Bottlenose dolphins (<u>Tursiops truncatus</u>) in Turneffe Atoll, Belize: occurrence, site fidelity, group size and abundance

Gregory S. Campbell^{1,2} Barbara A. Bilgre^{1,2} R. H. Defran^{1,2}

¹Cetacean Behavior Laboratory - Department of Psychology San Diego State University, San Diego, CA 92182-4611 USA

²Oceanic Society, Fort Mason Center - Building E San Francisco, CA 94123 USA

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 ($\overline{x} = 3.8$, 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 ($\overline{x} = 12.2$, SD = 14.33) ranged from one to 57, with 20% of the photographed population sighted only once and 37% photographed \geq 10 times. Dolphins photographed \geq two 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 that 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.

Introduction

Bottlenose dolphins (*Tursiops* spp.) are widely distributed in tropical and temperate waters, occupying 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 behavior patterns (Wells & Scott, 1999). Intraspecific 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 behavior. 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 bottlenose dolphins in a coral reef, mangrove and seagrass 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.

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 western side of the atoll contains numerous narrow openings called "creeks" maintained by strong tidal currents (Stoddart, 1962). The prevailing substrate is sandy seagrass (<u>Thalassia sp</u>.) interspersed with small patches of hexacorals and sponges. Surface water temperatures, which were recorded from 1993–1996, ranged from 20–35° C ($\overline{x} = 28.2$, SD = 1.98), and water depth from 1–12 m. Total area of the atoll is 531.4 km². 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 and 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

Campbell et al.

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 hrs and were conducted one to two times daily between 0800–1800 hrs. Survey vessels were from 6–9 m in length with 80–200 HP outboard engines. Four to eight onboard 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 behavior (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 coloration, 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 and 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 colorslide 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, behavior 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 = .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 #1 (lowest quality). An exception to this exclusion rule was made when the size of the fin was rated #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 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 behaviors, 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, the 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, in order 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 were also 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 hrs of effort were conducted in the Turneffe Atoll study area from March 1992 to March 1996. A total of 473.7 hrs (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 crescentshaped scars associated with shark attacks (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 150^{th} 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) (Figure 3). Twenty percent (n = 16) of the dolphins identified were photographed once, 43% (n = 35) 2–9 times, and 37% (n = 30) \ge 10 times. The number of study years in which identified dolphins were photographed (annual sighting frequency) averaged 2.5 yr (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 r = .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 ($\overline{x} = 50.8$, SD = 51.10). Forty-one percent (n = 25) of the dolphins sighted ≥ 2 times within ≥ 1 study year had 30 d or less between sightings, while 7% had an average of 100 d or more 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 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 yrs (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 yrs (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. 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 behavioral 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 ($\overline{x} = 3.8$) 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

Campbell et al.

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, patchily distributed 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 has also 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 lowdensity food resources and high predation risk exist, dolphin group size variation relative to micro-habitat usage patterns appears to be a mechanism for balancing predation risk with food availability (Wells et al., 1980; Wells et al., 1987; Heithaus, 2001a). 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, 2001a). 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, 2001b). 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-

Campbell et al.

group sizes thus appear to be a generalized characteristic of coastal bottlenose dolphins. In some cases larger calf-groups may provide greater protection for the young against aggressive male conspecifics (Connor, 1990), as well as the benefits of social learning for its 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 behavior in larger calf-groups may 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 may be an important factor in explaining the different community

Campbell et al.

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 labeled 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 use 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 km². 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, 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).

Acknowledgments

Numerous individuals made important contributions to this study. The authors first thank B. Winning and the Oceanic Society for funding and logistical support. The Belize Fisheries Department, the Belize Forestry Department, and R. Lightburn deserve recognition for their support of marine mammal research and conservation in Belize. We thank B. Würsig, K. Dudzinski and C. Graham of the Marine Mammal Research Program (MMRP) at Texas A&M University for their early work on this project and for making their data available for our analyses. We are grateful to E. Betancourt, R. Geban, K. Leslie and A. Small for their expertise in navigation and boat handling. The staff at Blackbird Caye Resort, as well as A. Dugan, S. Anderson, S. Christie, N. Crane, A. Molina and A. Sanders, provided invaluable field support. We thank M. Autrey, K. Dudzik, C. Faist, E. Howarth, K. Kerr, K. Liermann, J. Oswald, J. Roy and A. Toperoff for their assistance with photographic and data analysis. David Weller, K. Campbell, A. Lang, and G. Oliver graciously offered insightful and helpful remarks on drafts of this manuscript. We thank two anonymous reviewers for their helpful comments. Finally, this study would not have been possible without the participation and support of hundreds of Oceanic Society volunteers. This research was conducted under a marine scientific research permit issued to Oceanic Society from the Ministry of Agriculture & Fisheries, Government of Belize.

Literature Cited

- Arnbom, T. (1987) Individual identification of sperm whales. *Reports of the International Whaling Commission*. **37**, 201–204.
- Bearzi, G., Notarbartolo-Di-Sciara, G. & Politi, E. (1997) Social ecology of bottlenose dolphins in the Kvarneric (northern Adriatic Sea). *Marine Mammal Science*. 13, 650–668.
- Bertram, B. C. R. (1978) Living in groups: predators and prey. In: Krebs, J. R. & Davies, N. B., (eds.) *Behavioural Ecology: an Evolutionary Approach*, Blackwell Scientific Publications, Oxford, UK. pp. 279-309.
- Chao, A., Lee, M. S., & Jeng, S. L. (1992) Estimating population size for capturerecapture data when probabilities vary by time and individual animal. *Biometrics*. 48, 201–216.
- Cockcroft, V. G., Cliff, G. & Ross, G. J. B. (1989) Shard predation on Indian Ocean bottlenose dolphin Tursiops truncates off Natal, South Africa. *South African Journal of Zoology.* 24, 305-310.
- Connor, R. C. (1990) Alliances among male bottlenose dolphins and a comparative analysis of mutualism. Ph.D. dissertation. The University of Michigan, Ann Arbor, MI. 139 pp.
- Connor, R. C. (2000) Group living in whales and dolphins. In: Mann, J., Connor, R.C.,
 Tyack, P. L. & Whitehead, H., (eds.) *Cetacean Societies: Field Studies Of Dolphins And Whales*, University of Chicago Press, Chicago, II. pp. 199-218.
- Connor, R. C., Wells, R. S., Mann, J. & Read, A. J. (2000) The bottlenose dolphin: social relationships in a fission-fusion society. In: Mann, J., Connor, R.C., Tyack,

P. L. & Whitehead, H., (eds.) *Cetacean Societies: Field Studies Of Dolphins And Whales*, University of Chicago Press, Chicago, Il. pp. 91-126.

- Constantine, R. (2001) Increased avoidance of swimmers by wild bottlenose dolphins (*Tursiops truncatus*) due to long-term exposure to swim-with-dolphin tourism.*Marine Mammal Science.* 17, 689-702.
- Corkeron, P. J., Morris, R. J. & Bryden. (1987) Interactions between bottlenose dolphins and sharks in Moreton Bay. *Aquatic Mammals.* 13, 109-113.
- Cowlishaw, G. (1997) Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. Animal Behavior. **53**, 667-686.
- Defran, R. H., Shultz, G. M. & Weller, D. W. (1990) A technique for the photographic identification and cataloging of dorsal fins of the bottlenose dolphin (<u>Tursiops</u> <u>truncatus</u>). *Report of the International Whaling Commission*. (Special Issue 12), 53–55.
- Defran, R. H. & Weller, D. W. (1999) Occurrence, distribution, site fidelity, and school size of bottlenose dolphins (<u>Tursiops truncatus</u>) off San Diego, California. *Marine Mammal Science.* **15**, 366–380.
- Defran, R. H., Weller, D. W., Kelly, D. & Espinosa, M. A. (1999) Range characteristics of Pacific Coast bottlenose dolphins in the Southern California Bight. *Marine Mammal Science*. **15**, 381–393.
- Friday, N., Smith, T. D., Stevick, P. T. & Allen, J. A. (2000) Measurement of photographic quality and distinctiveness for the photographic identification of humpback whales, <u>Megaptera noveangliae</u>. *Marine Mammal Science*. **16**, 355–374.

- Hammond, P. S. (1986) Estimating the size of naturally marked whale populations using capture-recapture techniques. *Reports of the International Whaling Commission*. (Special Issue 8), 2553–282.
- Heithaus, M. R. (2001a) Shark attacks on bottlenose dolphins (*Tursiops aduncus*) inShark Bay, Western Australia: Attack rate, bite scar frequencies and attack seasonality.*Marine Mammal Science*. 17, 526-539.
- Heithaus, M. R. (2001b) Predator-prey and competitive interactions between sharks (order Selachii) and dolphins (suborder Odontoceti): a review. *Journal of Zoology,* (London). 253, 53-68.
- Jackson, J. B. C., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque,
 B. J., Bradbury, R. H., Cooke, R., Erlandson, J., Estes, J. A., Hughes, T. P., Kidwell,
 S., Lange, C. B., Lenihan, H. S., Pandolfi, J. M., Peterson, C. H., Steneck, R. S.,
 Tegner, M. J. & Warner, R. R. (2001) Historical overfishing and the recent collapse
 of coastal ecosystems. *Science*. 293, 629-637.
- Lima, S. L. & Dill, L. M. (1990) Behavioral decisions made under the risk of predation. *Canadian Journal of Zoology.* **68**, 619-640.
- Maze, K. S. & B. Würsig. (1999) Bottlenose dolphins of San Luis Pass, Texas: occurrence patterns, site-fidelity, and habitat use. *Aquatic Mammals*. **25**, 291–103.
- Norris, K. S. & Dohl, T. P. (1980) The structure and function of cetacean schools. In: L.
 M. Herman, (ed.) *Cetacean Behavior: Mechanisms And Functions*, John Wiley and Sons, New York, NY. pp 211–262.
- Otis, D. L., Burnham, K. P., White, G. C. & Anderson, D. R. (1978) Statistical inference from capture data on closed animal populations. *Wildlife Monographs*. **62**, 1–135.

- Pollock, K. H., Nichols, J. D., Brownie, C. & Hines, J. E. (1990) Statistical inference for capture-recapture experiments. *Wildlife Monographs*. 107, 1–97.
- Rexstad, E. & Burnham, K. (1991) User's guide for interactive program CAPTURE,Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University,Fort Collins, CO.
- Shane, S. H. (1980) Occurrence, movement and distribution of bottlenose dolphin, (Tursiops truncatus), in southern Texas. *Fishery Bulletin*. **78**, 593–601.
- Shane, S. H. (1990) Behavior and ecology of the bottlenose dolphin at Sanibel Island, Florida. In: S. Leatherwood & R. Reeves, (eds.) *The Bottlenose Dolphin*, Academic Press, Inc., San Diego, CA. pp 245–266.
- 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.
- Siegel, S. & Castellan, N. J. (1988) Non-Parametric Statistics For The Behavioral Sciences, McGraw-Hill, New York, NY.
- Slater, P. J. B. & Halliday, T. R. (1994) *Behaviour And Evolution*, Cambridge University Press, Cambridge, U.K.
- Smolker, R. A., Richards, A. F., Connor, R. C. & Pepper, J. W. (1992) Sex differences in patterns of association among Indian Ocean bottlenose dolphins. *Behaviour*. 123, 38-69.
- Stoddart, D. R. (1962) Three Caribbean atolls: Turneffe Islands, Lighthouse Reef, and Glover's Reef, British Honduras. *Atoll Research Bulletin.* 87, 1–147.
- Swingland, I. R. & Greenwood, P. J. (1983) The Ecology Of Animal Movement, Clarendon Press, U.K.

- van Schaik, C. P. & van Noordwijk, M. A. (1985) Evolutionary effects on the absence of felids on the social organization of the macaques on the island of Simeulue (*Macca fasicularis fusca*). Folia Primatologica. 44, 138-147.
- Weller, D. W. & Würsig, B. (in press) Bottlenose dolphins of Aransas Pass Texas:Annual and seasonal patterns of occurrence, site fidelity and behavior. *Fishery Bulletin*.
- Wells, R. S. (1986) The population structure of bottlenose dolphins. Ph.D. dissertation.University of California Santa Cruz, Santa Cruz, CA. 234 pp.
- Wells, R. S., Irvine, A. B. & Scott, M. D. (1980) The social ecology of inshore odontocetes. In: Herman, L. M., (ed.) *Cetacean Behavior: Meachanisms and Functions*, Wiley, New York. pp 263–317.
- Wells, R. S., Scott, M. D. & Irvine, A. B. (1987) The social structure of free-ranging bottlenose dolphins. In: H. Genoways, (ed.) *Current Mammalogy*. Vol. I., Plenum Press, New York and London. pp 247–305.
- Wells, R. S. & Scott, M. D. (1999) Bottlenose dolphin <u>Tursiops truncatus</u>. In: S. H. Ridgeway & R. J. Harrison, (eds.) *Handbook Of Marine Mammals: Volume VI, The Second Book Of Dolphins And Porpoises*, Academic Press, San Diego, CA. pp 137– 182.
- Whitehead, H. S., Gowans, S., Fauchner, A. & McCarrey, S. W. (1997) Population analysis of northern bottlenose whales in the Gully, Nova Scotia. *Marine Mammal Science*. 13, 173–185.

- Wilson, B., Thompson, P. W. & Hammond, P. S. (1997) Habitat use by bottlenose
 dolphins: Seasonal distribution and stratified movement patterns in the Moray Firth,
 Scotland. *Journal of Applied Ecology.* 34, 1365–1374.
- Wilson, B., Hammond, P. S. & Thompson, P. S. (1999) Estimating size and assessing trends in a coastal bottlenose dolphin population. *Ecological Applications*. 9, 288–300.
- Würsig, B. (1978) Occurrence and group organization of Atlantic bottlenose porpoises (<u>Tursiops truncatus</u>) in an Argentine bay. *Biological Bulletin*. **154**, 348–359.
- Würsig, B. (1986) Delphinid foraging strategies. In: R. J. Schusterman, J. A. Thomas and F. G. Wood, (eds.) *Dolphin Cognition And Behavior: A Comparative Approach*, Lawrence Earlbaum Associates, Hillsdale and London. pp 347–359.

	Rating					
Measure	# 1	# 2	# 3	# 4		
Focus	Blurry but general	Slightly blurred, soft	Sharp edge, adequate	N/A		
	fin outline visible	edge, small nicks	to detect small nicks			
Contrast	Shading similarities do not allow clear differentiation between fin and background	Fin and background similar in shading and fin edge obscured by glare	Fin and background similar in shading or fin edge obscured by glare	Fin and back- ground 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 1. Textual descriptions for each level of the four parameters used to rate photographic quality.

	Study	No.	Total	Dolphins /	Total	Groups /	G	roup Si	ize	Calf
	Period	Surveys	Dolphins	Survey	Groups	Survey	Mean	SD	Range	Percent
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%

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

	A	bundanc	No. Individuals	
Sample Periods	Estimate	SE	95% CI	Photographed
1992 & 1993	82	7.3	73-103	66
1994 & 1995/96	86	8.1	76-109	68

Table 3. Dolphin abundance estimation data and number ofindividuals photographed during the same two sample periods.



Figure 1. The Turneffe Atoll study area. Insets show study area location within Central America (A), and along the coast of Belize (B).



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.



Figure 3. Sighting frequencies for the 81 dolphins identified in Turneffe Atoll from 1992–1996.