Temporal variation in dwarf sperm whale (Kogia sima) habitat use and group size off Great Abaco Island, the Bahamas

Meagan Mná Dunphy-Daly

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TEMPORAL VARIATION IN DWARF SPERM WHALE (*Kogia sima*) HABITAT USE AND GROUP SIZE OFF GREAT ABACO ISLAND, THE BAHAMAS

A thesis submitted in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

in

BIOLOGY

by

Meagan Mná Dunphy-Daly

2008
To: Dean Kenneth Furton  
College of Arts and Sciences

This thesis, written by Meagan Mná Dunphy-Daly, and entitled Temporal Variation in Dwarf Sperm Whale (Kogia sima) Habitat Use and Group Size off Great Abaco Island, the Bahamas, having been approved in respect to style and intellectual content, is referred to you for judgment.

We have read this thesis and recommend that it be approved.

Maureen Donnelly

Douglas Wartzok

Michael Heithaus, Major Professor

Date of Defense: July 11, 2008

The thesis of Meagan Mná Dunphy-Daly is approved.

Dean Kenneth Furton  
College of Arts and Sciences

Dean George Walker  
University Graduate School

Florida International University, 2008
DEDICATION

I dedicate this thesis to my parents. They have inspired me to become the person and scientist that I am today. Their endless support, love, encouragement, and belief in me made the completion of this research possible.
ACKNOWLEDGMENTS

I would like to begin by thanking my major professor, Dr. Michael Heithaus, for his optimism, support, and confidence in my research. He never doubted my abilities and encouraged me throughout each step of this process. Diane Claridge welcomed me to her home and research site in Sandy Point and without her generosity and help this thesis would not have existed. I wish to thank the additional members of my committee, Dr. Maureen Donnelly and Dr. Douglas Wartzok, for their support and suggestions throughout my research and writing. Dr. John Durban also kindly provided advice and comments on a previous version of this manuscript.

I am grateful for the Earthwatch Institute volunteers and Bahamas Marine Mammal Research Organisation (BMMRO) scientific staff and research assistants that helped with data collection from 2000-2006 and made this project possible. I also would like to thank the members of my lab, particularly Derek Burkholder and Aaron Wirsing, for their advice, suggestions, proofreading skills, and friendship throughout my research. I am especially grateful to Jason Somarelli for his encouragement and support during my time in the Bahamas and while writing my thesis in Miami. Finally, I would like to thank my family for their love and their support of all of my adventures.

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ABSTRACT OF THE THESIS

TEMPORAL VARIATION IN DWARF SPERM WHALE (KOGIA SIMA) HABITAT USE AND GROUP SIZE OFF GREAT ABACO ISLAND, THE BAHAMAS

by

Meagan Mná Dunphy-Daly

Florida International University, 2008

Miami, Florida

Professor Michael Heithaus, Major Professor

Dwarf sperm whales, Kogia sima, are among the most commonly stranded yet least known pelagic cetaceans. I assessed seasonal and spatial variation in dwarf sperm whale group size and abundance off Great Abaco Island, the Bahamas. After correcting for survey effort and variation in sighting efficiency among sea states, I found that dwarf sperm whale group size and habitat use varied seasonally. In summer, dwarf sperm whale groups were small (median = 2.5, range = 1-8) and were found only in the two deep habitats within the study area (slope 400-900 m, deep 900-1600 m). In winter, group sizes increased (median = 4, range = 1-12) and sightings were almost six times higher in the slope habitat, where vertical relief is highest, than other habitats. My results suggest that studies of pelagic cetaceans and conservation plans must explicitly account for seasonal variation in group size and habitat use.
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PREFACE

A version of this thesis appears as:

1.1 INTRODUCTION

Increases in strandings of deep-diving cetaceans have generated considerable interest in poorly-known pelagic species. Of particular concern is minimizing anthropogenic effects, like noise and fishery interactions, which appear to be responsible for some strandings (e.g., Frantzis 1998, Balcomb and Claridge 2001, Cardonna-Maldonado and Mignucci-Giannoni 1999, Jepson et al. 2003, Fernández et al. 2005). For example, seventeen cetaceans (including beaked whales species, minke whales, *Balaenoptera acutorstrata*, and spotted dolphins, *Stenella frontalis*) stranded in the Bahamas during active sonar exercises by naval ships in 2000 (see Balcomb and Claridge 2001) and at least 12 Cuvier’s beaked whales (*Ziphius cavirostris*) stranded in the Mediterranean Sea during North Atlantic Treaty Organization (NATO) tests with low frequency active sonar in 1996 (Frantzis 1998). Fishery-induced mortality of pelagic cetaceans also is of considerable concern. In the United States, populations of deep diving species, such as Cuvier’s beaked whales, *Mesoplodon beaked whales* (*Mesoplodon sp.*), short-finned pilot whales (*Globicephala macrorhynchus*), and sperm whales (*Physeter macrocephalus*) are vulnerable to fishery mortality (Read and Wade 2000). Data on the impact of fishery interactions do not exist for many other deep-diving species.

In light of these anthropogenic impacts to pelagic cetaceans, studies of their habitat use and seasonal changes in their distribution and abundance are important for identifying places where, and times when, anthropogenic impacts are likely to be greatest. Although beaked whales have received considerable attention (e.g., Barlow and
Gisner 2006, MacLeod and D'Amico 2006), few studies have focused on dwarf sperm whales (*Kogia sima*) which are one of the most commonly stranded deep-diving cetaceans in temperate and tropical areas (Cardona-Maldonado and Mignucci-Giannoni 1999).

Dwarf sperm whales inhabit warm temperate and tropical waters and occur along the continental shelf and slope (see Willis and Baird 1998). In many locations, dwarf sperm whales are sympatric with pygmy sperm whales, *Kogia breviceps*. Both species of *Kogia* have a robust body and a discreet underslung jaw and are counter-shaded. *Kogia* are unique among marine mammals in that they have a sac within their lower intestine that is filled with dense, dark fluid (Caldwell and Caldwell 1989) that can be expelled in a dense cloud that may be a defense mechanism similar to that employed by squids (e.g., Caldwell *et al.* 1971).

Dwarf sperm whales are distinguished from pygmy sperm whales mainly by the size and position of their dorsal fin (see Willis and Baird 1998; Figure 1). The base height of the dorsal fin of dwarf sperm whales is greater than 5% of the total body length, whereas pygmy sperm whale dorsal fins are shorter and are less than 5% of the total body length (Willis and Baird 1998, McAlpine 2002). Furthermore, in dwarf sperm whales the dorsal fin is positioned more anteriorly than the dorsal fin of pygmy sperm whales (Willis and Baird 1998). Adult dwarf sperm whales can reach 2.7 m in length and can weigh between 136 and 272 kg (Handley 1966, Ross 1978). The larger pygmy sperm whale can grow to 4.25 m and 408 kg (Caldwell *et al.* 1971).
Most of what we know about dwarf sperm whales comes from stranded animals. Stranded animals commonly are entangled in gillnets (due to fisheries interactions), have experienced watercraft collisions, or have helminth loads in the esophagus and stomach, intestinal blockage, cardiomyopathy, or hemorrhage in the lungs, kidneys, spleen, and heart (Cardona-Maldonado and Mignucci-Giannoni 1999, Manire et al. 2004). Stomach contents from stranded animals suggest that they feed primarily on cephalopods and, to a lesser extent, on crustaceans and fish (see Nagorsen 1985, Willis and Baird 1998, Cardona-Maldonado and Mignucci-Giannoni 1999). Squid remains in stranded dwarf sperm whale stomachs represent over 15 different families of squid (see Willis and Baird 1998 for citations). It has been suggested that dwarf sperm whales feed on smaller squid and at shallower depths than pygmy sperm whales, although their diets overlap (see Willis and Baird 1998).

Despite frequent strandings in temperate and tropical locations (Cardona-Maldonado and Mignucci-Giannoni 1999), dwarf sperm whales are rarely identified at sea (Willis and Baird 1998, Baird 2005), probably because of their offshore habitat, small adult size (2.0-2.7 m), tendency to rest motionless at the surface, long dive durations, and propensity to avoid close approaches by boats (Willis and Baird 1998). Since most
information on dwarf sperm whales comes from strandings, studies of this species’
distribution and abundance at sea are particularly important.

Pelagic cetacean distributions are often correlated with bathymetric features that
may influence prey abundance and availability. For example, the abundance of Risso’s
dolphin (*Grampus griseus*) is highest in depths of 200-1000 m along the steep upper
continental slope (Baumgartner *et al.* 2001), humpback whale (*Megaptera novaeangliae*)
and minke whale distributions off Antarctica are correlated with high bathymetric slope
and high prey abundance (Friedlaender *et al.* 2006), and deep water and relatively steep
topographic features appear to be preferred by northern bottlenose whales (*Hyperoodon
ampullatus*) (Hooker *et al.* 2002). Habitat use and abundance of pelagic cetaceans also
may vary seasonally. For example, when faced with seasonal food shortages, sperm
whales often migrate hundreds of kilometers, resulting in seasonal and inter-annual

Oceanic islands provide an opportunity to study elusive pelagic species, such as
dwarf sperm whales, because of access to deep water using small, shore-based vessels
(*e.g.*, Baird 2005). Great Abaco Island, in the northeast Bahamas, is ideal for studies of
dwarf sperm whales because it sits upon a shallow carbonate bank that rapidly drops off
to deep canyons, providing easy access for small research vessels. The objectives of this
study were to 1) determine whether dwarf sperm whale relative abundance varied
temporally and spatially off Great Abaco Island, and 2) compare group sizes of dwarf
sperm whales across habitats, seasons, and years.
1.2 METHODS

Study site

The study was conducted off Great Abaco Island, in the northeast Bahamas (ca. 25° 55.0'N, 77° 20.0'W, Figure 2) where the deep waters of the Northwest Providence Channel, a branch of the Great Bahama Canyon, lie within 3 km of shore. A 6 x 21 km study grid, running parallel to shore and covering depths between 2-1600 m (Figure 3), has been the focus of long-term cetacean monitoring by the Bahamas Marine Mammal Research Organisation (BMMRO) since 1997. Within this area, average sea surface temperatures generally are below 24° C in the winter (November-April) and above 27° C in the summer (May-October).

Figure 2: The study was conducted off the southern end of Great Abaco Island, the Bahamas.
Field methods

From May 2001 to August 2005, randomized equal angle (70°) zigzag surveys and opportunistic surveys were conducted within the 6 x 21 km study area to assess dwarf sperm whale habitat use and group size. Although repeated transects parallel to depth contours are preferable for assessing habitat use patterns (e.g., Heithaus and Dill 2002), zigzag surveys were initiated by the BMMRO early in the study and these surveys were continued through 2005 to maintain methodological consistency. Analysis techniques were developed to overcome potential weaknesses of such surveys (see below). Randomized survey routes were pre-determined by randomly selecting a starting position along the southeast end of the study area and an initial heading (NE or SW). The direction in which surveys were run (i.e., from east to west or west to east) was...
determined by lighting and sea conditions at the start of the survey. Depending on the starting position, each survey consisted of 7 or 8 “legs” (Figure 4). Surveys were run in small boats (< 7 m) traveling ca. 28 km/hr with observers scanning 180° to both sides of the vessel.

Figure 4. Two examples of randomized zigzag survey tracks. The asterisk indicates the starting position of each example track.
Beaufort sea state and sea surface temperature were recorded at the beginning and end of each leg, and a Garmin 48 GPS recorded the position of the vessel every minute. No more than one survey was conducted per day; however, in many cases surveys were not completed in a single day. When this occurred, the survey was resumed on a subsequent day at the ending location. For the purposes of analysis (see below), each day was treated as a separate survey.

When a group of dwarf sperm whales was sighted, the GPS position on the survey line was recorded and the vessel left that position to approach the group. Group size was visually estimated by observers and the group’s GPS location was recorded, along with sea surface temperature and sea state. To confirm the species identification and group size, an attempt was made to photograph each group member using 35 mm SLR cameras with a 300 mm fixed lens or 200-400 mm zoom lens. Once the sighting was completed, the vessel returned to the point where the survey line was departed and the survey was resumed. In addition to quantitative surveys, sightings of dwarf sperm whale groups were recorded during non-random opportunistic surveys within the study area from 2001-2005.

Because no high-resolution bathymetry charts were available for the study site, I collected depth data in July and August of 2006 using a Furuno FCV1100 LCD echo sounder with a 28 kHz 3 kW transducer. A total of 12 bathymetry transects, each 21 km long and parallel to the study grid, were spaced 0.5 km apart within the 6 x 21 km grid. Depth and GPS position were recorded every 1 km along each transect (n = 264 points). One-hundred meter and 10 m bathymetry contours were created using ESRI ArcView GIS 3.2.
The study area was divided into three habitats based on 100 m contours and slope of the seafloor: shallow (2-400 m depth), slope (400-900 m depth), and deep (900-1600 m depth) (Figure 5). This division ensured adequate sampling area within each habitat type. The shallow habitat occupies ca. 24 km² of the study area and most depths are between 2-100 m. The waters of the deep habitat (ca. 70 km²) become progressively deeper offshore, but there is less bathymetric relief than in the slope habitat (ca. 32 km²). Depths for each dwarf sperm whale encounter within the study area were assigned using 10 m contours in GIS.

![Figure 5](image-url)

Figure 5. The study area with 100 m bathymetric contours and dwarf sperm whale sightings during randomized surveys (2001-2005). Habitat boundaries are bold. Circles are dwarf sperm whale sightings during randomized surveys in summer (June-August) and triangles are dwarf sperm whale sightings in winter (January-March).

Analysis

Survey tracks were downloaded at the completion of each day. Portions of the track before and after the survey, when the vessel broke the survey line, and during
cetacean sightings were excluded. Beaufort sea states were assigned to each one-minute GPS position point of the track using the sea state recorded at the beginning and end of a leg. If the sea state changed during a leg, it was assumed that the change occurred at the midpoint of the leg. All GPS one-minute effort points were imported into GIS and counted in each of the three habitats (shallow, slope, deep) for every sampling day. In each day, any habitat that had less than four effort points during appropriate conditions (see below) was excluded from analysis. Only days that sampled all three habitats adequately were used for analysis.

Since dwarf sperm whales are difficult to sight in poor weather conditions and only one dwarf sperm whale sighting occurred in seas greater than Beaufort 2, the habitat use analysis was restricted to sea states of Beaufort 0, 1, and 2. The mean distance between the location along the transect where a dwarf sperm whale group was sighted and the actual location of the group (measured in GIS) varied with sea state. Distances to groups in Beaufort 1 conditions (mean = 0.633 km ± 0.402 SD, n = 24 groups) were not significantly different from distances to groups sited in Beaufort 2 conditions (mean = 0.562 km ± 0.424 SD, n = 9; t = 0.44, df = 31, P = 0.66). However, groups were sighted at significantly greater mean distances in Beaufort 0 conditions (mean = 1.138 km ± 1.027 SD, n = 14; t = 2.54, df = 45, P = 0.015). Therefore, I corrected for variation in sighting conditions by weighting each GPS one-minute effort point by relative sighting efficiency of the sea state at that point using the 3rd quartile distance for sightings in Beaufort 0 conditions divided by the 3rd quartile distance for sightings in both Beaufort 1 and 2 conditions combined (effort points in Beaufort 0 = 1, Beaufort 1 and Beaufort 2 = 0.51). Beaufort 1 conditions and Beaufort 2 conditions were treated equally for effort
calculations because they were not statistically different from one another. For each habitat of every survey day, I calculated sightings per unit effort (SPUE) by dividing the number of dwarf sperm whale groups in a habitat by the sum of effort, corrected for sea state, in that habitat.

Because of unequal survey effort across months and years, I restricted my analyses of habitat use to three months in winter (January-March) and summer (June-August) during which effort was consistent across years. I used analysis of variance (ANOVA) to determine whether dwarf sperm whale relative abundance varied by habitat, season, year, and the interactions of these main effects. Habitat, season, and year were treated as fixed effects and SPUE data were square-root transformed to normalize variances. Non-significant interactions ($P > 0.10$) were removed from analysis. I also ran ANOVA with a collapsed data set (with an average SPUE value for each season of each year), but the general results were similar and are not presented here.

Temporal and spatial variation in dwarf sperm whale group size was investigated using both randomized survey data and opportunistic data collected inside the study area during January-March and June-August of 2001-2005. Photographs from dwarf sperm whale encounters were used to confirm field estimates of group size. Group sizes were square-root transformed to normalize the data and ANOVA was used to determine the effect of habitat, season, year, and their interactions (as described above).

Photographs from dwarf sperm whale encounters were examined to confirm group size and identify individuals. Individuals were identified using natural markings on their dorsal fins (e.g., Würsig and Würsig 1977; Figure 6). Animals with unmarked fins can sometimes be distinguished within an encounter but cannot be distinguished
between encounters. Therefore, to establish the minimum number of animals photographed, the number of dwarf sperm whales with clean fins and marked fins was determined for each encounter. Identification photographs were assigned a quality grade based on image size, focus, and lighting and only high quality photographs were used for site fidelity analysis.

Figure 6. An example of a marked and identifiable dwarf sperm whale dorsal fin (a) and an unmarked and unidentifiable dwarf sperm whale dorsal fin (b).

1.3 RESULTS

In total, 70 surveys were conducted across all three habitats for a total of over 107 hours (Table 1). Fifty-four dwarf sperm whale groups were encountered and the mean depth of encounters was 905.4 m ± 49.6 SE. Depths of encounters ranged from 302 m to 1535 m. Of all dwarf sperm whale encounters, 33 sightings occurred during surveys and 19 of these during target months from 2001-2005. Only five groups of pygmy sperm
whales were encountered from 2001-2005 and the mean depth of encounters was 746.7 m ± 347 SE.

Table 1. Survey effort off Great Abaco Island.

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Area (km²)</th>
<th>Season</th>
<th>Surveys</th>
<th>Hours</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shallow</td>
<td>24</td>
<td>Summer</td>
<td>39</td>
<td>14.38</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Winter</td>
<td>31</td>
<td>13.98</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Total</td>
<td>70</td>
<td>28.37</td>
</tr>
<tr>
<td>Slope</td>
<td>32</td>
<td>Summer</td>
<td>39</td>
<td>13.87</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Winter</td>
<td>31</td>
<td>11.37</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Total</td>
<td>70</td>
<td>25.23</td>
</tr>
<tr>
<td>Deep</td>
<td>70</td>
<td>Summer</td>
<td>39</td>
<td>29.20</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Winter</td>
<td>31</td>
<td>24.48</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Total</td>
<td>70</td>
<td>53.68</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td>70</td>
<td>107.28</td>
</tr>
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</table>

Photographs were taken of 216 potential individuals, but only 48 (22.2%) individuals had natural markings that facilitated identification. Seven of these 48 (18.9%) individuals were resighted once and two (5.4%) were resighted twice. Seven individuals were resighted in different years, including one resighted after almost six years.

The number of dwarf sperm whale groups encountered was influenced by an interaction between season and habitat (Table 2; Figure 7). During summer, dwarf sperm whale relative abundances were generally low. In winter, the overall sighting rate increased but primarily in the slope habitat, where sighting rates were almost six times
higher than in the shallow or deep habitats. Sighting rates did not vary significantly across years.

Table 2. ANOVA table of dwarf sperm whale habitat use.

<table>
<thead>
<tr>
<th>Factor</th>
<th>df</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Year</td>
<td>4,379</td>
<td>1.24</td>
<td>0.30</td>
</tr>
<tr>
<td>Season</td>
<td>1,379</td>
<td>5.75</td>
<td>0.017</td>
</tr>
<tr>
<td>Habitat</td>
<td>2,379</td>
<td>4.75</td>
<td>0.009</td>
</tr>
<tr>
<td>Season x habitat</td>
<td>2,379</td>
<td>4.67</td>
<td>0.010</td>
</tr>
</tbody>
</table>

In general, dwarf sperm whales were found in small groups (median = 3, range = 1-12, n = 54 groups), but groups were significantly larger in winter (median = 4, range = 1-12, n = 20 groups) than in summer (median = 2.5, range = 1-8, n = 34 groups) (Table 3; Figure 8). Group size did not vary with habitat and differences in group size among years were marginally significant (Table 3; Figure 9).
Figure 7. Spatial and temporal variation in dwarf sperm whale sightings per unit effort (SPUE) during randomized surveys. Units of effort are GPS one-minute effort points weighted by relative sighting efficiency in the sea state at that time. Error bars are ± SE.

Table 3. ANOVA table of dwarf sperm whale group size.

<table>
<thead>
<tr>
<th>Factor</th>
<th>df</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Year</td>
<td>4, 53</td>
<td>2.56</td>
<td>0.053</td>
</tr>
<tr>
<td>Season</td>
<td>1, 53</td>
<td>8.36</td>
<td>0.006</td>
</tr>
<tr>
<td>Habitat</td>
<td>2, 53</td>
<td>0.40</td>
<td>0.67</td>
</tr>
<tr>
<td>Season x habitat</td>
<td>2, 53</td>
<td>0.52</td>
<td>0.60*</td>
</tr>
</tbody>
</table>

*Removed from final model.
Figure 8. Seasonal variation in dwarf sperm whale group size. Thick bars represent the median, outside borders represent the 1\textsuperscript{st} and 3\textsuperscript{rd} quartile, error bars represent the range, and circles represent outliers.

1.4 DISCUSSION

Dwarf sperm whales are considered to be a pelagic species of the continental shelf and slope (see Willis and Baird 1998), but their specific habitat affinities have been poorly understood. I found that dwarf sperm whales were always found in waters deeper than 300 m and were distributed primarily along the upper canyon slope. However, dwarf sperm whale habitat use varied seasonally. During summer, dwarf sperm whale group sizes were small and sighting rates were low and spread relatively evenly among
deeper habitats. In winter, groups were larger and encounter rates increased, primarily in the slope habitat. Together, these results suggest net movement of individuals into the study area, possibly because of seasonal onshore-offshore movements, with most individuals found offshore and beyond the study area in summer. Future studies should include surveys that extend further offshore to assess this possibility.

Previous studies have presented two different views of dwarf sperm whale habitat use – one of a relatively nearshore species and one of an offshore, pelagic species. MacLeod et al. (2004) reported that the mean depth of ten dwarf sperm whale sightings off the east side of Great Abaco Island, the Bahamas was 247 m. In contrast, Baird (2005) recorded dwarf sperm whale sightings in much deeper waters off of Hawaii (mean $= 1565 \text{ m} \pm 1017 \text{ SD}$), and never in waters less than 450 m.

Despite the close proximity (ca. 100 km) of my study site to that of McLeod et al. (2004), I found dwarf sperm whale groups at a mean depth more than three times greater (905 m) and did not encounter groups in less than 300 m. This discrepancy in the mean depths over a relatively small spatial scale is surprising. However, differences may be associated with variation in sampling methods. First, I found that topographic maps, like those used by MacLeod et al. (2004) did not provide accurate depth data in my study area for fine-scale habitat use analysis. Second, my surveys were designed to sample depths in proportion to their availability and were conducted across seasons, while those off the east coast of Great Abaco Island were non-random, conducted only in summer months, and thus are of limited value for cross-site comparisons (MacLeod et al. 2004).

Future studies need to consider the effect of sea state on sighting efficiency and should strive to sample all accessible depths across seasons. By accounting for effort
(weighted by sighting biases) and examining the effect of season on habitat use, I found that dwarf sperm whales may occupy offshore habitats in the summer season and move into the slope region and shallow depths with higher relief during the winter season.

Physical features besides water depth likely make the slope habitat attractive to dwarf sperm whales. High relief, a sloping canyon wall, and other oceanographic features and processes may physically aggregate prey (Moser and Smith 1993, Logerwell and Smith 2001), although the small group sizes of dwarf sperm whales suggest that their prey probably do not occur in high densities. Alternatively, high relief areas provide structures on which to herd prey or may produce currents that reduce energetic costs of foraging in that area (e.g., Williams et al. 1996), both of which can increase the foraging efficiency of predators (Croxall et al. 1985). These mechanisms may explain the common association of cetaceans with high-relief habitats (e.g., sperm whales, Jaquet and Whitehead 1996; northern bottlenose whales, Hooker et al. 2002; bottlenose dolphins, Tursiops truncatus, Hastie et al. 2003), and may make the slope a high quality habitat for dwarf sperm whales.

Habitat use patterns of cetaceans have also been linked to changes in prey abundance (e.g., sperm whales, Jaquet et al. 2000; bottlenose dolphins, T. aduncus, Heithaus and Dill 2002, 2006; humpback and minke whales, Friedlaender et al. 2006). Therefore, variation in the abundance and distribution of prey may drive the seasonal influx of dwarf sperm whales into the study area. Squid are common prey of dwarf sperm whales in the Caribbean (Cardonna-Maldonado and Mignucci-Giannoni 1999), so seasonal movements of squid could cause inshore shifts in dwarf sperm whales. Although no data exist for the Bahamas, in other areas squid move inshore and into areas
of high bathymetric relief in winter. For example, schoolmaster gonate squid
(*Berryteuthis magister*) in the Bering Sea are found in low concentrations in the summer
but aggregate over the continental slope in the winter (Arkhipkin *et al.* 1996). Similarly,
in northwest Africa, mature European flying squid (*Todarodes sagittatus*) move to
continental slopes to spawn in winter months (Arkhipkin *et al.* 1999).

Seasonal changes in dwarf sperm whale habitat use and group size may be
influenced by factors other than the distribution or abundance of their prey. Predation
risk (Lima and Dill 1990), interspecific competition (e.g., Robertson 1996), and
reproductive and social behavior (e.g., Stamps 1991) all may influence habitat use and
group size. For example, bottlenose dolphins in Australia shift from productive but risky
shallow habitats to safer, deeper waters and increase group size when predatory tiger
sharks (*Galeocerdo cuvier*) are present (Heithaus and Dill 2002).

Dwarf sperm whales are at risk from killer whales (*Orcinus orca*) (Jefferson *et al.*
1991) and sharks (Willis and Baird 1998, Heithaus 2001). Killer whales were observed
attacking dwarf sperm whales in the study area in 2001 and 2005 (Figure 9), but they
have only been encountered twice in the study area since 1997. Both encounters were
during summer (BMMRO, unpublished data). It is possible that by occurring in smaller
groups and occupying deeper habitats in summer, dwarf sperm whales are able to avoid
detection by killer whales.
Although the threat of shark predation to dwarf sperm whales is often overlooked, parasites found in stranded individuals suggest that attacks may be more common than generally appreciated (see Gibson et al. 1998, Walker 2001, Anzar 2007). Sharks are the final host for larval cestodes (Cheung 1993, Caira and Healy 2004), such as *Phyllobothrium delphini*, that are commonly found encysted in dwarf sperm whale blubber (Nagorsen 1985, Cardonna-Maldonado and Mignucci-Giannoni 1999, Goold and Clarke 2000). In order for these parasites to be transmitted, shark predation and scavenging of dwarf sperm whale carcasses must be relatively frequent. Tiger sharks,
which are a major cetacean predator (Heithaus 2001), are present in the study area and could influence dwarf sperm whale habitat use and group size. However, there are no data on temporal variation in their numbers, and the possible effects of predation on dwarf sperm whales remain speculative.

Interspecific competition may also influence dwarf sperm whale habitat use and group size. Dwarf sperm whales are the most frequently encountered oceanic species in the study area (Claridge 2006), but pygmy sperm whales, Blainville’s beaked whales (M. densirostris), Cuvier’s beaked whales, and sperm whales are also encountered in the study area and their diets overlap somewhat with that of dwarf sperm whales (Willis and Baird 1998, Cardona-Maldonado and Mignucci-Giannoni 1999). Seasonal and spatial trends in the abundance of species other than dwarf sperm whales need to be determined in order to understand the potential influence of interspecific competition on dwarf sperm whales.

Finally, social behavior and reproductive considerations may influence habitat use and group sizes of dwarf sperm whales. Little is known about sociality in dwarf sperm whales, largely because of the difficulties in identifying individuals at sea, which is critical for determining social structure (e.g., Whitehead 1997). Although individual identification of this species is difficult due to their small size and propensity to avoid close approaches by boats (Willis and Baird 1998), Baird et al. (2006) were able to recognize individual dwarf sperm whales in eight out of ten encounters in Hawaii. The majority of dwarf sperm whales photographed (78%) in our study area did not have marked dorsal fins, making identification impossible. Nonetheless, we resighted nine of 48 identifiable individuals including one resighting after over five years, suggesting some
individuals remain in the study area or return seasonally. Therefore, dedicated photo-
identification efforts may help to elucidate dwarf sperm whale social behavior and
reproductive ecology, but other techniques (e.g., genetic sampling) may prove more
useful.

Pelagic and small-bodied cetaceans often are found in large groups of dozens to
hundreds of individuals (e.g., pantropical spotted dolphin, *S. attenuata*; spinner dolphin,
*S. longirostris*; short-beaked common dolphin, *Delphinus delphis*; see Scott and
Cattanach 1998) which likely function to dilute the risk of predation (see Heithaus 2001
for a review). It is therefore somewhat surprising that dwarf sperm whale group sizes are
small in the Bahamas (median = 3.46) and off of Hawaii (mean = 2.33, Baird 2005). The
presence of small groups in such apparently high-risk open habitats likely is driven by
relatively low food densities prohibiting the formation of large groups (e.g., Bertram
1978). Thus, further studies of dwarf sperm whales that integrate data on predator
abundance and prey availability may provide insights into the relative roles of predation
risk and foraging ecology on the evolution of group living and social structure on pelagic
cetaceans.
LITERATURE CITED


