistic approach duration, yielding a duration of approximately 3 min. Therefore, all samples without watercraft were of 3-min intervals, considering that no portion of the interval overlapped with the before, during, or after time periods of vessel approaches (Table 1B). From the beginning of the follow, control periods were started at a random number of seconds into the tape based on values generated by a random number table. These values changed for each follow. For each 3-min interval in which whistle rate was calculated there was a preceding 3-min interval that was not used. One-way ANOVA tests were performed to compare whistle rate between control periods and approach conditions.

During experimental boat approaches, S. M. Nowacek *et al.* (2001) found that there was a significantly higher incidence of heading and interanimal distance changes that occurred while dolphins were in shallow water than in deeper water. Building on this finding, I also considered habitat type as an additional factor in the analyses because, not only water depth, but substrate type and the presence of vegetation can affect sound transmission. Factorial ANOVAs were performed to determine if habitat type when added to vessel presence and individual (as a factor for range and duration only) affects whistle structure and production.

Received Noise Levels of Watercraft

Watercraft RLs recorded during the focal follows were used to determine the actual noise exposure associated with responses related to acoustic behavior. I examined the RLs of single and multiple vessel approaches when, by visual confirmation, the dolphin was in a position between the observation boat and the approaching vessel. Typically, the dolphin was 20 m from the observation vessel and on average, an approaching vessel was 125 m from the observation vessel. Therefore, the RL estimates should be underestimates because the dolphins were between the recording boat and the approaching vessel, but should approximate RL at the animal because the distance the dolphins were from the observation vessel was five times closer than their distance to an approaching vessel. Using the position criterion, I was certain that the dolphins were not receiving noise levels quieter than those recorded at the observation boat. Recordings of single and multiple approaches were processed with a high-pass filter at 1 kHz to eliminate most of the observation vessel's engine noise. Matlab was used to convert closest point of approach RLs of 1-sec segments to RMS (root mean square) voltage. Using the equation: $20 * \log(\text{RMS V}/1 \text{ V}) + 170 \text{ dB re } 1 \mu\text{Pa}$ (where $-170 \text{ dB re } 1 \mu\text{Pa}$ is the sensitivity of the hydrophones) voltage was converted into RMS dB units. The minimum RLs of vessels at various distances and speeds were calculated. RLs for approaches were compared to the RLs (also filtered at 1 kHz for engine noise) during non-approach conditions (<1 min before or after each approach) to create signal-to-noise ratios (SNR (dB), Table 1A). Signal-to-noise ratio is the comparison in dB of the boat noise to the ambient level whereas the RL is the sound pressure level at the location of the hydrophone. Logarithmic regression curves were generated to indicate SNR against distance of the vessels at closest approach.

RESULTS

Acoustic Behavioral Responses: Signature Whistle Frequency Range and Duration

In the summer of 2001 over 80 h of acoustic recordings were collected from 69 focal dolphin follows. Signature whistle frequency range (2.91–23.48 kHz) and duration (0.10–4.11 sec, mean: 0.80 sec) were measured from whistles obtained from recordings made during these follows. Signature whistles were stratified by opportunistic watercraft presence for analysis. Individual (with an identified signature whistle) and level of vessel presence (no watercraft, single, or multiple watercraft) were the categorical predictors for the analysis. Factorial, two-way ANOVAs were performed to examine the interactive effects of individual and level of vessel presence. Results show that only minimum whistle frequency changed significantly; there was an increase when vessels, either single or multiple, were present ($F_{2, 697} = 3.707, P = 0.025$). Individual as a factor was also significant ($F_{18, 697} = 41.890, P < 0.001$). However, the interaction term was significant ($F_{36, 697} = 3.363, P < 0.001$); individual animals responded to the presence of watercraft differently. This inconsistency in the data across all levels caused the main effect ANOVA tests to become inconsequential. Furthermore, vessel presence did not have a significant effect on maximum whistle frequency or overall frequency range (max. freq.: $F_{2, 697} = 0.314, P = 0.730$; freq. range: $F_{18, 697} = 1.887, P = 0.152$). There were still significant differences among individuals' signature whistles for these parameters (max freq.: $F_{18, 697} = 253.18, P < 0.001$; freq. range: $F_{18, 697} = 135.40, P = 0.001$). Interaction terms were significant for maximum frequency and frequency range as well (max freq.: $F_{36, 697} = 4.418, P < 0.001$; freq. range: $F_{36, 697} = 3.875, P < 0.001$). Thus, no consistent significant differences in minimum or maximum whistle frequency or frequency range were identified as a function of vessel approaches.

Whistle duration can change in two ways, either by stretching or shortening a whistle (*i.e.*, time warping) or by adding or deleting loops (*i.e.*, loop modification) to a whistle. Factorial, two-way ANOVAs were performed to test for time warping and loop modification for individual signature whistles. For the time warping analysis, single loop whistles from nine animals and double loop whistles from seven animals were compared during vessel approaches and in the absence of vessels. In both cases, there were no significant differences in whistle duration in the presence of watercraft (single loop: $F_{1, 350} = 0.163, P = 0.686$; double loop: $F_{1, 184} = 1.948, P = 0.164$). Additionally, to look at changes to whistle duration by a combination of time warping and loop modification, all signature whistles were combined whether they were single or multiple loops for each individual ($n = 19$). Individual was not a significant factor in this analysis ($F_{18, 714} = 1.225, P = 0.234$), so a one-way ANOVA was used to test whether the presence of watercraft affected whistle duration. While there was an increasing trend in whistle duration in the presence of vessels, and this is the direction predicted in terms of communication theory, it was not significant ($F_{1, 750} = 0.958, P = 0.328$). Thus, signature whistle duration does not vary significantly relative to vessel approaches.

Acoustic Behavioral Responses: Whistle Rate

I reexamined the selection of conditions (assigned as before, during, and after) in order to refine the analysis of whistle rate relative to vessel approaches. My

categorization of “before” was based on my ability to hear approaching vessels in the recordings. The breakpoint from “before” to “during” approach was the instance when a vessel was first heard underwater on the recordings. Given some of the factors affecting the quality of my recordings (the engine noise of the observation vessel and water flow noise around the hydrophones), and the superior hearing abilities of the dolphins, it is likely that approaching watercraft were audible to dolphins before they became audible on the recordings. Consequently, the “before” approach condition defined previously has been reassigned as “onset” of an approach.

For both single and multiple approaches there was a significant change in whistle rate across approach conditions (repeated measures ANOVA, single: $F_{2,66} = 5.838$, $P = 0.004$; multiple: $F_{2,30} = 3.589$, $P = 0.040$). For both single and multiple approaches, whistle rate for the “onset of an approach” condition was significantly higher than for the later conditions. During single approaches, distance of approaching watercraft to the animal and watercraft speed were not significant factors (distance: $F_{45,9} = 0.969$, $P = 0.570$; speed: $F_{3,51} = 1.221$, $P = 0.311$). This analysis was not performed for multiple approaches as each vessel in a group could not be treated separately so whistle rate data would have been shared, resulting in pseudoreplication (Kroodsma *et al.* 2001). Whistle rate appears to decrease as one or more vessels pass by the dolphin, without regard to watercraft distance or speed.

There was no significant difference in whistle rate for any condition between single and multiple approaches ($F_{1,144} = 0.171$, $P = 0.680$). For this reason, these data could be combined in order to increase the sample size used in the analysis. Again, there were significant differences in whistle rate at the onset, during, and after the presence of watercraft (Fig. 1). Dolphins whistled significantly more at the initial presence of a vessel compared to during and after approaches (Tukey's HSD *post-hoc* comparisons, onset *vs.* during: $P = 0.018$; onset *vs.* after: $P = 0.001$; during *vs.* after: $P = 0.631$). A subsequent analysis was performed which examined whistle rate data for the “onset of vessel approach(es)” compared to control periods when no vessels were present. Whistle rate for watercraft presence was significantly greater than when no watercraft were present (Fig. 1). Therefore, the full range of whistle response to vessel approaches appears to be an initial significant increase in whistle production as the vessel approaches, followed by a significant decline as the vessel passes and for a period thereafter.

The Role of Habitat on Whistle Structure and Production

To examine the role that habitat type coupled with vessel presence played on whistle structure and production, combined habitat conditions defined as either shallow (including sand and grass flats) or deeper areas (including channels, bays, and passes) were included as a factor for analysis. Results for minimum and maximum frequency, frequency range, and duration regarding watercraft presence were not significant. However, habitat alone was a significant factor for some parameters. A smaller dataset was used that included data for seven animals that produced whistles in both habitat types. There were significant differences in some whistle parameters between shallow and deeper areas. Minimum frequency of signature whistles was significantly lower in deeper habitat types (factorial ANOVA, habitat: $F_{1,342} = 5.989$, $P = 0.015$, individual: $F_{6,342} = 11.892$, $P < 0.001$). The interaction term was not significant ($F_{6,342} = 0.948$, $P = 0.461$).

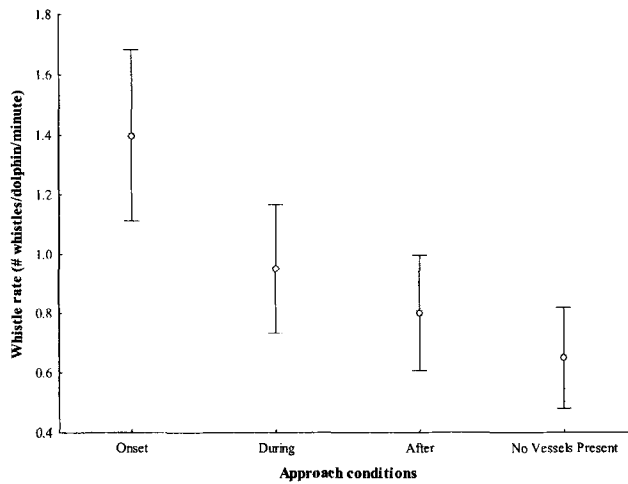


Figure 1. Mean whistle rate for onset, during, and after watercraft approaches. There were significant differences in whistle rate at onset, during, and after the presence of watercraft (repeated measures ANOVA: $F = 7.325$, $df = 2, 98$, $P = 0.001$). Whistle rate at the onset of approaches was double the rate when no boats were present (one-way ANOVA: $F = 27.201$, $df = 1, 141$, $P = 0.001$). Error bars represent standard error.

Likewise, deeper habitat types had a significant effect on the overall frequency range; the minimum frequency decreased causing the frequency range to expand (factorial ANOVA, habitat: $F_{1, 342} = 9.389$, $P = 0.002$; individual: $F_{6, 342} = 92.973$, $P < 0.001$). The interaction term was not significant ($F_{1, 342} = 4.838$, $P = 0.172$). Regarding maximum signature whistle frequency, individual dolphins did not consistently respond in the same direction, so although habitat type was a significant factor ($F_{1, 342} = 4.838$, $P = 0.028$), the interaction term was also significant ($F_{6, 342} = 2.238$, $P = 0.039$); there was no conclusive effect of habitat type on maximum frequency. Additionally, habitat type did not affect signature whistle duration ($F_{1, 366} = 2.001$, $P = 0.157$) or whistle rate ($F_{1, 199} = 0.9262$, $P = 0.337$). Overall, signature whistle frequency range increased and minimum frequency was significantly lower as a result of differences between shallow and deeper habitat types.

Received Noise Levels of Watercraft in Sarasota Bay

Minimum RLs from a variety of boats at the time and distance of closest approach were calculated for conditions of planing ($n = 33$, range: 115–138 dB re 1 μPa), plowing ($n = 6$; range: 114–121 dB re 1 μPa), and idling ($n = 4$, range: 113–116 dB re 1 μPa). Planing boats were louder than plowing and idling boats at all distances (SNR: planing: +13 dB; plowing: +9 dB; idling: +4 dB, Fig. 2). Regardless of speed, boats were loudest at closer estimated distances to the focal animal. Additionally, a subset of planing, jet-drive personal watercraft (PWC, $n = 7$) was compared to planing conventional boats ($n = 5$) at approximately the same distances from the observation boat. A non-linear regression was performed which showed that SNRs are significantly different between planing PWCs and boats at

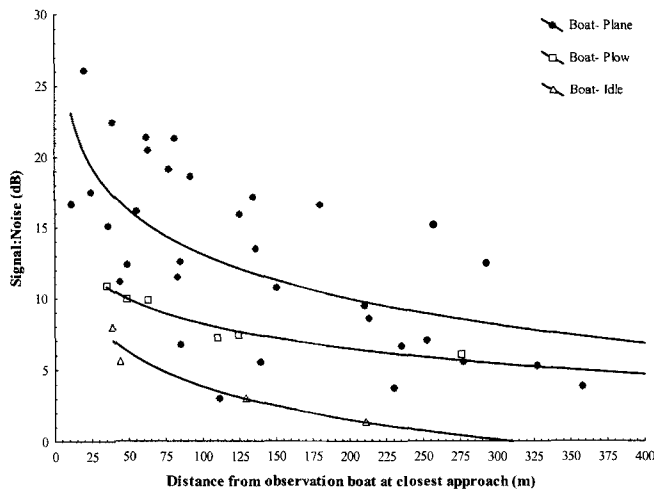


Figure 2. Signal-to-noise ratios of selected boat approaches at various distances and speeds. Boats were loudest at closer estimated distances to the focal animal. Planing boats were louder than plowing and idling boats. Best-fit trendlines are logarithmic, plane: $y = 19 - 0.04\ln(x)$; plow: $y = 11 - 0.02\ln(x)$; idle: $y = 8 - 0.03\ln(x)$.

similar distances ($\chi^2 = 8.48$, $df = 1$, $P = 0.003$). On average, planing boats were 18 dB louder than ambient conditions, whereas PWCs were only 9 dB above background levels, making the RL for a PWC about 9 dB quieter than a planing boat. Furthermore, all boats were heard over the observation vessel's engine noise unless the approaching boat was idling or >400 m away. Planing, plowing, and erratic (engaged in rapid heading changes) PWCs were heard only 51% of the time even though all approaches were <300 m away, providing additional evidence that jet-driven PWCs are quieter underwater than boats.

DISCUSSION

Bottlenose dolphins increased their rate of whistle production at the onset of a vessel approach, and then decreased production during and after it had passed, indicating that vessel approaches affect the acoustic behavior of dolphins. Increased whistle production may be a tactic to reduce signal degradation (Richardson *et al.* 1995) to insure that information is being communicated in a noisy environment, or, it may reflect heightened arousal in general, an increased motivation for animals to come closer together, with whistles functioning to promote reunions.

Turnbull and Terhune (1993) determined that for pinnipeds, call redundancy lowered the hearing threshold which implies that call repetition can increase the range of communication, thereby increasing the likelihood of information being received in a noisy situation. Whistles were produced within a frequency range of 3–23 kHz, and watercraft noise was recorded at 0.5–12 kHz. The average SNR for boat approaches ranged between 4 dB (idling) and 13 dB (planing) with some SNRs as much as 26 dB above the ambient noise level determined for this study. Therefore, because they share some frequency bands and generate above-ambient received levels, boat noise can play a role in signal masking, and this is most likely

to occur for close-approaching boats. Dolphins may increase their whistle rate as a boat approaches to increase the probability of detection of whistles before the boat noise more fully masks the whistles. Conversely, there were no changes in individual whistle duration or frequency range that could have potentially increased signal detectability during periods of watercraft activity. In terms of frequency range, results from this study indicated that dolphins responded to vessel presence in different directions. Because different vessel types have different frequency ranges of engine noise, and can overlap with the frequency range of dolphin whistles, dolphins may shift the frequency range of whistles in different directions depending on the frequency range of the vessel noise to avoid masking. Although this possibility was not examined fully in this study, it deserves further investigation.

Can an increase in call repetition be an expression of heightened arousal? A possible parallel to terrestrial mammals is from a study by Fischer *et al.* (1995) on Barbary macaques (*Macaca sylvanus*). Disturbance calls were defined as "given in sequences, the length of which seemed to be determined by the stimulus' presence . . . they might primarily express different levels of arousal." An increase in whistle production when a vessel is approaching may then be classified as a "disturbance call." Rendell and Gordon (1999) note a similar increase in whistle rate of pilot whales when they are exposed to sounds of a military sonar. When Barbary macaques were approached by an observer at night the mean call rate decreased after one minute of exposure (Fischer *et al.* 1995). There was a significant decrease in whistle rate from the "onset" to the "during" vessel approach conditions for dolphins. Similarly, reduced calling during other types of disturbance is a common response in other cetacean species as well. Sperm whales (*Physeter macrocephalus*) have ceased vocalizing in the presence of military sonar (Warkins *et al.* 1985). Long-finned pilot whales and sperm whales ceased calling during broadcasts of low-frequency sounds during the Heard Island Feasibility Test (Bowles *et al.* 1994). While data from the macaque study cannot be extrapolated directly to this study, it is interesting to note this trend in disturbance response.

S. M. Nowacek *et al.* (2001) noted that interanimal distance within a group decreased in the presence of watercraft so it is possible then that animals are sometimes within visual and even physical contact during a vessel approach. The close proximity between animals in a group may have been initiated by whistles, as a possible function of whistles is to facilitate or maintain group cohesion and vocal contact (*e.g.*, mother-calf separations/reunions, Smolker *et al.* 1993, Janik and Slater 1998). In turbid waters of the study area, visual contact is lost within a few meters, so close physical contact is the most effective means of maintaining group cohesion non-acoustically. This is another possible explanation for why there was a significant decrease in whistle rate from when the vessel was presumably first audible to when a vessel was passing by a group of dolphins.

Dolphins are frequently exposed to varying levels of watercraft noise and activity as many encounter a passing vessel every 6 min. PWCs can travel as fast or faster than motorboats and have access to extremely shallow water where most motorboats cannot venture (Burger and Leonard 2000). At approximately the same distances, planing PWCs are 9 dB quieter than planing boats. This poses an increased threat to dolphins, because not only can PWCs easily enter shallow habitats used for feeding and calf rearing, but also these data indicate that they are more difficult to detect than conventional powerboats. Habitat type played a role in structural changes to individuals' signature whistles. There was a significant increase in frequency range in deeper habitats than in shallower habitats. This can be explained

by frequency attenuation in shallow water environments in Sarasota Bay, where much of the signal is absorbed by the presence and density of sea grasses (D. P. Nowacek *et al.* 2001). Also, another possible factor can be that sound propagation is poor when the water depth is less than half of the wavelength of the transmitted whistle (Urick 1983). Consequently, the additive effects of boat noise and signal loss in a shallow environment can make communication less effective. Whistle repetition may have improved communication in these situations.

Noise generated by watercraft activity, unlike some other types of anthropogenic noise, is not a stationary or consistently present form of disturbance. On a diel scale, it may even be predictable to these animals. Watercraft can still pose a threat, however, as some boaters harass dolphins by chasing and feeding them, and 4% of the Sarasota dolphin community members have been struck by boats (Wells and Scott 1997). A main finding from my study proves that bottlenose dolphins in Sarasota Bay increased their whistle rate on approach, and it is also known that they swim in tighter groups during approaches, much like a social defense response to predation. Not only is there a threat of collision, but the behavioral mechanisms to respond to this threat, such as the energy and time required to produce the signal, also impose costs (Tyack 2000).

There are still questions that I was not able to answer during the course of this study: what is the threshold level at which watercraft become detectable to the dolphins, and at what level is a response elicited? Accurate measures of received noise level at the dolphin were not possible to obtain because I was unable to get an exact measure of the distance to the dolphin. Also, the observation vessel consistently approached dolphins and maneuvered at slow speeds during follows, however, the presence of the observation vessel itself is a likely source of disturbance that remains to be evaluated (S. M. Nowacek *et al.* 2001).

Advancements in technology are paving the way for future studies. Digital data archival tags (Johnson and Tyack 2003) can refine our understanding of when and how bottlenose dolphins respond to watercraft operating in their vicinity. These tags, attached by suction cups to the dorsal fin, can provide the ability to record sound levels at the dolphin along with compass heading, pitch, roll, and depth that allow direct comparisons of subtle short-term behavioral changes relative to received sound levels. Continued efforts, taken in new directions such as this, combined with information from past studies, can greatly enhance our understanding of certain factors or cues that trigger a response. Mitigation measures should not be based solely on short-term responses to human disturbance. However, the cumulative effects of repeated short-term responses, especially when vessel approaches occur every 6 min, must be considered by wildlife management agencies tasked with developing strategies to minimize the human impacts on marine mammals.

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