SIMULATED VESSEL APPROACHES ELICIT DIFFERENTIAL RESPONSES FROM MANATEES

JENNIFER L. MIKSIS-OLDS 1
PERCY L. DONAGHAY
Graduate School of Oceanography,
University of Rhode Island,
Narragansett, Rhode Island 02882, U.S.A.
E-mail: jmiksis@gso.uri.edu

JAMES H. MILLER
Department of Ocean Engineering
and
Graduate School of Oceanography,
University of Rhode Island,
Narragansett, Rhode Island 02882, U.S.A.

PETER L. TYACK
Woods Hole Oceanographic Institution,
Woods Hole, Massachusetts 02543, U.S.A.

JOHN E. REYNOLDS, III
Mote Marine Laboratory,
1600 Ken Thompson Parkway,
Sarasota, Florida 34236, U.S.A.

ABSTRACT

One of the most pressing concerns associated with conservation of the endangered Florida manatee is mortality and serious injury due to collisions with watercraft. Watercraft collisions are the leading identified cause of manatee mortality, averaging 25% and reaching 31% of deaths each year. The successful establishment and management of protected areas depend upon the acquisition of data assessing how manatees use different habitats, and identification of environmental characteristics influencing manatee behavior and habitat selection. Acoustic playback experiments were conducted to assess the behavioral responses of manatees to watercraft approaches. Playback stimuli made from prerecorded watercraft approaches were constructed to simulate a vessel approach to approximately 10 m in sea grass habitats. Stimulus categories were (1) silent control, (2) approach with outboard at idle speed, (3) vessel approach at planning speed, and (4) fast personal watercraft approach. Analyses of swim speed, changes in behavioral state, and respiration rate indicate

1 Present address of corresponding author: Jennifer L. Miksis-Olds, The Pennsylvania State University, Applied Research Laboratory, P. O. Box 30, State College, Pennsylvania 16804, U.S.A.
that the animals responded differentially to the playback categories. The most pronounced responses, relative to the controls, were elicited by personal watercraft. Quantitative documentation of response during playbacks provides data that may be used as the basis for future models to predict the impact of specific human activities on manatees and other marine mammal populations.

Key words: manatee, *Trichechus manatus latirostris*, disturbance, avoidance, playback experiment, watercraft approaches.

A pressing question regarding the conservation of Florida manatees (*Trichechus manatus latirostris*) is how to minimize both the lethal and nonlethal impacts on manatees in areas where watercraft operate. The lethal impacts of watercraft account for an average of 25% to more than 30% of identified manatee deaths each year (Ackerman *et al.* 1995, Reynolds 1999). The nonlethal impacts of boating on the physical health of manatees, as well as an indirect impact on food availability and communication, are controversial topics for which available data are inadequate. Identifying specific environments or behaviors that put manatees at a greater risk for boat collisions and quantifying manatee reactions to varying speeds and motor types of approaching vessels are necessary steps toward achieving the overall goal of minimizing the negative, lethal, and nonlethal impacts of boats and associated noise.

Manatees most commonly encounter relatively small boats: outboard or inboard/outboard leisure boats, personal watercraft (PWC), and fishing trawlers (Gorzelany 2004). PWC means a vessel <16 ft (4.9 m) in length that uses an inboard motor powering a water jet pump as its primary source of motive power and that is designed to be operated by a person sitting, standing, or kneeling on the vessel, rather than in the conventional manner of sitting or standing inside the vessel (2006 Florida Statutes, Title XXIV, Chapter 327, 327.02). The sounds produced by watercraft span a wide range of frequencies ranging from 10 Hz to 20,000 Hz, but the sound energy is typically concentrated below 2,000 Hz. The estimated 1/3-octave source levels at 1 m for small boats are 120–160 dB re 1 μPa at 1 m (Richardson *et al.* 1995, Gerstein 2002). Noise associated with PWC is unique compared to other commonly encountered outboard and inboard boats in that the impeller is not directly exposed to the water but housed inside the hull. This not only enables PWCs to travel into very shallow areas, but it also produces a different acoustic signature compared to outboard motors.

Despite the controversy concerning the frequency of peak hearing sensitivity, physiological, anatomical, and behavioral studies indicate that manatees appear to be able to detect approaching boats (Ketten *et al.* 1992; Nowacek *et al.* 2000, 2004a; Gerstein 2002). This is confirmed by field studies in which manatees responded to approaching boats (Reynolds 1981; Weigle *et al.* 1994; Nowacek *et al.* 2000, 2001a, 2004a). Nonetheless, some critical uncertainties remain in order for managers to understand and mitigate watercraft collisions. For example, under what conditions do manatees hear the noise produced from approaching boats in enough time to swim out of harm’s way? What frequencies are manatees capable of hearing, and how loud does the sound need to be at those frequencies?

Quantitative responses to boat approaches were documented by Nowacek *et al.* (2000, 2004a). Manatees detected boat presence from up to 1 km away and made gross changes in behavior at approximately 25–50 m from approaching watercraft.
Specifically, swimming speed increased and animals moved toward deeper channel waters in response to boat approaches. The distance from the manatees to the boat, water depth at the boat, and water depth at the manatees each had a significant effect on swimming speed, whereas the type of boat or boat speed did not have a significant effect.

Accurate detection of an approaching boat is only part of the problem for a manatee. In order to swim out of the direct path of the boat, the manatee must accurately localize the boat and respond appropriately. The physical characteristics of sound propagation in shallow water are complicated, and this can make it difficult to locate a sound source. From an acoustic standpoint, shallow water refers to areas where sound is propagated to distances at least several times the water depth, under conditions where both the surface and sediment boundaries have an effect on transmission (Urick 1983). Compared to deep-water environments, there is greater attenuation of sound in shallow water environments (Medwin and Clay 1998). Higher frequencies have shorter wavelengths and are therefore more directional than lower frequencies with respect to a sound source of a given size. High levels of sound reverberation in shallow water also make localization difficult for even those species that possess extremely accurate localization ability. For example, bottlenose dolphins (*Tursiops truncatus*), which have excellent acoustic localization capabilities, have been hit by boats in shallow water (Wells and Scott 1997, Buckstaff 2004). These observations suggest that successful localization of approaching boats is necessary, but not a sufficient component, for dolphins to safely avoid approaching watercraft. Localizing approaching boats may also be an important component for manatees to avoid collision.

Manatees that do manage to avoid collisions with watercraft still need to cope with other effects of boats. Boats that produce noise over the same frequencies as manatee vocalizations (Nowacek et al. 2003) can potentially mask communication signals. Motor noise can potentially mask communication signals. For example, if boat noise interferes with communication, females may lose contact with their calves or other members of a group, which could affect survival of the calves (Bengtson and Fitzgerald 1985). Manatees also are displaced from critical habitats with chronic boat disturbance (Provancha and Provancha 1988, Buckingham et al. 1999). Heavy vessel traffic may also cause manatees to expend more energy than they normally would (Reynolds 1999). For example, manatees significantly increase swim speed and move from shallow habitats to deeper channels during boat approaches (Nowacek et al. 2001a). Based on these findings, as well as observations of behavioral responses to opportunistic vessel approaches prior to the initiation of this study, three categories of response (slow swim, fast swim, and rolling dive) were defined prior to the initiation of the study. The magnitude and diversity of manatee responses to vessel traffic clearly indicate the need for playback experiments to demonstrate manatee responses to the acoustic component of vessel approaches.

**Materials and Methods**

**Stimulus Recordings**

All stimulus recordings were made using a single hydrophone suspended from a recording vessel anchored in a sea grass habitat adjacent to a boating channel. The recording hydrophone was a HTI-99-HF hydrophone with built-in preamplifier and had a 2 Hz–125 kHz frequency range and −178 dB re 1V/μPa sensitivity. The recording system was a National Instruments PCMcia DAQ Card-6062E used
Table 1. Characteristics of playback stimuli

<table>
<thead>
<tr>
<th>Category</th>
<th>Exemplar</th>
<th>Received level at 10 m (peak SPL)</th>
<th>Speed (mph)</th>
<th>Motor size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Idle</td>
<td>1</td>
<td>150 dB</td>
<td>5</td>
<td>115 hp</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>151 dB</td>
<td>5</td>
<td>100 hp</td>
</tr>
<tr>
<td>Planing</td>
<td>1</td>
<td>168 dB</td>
<td>35</td>
<td>115 hp</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>163 dB</td>
<td>35</td>
<td>100 hp</td>
</tr>
<tr>
<td>PWC</td>
<td>1</td>
<td>166 dB</td>
<td>40</td>
<td>1,235 cc</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>158 dB</td>
<td>25</td>
<td>1,235 cc</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>157 dB</td>
<td>25</td>
<td>1,235 cc</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>162 dB</td>
<td>40</td>
<td>1,235 cc</td>
</tr>
</tbody>
</table>

in conjunction with a Dell Inspiron 8100. The recording system had an overall frequency response of 20 Hz–22 kHz with a $-178$ dB re 1 V/$\mu$Pa sensitivity at 16-bit resolution. For each stimulus, the sound was recorded as a vessel approached the recording hydrophone at a constant speed from approximately 500–1,000 m away. The vessel approached to exactly 10 m away from the recording hydrophone and continued away at a constant speed for another 500–1,000 m. This method enabled calculation of received levels of the watercraft at 10-m distance (Table 1). The 10-m distance was the closest point of approach. Acoustic recordings of vessel approaches were made at two boat speeds: idle and full-throttle planing. Multiple exemplars from each category were recorded in order to ensure the generality of results and reduce pseudoreplication, defined as generalization from a study due to an animal responding to or learning from a single exemplar (Kroodsma 1989). Characteristics of each exemplar are summarized in Table 1. All vessels recorded possessed a 4-stroke motor, which provided an element of standardization across playback categories, regardless of engine size or vessel type. Two vessels were recorded for idle approaches. One vessel had a 115-hp outboard, and the other vessel had 100 hp. The same vessels were used to record two exemplars during a planing approach. Two separate 4-stroke PWCs were used to produce two planing approach recordings from each vessel for a total of four exemplars. Each PWC was recorded at two planing speeds: 25 mph (40 km/h) and 40 mph (64 km/h; Table 1).

The duration of all stimulus exemplars, regardless of stimulus category, was edited to 3 min to ensure the same length for each exemplar. This was done to control for the amount of time the playback subject was exposed to any sound coming from the playback system. Three-minute durations were chosen based on the longest audible approach sequence, which was the slow moving idle approach. For the idle approaches, 45 s of ambient noise preceded and followed the onset and offset of the stimulus signal, resulting in a total exemplar duration of 3 min. For planing and PWC approaches, ambient noise preceding and following the stimulus signal was appropriately included to produce a final stimulus duration of 3 min. The duration of ambient recording added prior to the stimulus onset was equal to that added after the signal offset. A silent control of 3 min was also constructed by creating a null vector (sound file containing 3 min of silence) at the same sample rate as the other stimuli. A silent control was selected to expose the subjects to any extraneous noise added by the transmit system that could potentially elicit a reaction. A control of only background noise was not included in the playback sessions because ambient noise preceded boat noise stimuli in all stimulus categories. If the animals were significantly
reacting to the background noise, there would have been a significant reaction to all category approaches. There was no significant response to the idle approach, which indicated that the animals were not reacting to either the boat noise or the background noise.

**Playback Categories**

The exemplars in the playback categories varied in several acoustic parameters. The stimulus categories differ not only in their acoustic envelopes, or overall amplitude shape, but also in their frequency characteristics (Fig. 1). The idle approaches had the longest stimulus duration but the lowest stimulus amplitude (Fig. 1a, b). The planing approaches had a more rapid rise time and higher amplitude than the idle approaches, but with a shorter acoustic envelope. The planing approaches also had a more gradual onset compared to the abrupt offset. The acoustic envelope of the PWC approaches was the shortest with the most rise time and approximately equal peak amplitude as the planing approaches.

The differences in frequency parameters were most evident in the spectrograms of Figure 1c. The idle approaches lacked a clearly defined broadband peak at the closest point of approach, and the U-shaped bands indicated the beta effect of sound during the approach and retreat (Tang 2005). The beta effect results in a decrease in signal frequency prior to the vessel’s closest point of approach and an increase in signal frequency during the retreat. From the perspective of the manatee, the beta effect could provide information about the position of the vessel. The planing and PWC approaches had a clear broadband peak at the closest point of approach.
This was preceded by a strong tonal, harmonic signal. In the PWC approaches, the tonal component of the approach was vastly reduced compared to that of the planing approaches, and the broadband peak of the PWC approach was also much narrower. Figure 2 further illustrates the difference in frequency spectra among the playback categories. Fifteen seconds prior to the closest point of approach, the PWC was approximately 10 dB quieter than both the idle and planing signals at 2–3 kHz (Fig. 2a). The magnitude of the idle and planing approaches was similar up to approximately 6 kHz. Above 6 kHz, the planing approach became about 10 dB louder than either the idle or PWC signals. Fifteen seconds prior to the closest point of approach, the planing approach transmitted the loudest signal in the higher frequencies. The planing approach was also clearly the loudest at the peak of approach by about 10 dB (Fig. 2b), with the exception of the PWC being the loudest between 2 and 3 kHz. The idle approach was the quietest at all frequencies during the peak of approach.

To better understand what the manatees detected during the vessel approaches, the power spectra of approaches were weighted by the only available manatee hearing thresholds as measured by Gerstein et al. (1999) (Fig. 3). Prior to the closest point of approach (Fig. 3a), planing signals were most salient above the background noise. The idle approach was above both the hearing threshold and noise floor for frequencies of approximately 2 kHz, whereas the PWC signature was either at or below detectable levels. At the closest point of approach (Fig. 3b), both the planing and PWC signals were well above threshold levels for all except the very lowest frequencies. The idle approach signal was loudest at approximately 2 kHz at the closest point of approach, but this level is 5 dB quieter than the planing and PWC levels over a band of 20 Hz to 20 kHz.

**Playback Experiments**

All playbacks were conducted in grass bed habitats that are commonly occupied by manatees. Restricting playbacks to one habitat type eliminated a confounding variable due to habitat type in the statistical analysis. In addition, playbacks were only performed with animals that were initially feeding or resting. The animals were relatively stationary during these two behaviors compared to traveling, milling, or social behaviors; therefore, changes in movement could be more easily observed and quantified. Restricting playbacks to two specific behavioral states also served to reduce the number of categories of analysis for statistical purposes, thus increasing the degrees of freedom within each category for each test.

The playback protocol was designed to simulate a boat approaching a manatee to 10 m. The same positional set-up was used for each playback regardless of which stimulus was used. The playback vessel was always positioned between the playback subject and the closest boating channel to simulate a boat approaching from deeper water and from the direction that a majority of boats would be traveling. Transmitted levels were adjusted for animal position so that the subject animal received appropriate received levels, as a function of stimulus type and exemplar (Table 1), regardless of the manatee's distance to the playback vessel, which was between 2 and 25 m from the manatee. Projection from a single, stationary transducer did not, however, allow for a directional motion component to the playback recording. If the manatees can localize the source accurately, the distance between the manatee and the playback vessel could have impacted the behavioral response. Due to the
Figure 2. Power spectra of vessel approach stimuli: (a) the comparison of 2-s clips measured 15 s before the closest point of approach; (b) the comparison of 2-s clips taken at the closest point of approach.
Figure 3. Spectra of vessel approaches weighted by the manatee hearing thresholds and smoothed in frequency plotted with ambient noise levels: (a) comparison of 2-s clips measured 15 s before the closest point of approach; (b) comparison of 2-s clips taken at the closest point of approach. For illustration purposes the manatee hearing sensitivity values for the frequencies measured in this paper are shown by the dashed-dotted line (data taken from Gerstein et al. 1999).
logistical constraints of the study design, this impact could not be addressed. Additional tests with stimuli simulating a rapid change in either direction or speed during the approach would provide valuable information that this study design was unable to offer.

During playback experiments, the focal animal (occurring as a single animal or in a pair) was observed for a minimum of 20 min before and after the exposure of the playback stimuli. Primary observers were blind to the stimulus presentation, as the transducer and observer were on opposite sides of the boat and the background noise in the boat masked the in-air component of the playback stimulus, which was audible at the amplifier. During this time the subject was either identified from previously catalogue animals or photographed for later identification. Playbacks were only conducted if no other animals were detected within visual range during the 20-min pre-exposure period. Pre- and poststimulus observation included 4-min interval sampling of focal animal course, heading, distance to boat, and behavioral state. Ventilation and vocalization rates were recorded continuously. Vocalization rates were not analyzed, however, because the transducer was on the same vessel as the recording hydrophone, and the playback saturated the hydrophone recording rendering the manatee vocalizations inaudible. Saturated vocalization recordings during the playback sessions did not allow for uninterrupted vocalization rate analysis. If the animals left the area during the pre-exposure period or during exposure to the playback stimuli, they were not followed.

Five minutes prior to the playback of any stimulus, the research vessel was anchored within 25 m of the focal animal and the sound source was deployed. An Aiwa model XP-V516C compact disc player connected to a Rockwood Detonator AMP-400 CRX amplifier delivered sound to a Lubell 9162 transducer, which projected the playback stimuli. This system was capable of producing a source level of approximately 190 dB re 1 μPa at 1 m in the frequency range of 240 Hz to 20 kHz. Response due to multiple boat interactions was avoided by only performing a playback when no other vessel had entered a 1-km radius for a 15-min period prior to the start of playback session. Each playback session consisted of four playback stimulus presentations presented 5 min apart. The 5-min stimulus presentation was chosen based on the knowledge that bottlenose dolphins in Sarasota Bay encounter a passing vessel every 6 min (Buckstaff 2004). Manatees would experience a similar or shorter interval between boat encounters depending upon the number of recreational vessels in the area at any particular time. One stimulus from each of the four categories (control, idle, plane, PWC) was presented in random order. If the focal animal moved outside of a 25-m radius before the presentation of the last stimulus, the research vessel re-anchored closer to the animal, and the remaining playback stimuli were presented followed by a 20-min poststimulus observation period. In an effort to reduce pseudoreplication, no manatee was a playback subject more than twice, and no animal ever received the same exemplar more than once (Table 2).

During the playback session, observations included point sampling of focal animal course, heading, distance to boat, ventilation, and behavior at the time of each surfacing. Visually observed responses to the playback stimuli generally fell into four categories: (1) investigate boat, (2) slow swim, (3) rolling dive, and (4) fast swim. Animals investigating the boat swam directly to the boat and interacted with it in some way. Slow swims were characterized by the animals changing position relative to the playback vessel without any visible wake or fluke prints. Rolling dives were identified by the arching of the manatee’s back and entire fluke leaving the water prior to a dive. Fast swims were characterized by a visible wake and strong fluke prints, often
Table 2. Summary of playback subjects, stimulus sequence, and response. In the "age" and "group composition" categories, A indicates adult, SA indicates subadult, C indicates calf.

<table>
<thead>
<tr>
<th>Session</th>
<th>Date</th>
<th>ID</th>
<th>Age</th>
<th>Number in Group</th>
<th>Group composition</th>
<th>Stimulus 1 Response</th>
<th>Stimulus 2 Response</th>
<th>Stimulus 3 Response</th>
<th>Stimulus 4 Response</th>
<th>Response</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>4 June 2004</td>
<td>Snuff</td>
<td>A</td>
<td>2</td>
<td>A, A</td>
<td>C</td>
<td>Idle2</td>
<td>PWC4</td>
<td>—</td>
<td>FS, LA</td>
</tr>
<tr>
<td>2</td>
<td>10 June 2004</td>
<td>Phish LA</td>
<td>A</td>
<td>1</td>
<td>Plane2</td>
<td>SS</td>
<td>C</td>
<td>Idle2</td>
<td>PWC2</td>
<td>SS</td>
</tr>
<tr>
<td>3</td>
<td>15 June 2004</td>
<td>Phish</td>
<td>A</td>
<td>1</td>
<td>PWC2</td>
<td>SS</td>
<td>Idle2</td>
<td>C</td>
<td>None</td>
<td>None</td>
</tr>
<tr>
<td>4</td>
<td>21 June 2004</td>
<td>DU723</td>
<td>A</td>
<td>2</td>
<td>Plane1</td>
<td>SS</td>
<td>Idle2</td>
<td>C</td>
<td>None</td>
<td>None</td>
</tr>
<tr>
<td>5</td>
<td>23 June 2004</td>
<td>623BB</td>
<td>A</td>
<td>2</td>
<td>C</td>
<td>SS</td>
<td>Idle1</td>
<td>Plane1</td>
<td>PWC3</td>
<td>None</td>
</tr>
<tr>
<td>6</td>
<td>25 June 2004</td>
<td>625A</td>
<td>A</td>
<td>2</td>
<td>PWC4</td>
<td>SS</td>
<td>Idle2</td>
<td>Plane2</td>
<td>C</td>
<td>None</td>
</tr>
<tr>
<td>7</td>
<td>28 June 2004</td>
<td>628A</td>
<td>A</td>
<td>2</td>
<td>PWC1</td>
<td>SS</td>
<td>Idle1</td>
<td>Plane1</td>
<td>Idle1</td>
<td>None</td>
</tr>
<tr>
<td>8</td>
<td>1 July 2004</td>
<td>DU723</td>
<td>A</td>
<td>2</td>
<td>C</td>
<td>SS</td>
<td>Idle1</td>
<td>PWC2</td>
<td>Plane1</td>
<td>None</td>
</tr>
<tr>
<td>9</td>
<td>6 July 2004</td>
<td>706AA</td>
<td>SA</td>
<td>1</td>
<td>PWC4</td>
<td>Idle1</td>
<td>C</td>
<td>Plane1</td>
<td>None</td>
<td>None</td>
</tr>
<tr>
<td>10</td>
<td>21 July 2004</td>
<td>721A</td>
<td>A</td>
<td>2</td>
<td>Idle1</td>
<td>None</td>
<td>None</td>
<td>None</td>
<td>None</td>
<td>FS, LA</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>---</td>
<td>---------------</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>11</td>
<td>22 July 2004</td>
<td>Clyde</td>
<td>A</td>
<td>2</td>
<td>A, A</td>
<td>C</td>
<td>PWC4</td>
<td>Plane2</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>None</td>
<td>SS</td>
<td>None</td>
<td>None</td>
<td>None</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>12</td>
<td>23 July 2004</td>
<td>723B</td>
<td>A</td>
<td>2</td>
<td>A, C</td>
<td>Plane2</td>
<td>C</td>
<td>PWC3</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>RD</td>
<td>None</td>
<td>RD</td>
<td>None</td>
<td>RD</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>13</td>
<td>23 July 2004</td>
<td>723A</td>
<td>A</td>
<td>2</td>
<td>A, C</td>
<td>PWC2</td>
<td>C</td>
<td>Plane2</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>RD</td>
<td>None</td>
<td>SS</td>
<td>LA</td>
<td>—</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>14</td>
<td>26 July 2004</td>
<td>726D</td>
<td>A</td>
<td>2</td>
<td>A, C</td>
<td>Plane1</td>
<td>Idle2</td>
<td>PWC1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>FS</td>
<td>SS</td>
<td>FS</td>
<td>None</td>
<td>None</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>15</td>
<td>26 July 2004</td>
<td>Phish</td>
<td>LA</td>
<td>A</td>
<td>2</td>
<td>A, A</td>
<td>C</td>
<td>Idle1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>None</td>
<td>None</td>
<td>FS</td>
<td>SS</td>
<td>None</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>16</td>
<td>27 July 2004</td>
<td>Splotch</td>
<td>A</td>
<td>2</td>
<td>A, A</td>
<td>PWC2</td>
<td>Idle1</td>
<td>C</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>FS</td>
<td>None</td>
<td>None</td>
<td>None</td>
<td>None</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>17</td>
<td>28 July 2004</td>
<td>727AA</td>
<td>SA</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>18</td>
<td>3 August 2004</td>
<td>803BB</td>
<td>A</td>
<td>2</td>
<td>A, SA</td>
<td>Plane2</td>
<td>C</td>
<td>Idle1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>RD</td>
<td>None</td>
<td>RD</td>
<td>None</td>
<td>SS</td>
<td>LA</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>19</td>
<td>4 August 2004</td>
<td>804C</td>
<td>SA</td>
<td>2</td>
<td>SA, SA</td>
<td>C</td>
<td>PWC4</td>
<td>Idle2</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>None</td>
<td>FS</td>
<td>None</td>
<td>None</td>
<td>None</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>20</td>
<td>5 August 2004</td>
<td>805BB</td>
<td>A</td>
<td>2</td>
<td>A, A</td>
<td>Idle1</td>
<td>Plane1</td>
<td>PWC1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>None</td>
<td>FS</td>
<td>FS</td>
<td>SS</td>
<td>SS</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>21</td>
<td>19 August 2004</td>
<td>823F</td>
<td>SA</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>None</td>
<td>SS</td>
<td>None</td>
<td>SS</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 2. Continued.
accompanied by a mud cloud stirred up from the bottom. Two retreating behaviors were also observed in relation to the playback vessel: (1) retreat to deep water and (2) pass by boat on the way to deep water. Direct retreats were characterized by the animal increasing distance from the playback vessel in the direction of deeper water. Passing by the boat on the way to deep water was a separate classification because the animal had to initially approach the playback vessel before retreating to deeper water. Passing by the boat on the way to deep water differed from the “investigate boat” response because the passing by the boat did not include any direct contact or interaction with the playback vessel by the manatee.

In addition to behavioral responses, a respiratory response to the playback stimuli was also calculated. An index of ventilation variability (index of variability) was calculated from the time series of visually observed surface breaths recorded continuously throughout the playback experiments. The poststimulus index of variability was calculated by adding the absolute values of the difference in time between breaths for the three consecutive breaths following the stimulus onset (poststimulus index of variability \( = |t_0 - t_1| + |t_1 - t_2| + |t_2 - t_3| \)). Higher values of poststimulus variability indicated a larger variability in ventilation. Traditional measures of ventilation rate and its associated variance were not utilized in this analysis because long submersions followed by quick successive breaths cancelled each other and masked the true breathing pattern. Inclusion of absolute values preserved the level of variability between breaths. Prestimulus index of variability was calculated in a similar manner. The index was calculated from a time series of triads consisting of three consecutive breaths preceding the first stimulus. The triad values were then averaged to produce a prestimulus index of variability (prestimulus index of variability \( = \left\{ \Sigma(|p_0 - p_1| + |p_1 - p_2| + |p_2 - p_3|)/n \right\} \)). Multiple, consecutive triads were used in the prestimulus index in order to establish the most accurate baseline index of variability. The poststimulus index only contained a single triad because this was the minimum number of surfacings observed between stimulus presentations during the playback session.

**Statistical Analysis**

The first level of analysis compared the frequency of animals either responding or not responding to each playback category and the control condition. Statistical significance was based on the binomial distribution. Differences in the frequency of behavioral responses between categories were investigated with a \( R \times C G \)-test for independence. Based on behavioral observations to opportunistic vessel approaches, the three categories of response (slow swim, fast swim, and rolling dive) were defined prior to the initiation of the playback study. \textbf{A priori} conditions were met, which justified the use of the \( R \times C G \)-test for independence used to assess the frequency of behavioral responses to the playback stimuli. Differences in the deviation between prestimulus and poststimulus index of variability across playback categories were tested with a single-factor analysis of variance (ANOVA).

**RESULTS**

Twenty-one playback sessions were conducted with 19 different subjects encountered either as single animals or in pairs (Table 2). A total of eighty stimuli were played: 21 Control, 10 Idle1, 10 Idle2, 11 Planing1, 8 Planing2, 6 PWC1, 5 PWC2, 5 PWC3, and 6 PWC4. Seventeen out of 21 animals (81%) showed no locomotor
response to the silent control (Table 2 and Figure 4). The difference between response or no response for all stimuli vs. the silent control was significant at the 95\% significance level based on a binomial distribution ($P < 0.001$). This indicated that the manatees were not significantly reacting to the exposure of the broadcasting system provided by the control stimulus. Manatees showed a marked locomotor response to the playback stimuli compared to the silent control. Thirteen of twenty animals (65\%) showed no response to the idle approach, whereas 35\% showed some type of locomotor response (i.e., slow swim, approach boat, fast swim, etc.) (Figure 4). This 35\% response rate was not significant at the 95\% significance level. During the planing approaches there was a significant locomotor response rate of 63\% ($P = 0.002$). Of the twelve animals that showed a locomotor response to the planing approach, two abandoned the area. All animals showed a locomotor response to the PWC approach ($P < 0.001$). Four of the twenty animals that responded (20\%) left the area.

An analysis of response orientation and heading of those animals that did show a locomotor response to the playback stimuli revealed a striking pattern (Fig. 4). Of the four animals that did respond to the control, all four investigated the boat. Seven animals of twenty responded to the idle approach. Of the seven, four (57\%) retreated directly to deep water, two (29\%) passed by the playback vessel on the way to deeper water, and one animal (14\%) retreated from the playback vessel to shallow water. During the planing and PWC approaches, the number of animals retreating directly to deep water increased, whereas the number of animals passing by the boat decreased. In general, manatees tended to respond to all approaches by retreating to deep water. The frequency of animals retreating directly to deep water increased in response to an increase in speed of the approaching vessel.

Behavioral analysis of the retreating animals showed a graded response in behavior associated with playback category (Fig. 5). No animals retreated during the controls, so this category was not included in the analysis. The frequency of animals retreating with a slow swim decreased from 71\% in response to the idle approach to 37\% for the
Figure 5. Behavioral response of retreating manatees to the playback categories. There is no response for the controls because no animals retreated during control presentations. * shows the significant decrease in the slow swim response associated with playback category (0.01 < P < 0.025). ** shows the significance increase in fast swim responses associated with playback category (0.01 < P < 0.025).

planing approach to finally 16% in response to the PWC approach (Fig. 5a). Analysis of frequency using a R × C G-test for independence revealed that the frequency of the slow swim response was dependent on playback category (0.01 < P < 0.025; Sokal and Rohlf 1995). Similarly, the increase seen in the frequency of fast swim response was dependent upon playback category (0.01 < P < 0.025). No animals responded to the idle approach with a fast swim, whereas 37% and 68% responded to the planing and PWC approaches, respectively (Fig. 5b). There was slight decrease in the frequency of rolling dive responses to the PWC approaches, but this decrease was not a significant pattern.

An ANOVA of the poststimulus index of variability showed a significant overall effect of stimulus type ($F_{3,82} = 2.72, P = 0.04$; Fig. 6). Post hoc multiple comparisons indicated an increase in variability between the prestimulus and both planing

Figure 6. Mean deviation from prestimulus/control variability for each playback category. The asterisk (*) indicates categories that differed significantly from the prestimulus/control values. Error bars represent standard error.
DISCUSSION

The most pronounced responses to the playback stimuli, relative to the controls, were elicited by the PWC. Significant behavioral and physiological responses were also seen in response to planing boat approaches, indicating that rapid vessel approaches do affect manatee behavior. Approaches by fast-moving vessels resulted in the disruption of feeding activity, an increase in energy expenditure inferred from swim speed, and in some cases a short-term avoidance of the feeding area. Avoidance reactions to approaching vessels are not unique to manatees, as disturbance responses to motorized vehicles have been documented in both marine and terrestrial species. In the marine environment, avoidance to motorized watercraft had been reported in manatees, cetaceans, and pinnipeds (manatees: Provancha and Provancha [1988], Buckingham et al. [1999], Nowacek et al. [2004a]; cetaceans: bottlenose dolphins, Janik and Thompson [1996], Nowacek et al. [2001b], Hastie et al. [2003], Buckstaff [2004]; killer whales, Orcinus orca, Kruse [1991], Williams et al. [2002a, b]; Hector’s dolphins, Cephalorhynchus hectori, Bejder et al. [1999]; beluga whales, Delphinapterus leucas, Finley et al. [1990]; pinnipeds: walruses, Odobenus rosmarus, Fay et al. [1984]; and harbor seals, Phoca vitulina, Reijnders [1981]). Documented disturbance reactions include increases in vocalization rate, increases in swim speed, longer dive durations, decreased interanimal distance, increased breathing synchrony, and displacement from haul-out sites. Terrestrial animals (bighorn sheep, Ovis canadensis canadensis, MacArthur et al. [1979]; white-tailed deer, Odocoileus virginianus, Richens and Lavigne [1978]; caribou, Rangifer tarandus, Murphy et al. [1993]; and penguins, Pygoscelis adelia, Culik et al. [1990]) were also found to avoid road vehicles, snowmobiles, and aircraft.

The manatees studied here showed the ability to discriminate and differentially react to the two different engine types and speeds simulated in the playback experiments. Nowacek et al. (2001a, 2004a) reported a generalized response by manatees to approaching boats involving turning toward or into deep water without specific regard to boat type, boat speed, distance from the manatee, the kind of habitat the boat was operating in, or the kind of habitat occupied by the manatee. Increases in swim speed were most prevalent in shallow water grassbeds when boats approached to between 0 and 9 m (Nowacek et al. 2004a). This study also showed that manatees reacted to simulated vessel approaches to within 10 m with an increase in swim speed and directed movement toward the closest deep water. The findings here differed from the previous study, however, because boat type and boat speed in this study appear to have a significant effect on swimming speed. This effect may not have been detected by Nowacek et al. (2004a) due to differences in study design and categorization of visible responses. This study differentiated between responses based on two different changes in swim speeds and the presence of rolling dives, which indicate deeper dives. Results presented here show that the manatees responded to slower idle approaches with a greater number of slow swim responses and a larger number of retreat paths that intersected with the playback vessel. In contrast, responses to fast approaching outboard motorboats or PWCs elicited a significantly greater frequency of response for fast swim speeds and retreat paths that avoided
the playback vessel. Because playback experiments only introduce the frequency and amplitude components of vessel signals (other potential components include visual information above and below water, and changes in the bearing of the acoustic signal), the frequency and amplitude information available to the animal prior to the closest point of approach can be used to explain how the animals may be discriminating and ultimately reacting to the different playback categories.

Fifteen seconds prior to the closest point of approach, the planing approaches were approximately 10 dB louder than the idle and PWC approaches for frequencies from 6 to 22 kHz. Similarly, the idle approach was approximately 12 dB louder than both the planing and PWC approaches at 2 kHz. Therefore, the slower rise times of the idle and planing approaches provide more information to the animals 15 s prior to arrival compared to the PWC approach. It is possible the manatees can extract the necessary information from these acoustic cues relating to speed, direction, and boat type in order to execute the most appropriate and energetically favorable response.

The most desirable responses are those that enable manatees to avoid collisions with watercraft. The playbacks provided an opportunity to observe responses to specific acoustic components of vessels approaching at a constant speed under controlled circumstances. Responses indicated that manatees are able to detect approaching vessels and execute appropriate responses to avoid vessel collisions by retreating to deep water where they can swim beneath the boat. Furthermore, manatees are able to discriminate between vessel types and speeds, which appeared to influence the degree and direction of response. Manatees tended not to respond to idle approaches. When animals did respond, most did so at a slow speed. By contrast, responses to PWC and planning approaches elicited a greater proportion of fast swims. Slower responses to slowly approaching vessels and quicker responses to faster-moving vessels would be appropriate in real-life situations, provided the vessels did not change speed. Manatee response is in marked contrast to that of right whales, which tend not to respond to approaching ships even though they do respond to alert signals (Nowacek et al. 2004b). Right whales responded to an alert signal during controlled exposures by swimming strongly to the surface, which is a response that is likely to increase rather than decrease the risk of collision.

The most energetically favorable response for a manatee to any vessel approach would be to minimize locomotor costs by not moving at all. However, this would not always be the most appropriate response in terms of avoiding vessel collisions. If a change in location is necessary, a response at swim speeds at or near the minimum cost of transport would be most efficient. It is often found that birds and mammals swim underwater at or near the speed of minimum cost of transportation (Williams et al. 1993, Ropert-Coudert et al. 2001, Lavvorn et al. 2004). Manatees generally cruise at speeds of 2–6 mph (3–10 km/h), although they have been recorded at speeds of 15 mph (24 km/h) for short bursts (Hartman 1979). Speeds of 2–6 mph would have been classified into the slow swim response in this study, so it appears that manatees responding to idle and many planing approaches acquire enough prior information to execute an energetically efficient response. The PWC acoustic signatures 15 s prior to arrival do not provide as much acoustic information compared to the idle and planing approaches.

The short rise time signal associated with PWC approaches does not differ greatly from ambient noise levels until 5 s before the peak, so it is possible that the manatees do not perceive these approaches in enough time to execute an energetically favorable response. Consequently, faster, less efficient responses are necessary to
retreat from a possible PWC collision. An alternative explanation is that the sharp rise time associated with the PWC approach elicits a startle response that causes manatees to retreat from the sound source without evoking a higher level of cognitive analysis. Avoidance responses to the short rise time signals have also been observed in sharks. Myrberg et al. (1978) reported that a silky shark (*Carcharhinus falciformis*) withdrew 10 m from a speaker broadcasting a 150–600-Hz sound with a sudden onset and a peak sound pressure level of 154 dB re 1 \(\mu\)Pa. These sharks also avoided a pulsed attractive sound when its sound level was abruptly increased by >20 dB. Finally, through prior encounters with PWCs, manatees may have learned to associate the PWC acoustic signal with vessels that are less predictable and more likely to approach them in shallow areas, thus requiring a more extreme response.

Regardless of the specific acoustic characteristic of the fast vessel approaches that elicit fast swim responses, these signals cause manatees to increase their swim speed. Swim speed, as well as breathing rates and heart rate, have been used to estimate the energies of free-ranging marine mammals (Sumich 1983, Kshatriya and Blake 1988, Williams et al. 1992, Hind and Gurney 1997). Assuming that manatees respond at maximum speeds and that the maximum aerobic energy used during locomotion can reach 4–11 times resting levels in marine mammals (Elsner 1986, Williams et al. 1993), consistent responses to vessel approaches potentially affect the energy budget of manatees in a significant way. Responses detected in this study are consistent with an energy cost, and future work quantifying energy expenditures will determine whether multiple reactions could have a long-term effect at the individual or population level.

Most playback experiments measure movement, visual, or vocal responses to the sound played. Behaviors most typically measured are orientation or movement relative to the sound source, vocalizations made in response to the playback, and previously defined behaviors or displays such as aggressive or sexual displays. Less frequently used, but possibly more objective, responses are changes in heart rate (birds: Davis [1986], Diehl [1992]; humans: Brown et al. [1976]; chimpanzees, *Pan troglodytes*: Berntson and Boysen [1989]; bottlenose dolphins: Miksis et al. [2001]) and hormone levels (Dufty 1982). Neither quantitative swim speed nor fluke rate or amplitude was measurable in this study. More accurate measurements of both swimming characteristics and physiological responses during playback responses are necessary in order to determine the degree to which repeated exposure to vessel approaches are affecting the manatee energy budget or stress levels. Technological advances in tag construction and measurement sensors may soon allow for the recording of these critical parameters (Johnson and Tyack 2003).

In summary, the playback technique presented here permits the investigation of numerous questions associated with manatee disturbance, threshold level, etc. without the risk of injury associated with the unpredictable behavior of wild animals during directed vessel approaches. This methodology has identified that vessel approaches, especially by PWCs and fast approaching watercraft, are a cause of manatee disturbance. This may be of regulatory concern, as harassment is prohibited in the United States by the Marine Mammal Protection Act. Manatees were also shown to hear and respond to boats approaching at idle speeds. Much more information is needed to determine how to minimize this disturbance in order to meet the criteria for species downlisting as outlined in the Florida Manatee Recovery Plan (U.S. Fish and Wildlife Service 2003). For example, the measured responses in this study were
only made during feeding and resting behaviors in grass bed habitats. Behavioral state and habitat type may have significant impacts on the motivation to react, and responses in other behavioral contexts (e.g., actively socializing) and habitats should be investigated.

ACKNOWLEDGMENTS

The success of this project would not have been possible without the help of numerous people. The interns and staff in the Manatee Research Program at Mote Marine Laboratory were critical to the field efforts. Special thanks are extended to Doug Nowacek for his input on initial project design. Thanks are also extended to Gretchen Hurst, Joe Gaspard, and Marie Chapla for their help with stimulus recordings. All playbacks were conducted under the guidelines of U.S. Fish and Wildlife permit MA071799-0 issued to Jennifer Miksis and comply with all current laws of the country. This project was funded by a National Defense for Science and Engineering Graduate (NDSEG) Fellowship, P.E.O. Scholar Award, and American Association for University Women (AAUW) Dissertation Writing Fellowship awarded to Jennifer Miksis.

LITERATURE CITED


Hartman, D. S. 1979. Ecology and behavior of the manatee (Trichechus manatus) in Florida. Special Publication 5, American Society of Mammalogists, Lawrence, KS.


Received: 9 May 2006
Accepted: 5 February 2007