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

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ABSTRACT

Dwarf sperm whales (*Kogia sima*) are among the most commonly stranded yet least known pelagic cetaceans. Few studies have occurred at sea, and none have quantified temporal and spatial variation in dwarf sperm whale abundance and group size. We assessed seasonal and spatial variation in dwarf sperm whale group size and abundance off Great Abaco Island, Bahamas using surveys within a 126 km^2 study area with depths between 2 and 1,600 m. After correcting for survey effort and variation in sighting efficiency among sea states, we 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 900–1,600 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. Our results suggest that studies of pelagic cetaceans and conservation plans must explicitly account for seasonal variation in group size and habitat use.

Key words: *Kogia sima*, dwarf sperm whale, seasonal distribution, habitat use, group size.

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, Cardona-Maldonado and Mignucci-Giannoni 1999, Balcomb and Claridge 2001, Jepson *et al.* 2003, Fernández *et al.* 2005). Therefore, studies of pelagic cetacean 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 (*e.g.*, *Mesoplodon densirostris*, *Ziphius cavirostris*) 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 for citations). Stomach contents from stranded animals suggest that they feed primarily on cephalopods and, to a lesser extent, on crustaceans and fish (see Cardona-Maldonado and Mignucci-Giannoni 1999). It has been suggested that dwarf sperm whales feed on smaller squid and at shallower depths than congeneric pygmy sperm whales (*K. breviceps*), 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). Unfortunately, most information on dwarf sperm whales comes from strandings, making studies at sea 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 dolphins (*Grampus griseus*) is highest in depths of 200–1,000 m along the steep upper continental slope (Baumgartner *et al.* 2001), baleen whale (humpback whale, *Megaptera novaeangliae*; minke whale, *Balaenoptera acutorostrata*) 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. When faced with seasonal food shortages, sperm whales (*Physeter macrocephalus*) often migrate hundreds of kilometers, resulting in seasonal and inter-annual variation in their abundance (Whitehead 1996, Jaquet *et al.* 2000).

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.

Methods

Study Site

The study was conducted off Great Abaco Island, in the northeast Bahamas (*ca.* 25°55.0′N, 77°20.0′W; Fig. 1A) where the deep waters of the Northwest Providence Channel, a branch of the Great Bahama Canyon, lie within 3 km of shore. A 6 by 21 km^2 study grid, running parallel to shore and covering depths between 2 and

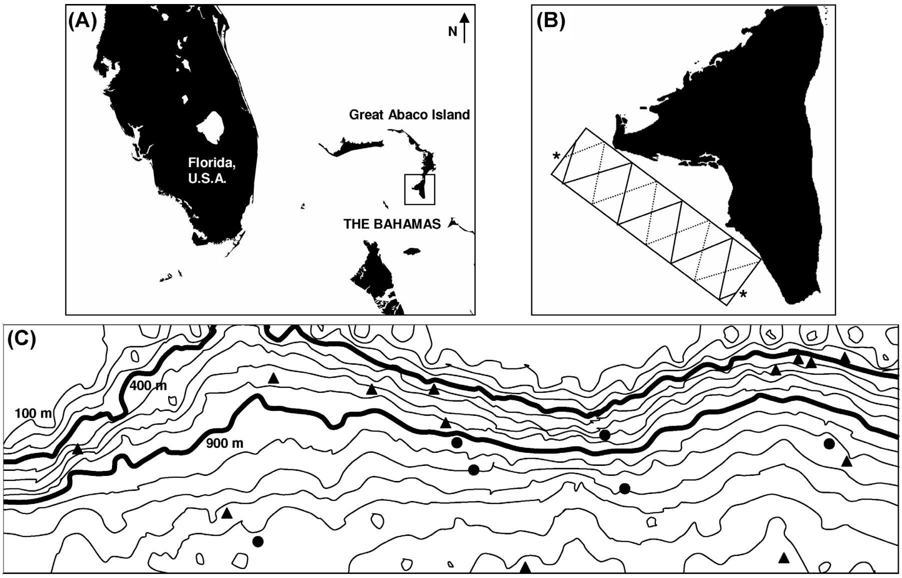

Figure 1. The study was conducted off (A) the southern end of Great Abaco Island, Bahamas inside (B) a 6×21 km^2 study area. Zigzag lines in (B) are two examples of randomized survey tracks. The asterisk indicates the starting position of each example track. (C) The study area with 100 m bathymetric 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).

1,600 m (Fig. 1B), has been the focus of long-term cetacean monitoring by the Bahamas Marine Mammal Research Organisation 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).

Field Methods

From May 2001 to August 2005, randomized equal angle (70°) zigzag surveys and opportunistic surveys were conducted within the 6×21 km^2 study area to assess dwarf sperm whale habitat use and group size. Randomized survey routes were predetermined 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 seven or eight "legs" (Fig. 1B). Surveys were run in small boats (<7 m) traveling *ca.* 28 km/h with observers scanning 180° to both sides of the vessel.

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. Not 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. Observers estimated group size visually and the group's GPS location was recorded, along with sea surface temperature and sea state. We attempted to photograph each group member to confirm the species identification and group sizing, using 35 mm SLR cameras with a 300 mm fixed lens or 200 to 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 nonrandom opportunistic surveys within the study area from 2001 to 2005.

Because no high-resolution bathymetry charts were available for the study site, we 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 6×21 km^2 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 somewhat arbitrarily into three habitats based on 100 m contours and slope: shallow (2–400 m depth), slope (400–900 m depth), and deep (900–1,600 m depth) (Fig. 1C). This division ensured adequate sampling area within each habitat type. The shallow habitat occupies *ca.* 24 km^2 of the study area and most depths are between 2 and 100 m. The waters of the deep habitat (*ca.* 70 km^2) become progressively deeper offshore, but there is less bathymetric relief than in the slope habitat (*ca.* 32 km^2). Depths for each dwarf sperm whale encounter within the study area were assigned using 10-m contours in GIS.

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 1-min 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, we assumed the change occurred at the midpoint of the leg. All GPS 1-min 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.

Because 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 $\pm$ 0.402 SD, $n = 24$ groups) were not significantly different from distances to groups sighted in Beaufort 2 conditions (mean $= 0.562$ km $\pm$ 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, we corrected for variation in sighting conditions by weighting each GPS 1-min effort point by relative sighting efficiency of the sea state at that point using the third quartile distance for sightings in Beaufort 0 conditions divided by the third 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, we 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.

Due to unequal survey effort across months and years, we restricted our analyses of habitat use to 3 months in winter (January–March) and summer (June–August) during which effort was consistent across years. We used ANOVA to determine whether dwarf sperm whale relative abundance varied by habitat, season, year, and their interactions. Habitat, season, and year were treated as fixed effects and SPUE data were square root transformed to normalize variances. Nonsignificant interactions ($P > 0.10$) were removed from analysis. We also ran ANOVA with a collapsed dataset (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 to 2005. Group size was 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).

Results

We conducted 70 surveys across all three habitats for a total of over 107 h (Table 1). We encountered 54 dwarf sperm whale groups at a mean depth of 905.4 m ± 49.6 SE. Of all dwarf sperm whale encounters, 33 sightings occurred during surveys and 19 of these during target months from 2001 to 2005.

The number of dwarf sperm whale groups encountered was influenced by an interaction between season and habitat (Table 2, Fig. 2). During summer, dwarf sperm

Table 1. Spatial and temporal distribution of survey effort.

Habitat	Area (km^2)	Season	Surveys	Hours
Shallow	24	Summer	39	14.38
		Winter	31	13.98
		Total	70	28.37
Slope	32	Summer	39	13.87
		Winter	31	11.37
		Total	70	25.23
Deep	70	Summer	39	29.20
		Winter	31	24.48
		Total	70	53.68
Total			70	107.28

Table 2. ANOVA table of dwarf sperm whale habitat use and group size.

	Habitat use			Group size		
Factor	df	*F*	*P*	df	*F*	*P*
Year	4,379	1.24	0.30	4,53	2.56	0.053
Season	1,379	5.75	**0.017**	1,53	8.36	**0.006**
Habitat	2,379	4.75	**0.009**	2,53	0.40	0.67
Season × habitat	2,379	4.67	**0.010**	2,53	0.52	0.60[a]

[a]Removed from final model. Statistically significant values are indicated in bold.

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.

In general, dwarf sperm whales were found in small groups (median = 3, range = 1–12, n = 54 groups), but they 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 2, Fig. 3). Group size did not vary with habitat and differences in group size among years were marginally significant (Table 2).

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. We found that dwarf sperm whales were always found in

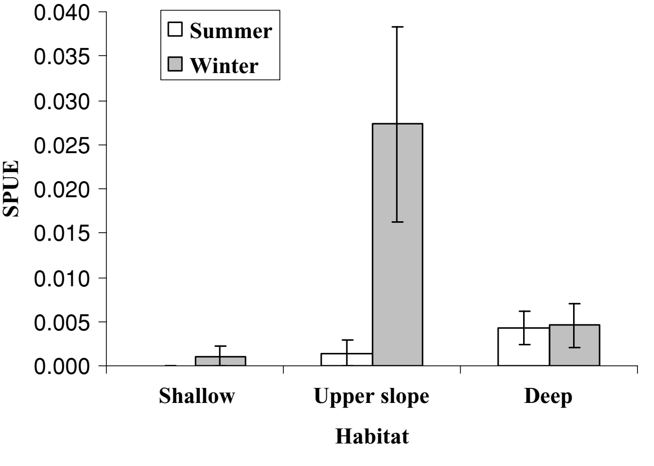

Figure 2. Spatial and temporal variation in dwarf sperm whale sightings per unit effort (SPUE) during randomized surveys. Units of effort are GPS 1-min effort points weighted by relative sighting efficiency in the sea state at that time. Error bars are ± SE.

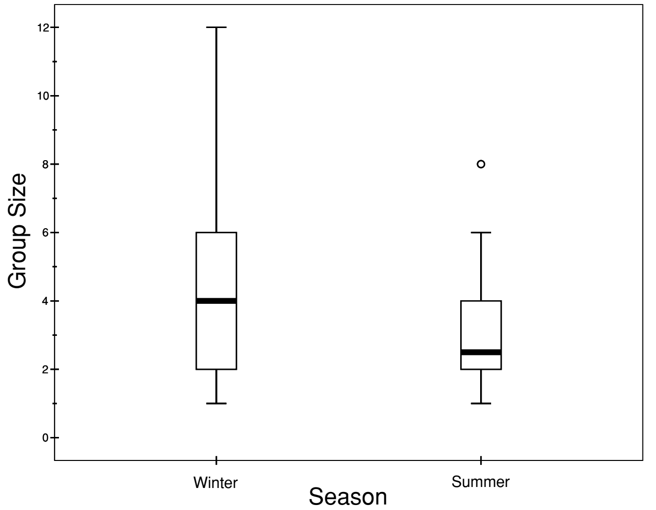

Figure 3. Seasonal variation in dwarf sperm whale group size. Thick bars represent the median, outside borders represent the first and third quartile, error bars represent the range, and circles represent outliers.

waters deeper than 300 m and were distributed primarily along the upper canyon slope (Fig. 1C). However, dwarf sperm whale habitat use varied seasonally. During summer, dwarf sperm whale group sizes were small (Fig. 3) and sighting rates were low and spread relatively evenly among deeper habitats (Fig. 2). In winter, groups were larger (Fig. 3) and encounter rates increased, primarily in the slope habitat (Fig. 2). 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 10 dwarf sperm whale sightings off the east side of Abaco Island, Bahamas was 247 m. In contrast, Baird (2005) recorded dwarf sperm whale sightings in much deeper waters off of Hawaii (mean = 1,565 m ± 1,017 SD), and never in waters less than 450 m.

Despite the close proximity (*ca*. 100 km) of our study site to that of McLeod *et al*. (2004), we 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 due to variation in sampling methods. First, we found that topographic maps, like those used by MacLeod *et al*. (2004) did not provide accurate depth data in our study area for fine-scale habitat use analysis. Second, our surveys were designed to sample depths in proportion to their availability and were conducted across seasons, while those off the east coast of Abaco were nonrandom, conducted only in summer months, and 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, we 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 may 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 (Cardona-Maldonado and Mignucci-Giannoni 1999), so seasonal movements of squid could cause inshore shifts in dwarf sperm whale habitat use. 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 (personal observation, Fig. 4), but they have only been encountered twice in the study area since 1997. Both encounters were during summer (Bahamas Marine Mammal Research Organisation, 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 *et al.* 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, Cardona-Maldonado and Mignucci-Giannoni 1999, Goold

Figure 4. Killer whale attack on a dwarf sperm whale in the study area off of Great Abaco Island, Bahamas on 27 July 2005 (photo credit: M. Dunphy-Daly, copyright Bahamas Marine Mammal Research Organisation).

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 (*Z. cavirostris*), 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. Therefore, dedicated photo-identification efforts may help to elucidate dwarf sperm whale social behavior and reproductive ecology, but other techniques 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, *Stenella 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.

Acknowledgments

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