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Nocturnal feeding of Atlantic spotted dolphins (*Stenella frontalis*) in the Bahamas

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The foraging habits of small delphinids, including the bottlenose dolphin (*Tursiops truncatus*), the dusky dolphin (*Lagenorhynchus obscurus*), and the spinner dolphin (*Stenella longirostris*), and others have been documented (Leatherwood 1975; Würsig and Würsig 1980; Norris *et al.* 1994; Young and Cockcroft 1994, 1995; Steiner 1995; Barros and Wells 1998; Vaughan *et al.* 2007). However, reports on the feeding habits of free-ranging spotted dolphins (*Stenella sp.*) are scarce (Bernard and Hohn 1989; Richard and Barbeau 1994; Fertl and Würsig 1995; Herzing 1996, 2004). Perrin *et al.* (1973) conducted stomach content analysis on spinner dolphins and pantropical spotted dolphins (*Stenella attenuata*) to identify preferred prey species and found evidence of specialization in prey choices and foraging patterns. Nocturnal feeding by spotted dolphins (*Stenella sp.*) in the Gulf of Mexico was described in 1994 by Richard and Barbeau but it was unclear whether the pantropical or Atlantic (*Stenella frontalis*) species was observed.

On the shallow banks of the Bahamas, a resident community of over 200 individually identifiable Atlantic spotted dolphins (*S. frontalis*) has been studied extensively for over two decades from May through September every year (Herzing 1996, 1997; Herzing and Johnson 1997; Elliser and Herzing 2012). These dolphins have been observed on the shallow sandbank during daytime hours feeding on a variety of prey items including both burrowing and schooling fish (Families: *Bothidae*, *Clinidae*, *Labridae*, *Hemiramphidae*, *Exocoetidae*; see Herzing 1996). Malinowski (2011) has additionally described the diurnal prey species of both Atlantic spotted dolphins and bottlenose dolphins in this area. A variety of hunting tactics, by prey type and

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habitat, have also been described for both delphinid species in this area of the Bahamas (Herzing 2004). In addition, dolphin regurgitation has been collected over the years and has included fish vertebrae, squid beaks (*Doryteuthis sp.* identified by N. Barros[2]), and large squid pens surpassing smaller reef squid size measurements, suggesting that these dolphins forage at least over deeper water when the Deep Scattering Layer (DSL) rises after dark. This paper describes nocturnal foraging activity of Atlantic spotted dolphins, recorded in the Bahamas between 1991 and 2004.

Research on Atlantic spotted dolphins has been conducted for 4 mo every summer on Little Bahama Bank (LBB), Bahamas, since 1985. The sandbank ranges in depths from 6 to 16 m and is adjacent to the deep waters of the Gulf Stream to the west and Grand Bahama Island to the South (Fig. 1). Dolphins were observed regularly during daytime hours on the shallow sandbank using a 20 m power catamaran. Nighttime observations (after 1900) were made when conditions were less than Beaufort 2 and the research vessel was located near the deep water edge. The research vessel motored along the edge of the sandbank where water depth typically drops, sometimes sharply, from $\leq$10 m to $\geq$200 m within 0.5–1.0 km. Engines were turned off and the research platform drifted passively in the northbound current along the edge of the sandbank. A hydrophone was deployed to detect any acoustic cues of dolphins in the area. Deck lights, and a floodlight located on the bridge, were used to facilitate

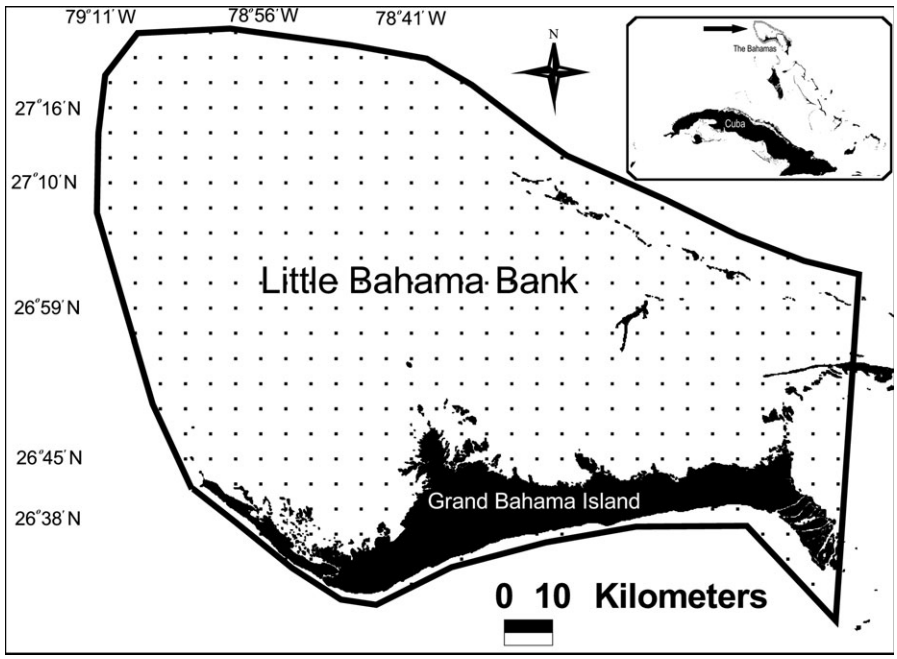

Figure 1. Study area. Dotted area indicates the shallow sandbank, surrounded by deep water. Arrow on the insert indicates the Bahamas study area.

[2]Personal communication from N. Barros (deceased), Mote Marine Laboratory and Aquarium, 1600 Ken Thompson Parkway, Sarasota, FL, 21 January 1994.

identification and observations of both the prey and the dolphins. Although disturbance of foraging behavior is possible with lights, on occasion both deck lights and generators were turned off during a drift and night-vision goggles allowed verification and detection of foraging dolphins. Once a drift offshore began, environmental conditions including location and water depth were recorded every 20 min. When dolphins were sighted from the boat, and often right next to the boat, group size was documented and age class composition and individual identifications were made when possible. Prey species were easily identified from the surface right next to the boat or underwater near the surface. Samples were collected using a dip net for verification during an observation or occasionally flew onto the deck during a chase by the dolphins. Divers regularly entered the water with cameras or an underwater video and hydrophones to document behaviors and sounds during feeding, as this is a semi-habituated community of dolphins. On occasion, usually due to dangerous jellyfish at the surface, divers did not enter the water but observed dolphins as they continued to chase and catch fish for hours next to the boat.

Table 1 lists the number of observed foraging events and their variation in depth, distance traveled, mean duration, and prey species. Between 1991 and 2004, we collected 48 observations of nocturnal feeding. Duration of the drifting events ranged from 10 min to over 9 h (for some all night drifts) with an average of 3:20 h:min. Actual observations of dolphins during these drifts ranged from 10 min to over 8:45 h:min, with an average of 1:49 h:min. During foraging events, water depth ranged from a mean ($\pm$ SD) minimum depth of 149.4 $\pm$ 75.9 m to a mean maximum depth of 307.6 $\pm$ 63.5 m. Observable groups (defined as animals engaged in similar behavior) of dolphins ranged in number from 1 to 15 with a mean of 6.8 $\pm$ 3.8 dolphins per foraging episode (Table S1).

The most common prey species observed were flying fish (Family Exocoetidae), and squid (*Doryteuthis* sp.), followed by needlefish (Family Belonidae) and ballyhoo/halfbeaks (Family Hemiramphidae) (Table 1). Dolphins were observed from the surface chasing and consuming flying fish. Squid were chased just below the surface often into the depths. Both types of chases were correlated with echolocation click trains often with a terminal buzz representing the targeting and closing in on prey (Verfuss *et al.* 2008) and these buzzes were recorded and verified with lone dolphins in close proximity. Although we rarely observed the consumption of squid in the water, previously collected regurgitated beaks and pens have been collected over the years during daytime observations suggesting that these chases are, at least in part, successful and squid is part of their diet.

Drift events covered a distance ranging from 1 to 24.7 km (mean 6.1 $\pm$ 5.1, Table 1), depending on starting position, duration of drift, the tidal states, currents, and winds, during which we encountered different identifiable dolphins as we passively drifted northward along the edge. Dolphins of both sexes and all developmental classes were observed foraging at night (Table S1). Dolphins could be individually identified by eye from spot patterns or body marks, from the surface, or on nighttime video and have been aged and tracked over the decades (Herzing 1997) as part of our regular summer research. Groups often included females whose reproductive status was known and monitored throughout the summer months by their size in girth and subsequent fall or spring calving. The majority of groups (43.8%) involved mixed sexes (n = 21). Single sex groups accounted for 14.6% (n = 7) and 41.7% were undetermined (n = 20). Mixed age groups were seen most often (68.8%, n = 33), with the most common composition including all age classes (n = 18, 37.5%). Groups of older adults only (fused: Herzing 1997) were

Table 1. Number of nocturnal foraging events, mean minimum and maximum depth (meters), and distance traveled during drift (kilometers), average time (hours:minutes), and prey species observed.

Year	No. foraging events	Mean minimum depth (m)	Mean maximum depth (m)	Mean distance drifted (km)	Mean duration (h:min)	Prey (# events with prey type)
1991	1	NA	NA	NA (3.2)[a]	NA	squid (1)
1992	4	NA	NA	2.7	2:07	needlefish (1), flying fish (2), ballyhoo (1), half beak (1)[b]
1993	4	109.1	209.7	7.1	3:55	needlefish (1), squid (2)[c]
1994	5	106	279.1	9.2	4:20	flying fish (4), squid (4), half beak (1)[b]
1995	8	131.4	304.6	4.5	2:44	needlefish (4), flying fish (7), squid (6)
1996	2	149.9	361.2	4.8	3:18	needlefish (2), flying fish (2), squid (2)
1997	1	NA	NA	NA (3.2)[a]	NA	needlefish (1), flying fish (1), ballyhoo (1)
1998	4	161.3	284.5	5.6	3:33	needlefish (4), flying fish (3), squid (4), ballyhoo (2)
1999	4	188.9	350.5	4.8	3:18	needlefish (3), flying fish (4), squid (3), ballyhoo (2)
2000	2	81.5	251.5	4.5	1:42	needlefish (2), flying fish (2), squid (2), ballyhoo (1)
2001	2	136.4	312.4	4.1	2:29	needlefish (1), flying fish (1), squid (2), ballyhoo (2)
2002	2	147.9	335.3	6.5	3:22	needlefish (1), flying fish (2), squid (2)
2003	4	170.2	330.9	12.5	4:20	needlefish (4), flying fish (4), squid (3)
2004	5	224.4	37.9	7.1	4:19	needlefish (5), flying fish (5), squid (5), ballyhoo (2)
All years	48	149.4	307.6	6.1	3:20	flying fish (37, 75.6%), squid (37, 75.6%), needlefish (29, 59.2%), ballyhoo (10, 20.4%), half beak (2, 4.1%)

Note: NA: either only one sample, or minimum and maximum were not recorded.

[a]Distance is for the one drift for that year.

[b]Indicates one event with no prey identified.

[c]Indicates two events with no prey identified.

encountered the least (14.6%, $n = 7$). Known cow/calf pairs, possibly baby-sitting dolphins, were observed in 35.4% ($n = 17$) episodes, sometimes in the company of additional calves. Newborns of the year were observed with their mothers offshore at night but calves were never observed foraging alone. Pregnant females were observed on five occasions ($n = 5$, 10.4%). Age class and reproductive states were easily documented; however, individual identification of all dolphins was difficult, thus for most events a small proportion of the group was identified. In addition, a sympatric species in the area with Atlantic spotted dolphins, the bottlenose dolphin (coastal ecotype) is observed in 15% of Atlantic spotted dolphin diurnal sightings (Herzing and Johnson 1997), yet has never been observed nocturnally or in depths >200 m along this edge alone or with Atlantic spotted dolphins and has never been observed feeding on flying fish or squid in this area, suggesting a separation of foraging niches for these two species.

Atlantic spotted dolphins in the Bahamas were observed foraging at night, in deep water, on a variety of species of fish and squid. Age, sex, and reproductive status were not limiting factors in the exploitation of deep-water resources off the shallow Bahamas sandbanks since males and females of all age classes, including newborns and calves and females of different reproductive states (nonreproductively active, pregnant, and nursing with a calf) engaged in nocturnal feeding in deep water. The sex and age class composition of groups, the majority including all age classes, is consistent with daytime encounters including all behaviors (Elliser and Herzing 2012).

Although this resident community of Atlantic spotted dolphins forages during daylight on bottom dwelling and schooling fish on the shallow sandbanks (Herzing 1996, 2004), the adjacent deep waters represent an additional food resource. Atlantic spotted dolphins are rarely encountered diurnally in deep water, which suggests that they exploit the variety of prey in the DSL. Another species that utilizes the DSL are Hawaiian spinner dolphins, where dolphins rest in the shallow sandy bay during the day until sunset, when they head out to deep water to forage, returning to the bay in the early morning (Norris *et al.* 1994). Although tiger sharks have been observed in the deep waters of the Bahamas at night with Atlantic spotted dolphins, nocturnal feeding off the edge of the sandbank appears to be an activity of all age classes of Atlantic spotted dolphins in the Bahamas to some degree.

It remains unclear if Atlantic spotted dolphins in the Bahamas are primarily (1) nocturnal feeders, with occasional instances of opportunistic diurnal feeding; (2) diurnal feeders with episodic nocturnal foraging; or (3) opportunistic with specialization based on experience or prey species availability. In the past the analysis of nocturnal foraging habits of dolphins has been determined primarily from the examination of the stomach contents of dead animals (Perrin *et al.* 1973, Barros and Wells 1998). The unique habitat in the Bahamas makes this area a new location for observing diurnal and nocturnal foraging habits of small delphinids.

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Supporting Information

The following supporting information is available for this article online: http://onlinelibrary.wiley.com/doi/10.1111/mms.12016/suppinfo.

Table S1. Group size and composition for nocturnal foraging events.