# Bottlenose dolphins (*Tursiops truncatus*) in Turneffe Atoll, Belize: occurrence, site fidelity, group size, and abundance

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## Abstract

Bottlenose dolphin (*Tursiops truncatus*) occurrence, site fidelity, group size, and population size were assessed within Turneffe Atoll, Belize, Central America during a 4-year photo-identification study. Five hundred and forty-nine photographic surveys were conducted between March 1992 and March 1996. Dolphin groups were encountered on 83% of surveys, and 2782 dolphins were observed in 732 separate groups. Group sizes ($\bar{x}$=3.8, SD=3.55) varied both annually and seasonally. Groups with calves were larger than groups without calves. Eighty-one dolphins were photographically identified, and the majority (81%) of these dolphins were documented by the 150th survey in which one or more identifiable dolphins were successfully photographed (June 1993). Sighting frequencies ($\bar{x}$=12.2, SD=14.33) ranged from one to 57, with 20% of the photographed population sighted only once and 37% photographed ≥10 times. Dolphins photographed ≥2 times in at least three of the four study years were labeled as residents, and comprised 30% of the identified population. Identified females (n=16) and males (n=10) had similar residency patterns. Abundance estimates, derived by using Chao's $M_{th}$ closed method, were similar for the first ($M_{th}$=82) and second ($M_{th}$=86) halves of the study. Small group sizes, low abundance estimates, and the limited residence pattern observed for dolphins in Turneffe Atoll suggest they depend on low-density food resources. Governmental and non-governmental concerns over potential human impacts on Turneffe's marine environment appear to be well placed.

Key words: bottlenose dolphins, *Tursiops truncatus*, photo-identification, occurrence, site fidelity, group size, abundance, Turneffe Atoll, Belize, Caribbean.

## Introduction

Bottlenose dolphins (*Tursiops* spp.) are widely distributed in tropical and temperate waters, occupy-ing a variety of coastal and offshore habitats (Shane *et al*., 1986; Rice, 1998). Ecological features, such as food resources and habitat type, are believed to be primary factors influencing dolphin behaviour patterns (Wells & Scott, 1999). Intra-specific variations in site fidelity, individual and group movements, group composition, and feeding patterns are thought to reflect adaptations to local ecology (Shane *et al*., 1986; Wells & Scott, 1999). Detailed field studies on bottlenose dolphins are needed to understand how differences in important ecological variables affect dolphin behaviour. Comparisons between well-studied dolphin populations in similar and different habitats provide an opportunity to evaluate the influence of specific habitat features and to refine existing generalities about this species.

Herein, we report the results of a 4-year, high-effort mark-recapture study of bottlenose dolphins in Turneffe Atoll, Belize, Central America. One goal of this research was to describe the occurrence, site fidelity, group size, and abundance of bottle-nose dolphins in a coral reef, mangrove, and sea-grass atoll. Additional goals of this research were to provide baseline information about these dolphins and broad characterizations of the availability of their food supply, both of which are needed for the management and conservation of this marine ecosystem.

## Materials and Methods

*Study area*
The study area (Fig. 1, 1A, 1B) was located within Turneffe Atoll (17°20′N; 87°50′W), 56 km off the mainland coast of Belize, Central America. Turneffe Atoll is separated from a long barrier reef by a 9.6–16.1 km wide channel that ranges in depth from 274–305 m (Stoddart, 1962). Numerous limestone-mangrove islands or 'cayes' occur within the atoll and form the boundaries of the Northern, Central, and Southern Lagoons. On the eastern side of the atoll there are large openings called 'bogues' that connect the lagoons with the sea, while the
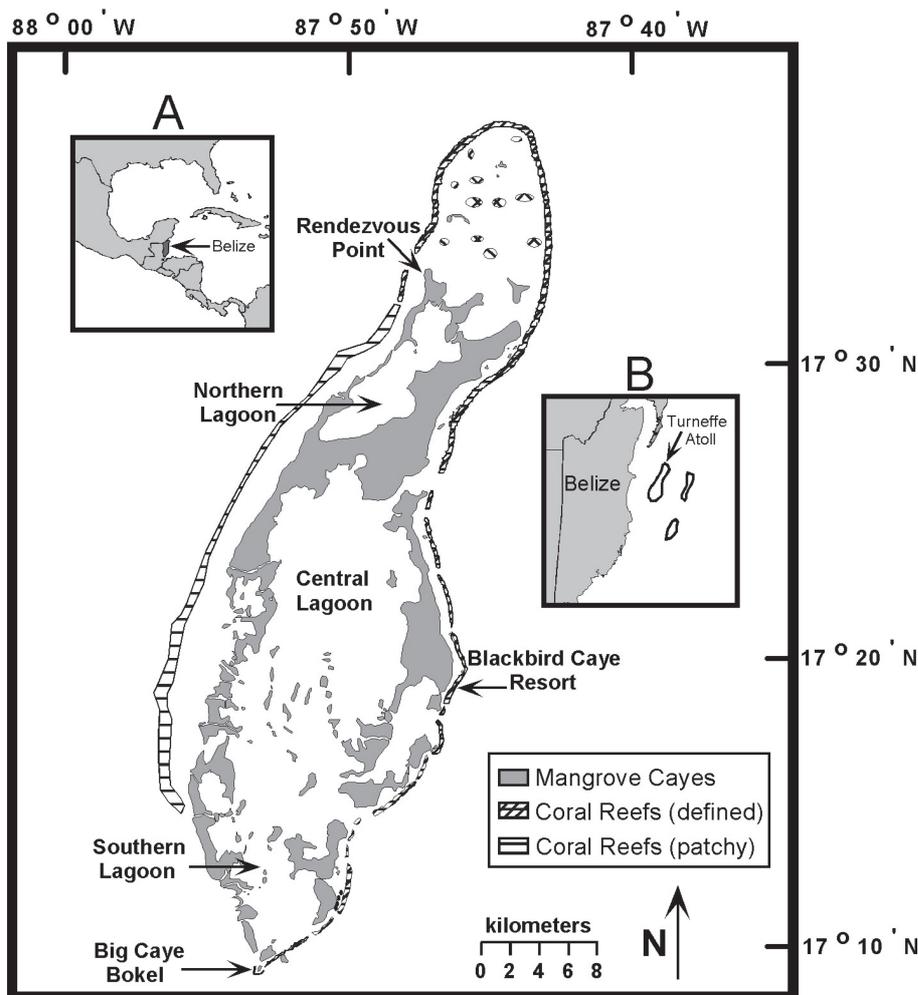
**Figure 1.** The Turneffe Atoll study area. Insets show study area location within Central America (A), and along the coast of Belize (B).

western side of the atoll contains numerous narrow openings called 'creeks' maintained by strong tidal currents (Stoddart, 1962). The prevailing substrate is sandy seagrass (*Thalassia* sp.) interspersed with small patches of hexacorals and sponges. Surface water temperatures, which were recorded from 1993–1996, ranged from 20–35°C ($\bar{x}$=28.2, SD=1.98), and water depth from 1–12 m. Total area of the atoll is 531.4 km$^2$. The study area included all areas within the atoll, except for the shallow and inaccessible waters of the Northern Lagoon and north of Rendezvous Point (Fig. 1).

*Photographic survey procedure*
Due to logistical and personnel constraints, three photographic sampling strategies were used during the 4-year study. Each strategy provided extensive coverage of the southern two-thirds of the atoll, bounded by Rendezvous Point in the north and Big Caye Bokel in the south. The eastern and western boundaries of the study area were defined by the coral reef system surrounding the atoll (Fig. 1). A meandering survey method (Shane, 1980, 1990; Weller & Würsig, in press) was employed from March 1992 through August 1993 to encounter and photograph as many dolphin groups as possible and to document substrate types, lagoons, sandbars, and small islands in the study area. Zone surveys, conducted from September 1993 through November 1994, consisted of systematically searching for dolphins in one to three randomly chosen zones per survey. Zones were selected from 21

pre-defined regions. Each zone was surveyed by following the same predetermined track-line in the same direction at least once per month. From March 1995 through March 1996, surveys were conducted along three predetermined routes selected to cover all areas. Survey routes were uniformly selected in the same order, but when time or weather constraints necessitated termination of a survey before the entire route was covered, the subsequent survey started from the point where the previous survey stopped.

Photographic surveys lasted 4–5 h and were conducted one to two times daily between 0800–1800 h. Survey vessels were from 6–9 m in length with 80–200 HP outboard engines. Four to eight on-board observers visually searched a 360° area around the boat until dolphins were sighted. Immediately after a sighting, the vessel was positioned approximately 30 m from the dolphins, where information on group size and composition, direction of movement, environmental conditions, latitude/longitude, and time was recorded. Dolphin groups were defined as all dolphins in close proximity (<100 m), moving in the same direction and often engaged in similar behaviour (Shane, 1990). Group size estimates included the total number of adults and calves. Calves were defined by three criteria: (1) physical appearance, including small body size, lighter colouration, and occasional presence of fetal folds; (2) physical ability, including immature swimming pattern and awkward head-up respiratory pattern; and (3) constant surface association with a particular adult dolphin (Weller & Würsig, in press).

Upon completion of initial data collection, the vessel was maneuvered to within 4–10 m of the dolphin group, and individual dorsal fins were photographed with 35-mm motor-driven cameras, 200- to 400-mm telephoto lenses, and either 200 ISO colour-slide or 400 ISO black-and-white film. Effort was made to acquire numerous quality photographs of each individual's dorsal fin, without regard to apparent distinctiveness. After completion of all photographic data collection, the vessel either continued on the original survey route or was positioned for underwater observations (see below). Identical procedures were repeated when additional dolphin groups were encountered.

*Underwater data collection*
Underwater observations of dolphins were conducted opportunistically. One to three observers wearing skin-diving equipment entered the water 10–20 m from dolphins and swam slowly toward the group, attempting to limit disruption of natural activities. Notes on individual markings, behaviour and gender were recorded using clipboards and underwater markers. Females were identified through observations of distinct urogenital and mammary slits or by repeated photographs with a calf. Males were identified based on observations of a penis and/or distinct penile and anal slits. Gender identification was completed when an identifiable dorsal fin photograph was obtained of a dolphin meeting gender identification criteria.

*Photographic data analysis*
Photo-identification analyses closely followed techniques described by Defran *et al.* (1990) and are briefly summarized as follows: Clear photographs of distinctively marked dorsal fins were sorted by recognizable notch patterns, and the best photograph of each dolphin was selected as the 'type photo' to which all other photographs were compared. Subsequently, only unambiguous matches with the 'type photo' were accepted as re-identifications of a known individual.

*Population estimation*
Standard mark-recapture models for estimating abundance assume that within a sample, a marked animal will be recognized with certainty if recaptured (Pollock *et al.*, 1990). If the probability of capture is not equal among members of a population, which can occur if poor quality photographs are used to identify individuals, the resulting abundance estimates are negatively biased (Hammond, 1986). Several cetacean mark-recapture studies have addressed the issue of photographic quality through the development and application of photo-quality rating systems (Arnbom, 1987; Whitehead *et al.*, 1997; Wilson *et al.*, 1999; Friday *et al.*, 2000). To reduce bias toward highly distinctive individuals in our analyses, we developed a textual rating system and accompanying set of reference photos for judging four measures of photographic quality (Table 1). To ensure high inter-observer reliability, four experienced photographic analysts participated in four pre-tests using different sets of 40–100 dorsal fin images. Good to substantial agreement among individual judges across all categories (Kappa statistic: $K = 0.70–1.0$) was established (Siegel & Castellan, 1988) before we applied photo-quality ratings to the data set. Photographs were not used in the population estimate if focus, contrast, proportion of fin, or size of the fin within the negative were rated a number 1 (lowest quality). An exception to this exclusion rule was made when the size of the fin was rated number 1, but all other measures of photographic quality received the highest possible rating.

Analyses of our photographic data suggested that the dolphin population in Turneffe Atoll was finite (see rate of discovery analysis–results section) and exhibited little or no permanent immigration or emigration. Since bottlenose dolphins have a long

**Table 1.** Textual descriptions for each level of the four parameters used to rate photographic quality.

| Measure | Rating | | | |
| --- | --- | --- | --- | --- |
| | No. 1 | No. 2 | No. 3 | No. 4 |
| Focus | Blurry but general fin outline visible | Slightly blurred, soft edge, small nicks difficult to discern | Sharp edge, adequate to detect small nicks | N/A |
| Contrast | Shading similarities do not allow clear differentiation between fin and background | Fin and background similar to shading and fin edge obscured by glare | Fin and background similar in shading or fin edge obscured by glare | Fin and background easily distinguished |
| Proportion of fin area visible | 1/3 of the fin is visible | 2/3 of the fin is visible | All or nearly all of the fin is visible | N/A |
| Dorsal fin size | Fin occupies 1–5 grid squares | Fin occupies 6–19 grid squares | Fin occupies 20+ grid squares | N/A |

**Table 2.** Summary information on annual and seasonal survey effort, encounter rate, sighting data, and group size.

| | Study period | No. surveys | Total dolphins | Dolphins/ survey | Total groups | Groups/ Survey | Group size | | | Percent calf |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | | | | | | | Mean | SD | Range | |
| Annual | 1992 | 117 | 515 | 4.4 | 167 | 1.4 | 3.1 | 2.74 | 1–20 | 7% |
| | 1993 | 143 | 892 | 6.2 | 199 | 1.4 | 4.5 | 4.25 | 1–20 | 12% |
| | 1994 | 165 | 913 | 5.5 | 215 | 1.3 | 4.2 | 4.01 | 1–27 | 14% |
| | 1995/1996 | 124 | 462 | 3.7 | 151 | 1.2 | 3.1 | 2.13 | 1–16 | 10% |
| Seasonal | Spring | 207 | 858 | 4.1 | 267 | 1.3 | 3.2 | 2.97 | 1–20 | 11% |
| | Summer | 128 | 529 | 4.1 | 178 | 1.4 | 3 | 2.64 | 1–20 | 9% |
| | Fall | 214 | 1395 | 6.5 | 287 | 1.3 | 4.9 | 4.25 | 1–27 | 13% |
| | Overall | 549 | 2782 | 5.1 | 732 | 1.3 | 3.8 | 3.55 | 1–27 | 11% |

life span and low reproductive rates (Shane *et al.*, 1986; Wells & Scott, 1999), births and deaths were assumed to be infrequent. Thus, for the purposes of conducting population estimates, dolphins in Turneffe Atoll were treated as members of a closed population. Inherent differences in individual behaviours, such as preferences for certain areas, were assumed to affect the probability of identifying individuals during our sampling periods. In addition, individual variations in boat avoidance techniques and surfacing rates were assumed to affect the probability of capture during encounters (Hammond, 1986; Wilson *et al.*, 1999). Therefore, Chao's closed model $M_{th}$ (time and heterogeneity), which allows capture probabilities to vary with time (sampling period) and by individual, was chosen as the most appropriate population estimator (Chao *et al.*, 1992). Abundance estimates were carried out using the program CAPTURE (Otis *et al.*, 1978; Rexstad & Burnham, 1991).

Short sampling periods were selected so that the probability of changes in the population size was minimized. Sighting data were divided into three seasonal periods for each of the four study years: March–May (spring), June–August (summer), and September–December (fall). Thus, each study year contained three sampling periods with a total of 12 sampling periods across the 4-year study. Abundance estimates were carried out for the first-half (1992/1993) and the second-half (1994/1995&96) of the study with each 2-year study period represented by six samples.

*Data set partitioning and analysis*
To analyze annual patterns of site fidelity and group size, data were divided based on four time periods: March–December 1992 (data collected by C. Graham & K. Dudzinski–MMRP, TAMU); March–December 1993; March–December 1994; and March–December 1995 & February–March 1996 (Table 2). Due to limited surveying opportunities in Turneffe Atoll from December to February, surveys conducted in the months of December 1992–1995 were combined with the fall data, and surveys conducted in February 1996 were combined with the spring data. Thus, seasonal

analyses of group size were conducted by dividing each study year based on three seasonal periods: spring (February–May), summer (June–August), and fall (September–December).

Data on group size, number of sightings and annual sighting frequencies were not normally distributed. Therefore, to conduct parametric ANOVA tests, we transformed the data into standardized z-score values. Annual and seasonal analyses of group size were conducted using the z-scores as input values for a two-way nested ANOVA (season nested within year). Analysis of group size differences relative to the presence or absence of one or more calves was conducted using the z-scores as input values for a one-way ANOVA. Analyses of both the number of sightings and annual sighting frequency as a function of gender also were conducted using z-scores as input for a one-way ANOVA.

## Results

### Survey effort, encounter rate and group size

Five hundred and forty-nine surveys totaling 1980.7 h of effort were conducted in the Turneffe Atoll study area from March 1992 to March 1996. A total of 473.7 h (24.0%) was spent in direct observation of 2782 dolphins (field estimate). Table 2 provides additional details of annual and seasonal survey efforts, encounter rates, and sighting data.

Group size for the 732 dolphin groups observed between 1992–1996 averaged 3.8 individuals (SD=3.55, median=2.5, mode=2) (Table 2). Sixty-three percent (n=462) of all groups encountered contained one to three individuals, and groups of ≤10 dolphins comprised 93% of all sightings. Annually, larger groups were observed in 1993 and 1994, and smaller groups were observed in 1992 and 1995/1996 ($F_{(3,720)}=6.48$; $P<0.001$) (Table 2). Group size also varied seasonally, with larger groups observed in fall and smaller groups observed during spring and summer ($F_{(8,720)}=6.96$; $P<0.001$) (Table 2). Eleven percent (n=323) of the dolphins encountered were judged to be calves, and 30% (n=223) of the groups observed during the study contained at least one calf. Groups with one or more calves ($\bar{x}=6.4$, SD=4.54) were significantly larger than groups with no calves ($\bar{x}=2.7$, SD=2.23) ($F_{(1,730)}=228.57$; $P<0.01$).

All Turneffe dolphins encountered during photo-identification surveys, as well as underwater data collection, were examined for the presence of the distinctive crescent-shaped scars associated with shark attacks (see Fig. 4.5 in Connor *et al.*, 2000). No such scarring or other evidence of predation or attack was evident during any of the surface or underwater observations made during the study period.

## Photographic Data

### Rate of discovery

The rate at which individual dolphins were identified between 1992–1996 was examined across surveys in which at least one dolphin was photographically identified (n=322 surveys, Fig. 2). Rate of discovery, plotted as the cumulative number of newly identified individuals across blocks of 10 surveys, indicates that a majority (81%, n=66) of the dolphins identified during the study were photographed by the 150th survey (June 1993). Fifteen new dolphins (19%) were identified in the remaining 33 months of the study (blocks 16–32).

### Sighting frequency and site fidelity

Sighting frequencies for the 81 dolphins identified during the study ranged from 1–57 ($\bar{x}=12.2$, SD=14.33) (Fig. 3). Twenty percent (n=16) of the dolphins identified were photographed once, 43% (n=35) 2–9 times, and 37% (n=30) ≥10 times. The number of study years in which identified dolphins were photographed (annual sighting frequency) averaged 2.5 years (SD=1.24, range=1–4). Thirty-two percent (n=26) of the identified population was photographed during only one year, and 32% (n=26) was observed during all four years. There was a significant, positive correlation between the total number of sightings and annual sighting frequencies (Pearson's r=0.689; $P<0.01$).

The mean number of days between sightings within each study year for the 61 dolphins photographed ≥2 times within ≥1 study year ranged from 9–267 d ($\bar{x}=50.8$, SD=51.10). Forty-one percent (n=25) of the dolphins sighted ≥2 times within ≥1 study year had ≤30 d between sightings, while 7% had an average of ≥100 d between sightings.

Individuals were divided into residency classes based on their photographic sighting histories. Data on the two most extreme categories, residents and transients, are presented here. Residents were dolphins photographed ≥2 times in at least 3 of 4 study years, and comprised 30% (n=25) of the identified population. For residents, the mean number of sightings was 30.3 (SD=12.90), and the mean number of days between sightings within each study year was 26.4 (SD=36.51). Transients, which were dolphins photographed only one time, made up 20% (n=16) of the identified population.

The affiliation patterns of the 16 dolphins classified as transients were examined to determine if these individuals were observed together at the same time and location, or were observed randomly with other known dolphins. Our analysis indicated that 75% (n=12) of these dolphins were never photographed together or within the same 7-day period, while the remaining 25% (n=4) were sighted
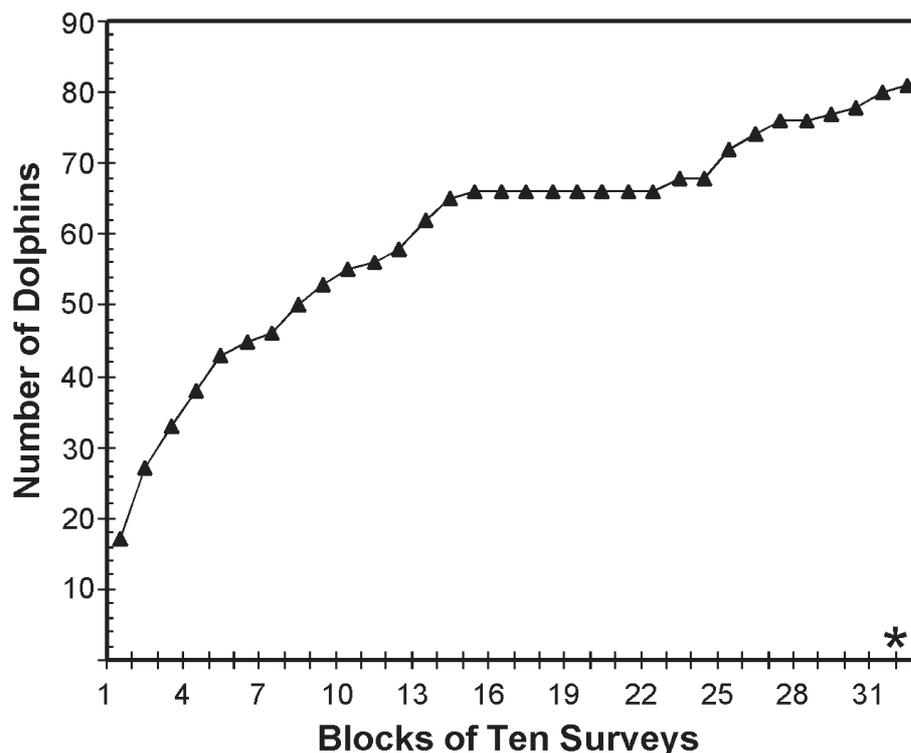
**Figure 2.** Cumulative number of dolphins identified over blocks of 10 surveys where at least one dolphin was photographically identified. Block 32 (*) contains data from 12 surveys.

together as members of an anomalous group. Further examination of the affiliation patterns for the 12 transient dolphins sighted independently of one another showed that these animals were always observed with other more frequently sighted dolphins. Sightings of transient dolphins showed no seasonal or annual trends.

*Gender comparisons*

Gender was determined for 26 (32%) of the 81 identified dolphins. Identified females (n=16) were sighted an average of 27.8 times (SD=18.34, range=4–57) and had a mean annual sighting frequency of 3.4 years (SD=0.72, range=2–4). Sighting data were similar for males (n=10), who had an average of 26.1 sightings (SD=10.75, range= 9–39) and an average annual sighting frequency of 3.8 years (SD=0.42, range=3–4). No significant gender-based differences in annual or overall sighting frequencies were present.

*Population estimates*

Mark-recapture abundance estimates, derived by using Chao's $M_{th}$ closed method, were similar for the first ($M_{th}$=82) and second ($M_{th}$=86) halves of

the study (Table 3). Both estimates obtained from the $M_{th}$ model were larger than the number of individuals identified during that sample period. The $M_{th}$ estimates, as well as the direct counts, suggest that between 1993–1996, the dolphin population size in Turneffe Atoll was relatively small and stable across the study period.

**Discussion**

Ecosystem specific adaptations are important in determining the site fidelity and social structure of mammals, including several cetacean species (Swingland & Greenwood, 1983; Connor, 2000). Bottlenose dolphins have been studied in a variety of locations and habitat types, with some of the most detailed information derived from work in Sarasota Bay, Florida (Wells, 1986), along the Texas coastline (Maze & Würsig, 1999; Weller & Würsig, in press), in Shark Bay, Western Australia (Connor, 1990), and across coastal areas of Southern California (Defran & Weller, 1999; Defran *et al.*, 1999). Turneffe Atoll is a unique environment with characteristics that both overlap and contrast with these and other study sites.
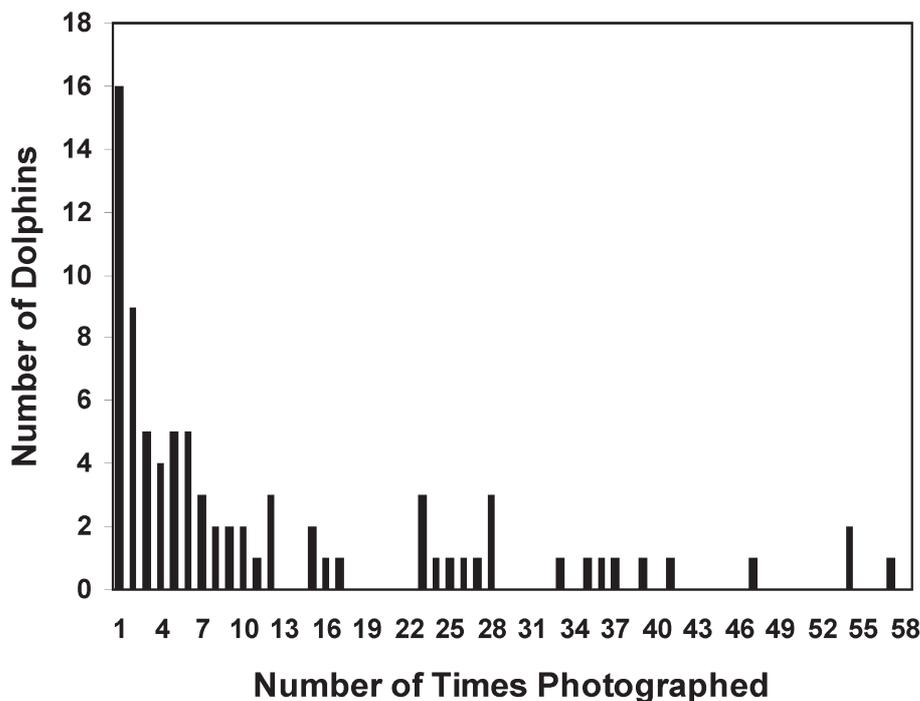
**Figure 3.** Sighting frequencies for the 81 bottlenose dolphins identified in Turneffe Atoll from 1992–1996.

**Table 3.** Bottlenose dolphin abundance estimation data and number of individuals photographed during the same two sample periods.

| Sample periods | Abundance | | | No. individuals photographed |
| --- | --- | --- | --- | --- |
| | Estimate | SE | 95% CI | |
| 1992 & 1993 | 82 | 7.3 | 73–103 | 66 |
| 1994 & 1995/96 | 86 | 8.1 | 76–109 | 68 |

Variations in the patterns of occurrence, site fidelity, group size and population size between Turneffe Atoll and other study sites suggest trends in the way that habitat differences influence the behavioural ecology of this species.

*Group size*
Group sizes reported for coastal bottlenose dolphins vary widely, with average sizes ranging from three to over 100 individuals (Connor *et al.*, 2000). In Turneffe Atoll, the small mean group size ($\bar{x}=3.8$) and the frequent occurrence of groups composed of one to four individuals indicated that this community was divided into small social and foraging units. These grouping patterns were similar to those reported for dolphins in other protected

areas, such as the west coast of Florida (Wells, 1986; Shane, 1990), along the Texas coast (Maze & Würsig, 1999; Weller & Würsig, in press), and in Shark Bay, Western Australia (Connor, 1990). These study sites and Turneffe Atoll all have predominantly sandy and seagrass substrates occurring within sheltered waters. Low-density, predictable food resources typical of this habitat type likely provide strong selective pressure for small group sizes (Shane *et al.*, 1986; Wells & Scott, 1999); and the formation of smaller foraging groups effectively reduces competition among conspecifics when prey density is low (Bertram, 1978; Connor, 2000).

In open waters, patchy, but rich food resources likely provide selective pressure for the formation of

larger groups. Increased group size allows dolphins to take advantage of integrated sensory information and feed cooperatively, thus increasing the energy intake of each group member (Würsig, 1986; Defran & Weller, 1999; Wells & Scott, 1999). For example, bottlenose dolphins along the Southern California coast form larger groups, and engage in extensive back and forth coastal movement, presumably to exploit their patchy, grouping prey items (Defran *et al.*, 1999).

In addition to energy intake, predation risk is a primary factor that can influence group size (Bertram, 1978; van Schaik & van Noordwijk, 1985; Lima & Dill, 1990). Larger groups provide greater protection to group members through improved predator detection and defense. There are many examples of group size increases successfully reducing predation in the terrestrial environment (e.g., van Schaik & van Noordwijk, 1985; Lima & Dill, 1990) and predation risk also has been suggested as an important determinant of group size in some odontocetes (Norris & Dohl, 1980; Shane *et al.*, 1986; Wells & Scott, 1999).

There is an inevitable trade-off between optimizing foraging efficiency and reducing predation risk (Bertram, 1978; Lima & Dill, 1990; Cowlishaw, 1997). For example, in Sarasota Bay, Florida and Shark Bay, Western Australia, where both low-density food resources and high predation risk exist, dolphin group size variation relative to microhabitat usage patterns appears to be a mechanism for balancing predation risk with food availability (Wells *et al.*, 1980; Wells *et al.*, 1987; Heithaus, 2001*a*). In Turneffe Atoll, the absence of shark injuries among dolphins is comparable to Moray Firth, Scotland (Wilson *et al.*, 1997) and the Adriatic Sea (Bearzi *et al*, 1997) where predators are rare. This is in marked contrast with the frequent observation of shark bite scars on dolphins in Moreton Bay, Eastern Australia (36%) (Corkeron *et al.*, 1987) Natal, South Africa (19%) (Cockcroft *et al.*, 1989), Sarasota Bay, Florida (31%) (Urian *et al.*, 1998) and Shark Bay, Western Australia (74%) (Heithaus, 2001*a*). The fact that no shark bite scars were observed in Turneffe Atoll suggests that, as in Moray Firth and the Adriatic Sea, predator risk for dolphins is minimal (see Heithaus, 2001*b*). If predation risk in Turneffe is indeed low, a primary factor influencing group size is likely to be energy intake. Therefore, group sizes in Turneffe likely provide a less confounded index of food resource characteristics than in locations where predation risk is greater and thus more influential on group formation.

The size of groups with calves in Turneffe Atoll was larger than groups without calves, as they were in California (Defran & Weller, 1999), Texas (Maze & Würsig, 1999), the Adriatic Sea (Bearzi

*et al.*, 1997), and Florida (Wells, 1986). Larger calf-group sizes thus appear to be a generalized characteristic of coastal bottlenose dolphins. In some cases, larger calf-groups could provide greater protection for the young against aggressive male conspecifics (Connor, 1990), as well as the benefits of social learning for young members (Shane, 1980; Norris & Dohl, 1980; Wells, 1986). In environments with low prey availability, such as those hypothesized to be characteristic of Turneffe Atoll, allomaternal behaviour in larger calf-groups could also increase the foraging efficiency of nursing mothers who are constrained by their maternal responsibilities.

*Site fidelity*

Site fidelity patterns for Turneffe dolphins are similar to those reported for dolphins along the Texas coast where some individuals are residents, while most others appear to be transients or infrequent visitors (Maze & Würsig, 1999; Weller & Würsig, in press). These site fidelity patterns contrast with those reported from Sarasota Bay, where many dolphins in that community display long-term site fidelity. Further, no gender differences in site fidelity patterns were documented among Turneffe dolphins, a finding that contrasts with Sarasota Bay where females exhibited a higher degree of site fidelity to the study area (Wells, 1986).

Protected areas, such as Turneffe Atoll and Sarasota Bay, vary considerably in the degree to which they are geographically open to surrounding oceanic waters. The barrier island environment of Sarasota Bay, with few and narrow openings to the Gulf of Mexico, is considerably more sheltered than Turneffe Atoll which has numerous 'cuts' and 'bogues' that open to the Caribbean Sea (Fig. 1). These variations in habitat openness could be an important factor in explaining the different community and gender-based site fidelity patterns observed between Sarasota and Turneffe. Dolphins inhabiting the relatively closed bay system of Sarasota could have fewer opportunities for movement into and out of the study area, while dolphin movement patterns in Turneffe Atoll are not as limited by geographic barriers.

The number of surveys and the number of groups encountered in the current study represent a considerable field effort (Table 2). It is unlikely, therefore, that the high proportion (70%) of dolphins not labelled as residents was the result of missed photographic opportunities. Rather, it appears that many of the dolphins photographed at Turneffe have ranges that include, but are not limited to the atoll. Sporadic visitors may exploit coastal waters along the Belize barrier reef or the more pelagic waters east of the atoll.

*Rate of discovery and population size*

The rate at which newly identified dolphins were discovered increased steadily until June 1993, when an apparent leveling trend in the discovery curve was observed. The apparent asymptote in the slope of the curve suggests that a small and finite population of dolphins uses the atoll, most of which were photographed by the end of the study. Thus, it appears that dolphins in Turneffe Atoll are members of a population that is demographically closed, but geographically open.

The abundance estimates obtained using Chao's $M_{th}$ closed model along with direct counts of photographically identified individuals also suggest that a small and finite population of dolphins uses Turneffe Atoll. Though site fidelity data indicate that there are fluctuations in the number of individuals present at any given time, abundance estimates over biannual sampling periods provided evidence of stability in the number of dolphins that inhabit the atoll. The small population size estimated for Turneffe Atoll suggests that overall dolphin density in the study area is very low–calculated at 0.16 dolphins per $km^2$. This density is similar to that in the Adriatic Sea (Bearzi *et al.*, 1997), but is one order of magnitude lower than in most places where bottlenose dolphin populations have been studied (Shane *et al.*, 1986; Wells *et al.*, 1987; Smolker *et al.*, 1992). Turneffe Atoll thus, appears to be a habitat that supports a low density of dolphins occurring in small groups due to low predation rates, low food availability or a combination of both factors.

The small, developing nation of Belize, in Central America, where this study took place, is a region targeted for increased tourism and development. Governmental and non-governmental organizations have expressed great concern over potential human impacts on Turneffe's marine environment that could occur with increased tourism in the region. Considering the very small group sizes formed by Turneffe dolphins, along with their small population size and the low proportion of residents, these concerns may be well-placed. Conservation measures are needed to protect these dolphins and their habitat from the possibly negative impacts of increased levels of tourism (Constantine, 2001) and fishing activities (Jackson *et al.*, 2001).

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