MARINE MAMMAL SCIENCE, 28(4): E444–E455 (October 2012)  
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DOI: 10.1111/j.1748-7692.2011.00560.x

Passive acoustic density estimation of sperm whales in the Tongue of the Ocean, Bahamas

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ABSTRACT

Long-term passive acoustic monitoring of marine mammals on navy ranges provides the opportunity to better understand the potential impact of sonar on populations. The navy range in Tongue of the Ocean (TOTO), Bahamas contains extensive hydrophone arrays, potentially allowing estimation of the density of deep diving, vocally active species such as the sperm whale (*Physeter macrocephalus*). Previous visual surveys in TOTO have been of limited spatio–temporal coverage and resulted in only sporadic sightings of sperm whales, whereas passive acoustic observations suggest the species is present year round. However, until now the means of acoustically determining the specific number of individuals in each cluster has been limited. We used recently developed algorithms to identify the number of echolocating whales present during a 42 d study period. We screened a 297 h acoustic data set to determine the proportion of time animals were present; fifty 10 min samples during presence were analyzed to estimate the number of individuals vocalizing during each sample. These counts were combined with an independent estimate of the proportion of 10 min periods when tagged animals vocalize. The estimated average density was 0.16 whales/1,000 km² (CV 27%; 95% CI 0.095–0.264). The method is potentially applicable to other areas containing dense hydrophone arrays.

Key words: animal density, population size, sperm whale, *Physeter macrocephalus*, passive acoustic array.

Our knowledge of the distribution and density of most marine mammals comes mostly from visual observations. Dedicated visual surveys are expensive, labor-intensive, weather dependent, and usually limited to daylight hours—all of which

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limits spatial and temporal coverage. Aerial surveys present a significant safety risk. In addition, several marine mammal species are not always available for visual detection because of their diving behavior. Sperm whales (*Physeter macrocephalus*), for example, dive to great depths using repetitive, distinct vocalizations for echolocation and communication, but spend little time at the surface, reducing the likelihood of visual sighting. Passive acoustic methods using fixed sensors have been used extensively to monitor seasonal presence and relative abundance of marine mammals (Mellinger et al. 2007), but only recently have they been used to estimate absolute density and population size (e.g., Marques et al. 2009, Moretti et al. 2010). Here, we develop and demonstrate a method for long-term population monitoring of sperm whales in an area where a fixed array of hydrophones is available such that animals vocalizing within the array boundary can be detected with certainty and those outside it can be excluded.

Our study area is the Tongue of the Ocean (TOTO), Bahamas, a deep water trough that contains the U.S. Navy’s Atlantic Undersea Test and Evaluation Center (AUTEC) testing range. The range is used regularly for navy exercises; hence, given the general concern about the effect of anthropogenic noise including navy sonar on marine mammals (NOAA 2001) there is a need for effective long-term monitoring of species’ population density in this area. Methods based on passive acoustics have already been developed for beaked whales (Marques et al. 2009, Moretti et al. 2010), but relied heavily on data from digital acoustic recording tags to help estimate probability of detecting vocalizations and vocalization rate or dive rate. Here we make use of the fact that sperm whale clicks are louder than those of beaked whales to reduce our dependence on tag data, although we still require such data to estimate the proportion of time spent vocalizing.

Sperm whale groups sighted by the authors in the TOTO typically consist of adult females and/or subadults of unknown sex. The Northeast and Northwest Providence Channels, at the northern entrance to the TOTO, provide year-round habitat for sperm whales. The overall mean cluster size for sperm whales in the Bahamas is 5.37 (SE = 0.28, range = 1–19, median = 5, mode = 1, n = 204), whereas in the TOTO the mean cluster size is 3.38 (SE = 0.40, range = 1–6, median = 3, mode = 3, n = 20; D. Claridge and C. Dunn, unpublished data). Females and subadults often travel and forage together in diffuse groups within which smaller clusters of 1–3 individuals may be sighted at the surface, diving synchronously, and remaining within 100 m of each other (Christal and Whitehead 2001). Across multiple populations, sperm whales on average spend 72% of their time in foraging dive cycles, producing regular clicks for approximately 81% of a dive (Watwood et al. 2006). Clicking begins within minutes after a dive starts and the typical interclick interval (ICI) is 0.5–2 s for the duration of the dive until beginning to ascend (Zimmer et al. 2003). Sperm whales produce broadband, directional clicks with measured source levels greater than 220 dB re. 1 uPa @ 1 m, and source level differences of 35 dB for the same click received in different directions (Møhl et al. 2000, Zimmer et al. 2005).

Sperm whales have been detected acoustically using bottom mounted hydrophones in the TOTO since the inception of the Marine Mammal Monitoring on Navy Ranges signal processing system in 2001 (Ward 2002). Their distinct foraging clicks are easily detected and classified to species level; however, association of clicks to an individual whale is more problematic. Click structure is correlated to animal size, click-to-click variation in source level, and off-axis angle from the main axis of the whale’s melon (Møhl et al. 2000, Zimmer et al. 2005). The association problem is further complicated by the reception of surface and bottom
reflected clicks in addition to the direct path received click on each hydrophone (Baggenstoss 2011a).

Our objective is to estimate the average sperm whale density at AUTEC during a period of 42 d (15 August to 27 September 2007). The method involves detecting clusters of vocalizing sperm whales within the array and associating clicks to individuals, providing the number of vocal members in the diving cluster. Initial visual screening of spectrograms from a 297 h acoustic data set identified periods when sperm whales were thought to be present. Specialized algorithms that detect, classify, and associate sperm whale clicks to an individual are applied to a subset of 50 randomly selected 10 min samples to determine the number of vocalizing whales within the acoustically monitored area for each sample. These results are combined with sperm whale dive and vocalization information known from digital acoustic recording tags (DTag) to estimate the density of whales present within the AUTEC range during the recording period.

**Material and Methods**

**Study Location**

This study presents data collected by the U.S. Navy at AUTEC in the TOTO, Bahamas during the 2007 Behavioral Response Study (BRS) from 15 August to 26 September 2007 (Boyd et al. 2007). The TOTO is a deepwater trough with depths up to 1,600 m and only one deepwater entrance, to the north. Passive acoustic data were recorded on a grid of 82 deepwater bottom mounted hydrophones arranged with an average 3.8 km spacing (Fig. 1). Given the steady production of clicks at source levels in excess of 220 dB during foraging dives, all vocalizing sperm whales within a 3.8 km radius of a hydrophone are assumed to be detected, resulting in a monitoring area (A) of 1,340 km².

**Passive Acoustic Monitoring**

Multiple recordings from all 82 hydrophones were taken throughout the study period, with each recording varying from 1 h to 22 h in duration. All data were processed through the Marine Mammal Monitoring (M3R) software, a real-time tool set for detection, localization, and monitoring of whales in the open ocean (Morrissey et al. 2006). Throughout the study period, M3R operators, as well as visual observers aboard surface vessels, logged periods of apparent sperm whale presence. Recordings were also manually reviewed posttest using M3R’s spectrogram analysis tool, and those containing possible sperm whale clicks were noted. Recordings corresponding to periods where no sperm whales were noted by any of the above means were not processed further, and it was assumed that no sperm whales were present on the range during these periods. Conversely, recordings containing possible sperm whale clicks were processed further.

A systematic sample, with random start point, of fifty 10 min periods was selected from the recordings where sperm whales were potentially present. This sample was processed through a separate algorithm (Baggenstoss 2008) that detected, classified, and extracted each sperm whale click received. The spectrogram of each 10 min period was visually evaluated to identify hydrophones with sperm whale clicks present. Each sample period with sperm whales present was analyzed using algorithms developed
Figure 1. Atlantic Undersea Test and Evaluation Center (AUTEC) hydrophones with area of certain detection (A) indicated in gray. Numbers indicate how many simultaneous sperm whale click trains observed per sample at each location. Circles outlining hydrophones indicate sperm whales detected outside the certain detection area. Depth contours at 200 m intervals.

by Baggenstoss (2011a) to associate each click with a “click train” from an individual and then classify the click train as direct path, surface reflection or reverberation. The number of temporally overlapping, direct path trains was used to estimate the number of whales clicking. If more than one cluster of sperm whales was clicking within the monitoring area, the process was repeated for each cluster to determine the total number of whales present. The click trains were then localized (Baggenstoss 2011b) to determine if the vocalizing cluster was within the study area. In many instances, the cluster was localized, rather than individual whales, and the number of whales in the cluster was derived from the number of simultaneous click trains present within the sample period. Occasionally, there would only be a few click trains on hydrophones along the outer perimeter of the study area, but not enough to localize a position. This is the result of whales outside the study area and these click trains were not used. The location and number of whales vocalizing in each 10 min sample were recorded.

Proportion of Time Clicking

To convert the number of whales vocalizing into a total number of whales present requires an estimate of the proportion of time spent vocalizing. This cannot be
obtained from the AUTEC hydrophones, as we only know a whale is present when it is clicking. Instead, we obtained it from DTag data, gathered on 25 whales in the Gulf of Mexico in 2001–2003 and on 6 from the east coast of the United States in 2003. The timing of each click emitted by the tagged animal was recorded. The deployment times were divided into 10 min intervals (10 min being the length of the sample periods used when processing AUTEC hydrophone recordings), and for each whale, the proportion of intervals containing one or more clicks was calculated. A weighted mean proportion was calculated, weighting by number of 10 min intervals per whale, together with a weighted standard error.

**Density Estimation**

Assuming that all periods of whale presence were identified during the initial screening, that all individuals vocalizing within the study area in each 10 min sample are counted, and that none from outside the study area are included, the average density of animals can be estimated by

\[
\hat{D} = \frac{np_p}{Ak\hat{p}_v},
\]

(1)

where \(n\) is the number of individuals counted over \(k\) sample periods within study area \(A\), \(p_p\) is the proportion of the total time monitored where sperm whales were thought to be present, and \(\hat{p}_v\) is the estimated proportion of time an individual whale vocalizes at least once in a 10 min interval, an estimation based on DTag data recordings of individual whales. This estimator can be justified intuitively as follows: \(n/k\) is the mean number of whales detected over the sample periods. If animals vocalized continuously and so were always detectable, and if the sample periods were distributed at random throughout the entire time period of interest, then \(n/k\) would be an estimate of mean abundance in the study area, and \(n/Ak\) would estimate mean density. However, on average, only a proportion of animals vocalize, and hence mean abundance in the sample periods is estimated by \(n/Ak\hat{p}_v\) and mean density by \(n/Ak\hat{p}_v\). Also, the sample periods were not randomly distributed through the whole time period of interest: they were randomly distributed through proportion \(p_p\) of the period, whereas abundance and density in the rest of the period was zero. Hence mean density is an average of the density during the time period \(p_p\) that was sampled, and the zero density during time period \((1 - p_p)\) that was not sampled:

\[
\hat{D} = \left(\frac{n}{Ak\hat{p}_v}\right) p_p + (0) (1 - p_p) = n p_p / Ak\hat{p}_v.
\]

(2)

The coefficient of variation (CV) on \(D\) can be estimated using the delta method (Buckland et al. 2001), with the two random components being \(n\) and \(\hat{p}_v\):

\[
CV(\hat{D}) = \sqrt{CV(n)^2 + CV(\hat{p}_v)^2},
\]

(3)

where \(CV(n)\) was estimated using the between-sample variance in encounters: \(CV(n) = \text{vär}(n)/n\), where

\[
\text{vär}(n) = \frac{k}{k - 1} \sum_{i=1}^{k} \left( n_i - \frac{n}{k} \right)^2
\]

(4)
and where \( n_i \) is the number of individuals counted in the \( i \)th sample period. CV(\( \hat{p}_v \)) was estimated from the between-whale variation in proportion of time vocalizing (weighted by length of tag deployment):

\[
\text{CV}(\hat{p}_v) = \frac{\text{vâr} (\hat{p}_v)}{\hat{p}_v},
\]

(5)

where

\[
\text{vâr}(\hat{p}_v) = \frac{1}{L-1} \sum_{j=1}^{J} l_j (p_{v,j} - \hat{p}_v)^2
\]

(6)

and where \( p_{v,j} \) is the proportion of time vocalizing on the \( j \)th tag, with deployment length, \( l_j \), and \( L \) is the total tag deployment length. Note that \( p_0 \) does not contribute to the estimated CV of \( \hat{D} \) because no uncertainty is added in going from the estimate of average density during the time period sampled (\( n/Ak \hat{p}_v \)) to average density over the entire sample period of interest as density in the time period not sampled is known (by assumption) to be zero. Confidence intervals on \( D \) can be obtained by assuming it follows a lognormal distribution (Buckland et al. 2001).

**RESULTS**

In total, 28 recordings on the hydrophone array were available for analysis, with a total recording period of 297.3 h. The distribution of available data was not uniform over the day, with 58% of it coming from daylight hours (Fig. 2). Operator logs and subsequent visual spectrogram review yielded eight recordings totaling 113.7 h where sperm whales were acoustically detected at some point during the recording; hence \( p_v = 0.382 \). Sperm whales were detected throughout the day and night. Of the \( k = 50 \) samples taken from the processed recordings, 26 samples had at least one whale clicking sufficiently loud enough to detect click trains and 13 had sperm whale individuals or clusters localized within the range area, resulting in \( n = 18 \) animals being counted (CV(\( n \)) = 26.0%). At most two direct path click trains were simultaneously observed, suggesting cluster sizes of 1–2 individuals. Removing samples with no whales present, a mean cluster size of 1.4 individuals was observed (SD = 0.5, \( n = 26 \)). The detected clusters were located predominantly in the northeastern quadrant of the range over the deepest water in the TOTO canyon, adjacent to the steep canyon wall (Fig. 1). Additional vocalizations were detected off-range in the southeastern corner, but no sperm whales were detected on the western perimeter of the range.

For estimating the proportion of time vocalizing, \( p_v \), the 31 tag deployments yielded a total of 924 intervals of 10 min each (Table 1). The weighted mean proportion of intervals containing vocalizations was \( \hat{p}_v = 0.649 \) (SE = 0.038, CV(\( \hat{p}_v \)) = 5.5%). This proportion was similar between the 25 Gulf of Mexico animals (0.654, SE = 0.043) and the 6 east coast animals (0.614, SE = 0.082).

Substituting these quantities into equations (1) and (2) yields a density estimate of 0.158 animals/1,000 km\(^2\), with CV 26.6% and 95% CI 0.095–0.264 animals/1,000 km\(^2\).
Figure 2. Diel distribution of recording effort and sperm whale click presence for the hydrophone recordings (top) and for the 50 sample periods (bottom). The hashed lines indicate night. Gray bars indicate times with sperm whale clicks detected visually using spectrogram evaluation (top) and using the automated methods of Baggenstoss (2011a, b) (bottom). The black bars on the bottom figure indicate times with sperm whales localized within the study area A.

**DISCUSSION**

The estimate of sperm whale density at TOTO is nearly an order of magnitude lower than the average global estimate for all areas surveyed using visual techniques, 1.4 whales/1,000 km², and is lower than any of the estimates reviewed by Whitehead (2002). However, it was not unexpected that a small, rather isolated area of deep oligotrophic (Cannizzaro and Carder 2006) water surrounded by shallows might have a lower density than the open ocean. Sperm whale populations are best described on an ocean basin scale, as they range widely and can cover up to 70 km in a day (Whitehead 2003). The density of females, especially at low latitudes, has been found to vary widely on time scales of months and years (Whitehead 2003). Therefore, the
low density estimated during the limited sample period of this study may simply reflect a transient time of low abundance or a long-term trend. Extended observation over a longer time period using the tools presented here is necessary to resolve this question. We do not think that the low value necessarily indicates a difference because of acoustic vs. visual detection of animals: so long as both methods give unbiased density estimates, then they are measuring the same quantity. We discuss potential sources of bias in our method below.

Previous attempts at acoustic line transect density estimation of sperm whales found that acoustic observation provided an excellent means of increasing the observation of sperm whale clusters, but visual identification was still necessary to determine cluster size (Barlow and Taylor 2005). Our method resolves this prior

Table 1. Summary of vocalization data from DTags placed on sperm whales used in deriving estimate of proportion of time clicking ($\hat{p}_v$).

<table>
<thead>
<tr>
<th>Tag no.</th>
<th>Location</th>
<th>Tag on time</th>
<th>$n$ periods$^b$</th>
<th>$n$ vocal periods$^b$</th>
<th>$\hat{p}_v$</th>
</tr>
</thead>
<tbody>
<tr>
<td>sw01_200</td>
<td>GM</td>
<td>19 July 2001 1558</td>
<td>49</td>
<td>33</td>
<td>0.67</td>
</tr>
<tr>
<td>sw01_204</td>
<td>GM</td>
<td>23 July 2001 1418</td>
<td>31</td>
<td>24</td>
<td>0.77</td>
</tr>
<tr>
<td>sw01_208b</td>
<td>GM</td>
<td>27 July 2001 1642</td>
<td>16</td>
<td>6</td>
<td>0.38</td>
</tr>
<tr>
<td>sw01_209c</td>
<td>GM</td>
<td>28 July 2001 1358</td>
<td>16</td>
<td>14</td>
<td>0.88</td>
</tr>
<tr>
<td>sw02_235c</td>
<td>GM</td>
<td>23 August 2002 1703</td>
<td>7</td>
<td>7</td>
<td>1.00</td>
</tr>
<tr>
<td>sw02_237a</td>
<td>GM</td>
<td>25 August 2002 1123</td>
<td>19</td>
<td>10</td>
<td>0.53</td>
</tr>
<tr>
<td>sw02_238a</td>
<td>GM</td>
<td>26 August 2002 0922</td>
<td>21</td>
<td>18</td>
<td>0.86</td>
</tr>
<tr>
<td>sw02_238b</td>
<td>GM</td>
<td>26 August 2002 1623</td>
<td>13</td>
<td>12</td>
<td>0.92</td>
</tr>
<tr>
<td>sw02_239a</td>
<td>GM</td>
<td>27 August 2002 1040</td>
<td>73</td>
<td>59</td>
<td>0.81</td>
</tr>
<tr>
<td>sw02_239b</td>
<td>GM</td>
<td>27 August 2002 1738</td>
<td>6</td>
<td>4</td>
<td>0.67</td>
</tr>
<tr>
<td>sw02_240a</td>
<td>GM</td>
<td>28 August 2002 1134</td>
<td>5</td>
<td>4</td>
<td>0.80</td>
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<tr>
<td>sw02_240c</td>
<td>GM</td>
<td>28 August 2002 1703</td>
<td>29</td>
<td>26</td>
<td>0.90</td>
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<tr>
<td>sw02_248a</td>
<td>GM</td>
<td>5 September 2002 1811</td>
<td>8</td>
<td>5</td>
<td>0.63</td>
</tr>
<tr>
<td>sw02_249a</td>
<td>GM</td>
<td>6 September 2002 0845</td>
<td>12</td>
<td>9</td>
<td>0.75</td>
</tr>
<tr>
<td>sw02_253a</td>
<td>GM</td>
<td>10 September 2002 1638</td>
<td>21</td>
<td>16</td>
<td>0.76</td>
</tr>
<tr>
<td>sw02_254a</td>
<td>GM</td>
<td>11 September 2002 1109</td>
<td>67</td>
<td>52</td>
<td>0.78</td>
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<tr>
<td>sw02_254b</td>
<td>GM</td>
<td>11 September 2002 1028</td>
<td>74</td>
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<tr>
<td>sw02_254c</td>
<td>GM</td>
<td>11 September 2002 1034</td>
<td>74</td>
<td>48</td>
<td>0.65</td>
</tr>
<tr>
<td>sw03_156a</td>
<td>GM</td>
<td>05 June 2003 1006</td>
<td>28</td>
<td>26</td>
<td>0.93</td>
</tr>
<tr>
<td>sw03_162a</td>
<td>GM</td>
<td>11 June 2003 1726</td>
<td>6</td>
<td>4</td>
<td>0.67</td>
</tr>
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<td>sw03_163a</td>
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<td>12 June 2003 1754</td>
<td>39</td>
<td>5</td>
<td>0.13</td>
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<tr>
<td>sw03_164a</td>
<td>GM</td>
<td>13 June 2003 0947</td>
<td>75</td>
<td>58</td>
<td>0.77</td>
</tr>
<tr>
<td>sw03_165a</td>
<td>GM</td>
<td>14 June 2003 1606</td>
<td>82</td>
<td>50</td>
<td>0.61</td>
</tr>
<tr>
<td>sw03_167a</td>
<td>GM</td>
<td>16 June 2003 1526</td>
<td>15</td>
<td>15</td>
<td>1.00</td>
</tr>
<tr>
<td>sw03_173b</td>
<td>GM</td>
<td>22 June 2003 1449</td>
<td>35</td>
<td>6</td>
<td>0.17</td>
</tr>
<tr>
<td>sw03_197a</td>
<td>E</td>
<td>16 July 2003 1044</td>
<td>12</td>
<td>10</td>
<td>0.83</td>
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<td>sw03_197b</td>
<td>E</td>
<td>16 July 2003 1210</td>
<td>13</td>
<td>8</td>
<td>0.62</td>
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<tr>
<td>sw03_201b</td>
<td>E</td>
<td>20 July 2003 1515</td>
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<td>12</td>
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<tr>
<td>sw03_202a</td>
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<td>21 July 2003 1210</td>
<td>13</td>
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<td>0.23</td>
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<tr>
<td>sw03_206c</td>
<td>E</td>
<td>25 July 2003 1312</td>
<td>15</td>
<td>15</td>
<td>1.00</td>
</tr>
<tr>
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<td>E</td>
<td>26 July 2003 1128</td>
<td>37</td>
<td>20</td>
<td>0.54</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td></td>
<td></td>
<td><strong>930</strong></td>
<td><strong>620</strong></td>
<td><strong>0.67</strong></td>
</tr>
</tbody>
</table>

*Note:* GM = Gulf of Maine, E = east coast United States.

$^a$Form is date time.

$^b$n periods is the number of 10 min periods available from that tag; n vocal periods is the number of these 10 min periods for which the animal produced one or more click.
deficiency by determining the number of simultaneous whales clicking through the elimination of multipath and assigning clicks to individual whales on the basis of interclick similarity (Baggenstoss 2011a). Clusters of one to two animals were acoustically detected. These clusters may be part of a larger group of sperm whales diving either synchronously or not. Although previous visual observations in the TOTO (D. Claridge and C. Dunn, unpublished data) lead one to expect a larger cluster size, the acoustically detected cluster size in this study is consistent with the mode observed in the Bahamas and with the behavior observed by Christal and Whitehead (2001) for adult females foraging with subadults. We acknowledge, however, that it would be somewhat harder to determine the number of individuals if diving groups were larger (as discussed by Baggenstoss 2011b), and hence this method will not work well in all circumstances.

Our method assumes that all whales vocalizing in each 10 min period within the study area are detected and counted, and none from outside the range are included. We also assume that the composition of each cluster does not turn over during a 10 min period. (This would happen if, for example, an animal diving at the beginning of the interval started to ascend and stop clicking, whereas another not diving at the beginning dove and started clicking soon after the first one stopped.) Each sample can be viewed as a “snapshot” of the number of vocalizing animals in the study area—when this is divided by the probability that an animal is vocalizing ($p_v$), we obtain an estimate of the number of animals present. The length of period chosen was therefore a compromise between two competing needs: to have a period long enough that animals diving close to one another would produce one or more overlapping click trains (so that we could accurately obtain the number in each cluster), while being short enough that cluster composition would not turn over.

One potential source of bias is that the opportunistic nature of the hydrophone recording data meant we did not obtain a uniform sample throughout the day (Fig. 2, top panel). One solution to this would be to model density as a function of time of day, but a better one would be to improve the data acquisition protocol so as to obtain uniform coverage. For this study, given that animals were detected throughout the day and night in approximate proportion to the amount of surveying (Fig. 2, top panel), we suggest that any possible bias from uneven sampling is small.

Sperm whale foraging behavior is remarkably similar among geographically diverse populations (Watwood et al. 2006). Sperm whales tagged in the western North Atlantic Ocean, Gulf of Mexico, and Ligurian Sea had no significant differences in the duration of foraging or percentage of the dive duration in the foraging phase (Watwood et al. 2006). In this study, we found the proportion of time spent vocalizing to be very similar between Gulf of Mexico and western North Atlantic animals. Previous acoustic monitoring of sperm whales indicates that click production depends on the behavior state with the “primary” state consisting of small clusters (<3 whales) diving, the “social” state with larger clusters at or near the surface, and a third “intermediate” state (Whitehead and Weilgart 1990). They estimated a 0.70 probability of clicking during the “primary” state, which occurred 80% of the day, a 0.46 probability during the “intermediate” state, and a 0.05 probability during the “social state.” Averaged over 24 h, this results in a 0.611 probability of clicking, which is consistent with the $\hat{p}_v = 0.649$ estimated here. There was some evidence from the tag data that proportion of time spent vocalizing varied diurnally; however, for practical reasons, tag deployments tend to take place during daylight hours and hence the nighttime sample size was only approximately 10% of that obtained during daytime. Ideally, with more data, we could model proportion of
time vocalizing as a function of time of day, and hence estimate a \( p_v \) weighted for the

times of day the 50 acoustic samples were taken.

The methods presented here provide the ability to quantitatively assess short-term
reactions of sperm whales to range military use (e.g., density before, during and after
operations), as well as a means for long-term monitoring of changes in population
density and distribution within the TOTO. The methods can also be extended to
other areas with similar dense hydrophone arrays such as the U.S. Navy’s Pacific
Missile Range Facility. Sperm whale distribution, cluster size, and click production
can be effectively studied over periods from hours to years. Future work should extend
the period of observation beyond the small study period evaluated here to determine
time varying trends of sperm whale occurrence within the TOTO. We note, however,
that the CV of our density estimate, at 26.6%, is rather high and a lower CV would
be desirable in future. Almost all of this uncertainty came from variation between
the 50 samples in the number of whales present (CV(\( n \)) = 26.6%), whereas very little
came from estimation of the proportion of time spent vocalizing (CV(\( \hat{p}_v \)) = 5.5%).
In future studies, CV(\( n \)) could be reduced by stratifying the sample of intervals, if it
were known in advance that there were periods of high and low density, or by taking
a larger sample of the data to process in detail.

This method is one of several with potential use in situations where there is a
dense array of hydrophones, such that vocalizations from inside a defined area can
be detected with certainty, whereas those from outside can be localized sufficiently
accurately to be excluded. This method requires that successive vocalizations from
the same animal can be linked (e.g., clicks linked to form click trains), and that false
positive detections can be excluded. In other situations, it may not be possible to
determine whether successive vocalizations come from the same animal, but it may
be possible to determine the hydrophones on which an individual vocalization was
detected. In this case, there is the potential to use methods based on spatially explicit
capture recapture (SECR), as demonstrated by Marques et al. (2011) on minke whales
at a navy testing range in Hawaii. This method yields the density of vocalizations, and
hence requires an independent estimate of vocalization rate to convert to density of
individuals. When detectability is low enough that vocalizations are rarely detected
on multiple hydrophones then it is necessary to model the detection probability
by making assumptions about source levels, propagation conditions and detector
characteristics (Küsel et al. 2011), or by using external information such as from
tagging studies (Marques et al. 2009). An estimate of vocalization rate is again
required to convert from density of vocalizations to density of individuals. Given the
increasing portfolio of methods available to estimate absolute density from passive
acoustic recordings, we anticipate that their use may become widespread. However,
the availability of the required auxiliary information, such as proportion of time
spent vocalizing or vocalization rates, remains a significant limitation.

Acknowledgments

These data were collected during the 2007 BRS funded by the Chief of Naval Operations
Environmental Readiness Division, Office of Naval Research, NAVSEA PEO-IWS 5, and the
Strategic Environmental Research and Development Program. We thank the entire field team
that participated in the 2007 BRS. This work is part of the DECAF project, funded under the
National Oceanographic Partnership Program jointly by the Joint Industry Program of the
International Association of Oil and Gas Producers and the U.S. National Marine Fisheries
Service.
LITERATURE CITED


Received: 14 March 2011
Accepted: 20 October 2011