

Observations of rough-toothed dolphins (*Steno bredanensis*) off the coast of Utila, Honduras

Stan A. Kuczaj II* and Deirdre B. Yeater

Department of Psychology, Marine Mammal Behavior and Cognition Laboratory, 118 College Drive #5025, University of Southern Mississippi, Hattiesburg, MS 39406-5025, USA. *Corresponding author, e-mail: s.kuczaj@usm.edu

Local dive shop operators and fishermen report that rough-toothed dolphins (*Steno bredanensis*) are frequently encountered off the coast of Utila, Honduras, (16° 05' 46.5" N 86° 55' 47.8" W). Our observations suggest that at least some of these animals may constitute a resident population, although the extent of the resident group's home range has not been determined. Twenty-eight rough-toothed dolphins were identified using photo-identification techniques, 15 of which were re-sighted on two or more occasions. The 12 animals that were re-sighted four or more times were typically seen together, suggesting that they constitute a stable social group. At least one of these dolphins is an adult male, and his continued presence in this social group may reflect a social structure for rough-toothed dolphins that differs from that described for other dolphin species. Social interactions often involved tactile behaviours such as pectoral fin rubbing and side rubbing. The observed dolphins sometimes expressed interest in the research vessel and other boats by approaching, and on separate occasions examined a hydrophone and slow moving propeller visually and echoically. Overall, our behavioural observations suggest: (1) synchronous behaviours and 'tight' groupings are common while rough-toothed dolphins are travelling; (2) tactile contact is an important aspect of social interactions for rough-toothed dolphins; (3) cooperative behaviour occurs during play; and (4) rough-toothed dolphins are curious.

INTRODUCTION

The literature concerning rough-toothed dolphins (*Steno bredanensis*) is replete with comments concerning how little is known about this species (Evans, 1987; Waring et al., 1997; Jefferson, 2002). For example, the world-wide distribution and seasonal migratory patterns (if any) of this species are unknown (Maigret, 1994; Carwardine, 1995). Rough-toothed dolphins are most typically found in deep tropical, subtropical, and warm temperate offshore waters, but are also found in cooler waters (Ritter, 2002). Although rough-toothed dolphins are more likely to be sighted in deep offshore waters, they have also been observed in relatively shallow coastal waters off Brazil (Lodi, 1992; Ott & Danilewicz, 1996; Flores & Ximenez, 1997; Lodi & Hetzel, 1999), Japan (Miyazaki, 1980), and Mauritania (Maigret et al., 1976; Addink & Smeenk, 2001), as well as near the shores of islands with deep drop-offs (Ritter, 2002; Gannier & West, 2005; Götz et al., 2005; Webster et al., 2005). The extent to which rough-toothed dolphins visit shallow waters is not clear. Ritter (2002) reported that the dolphins were rarely sighted in waters less than 50 m deep off La Gomera, Canary Islands, while the dolphins observed by Webster et al. (2005) in the Hawaiian Archipelago were never sighted in water less than 501 m. However, off of the coast of Brazil, Lodi (1992) reported rough-tooth dolphins in waters 20 m deep, while Lodi & Hetzel (1999) found rough-toothed dolphins in 5–11 m deep water.

The lack of certainty concerning rough-tooth dolphin habitat use reflects the relative paucity of field studies on

this species, perhaps because they are considered difficult to observe at sea (Miyazaki & Perrin, 1994). Consequently, Jefferson (2002) concluded that 'essentially nothing is known about population or stock structure in this species. In fact, the ecology and biology of the species are poorly studied (p. 1056).

Efforts in recent years have suggested possible home ranges for these animals. Ritter (2002) reported year-round abundance of rough-toothed dolphins off La Gomera, Canary Islands, and Gannier & West (2005) found rough-toothed dolphins year-round near Tahiti and Moorea. Neither of these studies involved photo-identification of individual animals, and so it is not clear if different rough-toothed dolphins pass through these areas throughout the year or if resident groups of rough-toothed dolphins reside in each of these areas. Webster et al. (2005) used photo-identification techniques to identify 328 rough-toothed dolphins in the Hawaiian Archipelago. There were 223 individuals identified off the coast of Kaua'i/Ni'ihau, 16 individuals identified off the coast of O'ahu, and 89 individuals identified off the coast of Hawai'i. Re-sightings were only reported for Hawai'i, with 37 within-year re-sightings and 19 between-year re-sightings. There were no inter-island re-sightings, suggesting site fidelity for specific islands.

The social structure of rough-toothed dolphin groups is poorly understood. Small groups of rough-toothed dolphins sometimes maintain close spatial proximity while travelling (Addink & Smeenk, 2001; Pitman & Stinchcomb, 2002; Ritter, 2002; Götz et al., 2005), an arrangement

Table 1. *Description of behavioural events produced by rough-toothed dolphins.*

Behaviour	Description
Aerial	Animal performs an out of water movement
Approach human	Animal approaches human(s)
Approach hydrophone	Animal approaches the hydrophone
Breach	Animal comes up out of the water and slaps down on one of its sides
Bow-riding	Animal swimming at bow of boat as it moves
Chase	One animal follows another at a fast speed
Chase fish	Animal chases after fish
Chin slap	Animal brings head above water and slaps chin (bottom portion of the rostrum) down
Chuff	Animal forces air out of its blowhole making a chuffing noise
Consume fish	Animal eats fish
Dive	Animal dives down into the water
Fluke-in dive	Animal dives from surface with tail not breaking the surface of the water
Fluke-out dive	Animal dives from surface with tail out of the water at apex of dive
Fluke slap	Animal slaps object with its fluke
Group social ball	3+ animals engage in energetic social behaviour, usually involves surface splashing in the same area continually for a few seconds or more
Group swim	Three or more animals swim together
Other	Behaviour not specified here
Pair swim	Two animals swim together
Pec slap	Animal slaps object with its pectoral fin
Pec wave	Animal waves pectoral fin in the air above the water surface
Play with object	Animal plays with an object
Porpoising	Animal porpoises through the water while swimming
Produce bubble	Animal blows one or more bubbles
Rest at surface	Relatively motionless at surface
Spin	Animal rotates roughly 360 degrees or more out of the water
Spy hop	Bobbing vertical at surface emerging to about dorsal fin
Solo swim	Animal swims alone
Sexual	Animal demonstrates a sexual behaviour
Tactile	Non-sexual contact between animals
Ttail wave	Animal waves tail in the air above the water surface
Vocalize	Animal makes a vocalization
Wake-riding	Animal swimming through wake that boat produces as it moves

that may reduce energy costs (Weihs, 2004) and facilitate ‘eavesdropping’ on echoes from sonar signals from conspecifics (Götz et al., 2005). In addition, such ‘tight’ formations may increase opportunities for various forms of tactile contact, which in turn may play important roles in communication, social bonding, and social maintenance (Dudzinski, 1998; Johnson & Moewe, 1999; Sakai et al., 2006). However, the demographics of the individuals in the tight group formations exhibited by some rough-toothed dolphin groups have yet to be determined, which makes it difficult to determine the social significance (if any) of these ‘tight’ spatial configurations.

Information concerning the behaviour of rough-toothed dolphins is sparse, but it nonetheless paints an intriguing picture of this species. Their social interactions involve visual displays such as ‘belly-flashing’, tactile behaviours such as fluke-stroking, and high-energy behaviours such as chases (Addink & Smeenk, 2001). Rough-toothed dolphins also occasionally produce high-energy surface behaviours such as breaches, and sometimes approach boats and engage in bow-riding or wake-riding (Watkins et al., 1987; Steiner;

1995; Lodi & Hetzel, 1999; Ritter, 2002). These behaviours, coupled with their play with objects ranging from plastic bags to turtles and puffer fish, may reflect this species’ natural curiosity (Ritter, 2002; Steiner, 1995).

Rough-toothed dolphin foraging appears to be flexible and opportunistic (Lodi & Hetzel, 1999; Addink & Smeenk, 2001; Ritter, 2002). They appear to cooperate in a variety of ways to increase foraging success (Brower & Curtsinger, 1979; Smeenk et al., 1995; Steiner, 1995; Lodi & Hetzel, 1999; Addink & Smeenk, 2001; Pitman & Stinchcomb, 2002), and may even actively teach calves and juveniles to forage (Smeenk et al., 1995; Lodi & Hetzel, 1999; Addink & Smeenk, 2001). Cooperative behaviour has been observed in other contexts as well. Epimeletic behaviour consisting of a female rough-toothed dolphin supporting a dead adult female dolphin at the surface for approximately two hours was reported by Lodi (1992), and cooperative play behaviour among two adults and a juvenile rough-toothed dolphin was described by Kuczaj & Highfill (2005).

In this paper, we report on observations of rough-toothed dolphins conducted in the waters near Utila, Honduras,

Table 2. Behavioural states and definitions used in this study.

Behaviour state	Definition
Travel	Moving steadily in one direction
Feed	Any of a variety of behaviours distinguished by such things as repeated dives in varying directions in one location, feeding circles, feeding splashes, fish kicks, feeding rushes, and fish tosses
Social	Some or all pod members in almost constant physical contact with one another, oriented toward one another, and often displaying surface behaviours, no forward movement
Rest	Moving very slowly or drifting in one direction
Mill	Moving in varying directions in one location but showing no surface behaviours and no apparent physical contact between individuals, usually staying close to the surface
With boat	Dolphins approach or travel alongside a boat and may be either bow-riding or wake-riding
Sexual	Any behaviour that involves genital to genital contact, rostrum to genital inspection, erection, and/or actual copulation
Acrobatics	Surface displays that involve slapping a body part on the water surface including aerials and breaches
Play with object	Dolphins manipulate or interact with a foreign object with any body part

between June 2004 and June 2006. We discuss the identification of individual animals, their behaviour, and their social affiliations. We also consider possible evidence for site fidelity for some of these animals.

MATERIALS AND METHODS

Surveys were conducted near Utila, Honduras (16°05'46.5" N 86°55'47.8"W). Utila is an island that lies approximately 28.9 km from the northern coast of the Honduran mainland. The island is 41 km² in size and is the smallest of the Honduran Bay Islands. Visibility under water is normally 24 to 37 m, which provides opportunities for both underwater and surface observations. Water temperatures range from 27 to 29°C for most of the year (Behrens, 2002). Water depth ranges from less than 10 m (close to shore) to more than 1500 m due to nearby steep drop-offs.

Surveys were conducted on 10 days in June 2004, 6 days in September 2004, 16 days in May 2005, 5 days in August 2005, 6 days in March 2006, and 18 days in May 2006 using either a 13 m fishing vessel or a 10 m dive boat as a research platform. Supplemental information was provided by local dive shops that are collaborating with the authors. Personnel at these dive shops were trained by the authors to conduct surveys when the authors are not in the field, and do so when time and conditions permit.

Each survey included the circumnavigation of the entire island. However, the specific search pattern for each survey was variably determined by weather conditions at the time. During a survey, observers scanned the sea while looking for indications of dolphin surface activity. If dolphins were sighted, the research vessel carefully approached in order to obtain digital photographs of dorsal fins and digital video recordings of dolphin behaviour. If conditions permitted, swimmers sometimes entered the water in order to obtain underwater photographs and video. For each sighting, behavioural data were recorded continuously using an ethogram that allowed us to tally behavioural events (e.g. spy hop, fluke slap, chase other dolphin, bow-ride, breach, and pair swim, Table 1). This information was also used to determine the behavioural state of each sighted dolphin group. Behavioural states included travel, feed, mill, rest, social, sexual, with boat, acrobatics, and play with objects.

Operational definitions of these states are consistent with those provided by Shane et al. (1986) (Table 2).

Equipment and methods of analyses

A Garmin® GPS (Global Positioning System), Garmin® Mapsource® Blue Chart software, and Arc View were used to record the locations of dolphin sightings and the track lines for each survey. Surface behavioural video data were collected using a Sony® digital video camcorder. For underwater videography, a custom-made underwater video and acoustic array was used (Dudzinski et al., 1995), which included a Sony® Handycam® camcorder and a Sony® digital audio tape recorder. Noldus The Observer® was used to code and analyse behaviours recorded on video. Digital photographs of the dolphins' dorsal fins were obtained with a Canon EOS 10D digital camera equipped with a 100–400 mm zoom lens. The mark–recapture methodology was used (Markowitz et al., 2003) and photographs were categorized and matched using Adobe Photoshop. All dolphin identifications and resightings from photographs were confirmed by three independent researchers before being entered into our data base. MATLAB® SOCPROG 2.2 was used to analyse association patterns within dolphin social groups (Whitehead et al., 2005).

RESULTS

Species sighted

Species sighted during surveys included rough-toothed dolphins, long-snouted spinner dolphins (*Stenella longirostris*), bottlenose dolphins (*Tursiops truncatus*), and short-finned pilot whales (*Globicephala macrorhynchus*). Local dive boats have also photographed killer whales (*Orcinus orca*) and sperm whales (*Physeter macrocephalus*) near Utila during the past two years. Spinner dolphins and rough-toothed dolphins were the most commonly observed species.

Rough-toothed dolphin sightings

During June 2004, 60 h of effort resulted in a total of eight hours of observations of rough-toothed dolphins on five separate days. During September 2004, 41 h of effort yielded ten hours of observations of rough-toothed dolphins



Figure 1. Locations at which rough-toothed dolphins were sighted.

on three separate days. During May 2005, 114 h of effort failed to produce a rough-toothed dolphin sighting. During August 2005, 17 h of effort resulted in ~2 h of rough-toothed dolphin observations during a single encounter. Thirty hours of effort in March 2006 resulted in 1½ h of rough-toothed dolphin observations during a single encounter. Finally, 109 h of effort in May 2006 yielded four hours of observations. Therefore, approximately 25.5 h of observations of rough-toothed dolphins have been obtained since we began our observations in June 2004. During these observations, 701 min of surface video and 113 min of underwater video were obtained.

Figure 1 shows the locations at which rough-toothed dolphins were first sighted during surveys: four of the sightings were recorded by our dive shop collaborators, and are confirmed by photographic records. As shown in Figure 1, rough-toothed dolphins were most commonly sighted towards the eastern half of Utila, but were also seen at other locations around the island. Water depth for these initial sightings ranged from 6 to 122 m deep. The dolphins often ventured into much deeper water as they travelled and were sometimes in water deeper than 1500 m during our observations.

Identification and re-sightings of individuals

Photographs of dorsal fins were used to identify 28 individual rough-toothed dolphins, 15 of which were re-

sighted. Specifically, three dolphins were sighted on two occasions, four dolphins were sighted on four occasions, two dolphins were sighted on five occasions, one dolphin was sighted on seven occasions, two were seen on eight occasions, and one animal was observed on nine occasions. Given that there were 15 sightings of groups of rough-toothed dolphins, one might expect the number of re-sightings to be higher if some of these dolphins constitute a resident population for this area. Although photographs were taken during each of these observations, the number of dolphins that could be reliably identified from these photographs ranged from zero (one encounter) to 16 (one encounter), with a mean of 6.4 dolphins identified per sighting. Given these limitations, the numbers of re-sightings across years suggests that some of these animals may constitute part of a resident population. Fifteen animals were identified from our observations in 2004. Of these, six dolphins were re-sighted in 2005 and in 2006. Another six animals were re-sighted in 2006, but not in 2005. The remaining three animals from 2004 have not been re-sighted. All six animals that were identified in 2005 had been identified in 2004. Of the 24 dolphins identified in 2006, 12 had been previously identified in 2004 (six of these had also been seen in 2005). The remaining 12 animals were identified for the first time in 2006.

Group size and composition

Group size ranged from a minimum of five to a maximum of 30 individuals, with eight to 12 animals being the most common group size. As noted above, we identified 28 individual dolphins, over half of which were re-sighted. In order to determine associations among re-sighted dolphins, we selected the 12 animals that had been re-sighted four or more times. Half-weight associations were determined using SOCPROG (Whitehead et al., 2005). Associations ranged from 0.44 to 1.0 (Table 3), demonstrating that these 12 animals were typically observed with one another during our observations.

We also assessed ‘close’ associations between individuals within the same larger group. For this analysis, dolphins that were within ~1 m of each other were considered to be closely associated. Although the duration of these associations varied, in virtually all cases they exceeded 60 s. Half-weight

Table 3. Half-weight associations for the twelve dolphins re-sighted a minimum of four times.

ID	Dolphin ID											
	1	4	5	9	10	14	15	16	18	19	20	23
1	–	1	0.62	0.5	0.75	0.75	0.73	0.6	0.44	0.6	0.5	0.67
4		–	0.62	0.5	0.75	0.75	0.73	0.6	0.44	0.6	0.5	0.67
5			–	0.82	0.62	0.62	0.75	0.67	0.71	0.8	0.82	0.57
9				–	0.67	0.5	0.53	0.71	0.62	0.71	0.88	0.62
10					–	0.75	0.55	0.6	0.67	0.8	0.67	0.67
14						–	0.73	0.8	0.67	0.8	0.67	0.89
15							–	0.62	0.67	0.77	0.67	0.67
16								–	0.55	0.67	0.86	0.91
18									–	0.91	0.77	0.6
19										–	0.86	0.73
20											–	0.77
23												–

Table 4. Half-weight associations for dolphins in close proximity to one another.

	0.30–0.39	0.40–0.49	0.50–0.59
Dolphin IDs	1 ↔ 10	18 ↔ 19	4 ↔ 23
	4 ↔ 15	14 ↔ 23	5 ↔ 28
		9 ↔ 15	
		18 ↔ 20	

associations were determined using SOCPROG, and revealed that even though dolphins may have been part of the same social group, they were not necessarily seen in close proximity to one another. For example, Dolphins 1 and 4 were highly associated in terms of being in the same group, but were not seen in close proximity to one another (Table 4).

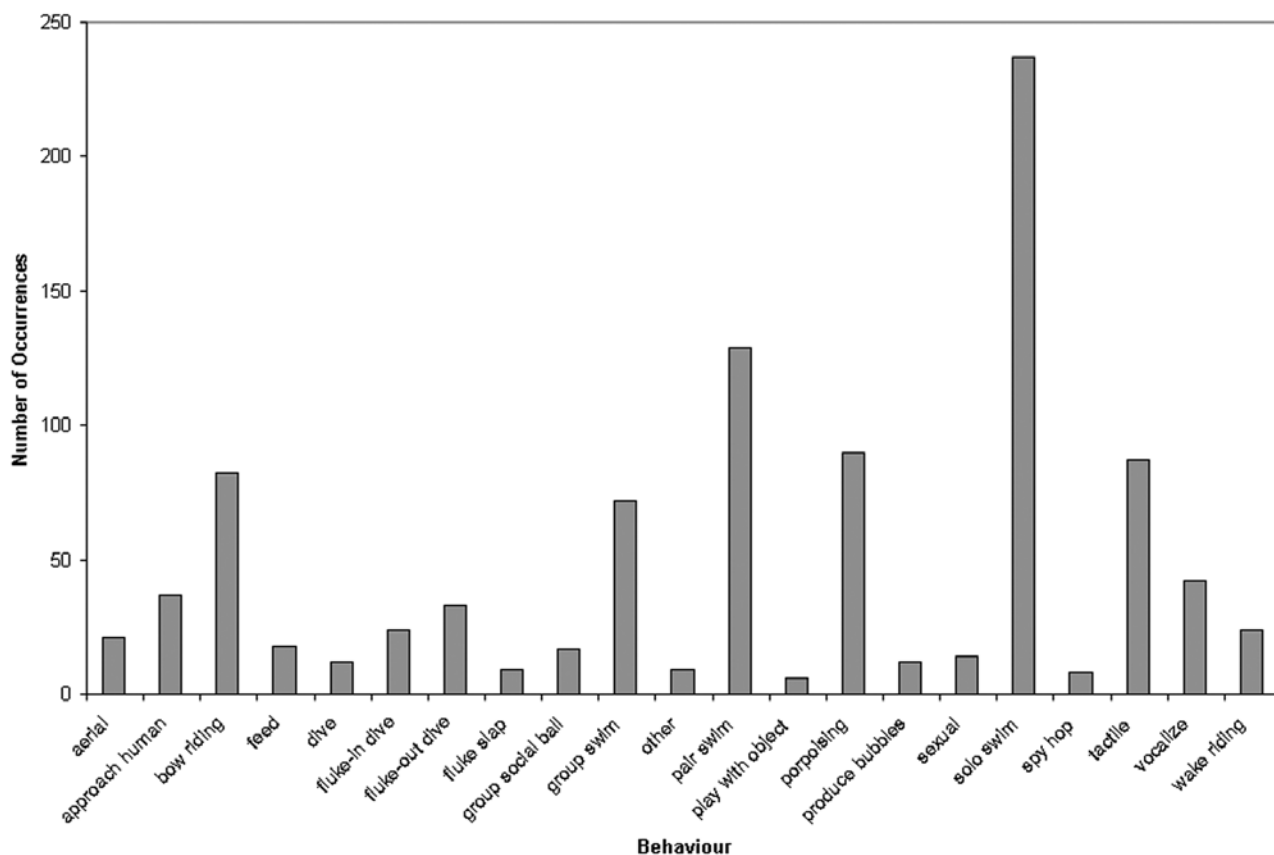
Although we positively identified the gender of only one animal (an adult male), this male was observed in 2004, 2005, and 2006, and appears to be a permanent member of a social group consisting of adult animals, as well as juveniles and calves of unknown sex. We believe that three of these dolphins are females, and possibly mothers, due to their close associations and multiple re-sightings with calves or juvenile dolphins. The echelon position was often observed, which supports the notion that some of the dolphins were mother and calf pairs. Calves were observed nursing on two occasions from the adults presumed to be mothers. With

one exception, each rough-toothed dolphin group that was observed included one or more calves and a single juvenile dolphin.

Behavioural states and events

The most common behavioural states of the observed dolphin groups were travel (26.6%), with boat (17.5%), and feed (14.9%). Social (11%), rest (9.7%), and mill (9%) were the next most common states. Object play (7.1%) and sexual (3.8%) were the least common states. Within each of these states, a variety of behavioural events were documented. The frequency of occurrence of the most common behavioural events is summarized in Figure 2.

Dolphins were most likely to produce solo swims while travelling (Figure 2). However, they also produced many pair swims and group swims. During pair and group swims, the dolphins typically maintained tight spatial configurations in which the animals were less than one body width from one another. In fact, they were often touching while in such tight formations. Dolphins in these formations often engaged in synchronous surfacing, and one observation illustrates how certain animals may influence the behaviours of others. A group of ten dolphins was swimming in synchrony near the surface. One dolphin (dolphin no. 5 in our catalogue) changed direction and immediately began what was to become a deep dive. The other nine dolphins in the group immediately changed direction and followed Dolphin 5. We believe that Dolphin 5 is a mother with a young calf, and she is often observed with other dolphins. Whether she is one of the leaders of this group remains an open question.

**Figure 2.** Frequency of most commonly observed behavioural events.

The dolphins also frequently engaged in various forms of tactile contact with one another. These included swimming or resting with parts of the body touching, pectoral fin rubbing, side rubbing, and mouthing. Mouthing consisted of one dolphin gently 'rubbing' another dolphin's body with its open mouth. Full body rubs were also observed on multiple occasions. These occurred when two dolphins were slowly swimming in opposite directions while rubbing the entire length of their bodies against one another. These tactile interactions were believed to be affiliative rather than combative or aggressive given the slow speed with which the interactions occurred, the absence of loud or harsh vocalizations (such as squawking), and the absence of fast chases and jerking movements.

Dolphins often approached the research vessel to bow-ride or wake-ride, and were also observed swimming alongside the research vessel or other boats. They followed the boat during two encounters, and on one occasion oriented towards and echolocated on the boat's propeller (the propeller was moving quite slowly at the time). Three individuals also oriented towards the hydrophone used during another encounter. One or more of these dolphins echolocated on the hydrophone.

The dolphins occasionally exhibited interest in human swimmers on occasions during which swimmers were in the water. Individual dolphins sometimes changed course to swim in close proximity to swimmers, often orienting towards a swimmer and occasionally echolocating on a swimmer. Four dolphins encircled human swimmers on separate occasions during which time the dolphin swam in circles around a human swimmer, orienting toward the human while doing so.

The rough-toothed dolphins were observed playing with objects on numerous occasions. On one occasion, an adult dolphin held a piece of plastic in its mouth, dropped it, and then retrieved it with its pectoral fin. Similar behaviours were observed with pieces of seaweed and seagrass. Dolphins also sometimes tossed a fish in the air and then retrieved it, occasionally repeating the sequence over and over. Kuczaj & Highfill (2005) observed cooperative play between one juvenile and two adult rough-toothed dolphins during one of their observations. The adults were playing with a piece of plastic, passing it back and forth as they swam. Each adult involved the juvenile in this game by releasing the plastic close to the young dolphin's mouth, thereby making it easier for the juvenile to catch the plastic. This episode of cooperative play lasted approximately 15 min.

DISCUSSION

The observations reported above support the notion that rough-toothed dolphins frequently visit the waters near the coast of Utila. Although we did not find rough-toothed dolphins each day that we surveyed these waters for marine mammals, we did sight them on numerous occasions. Furthermore, sightings of rough-toothed dolphins were often reported by individuals on other vessels on days during which we failed to find rough-toothed dolphins. Although we cannot be certain that the rough-toothed dolphins spotted by other vessels are part of the group we normally observed, our re-sightings of 15 animals over a three year

period demonstrates that this area has high site fidelity for at least some of these dolphins. Some of the animals that we have observed off Utila were also observed in a shallow water bay at a neighbouring island, Roatan, during March 2006, suggesting that their home range extends to at least the waters surrounding these two islands.

Site fidelity has been reported for a variety of cetaceans, including bottlenose dolphins (e.g., Bearzi et al., 1997; Connor et al., 2000a; Gubbins 2002; Kerr et al., 2005), Hector's dolphins (*Cephalorhynchus hectori*; Brager et al., 2002), common dolphins (*Delphinus delphis*; Neumann et al., 2002), and killer whales (*Orcinus orca* Bigg et al., 1987; Bigg et al., 1990). Webster et al. (2005) reported high-site fidelity for rough-toothed dolphins off the Hawaiian Archipelago, which is consistent with our findings for Utila. However, Webster et al. believed that the rough-toothed dolphins in their study area exhibited high site-fidelity for individual islands, whereas at least some of the dolphins we have studied visited at least two of the islands in our study area. Clearly, more work is needed to determine the range of home areas for groups of rough-toothed dolphins, as well as the ecological characteristics of these home ranges. Consequently, we plan to expand our survey efforts to include the Honduran Bay Island area (Utila, Roatan, Guanaja, and Cayos Cochinos) in order to better understand the home range of the group of dolphins that we have described here.

Although the dolphins in this study were found in much more shallow water than has been observed by others, the behaviours exhibited by the rough-toothed dolphins we observed were nonetheless consistent with those reported in the literature. Group size ranged from 5–30 dolphins, which is consistent with reports that small groups of rough-toothed dolphins are more common than larger groups of 50 or more (Watkins et al., 1987; Miyazaki & Perrin, 1994; Acevedo-Gutiérrez, 2002; Jefferson, 2002; Gannier & West, 2005). During our observations, the dolphins frequently engaged in synchronous swimming among tightly spaced subgroups, a behaviour that may characterize this species (Addink & Smeenk, 2001; Pittman & Stinchcomb, 2002; Ritter, 2002 Götz et al., 2005). Synchronized swimming in tight formations may signal group cohesion (Ritter, 2002), and perhaps also serve to strengthen social bonds. In addition, Götz et al. (2005) suggested that these tight formations might facilitate 'eavesdropping' on the echolocation efforts of dolphins within the group. Rough-toothed dolphins appear to value tactile contact, and tight formations may increase opportunities for such forms of interaction.

Dolphins frequently approached the research vessel or other boats during our observations, and often engaged in bow-riding or wake-riding. Similar behaviours have been reported by Lodi & Hetzel (1999), Ritter (2002), Steiner (1995) and Watkins et al., (1987). The rough-toothed dolphins that we observed occasionally produced high energy surface behaviours, such as breaches and leaps. Similar behaviours by rough-toothed dolphins were also reported by Ritter (2002).

The playful nature of rough-toothed dolphins stood out in our observations. The dolphins played with a variety of objects, including pieces of plastic, seaweed, seagrass, and whole fish. They have also been observed playing with an

inflated puffer fish (Steiner, 1995; Lodi & Hetzel, 1999), a jelly fish and a sea turtle (Ritter, 2002). The cooperative play we witnessed (Kuczaj & Highfill, 2005) has not been reported by others, but cooperative foraging has been documented (Brower & Curtsinger, 1979; Steiner, 1995; Pittman & Stinchcomb, 2002). Cooperation during play may serve to facilitate cooperation during foraging. Or, perhaps rough-toothed dolphins engage in a variety of cooperative behaviours, and we have only scratched the surface of such behaviour for this species. A better understanding of rough-toothed dolphin cooperation, particularly the manner in which calves and juveniles learn to cooperate, would further our understanding of cetacean culture (Rendell & Whitehead, 2001).

The curiosity of rough-toothed dolphins was also evident in our observations. They approached and followed the boat, and investigated a slow moving propeller and a hydrophone (see Ritter, 2002, for a description of similar behaviours). They also appeared interested in human swimmers, often approaching them as if to get a 'better look'. In such cases, a dolphin swam directly towards or underneath a human swimmer, oriented its head toward the swimmer, and sometimes echolocated on the swimmer. Captive bottlenose dolphins are known to seek novelty (Kuczaj et al., in press), and captive rough-toothed dolphins can be trained to produce novel behaviours (Pryor et al., 1969). Novelty is also likely to be important for wild dolphins, for an interest in novelty facilitates flexible problem solving, which in turn enhances flexible foraging abilities (Kuczaj & Walker, 2006).

Perhaps the most unique aspect of our observations concerns the continual presence of an adult male in the social group. This contrasts sharply with what is known about bottlenose dolphins. Male bottlenose dolphins are not long-term members of social groups that also contain females and calves. Male bottlenose dolphins typically associate with one or two other males, and interact with female groups only when seeking mates (Connor et al., 2000b). The consistent presence of an adult male in the observed group of rough-toothed dolphins off Utila suggests that the social structure of rough-toothed dolphins may differ from that of bottlenose dolphins. This rough-toothed dolphin male has been observed copulating with different females in the group, and so may have sired at least some of the young dolphins. If this is the case, the male is a member of the social group as well as presumably the father of some members of the group. We do not yet know if he is the sole adult male, but hope to determine the gender of the remainder of the group during future field trips. Regardless, based on these observations it seems that rough-toothed dolphin social structure involves adult males as well as adult females and juveniles and calves of both sexes. Although some killer whale males remain in groups containing females and the females' offspring (Connor et al., 2000b), the males are sons or grandsons of some of the females, and are not the fathers of the young animals in the group. Thus, if the rough-toothed male is indeed the father of any of the offspring in the group, rough-toothed dolphin social structure may be unique among the cetaceans studied to date.

Although recent years have witnessed a gradual accumulation of information concerning rough-toothed

dolphins, there are still many more questions than answers. It remains the case that relatively little is known about their social structure, behavioural repertoire, extent of their home range, effect of seasonality on site fidelity, and world-wide distribution. There is clearly much work to be done, and we suspect that many interesting discoveries lie ahead.

We acknowledge the Dolphin Cognition and Communication Fund, the Office of International Studies, and the Lucas Award for Faculty Excellence at The University of Southern Mississippi for their support of this project. We also thank the numerous undergraduate and graduate students who assisted with data collection and analyses. Our local boat captain, Tuleo Munoz, willingly shared his knowledge of the area and proved aptly capable of providing a stable platform from which to conduct our observations, even in rough seas. Special thanks go to Regina Greene, Jules Page, Tania Brunet and Dan Cain of the Utila Dive Center for their enthusiastic efforts to conduct dolphin surveys and gather information about sightings from local dive boats. They are superb collaborators, and together we hope to answer some of the questions we have raised in this paper. Finally, we thank the three referees of a previous version of this paper for their many helpful comments and suggestions.

REFERENCES

- Acevedo-Gutiérrez, A., 2002. Group behavior. In *Encyclopedia of marine mammals* (ed. W.F. Perrin et al.), pp. 537–544. San Diego: Academic Press.
- Addink, M.J. & Smeenk, C., 2001. Opportunistic feeding behaviour of rough-toothed dolphins *Steno bredanensis* off Mauritania. *Zoologica Verb Leiden*, **334**, 38–48.
- Bearzi, G., Notarbartolo di Sciarra, G., & Politi, E., 1997. Social ecology of bottlenose dolphins in the Kvarneric (northern Adriatic Sea). *Marine Mammal Science*, **13**, 650–668.
- Behrens, D., 2002. *Diving and snorkeling Honduras' Bay Islands*, pp. 11–17. Oakland, California: Lonely Planet Publications.
- Bigg, M.A., Ellis, G.M., Ford, J.K.B. & Balcomb, K.C., 1987. *Killer whales: a study of their identification, genealogy, and natural history in British Columbia and Washington State*. Nanaimo, BC: Phantom Press.
- Bigg, M.A., Olesiuk, P.F., Ellis, G.M., Ford, J.K.B. & Balcomb, K.C., 1990. Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. In *Individual recognition of cetaceans: use of photo-identification and other techniques to estimate population parameters* (ed. P.S. Hammond et al.), pp. 383–405. *Reports of the International Whaling Commission*, Special Issue no. 12. Cambridge: International Whaling Commission.
- Brower, K. & Curtsinger, W.R., 1979. *Wake of the whale*. New York: Friends of the Earth.
- Brager, S., Dawson, S., Sooten, E., Smith, S., Stone, G., & Yoshinaga, A., 2002. Site fidelity and along-shore range in Hector's dolphin, an endangered marine dolphin from New Zealand. *Biological Conservation*, **108**, 281–287.
- Carwardine, M., 1995. *Dorling Kindersley handbook of whales, dolphins, and porpoises*, pp. 182–183. New York: Dorling Kindersley Publishing, Inc.
- Connor, R., Wells, R., Mann, J., & Read, A., 2000a. The bottlenose dolphin: social relationships in a fission-fusion society. In *Cetacean societies: field studies of dolphins and whales* (ed. J. Mann et al.), pp. 91–127. Chicago: University of Chicago Press.
- Connor, R., Read, A., & Wrangham, R., 2000b. Male reproductive strategies and social bonds. In *Cetacean societies: field studies of dolphins and whales* (ed. J. Mann et al.), pp. 247–269. Chicago: University of Chicago Press.

- Dudzinski, K.M., 1998 Contact behavior and signal exchange in Atlantic spotted dolphins (*Stenella frontalis*). *Aquatic Mammals*, **24**, 129–142.
- Dudzinski, K.M., Clark, C.W., & Würsig, B., 1995. A mobile video/acoustic system for simultaneous underwater recording of dolphin interactions. *Aquatic Mammals*, **21**, 187–193.
- Evans, P., 1987. *The natural history of whales and dolphins*. New York: Facts on File Publications.
- Flores, P.A. & Ximenez, A., 1997. Observations of the rough-toothed dolphin *Steno bredanensis* off Santa Catarina Island, southern Brazilian coast. *Biotemas*, **10**, 71–79.
- Gannier, A. & West, K.L., 2005. Distribution of the rough-toothed dolphin (*Steno bredanensis*) around the Windward Islands (French Polynesia). *Pacific Science*, **59**, 17–24.
- Götz, T., Verfuß, U., & Schnitzler, H., 2005. 'Eavesdropping' in wild rough-toothed dolphins (*Steno bredanensis*)? *Biology Letters*, **2**, 1–3.
- Gubbins, C., 2002. Use of home ranges by resident bottlenose dolphins (*Tursiops truncatus*) in a South Carolina estuary. *Journal of Mammalogy*, **83**, 178–187.
- Jefferson, T.A., 2002. Rough-toothed dolphin *Steno bredanensis*. In *Encyclopedia of marine mammals* (ed. W. Perrin et al.), pp. 1055–1059. New York: Academic Press.
- Johnson, C.M. & Moewe, K., 1999. Pectoral fin preference during contact in Commerson's dolphins (*Cephalorhynchus commersonii*). *Aquatic Mammals*, **25**, 73–77.
- Kerr, K., Defran, R., & Campbell, G., 2005. Bottlenose dolphins (*Tursiops truncatus*) in the Drowned Cayes, Belize: Group size, site fidelity, and abundance. *Caribbean Journal of Science*, **41**, 172–177.
- Kuczaj, S.A. II & Highfill, L., 2005. Dolphin play: Evidence for cooperation and culture? *Behavioral and Brain Sciences*, **28**, 705–706.
- Kuczaj, S.A. II, Makecha, R.N., Trone, M., Paulos, R.D., & Ramos, J.A., in press. The role of peers in cultural transmission and cultural innovation: evidence from dolphin calves. *International Journal of Comparative Psychology*.
- Kuczaj, S.A. II & Walker, R., 2006. Problem solving in dolphins. In *Comparative cognition: experimental explorations of animal intelligence*, (ed. T. Zentall and E. Wasserman), pp. 580–601. Cambridge, MA: MIT Press.
- Lodi, L., 1992. Epimeletic behaviour of free-ranging rough-toothed dolphins, *Steno bredanensis*, from Brazil. *Marine Mammal Science*, **8**, 284–287.
- Lodi, L. & Hetzel, B., 1999. Rough-toothed dolphin, *Steno bredanensis*, feeding behaviours in Ilha Grande Bay, Brazil. *Biociencias, Porto Alegre*, **7**, 29–42.
- Maigret, J., 1994. Marine mammals and fisheries along the West African coast. *Reports of the International Whaling Commission, Special Issue*, **15**, 307–316.
- Maigret, J., Trotignon, J., Duguy, R., 1976. *Observations de cétacés sur les côtes de Mauritanie (1971–1975)*. Conseil International pour l'Exploration de la Mer, Comité des Mammifères Marins CIM, pp. 1–6.
- Markowitz, T., Harlin, A., and Würsig, B., 2003. Digital photography improves efficiency of individual dolphin identification. *Marine Mammal Science*, **19**, 217–223.
- Miyazaki, N., 1980. Preliminary notes on age determination and growth of the rough-toothed dolphin, *Steno bredanensis*, off the Pacific coast of Japan. *Reports of the International Whaling Commission, Special Issue*, no. 3, 171–179.
- Miyazaki, N. & Perrin, W.F., 1994. Rough-toothed dolphin *Steno bredanensis* (Lesson, 1828). In *Handbook of marine mammals Vol. 5. The first book of dolphins* (ed. S.H. Ridgeway and R.J. Harrison). London: Academic Press.
- Neumann, D., Leitenberger, A., & Orams, M., 2002. Photo-identification of short-beaked common dolphins (*Delphinus delphis*) in north-east New Zealand: a photo-catalogue of recognizable individuals. *New Zealand Journal of Marine and Freshwater Research*, **36**, 593–604.
- Ott, P.H. & Danilewicz, D., 1996. Southward range extensions of *Steno bredanensis* in the Southwest Atlantic and new records of *Stenella coeruleoalba* for Brazilian waters. *Aquatic Mammals*, **22**, 185–189.
- Pitman, R. & Stinchcomb, C., 2002. Rough-toothed dolphins (*Steno bredanensis*) as predators of Mahimahi (*Coryphaena hippurus*). *Pacific Science*, **56**, 447–450.
- Pryor, K.W., Haag, R. & O'Reilly, J., 1969. The creative porpoise: training for novel behavior. *Journal of the Experimental Analysis of Behavior*, **12**, 653–661.
- Rendell, L. & Whitehead, H., 2001. Culture in whales and dolphins. *Behavioral and Brain Sciences*, **24**, 309–324.
- Ritter, F., 2002. Behavioral observations of rough-toothed dolphins (*Steno bredanensis*) off La Gomera, Canary Islands (1995–2000), with special reference to their interactions with humans. *Aquatic Mammals*, **28**, 46–59.
- Sakai, M., Hishii, T., Takeda, S., & Kohshima, S., 2006. Laterality of flipper rubbing behaviour in wild bottlenose dolphins (*Tursiops aduncus*): caused by asymmetry of eye use? *Behavioral Brain Research*, **170**, 204–210.
- Shane, S.H., Wells, R.S., & Würsig, B., 1986. Ecology, behavior and social organization of the bottlenose dolphin: a review. *Marine Mammal Science*, **2**, 34–63.
- Smeenck, C., Addink, C.M., & Richards, H., 1995. Some observations of the behaviour of wild rough-toothed dolphins *Steno bredanensis*. Paper presented at the biennial meeting of the Society for Marine Mammalogy, Orlando, FL.
- Steiner, L., 1995. Rough-toothed dolphin, *Steno bredanensis*: a new species record for the Azores, with some notes on behaviour. *Arquipélago*, **13A**, 125–127.
- Waring, G., Palka, D., Mullin, K., Hain, J., Heansen, L., & Bisack, K., 1997. *US Atlantic and Gulf of Mexico Marine Mammal Stock Assessments—1996*. NOAA Technical Memorandum NMFS-NE-114, pp. 206–208.
- Watkins, W.A., Tyack, P., Moore, K.E. & Notarbartolo-di-Sciara, G., 1987. *Steno bredanensis* in the Mediterranean Sea. *Marine Mammal Science*, **3**, 78–82.
- Webster, D., Baird, R., McSweeney, D., Ligon, A., & Schorr, G., 2005, December. *High Site-Fidelity of a Deep-Water Dolphin: Rough-Toothed Dolphins in the Hawaiian Archipelago*. Poster presented at the biennial meeting of the Society for Marine Mammalogy, San Diego, CA.
- Weih, D., 2004. The hydrodynamics of dolphin drafting. *Journal of Biology*, **3**, 8.
- Whitehead, H., Bejder, L., & Ottensmeyer, A., 2005. Testing association patterns: issues arising and extensions. *Animal Behaviour*, **69**, 1–6.

Submitted 16 June 2006. Accepted 17 October 2006.