Aquatic Mammals 1997, **23.3,** 163-170

Habitat use by bottlenose dolphins (*Tursiops truncatus*) at Turneffe Atoll, Belize

E. Grigg and H. Markowitz

San Francisco State University, Department of Biology, 1600 Holloway Avenue, San Francisco, CA 94132, USA

Abstract

Site preference and habitat use by bottlenose dolphins (*Tursiops truncatus*) at Turneffe Atoll, Belize were investigated using survey routes and counts of animals seen. Ten sites were the focus of this study, covering a range of locations throughout the southern two-thirds of Turneffe Atoll and encompassing four key habitat types. Data were collected from Fall 1995 through Spring 1996; counts and a variety of environmental and behavioral observations were made from small boats. It was found that dolphin group size is dependent on location, and further, that dolphin group size is dependent on habitat type. The data indicate that some areas of the atoll are favored by groups of a certain size; this relationship, combined with the relationship between habitat type and group size suggests that certain areas of the atoll are used by the dolphins preferentially for specific activities. This finding is comparable to that of other studies on coastal *T. truncatus* that have noted a relationship between environmental variables, group size, and behavior. Average group size and sighting rates by season are also given.

Introduction

Bottlenose dolphins (*Tursiops truncatus*) are highly adaptable cetaceans, found throughout the world, absent only from polar regions. The behavior of these dolphins is closely tied to local ecology (Shane *et al*., 1986), and *Tursiops* exhibit widely ranging patterns of behavior. Bottlenose dolphins are, as a rule, opportunists; they adapt their behavioral regime to take advantage of local opportunities. Food resources are a primary factor in determining site fidelity, individual and group movements, and feeding patterns of these animals in their various habitats across the globe (Shane *et al*., 1986; Wells *et al*., 1980).

Generally, group size for coastal bottlenose dolphins ranges between 2–15 animals; habitat structure and activity patterns (i.e., feeding vs socializing) are the major factors determining group size (Shane *et al*., 1986). For example, groups in deeper water tend to be larger, often feeding cooperatively, while groups in shallow water tend to be smaller, and dolphins sighted in shallow water are often feeding individually or in small groups; this was found to be the case in Argentina (Würsig & Würsig, 1979), South Africa (Saayman & Tayler, 1973), and Florida (Scott *et al*., 1990). Shane (1977, 1990) notes that at both her Texas and Florida study sites, socializing dolphin groups were larger than groups involved in other activities. This trend is not observed in all *Tursiops* study areas, however. Food patchiness and/or the presence of other potentially competitive dolphin species can also influence group size (Corkeron, 1990); the size of the patches and the degree of competition for food can serve as a limiting factor on *Tursiops* group size.

Often, particular activities of coastal bottlenose dolphins are associated with particular depths; in many sites, feeding is primarily concentrated close to shore, where the presence of estuaries, mangroves, or physical barriers such as mud banks can provide higher prey density and opportunities for 'corralling' prey (Shane, 1990). Socializing and traveling are often observed further offshore: traveling, socializing and social traveling increase as water depth increases. In addition, different age and sex classes may vary in site preference (Irvine *et al*., 1981).

This study focused on the habitat use and site preference of bottlenose dolphins located at Turneffe Atoll, 32 km off the coast of Belize, in the Caribbean Sea (Fig. 1). This area presents an excellent opportunity for studying habitat use by these animals, due to the rich natural environment available to them, and to the limited human encroachment (thus far) into the area. The atoll provides the dolphins with extensive seagrass beds, productive mangrove shorelines, and a flourishing coral reef. Each of these areas was examined in the course of the study, using survey routes designed to encompass representatives of each habitat type found within the atoll.

Behavioral and sighting data were collected throughout Turneffe Atoll, although (due to the large size of the atoll, and the relatively inaccessible nature of much of the atoll's northern portion) the data collection was concentrated on the southern two-thirds of the atoll.

This project represents a subset of the work done for the Belize Bottlenose Dolphin Project. One of the overall goals of the four-year Turneffe study is an increased knowledge of the habitat use patterns of *Tursiops truncatus* in and around the atoll. The working hypothesis of this project was that the probability of sighting bottlenose dolphins at a particular site within the dolphins' range can be predicted from the nature of physical and biological characteristics of that site.

Other studies have recognized differential importance of certain sites over others: such studies have recognized that certain localities may be of 'high value' to the bottlenose dolphin for shelter, social interaction, and feeding (Lear & Bryden, 1980), and have used dolphin presence and density as an indicator of 'high value' habitat areas. Identifying these areas can be problematic, however, and Lear & Bryden (1980) note that physically similar areas within their study area do not have high dolphin density, the reasons for which are unknown.

Study area

Turneffe Atoll is a large atoll which covers an area of 531.4 km^2, the largest of three atolls located off the coast of the small Central American nation of Belize. Turneffe is separated from mainland Belize by a barrier reef and a channel which descends to a depth of 305 m (Gibson, 1990). The atoll itself is composed of many mangrove islands or 'cayes' surrounding three shallow lagoons: the relatively inaccessible northern lagoon, the southern lagoon, and the large central lagoon. On the eastern side of the atoll, large openings between the mangrove cayes connect the lagoons and the open ocean and are called 'bogues'; on the western side, the openings are much narrower, and are called 'creeks'. The substrate covering the majority of the central and southern lagoons, the two lagoons surveyed in this study, consists of sand and seagrass (*Thalassia* sp.), with occasional coral patches. The atoll is surrounded by a coral reef, well-defined on the eastern (windward) side and patchy on the western (leeward) side. The site is shallow overall (maximum depth is roughly 30 ft); dolphins are sighted year-round in many locations around the atoll. Bottlenose dolphins are comfortable in shallows; *Tursiops* are frequently seen in depths of less than 1 m in marshlands, lagoons, and mangrove swamps (Leatherwood, 1975).

Human encroachment into the atoll is minimal, consisting of three small resorts catering to scuba divers, sport fishermen, and ecotourists. There is also a coral reef conservation study underway at the atoll, based out of a small camp on one of the cayes. Other human presence at Turneffe consists of the numerous small fishing camps scattered throughout the atoll; small-scale commercial fishermen collect spiny lobster (*Panulirus argus*) and conch (*Strombus* sp.), and fish for snapper (*Lutjanus* sp., *Ocyurus chrysurus*) and grouper (*Epinephelus* sp., *Mycteroperca* sp.). Dolphins have been observed to interact with these fisheries, rolling lobster traps and fish traps in an attempt to get to the catch inside.

Methods

Daily trips along pre-determined survey routes (covering a range of habitat types) were conducted from September 1995 to May 1996. Survey routes were not limited to those areas where dolphins are commonly observed, but covered all habitat types found within the atoll. Ten study sites were specifically addressed for the purposes of this study (Fig. 1); a brief description of the key environmental considerations at each of the sites is found in Table 1. Sites were chosen to represent a cross-section of habitat types found at Turneffe, and fell into four general habitat categories (Table 2). Sites were defined and equalized in size using GPS readings: each site consisted of one longitudinal minute E–W and two latitudinal minutes N–S. For example, site 1 (Northern Bogue 1) covers W87°48′00″ to W87°49′00″ and N17°25′00″ to N17°27′00″.

The number of animals present at each site was recorded. Counts were taken from a small boat (21 ft Mako) and the number of animals present was agreed upon by the boat driver and the researcher. Each time animals were sighted, location was recorded using a handheld Global Positioning System (GPS) receiver. Weather, sea/surface conditions, temperature, tidal state, water depth, sky conditions, substrate type, wind direction and speed were recorded at each area where dolphins were sighted. Sites were assigned to habitat type categories based primarily on location within the atoll, predominant sea/surface conditions (i.e., whether the area was generally protected or exposed), and substrate type.

In order to examine whether the number of dolphins sighted was independent of location, a 4×10 chi-square contingency table was run on group sizes (including zero animals, i.e., no dolphins sighted) vs site (Zar, 1996). Dolphin groups were divided into four categories: 0, 1–3 animals, 4–6 animals, and greater than 6 animals. The 10 sites were then grouped into the four habitat

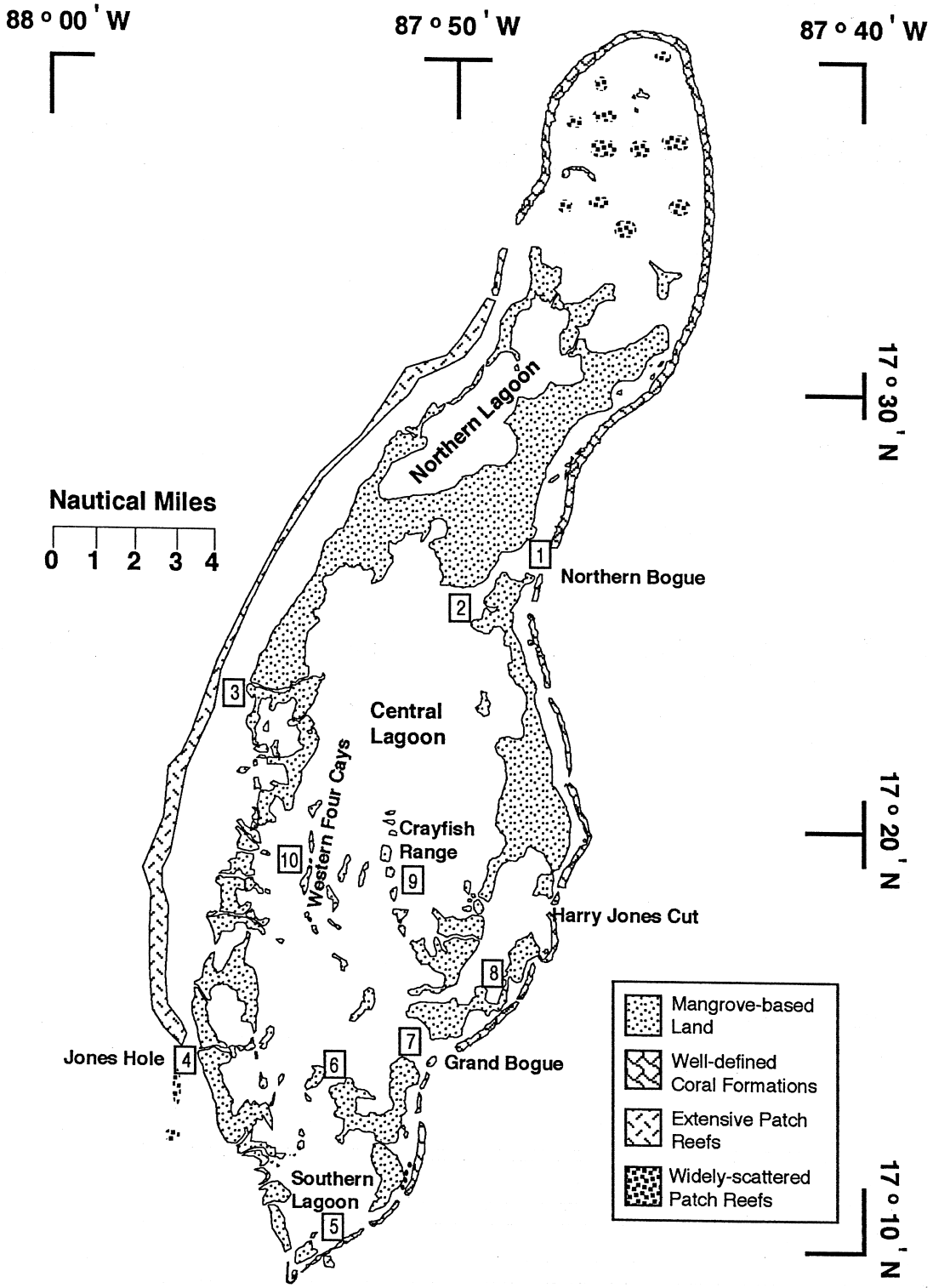

Figure 1. Map of Turneffe Atoll, showing ten focal study sites. (Map courtesy of the Cetacean Behavior Laboratory, San Diego State University.)

Table 1. Descriptions of study sites

Site number	Site name	Descriptive characteristics
1	Northern Bogue 1	Largely sand and coral substrate; exposed; adjoining coral reef; resort in area; windward side of atoll
2	Northern Bogue 2	Sand, seagrass substrate; relatively protected
3	West of Crikazeen Creek	Seagrass substrate; relatively protected; adjoining coral reef; western edge of mangrove creek; leeward side of atoll
4	Jones Hole	Sand, patch coral, seagrass substrate; somewhat protected; western edge of mangrove creek; leeward site of atoll
5	Southern Lagoon	Sand, patch coral, some seagrass substrate; adjoining coral reef; exposed; resort in area
6	Pigeon Caye Bogue	Thick seagrass substrate; protected; access to Grand Bogue/open ocean
7	Grand Bogue	Sand, seagrass, and abundant patch coral substrate; exposed; adjoining coral reef; windward side of atoll
8	Long Bogue	Seagrass substrate; protected; access to both Harry Jones Cut and Grand Bogue
9	Crayfish Cayes	Thick seagrass substrate; protected; adjoins lagoon mangrove cayes; access via bogues to windward side of atoll
10	Western Four Cayes	Thick seagrass substrate; protected; adjoins lagoon mangrove cayes; access via creeks to leeward side of atoll

A brief description of notable environmental characteristics of each site is given here. Descriptive characteristics compiled from personal observations, information provided by boat drivers and fishermen familiar with the area, and maps whenever available.

Table 2. Habitat type groupings

Habitat type	Sites included	Defining characteristics
1	9, 10	*Central lagoon sites*; protected; thick seagrass substrate
2	2, 6, 8	*Easy access to bogue/open ocean*; protected; thick seagrass substrate
3	1, 5, 7	*Bogues*; exposed; *windward side of atoll*; sand, some seagrass, and lots of patch coral; coincide with reef breaks
4	3, 4	*Creek mouths*; *leeward side of atoll*; seagrass, some patch coral; adjoin reef

This table represents a rough grouping of sites into overall habitat types; there inevitably exists some overlap in habitat characteristics between the different sites. The primary defining characteristic used was location relative to the atoll, shown here in italics; e.g., the central lagoon sites were located well within the 'protection' of the atoll, vs the bogues, which are quite exposed and offer immediate access to the fringing reef and the open ocean.

groupings (Table 2), and a 4×4 chi-square contingency table was run on group size vs habitat type.

Results

Dolphin sighting data by site are shown in Table 3. Using grouped data from Fall 1995 and Spring 1996, it was found that dolphin group size is dependent on location ($\chi^2=47.854$, df=27, $P<0.01$); the Spring data alone also demonstrated this relationship ($\chi^2=45.421$, df=27, $P<0.025$). Noteworthy observations made while comparing the 10 sites include: sites 4 and 7 had the lowest number of visits with no dolphins sighted; a markedly higher number of small groups (1–3 animals) was seen at site 7; no larger groups (greater than six

Table 3. Dolphin sighting data by site

	Dolphin group size			
Site number	0	1–3	4–6	>6
1	17	6	1	0
2	14	11	4	1
3	16	1	3	2
4	12	11	2	5
5	14	12	3	1
6	19	2	2	3
7	10	17	2	3
8	18	5	4	0
9	16	5	1	2
10	17	3	0	2

Table 4. Summary data for Fall 1995 and Spring 1996

	Fall 1995	Spring 1996
Time spent in field (hr)	135.6	220.4
Time spent with dolphins (hr)	37.37	49.3
Total number of sightings	64	97
Total number of dolphins seen	307	247
Average group size	4.3	2.9
Standard deviation	3.61	2.17
Number of dolphins/effort hour	2.26	1.12

Note that, despite the longer time spent in the field in Spring 1996 vs Fall 1995, the total number of dolphins seen in the Fall (307) was higher than in the Spring (247). This trend is also seen in the average group size, which is higher in the Fall (4.3) than in the Spring (2.9), and in the number of dolphins seen per effort hour (2.26 in the Fall vs 1.12 in the Spring).

dolphins) were seen at sites 1 and 8. Total number of survey hours, number of sightings and number of dolphins sighted throughout Turneffe Atoll for Fall 1995 and Spring 1996 are shown in Table 4.

The Fall 1995 data were then analyzed at the most basic level of zero animals seen vs one or more seen, using a 2×10 chi-square contingency table. The Fall data, when grouped at this level, demonstrated that whether or not dolphins were sighted is dependent on location ($\chi^2=17.352$, df=9, $P<0.05$).

One question that arose at this point was the potential difference in time spent at each site, due to the survey/sampling methods. Although the survey boat moved at a constant speed throughout the study area, when dolphins were sighted we almost invariably stopped and observed them. Remaining in a given area to observe the dolphin group may increase the probability of sighting a second group in this same area (vs, for example, simply sighting the animals and continuing on along the survey route without stopping). In order to be sure that our results were not colored by this phenomenon, we returned to the data and eliminated all the subsequent sightings at any one site; we then analyzed only the first sighting at each site (i.e., only the times when we came upon dolphins in a given area) for the Fall and the Spring data. As this meant eliminating data from the limited data bank, we analyzed at the most basic level of zero animals vs one or more animals seen. Results fell into the same pattern as the complete data (encompassing all sightings): we were not able to reject the null hypothesis (that dolphin presence was independent of location) for the Fall data alone ($\chi^2=10.762$, df=9, $P>0.25$), were able to reject for the Spring ($\chi^2=17.724$, df=9, $P<0.05$), and were able to reject for the pooled data ($\chi^2=22.985$, df=9, $P<0.01$).

Dolphin sighting data by habitat type are shown in Table 5. Analysis of group size vs habitat type showed that dolphin group size is dependent on the habitat type in which the animals are found ($\chi^2=18.751$, df=9, $P<0.05$). This is based on pooled 1995 and 1996 data (homogeneity $\chi^2=8.168$, df=9, $P<0.75$). Highest number of visits with no sightings was recorded in habitat type 1. Small groups (one to three animals) were more frequently seen in habitat type 3. Medium groups of four to six animals were seen with comparable frequency in habitat types 2 through 4, but almost never seen in habitat type 1. Large groups (six or more animals) were more frequently seen in habitat type 4.

We then examined the differences between the Fall data and those of Spring 1996. As indicated in Table 4, less time was spent in the field in the Fall of 1995 and fewer sightings were recorded. In order to examine the degree to which small sample size was problematic for the Fall data, we ran a test for minimum adequate sample size on the number of sightings per site. Sample size for the Fall was indeed found to be well below the predicted sample size necessary to reject the null hypothesis for the Fall data.

Interestingly, however, a higher total number of dolphins was recorded in the Fall vs the Spring, and the number of dolphins per unit effort was higher in the Fall. A chi-square analysis was run on the number of dolphins seen in the Fall vs in the Spring,

Table 5. Dolphin sighting data by habitat type

	Dolphin group size			
Habitat type	0	1–3	4–6	>6
1	33	9	1	4
2	51	22	10	4
3	41	35	6	4
4	28	12	5	7

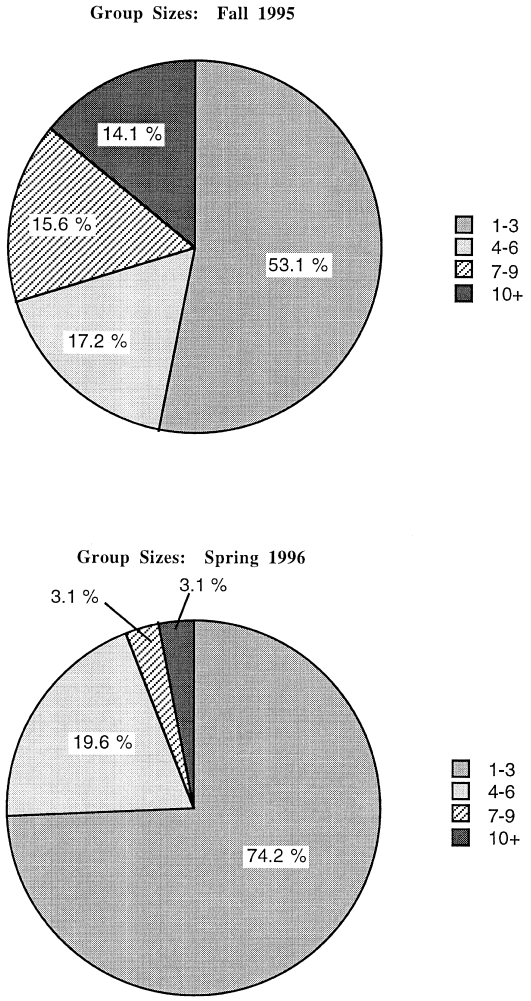

Figure 2. Dolphin group sizes in Fall 1995 and Spring 1996. Note that the percentage of small groups (1–3 animals) was higher in the Spring (74.2%) than in the Fall (53.1%), and the percentage of larger groups (4 or more animals) was higher in the Fall (with a total of 46.9%) than in the Spring (total 25.8%). This trend is particularly notable in the larger (and potentially socializing) groups of seven or more animals.

with proportional adjustment for the number of hours sampled. Number of dolphins seen in the Fall proved to be higher than the number seen in the Spring ($\chi^2 = 52.34$, df = 1, $P < 0.001$). Average size of group sighted was also higher in the Fall than in the Spring, as seen in Table 4 and Figure 2.

Discussion

Since dolphin presence was not independent of location, the data suggest that some environmental variable or variables are influencing where the dolphins are found. Certain areas represent quality habitat for these animals, and dolphins are found more frequently in such habitats. For example, dolphins were most consistently sighted when surveying site 4 (Jones Hole) and site 7 (Grand Bogue). Both sites are associated with breaks in the fringing reef surrounding Turneffe; Jones Hole is located at the mouth of a mangrove creek, and such creeks have been found to possess a high biomass of fish at other comparable areas in Belize (Sedberry & Carter, 1993). Grand Bogue represents an area with abundant coral reef patches, with strong tidal movements pulling water from the fringing reef and beyond into the central lagoon, and from the seagrass beds and mangrove shoreline of the central lagoon out towards the reef. Both the presence of coral patches and tidal movements present feeding opportunities for dolphins in this area. Dolphins (including bottlenose in Belize) have been found feeding in association with coral reefs (Dudzinski *et al.*, 1995; Hansen, 1990). Fish movements (and therefore bottlenose dolphin feeding activities) may be influenced by tides: in one similar study of bottlenose habitat use, striped mullet (frequently listed as a favorite food item of coastal *Tursiops*) are often found in small groups on the shallow banks of bays and estuaries during flood tide, and gather into larger schools in deeper water as tide begins to ebb (Würsig & Würsig, 1979). Dolphin movements and feeding activities cannot yet be directly correlated with fish distributions in our study area, but this is one of the aims of the ongoing Belize Bottlenose Dolphin Project. Such correlations have been reported for nearshore groups of bottlenose (Würsig & Würsig, 1979) and humpback dolphins (Saayman & Tayler, 1973). Presence of competitive dolphin species is unlikely to be a factor in site preference; other species (*Stenella frontalis* and *S. clymene*) are only rarely seen in and around the atoll.

Both Grand Bogue and Jones Hole provide easy access to the fringing reef and open ocean on one side, and the seagrass beds and mangrove shorelines of the atoll on the other. Both sites may serve as travel routes into and out of the atoll, or as prime habitat for feeding or some other activity: seagrass beds and mangrove shorelines are known to be important nursery habitats for juvenile reef and seagrass fishes, and are known to exhibit high biomass and productivity (Sedberry & Carter, 1993). Resolution of how the animals are using these areas will require looking at the behavior of the animals in this area, rather than simply presence or absence of dolphins there.

The data suggest that certain group sizes are associated with particular locations. For example, a markedly higher number of small groups of one to three animals was seen at sites 7 (Grand Bogue),

2 (Northern Bogue 2) and 5 (Southern Lagoon). As mentioned above, other studies have shown that behavior is correlated with group size; for example, large groups are often socializing, and small groups are often feeding/foraging (Shane *et al*., 1986). Cooperative feeding by larger groups was not seen at Turneffe. Sites 7, 2 and 5 may be used mainly by small groups of foraging dolphins. Certain locations at Turneffe are better suited than others for certain dolphin activities (feeding, mating/socializing, resting, etc.), and again in this way may constitute 'quality habitat' for the Turneffe bottlenose. Both small (1–3) and larger groups (4 or more) are seen fairly frequently at site 4 (Jones Hole); this site appears to be regularly utilized by the dolphins for a range of activities.

The results for group size vs habitat type are equally complex, but possible conclusions include noting that habitat type 1 (central lagoon sites) had the highest number of visits with no sightings, and this may be due to lower dolphin density in these areas. Habitat type 1 did, however, have similar numbers of sightings in the larger (>6) group sizes (compared to the other three habitat types), suggesting that large, possibly socializing groups do occasionally make uses of these areas. The relatively high numbers of large (>6) group sightings in habitat type 4 (creek mouths, outside and on the leeward site of the atoll) suggests that dolphins frequently use these areas for social activity. Large groups of actively socializing dolphins were frequently seen loitering in these areas or moving slowly north or south along the outer western edge of the atoll.

The differences in group size between the Spring and the Fall are related to social patterns in the bottlenose population at Turneffe (Figs 2 and 3). Our observations corroborate those of previous researchers (Bilgre, personal communication) who have noted the peak in calf births at Turneffe during the Fall season. Bottlenose dolphin gestation is approximately one year, and during this same season, large groups of dolphins engaged in active social and sexual behavior are frequently observed in the area. The higher number of dolphins seen, and the larger average group size, appear to be a result of the presence in the Fall months of these large socializing groups. The reasons for this Fall peak are not known, as abiotic conditions at Turneffe do not vary widely throughout the year; the peak may have to do with seasonal availability of a favored prey item or items. Bottlenose dolphins around the world exhibit flexible patterns in reproductive timing, as in many other aspects of their lives; this relationship between peaks in reproductive activity and resource availability has been suggested elsewhere (Urian *et al*., 1996).

Increased knowledge of the Turneffe dolphin population and the benefits of the atoll will be used to help the government of Belize evaluate Turneffe as a site for a marine sanctuary. The researchers at Turneffe hope that information about how the dolphins are using the area will help the Belizian government make informed decisions about the management of the waters off the mainland coast, and help them to make the decision to protect the atoll's still-unspoiled marine ecosystem. Knowing which areas of the atoll present a high probability of dolphin presence can be used in evaluating various areas of Turneffe for future preservation or development; ideally, areas which are frequently used by these animals (sites that have a high probability of dolphin sighting, and represent 'quality habitat' for the animals) would be spared further development, and areas which are rarely used (sites which have a low probability of dolphin sighting) will be chosen preferentially for future human use. With this increased understanding of the Atoll ecosystem, we are in a stronger position to argue for its preservation, or at the very least to advise those responsible for the management of the system on the dolphins' habitat requirements.

Acknowledgements

The work at Turneffe Atoll was funded by Oceanic Society Expeditions (OSE) of San Francisco, California, and conducted with the permission of the Belize Department of Fisheries. In addition, a grant from the Graduate Assistance in Areas of National Need (GAANN) provided research and living support for E. Grigg during much of the course of the study. The data collection would not have been possible without the support and participation of the dedicated volunteers who came to Belize through OSE and Elderhostel. Advice and encouragement on field methods was generously given by Alison Sanders of SFSU, and Birgit Winning of OSE; Dr Stan Williams and Régan Rostain of SFSU, and Anita Gavazzi of University of California at Davis provided help and advice on the data analysis portion of the study.

References

Ballance, L. T. (1990) Residence patterns, group organization, and surfacing associations of bottlenose dolphins in Kino Bay, Gulf of California, Mexico. In: S. Leatherwood & R. R. Reeves (eds) *The bottlenose dolphin*. Academic Press, Inc: San Diego.

Ballance, L. T. (1992) Habitat use patterns and ranges of the bottlenose dolphin in the Gulf of California, Mexico. *Marine Mammal Science* **8**(3), 262–274.

Corkeron, P. J. (1990) Aspects of the behavioral ecology of inshore dolphins *Tursiops truncatus* and *Sousa chinensis* in Moreton Bay, Australia. In: S.

Leatherwood & R. R. Reeves (eds) *The bottlenose dolphin*. Academic Press, Inc: San Diego.

Dudzinski, K. M., Frohoff, T. G. & Crane, N. L. (1995) Behavior of a lone female bottlenose dolphin (*Tursiops truncatus*) with humans off the coast of Belize. *Aquatic Mammals* **21**(2), 149–153.

Gibson, J. P. (1990) Status report on Turneffe Islands. Fisheries Department, Belize. 127 p.

Hansen, Larry J. (1990) California coastal bottlenose dolphins. In: S. Leatherwood & R. R. Reeves (eds) *The bottlenose dolphin*. pp. 403–420. Academic Press, Inc: San Diego.

Irvine, A. B., Scott, M. D., Wells, R. S. & Kaufmann, J. H. (1981) Movements and activities of the Atlantic bottlenose dolphin, *Tursiops truncatus*, near Sarasota, Florida. *Fishery Bulletin* **79**(4), 671–688.

Lear, R. J. & Bryden, M. M. (1980) A study of the bottlenose dolphin *Tursiops truncatus* in eastern Australian waters. Australian National Parks and Wildlife Service (4): pp. 1–25.

Leatherwood, S. (1975) Some observations of feeding behavior of bottlenosed dolphins (*Tursiops truncatus*) in the northern Gulf of Mexico and (*Tursiops* cf. *T. gilli*) off southern California, Baja California, and Nayarit, Mexico. *Marine Fisheries Review* **37**(9), 10–16.

Saayman, G. S. & Tayler, C. K. (1973) Social organization of inshore dolphins (*Tursiops aduncus* and *sousa*) in the Indian Ocean. *Journal of Mammalogy* **54**(4), 993–996.

Scott, M. D., Wells, R. S. & Irvine, A. B. (1990) A long-term study of bottlenose dolphins on the west coast of Florida. In: S. Leatherwood & R. R. Reeves (eds) *The bottlenose dolphin*. Academic Press, Inc: San Diego.

Sedberry, G. R. & Carter, J. (1993) The fish community of a shallow tropical lagoon in Belize, Central America. *Estuaries* **16**(2), 196–215.

Shane, S. H. (1977) The population biology of the Atlantic bottlenose dolphins, *Tursiops truncatus*, in the Aransas Pass area of Texas. M.Sc. thesis, Texas A&M University, College Station, TX 77843.

Shane, S. H. (1990) Behavior and ecology of the bottlenose dolphin at Sanibel Island, Florida. In: S. Leatherwood & R. R. Reeves (eds) *The bottlenose dolphin*. Academic Press, Inc: San Diego.

Shane, S. H., Wells, R. S. & Würsig, B. (1986) Ecology, behavior, and social organization of the bottlenose dolphin: a review. *Marine Mammal Science* **2**(1), 34–63.

Urian, K. W., Duffield, D. A., Read, A. J., Wells, R. S. & Shell, E. D. (1996) Seasonality of reproduction in bottlenose dolphins, *Tursiops truncatus. Journal of Mammalogy* **77**(2), 394–403.

Wells, R. S., Irvine, A. B. & Scott, M. D. (1980) The social ecology of inshore Odontocetes. In: L. M. Herman (ed.) *Cetacean behavior: mechanisms and functions*. John Wiley and Sons: New York.

Würsig, B. & Würsig, M. (1979) Behavior and ecology of the bottlenose dolphin, *Tursiops truncatus*, in the south Atlantic. *Fisheries Bulletin* **77**(2), 399–412.

Zar, J. H. (1996) *Biostatistical analysis* (3rd edn). Prentice-Hall, Inc: Engelwood Cliffs.