

Inshore and offshore bottlenose dolphin (*Tursiops truncatus*) communities distinguished by association patterns near Grand Bahama Island, Bahamas

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Abstract: Little is known about the behavior of offshore dolphin populations. Our purpose was to distinguish and describe stable social groups of bottlenose dolphins (*Tursiops truncatus*) between inshore and offshore West End, Grand Bahama Island (26°42'N, 79°00'W). Photoidentification was conducted from May to September, 1994 to 1996. A simple ratio index described association patterns between dolphins. Multidimensional scaling of association indices ($n = 1711$ dolphin pairs) distinguished two dolphin communities consisting of 28 dolphins (19 of known sex) found inshore and 15 dolphins (12 of known sex) found ≥ 27 km offshore. Eight of the 15 offshore dolphins were opportunistically photographed in the same region between 1986 and 1990. The two communities were found at different water depths (Mann-Whitney U test, $p < 0.01$), over distinct bottom types (Kruskal-Wallis test, $p < 0.01$), and used different bottom-foraging strategies. Long-term site fidelity of up to 10 years and repeated dolphin associations of up to 8 years occurred ≥ 27 km from shore. Dolphins sighted ≥ 15 times averaged 48 associates (SD = 11, $n = 28$). A dolphin's closest associate was of the same gender 74% of the time. This study is the first to report long-term site fidelity and association patterns of bottlenose dolphins found far from shore.

Résumé : Le comportement des dauphins au large des côtes est mal connu. Nous avons cherché à distinguer et à décrire les groupes sociaux stables chez des Dauphins à gros nez (*Tursiops truncatus*), sur la côte et au large de la côte, dans l'extrémité ouest de l'île Grand Bahama (26°42'N, 79°00'O). Les dauphins ont été identifiés par photographie entre mai et septembre, en 1994-1996. Des indices basés sur des rapports simples ont servi à décrire les associations entre individus. Une échelle multidimensionnelle des indices d'association ($n = 1711$ paires de dauphins) a fait ressortir deux communautés de dauphins composées respectivement de 28 individus (19 de sexe connu) sur la côte et de 15 individus (12 de sexe connu) trouvés ≥ 27 km de la côte. Huit des 15 dauphins de la communauté du large ont été photographiés occasionnellement dans la même région entre 1986 et 1990. Les deux communautés fréquentent des eaux de profondeurs différentes (test U de Mann-Whitney, $p < 0,01$), sur des substrat distincts (test de Kruskal-Wallis, $p < 0,01$) et elles utilisent des stratégies distinctes de recherche de nourriture sur le substrat. Les dauphins du large se sont avérés fidèles au site, parfois pendant 10 ans, et des associations d'individus ont persisté pendant près de 8 ans trouvés ≥ 27 Km de la côte. Des dauphins aperçus ≥ 15 fois étaient associés en moyenne à 48 individus (écart type = 11, $n = 28$). Le partenaire le plus proche était du même sexe dans 74% des cas. Il s'agit là de la première étude à mentionner la fidélité à long terme au site et à mettre en lumière les patterns d'associations chez des Dauphins à gros nez vivant au large des côtes.

[Traduit par la Rédaction]

Introduction

Patterns of association between individual bottlenose dolphins (*Tursiops truncatus*) vary from dynamic and temporary to stable and long term (Würsig 1978; Wells et al. 1987; Ballance 1990; Würsig and Harris 1990; Weller 1991; Smolker et al. 1992; Bräger et al. 1994; Harzen 1995). Association

patterns are useful in defining a community (Wells et al. 1987). Community members typically interact closely and frequently with one to several particular individuals, less so with other members of the community, and least with dolphins of surrounding communities (Wells et al. 1987).

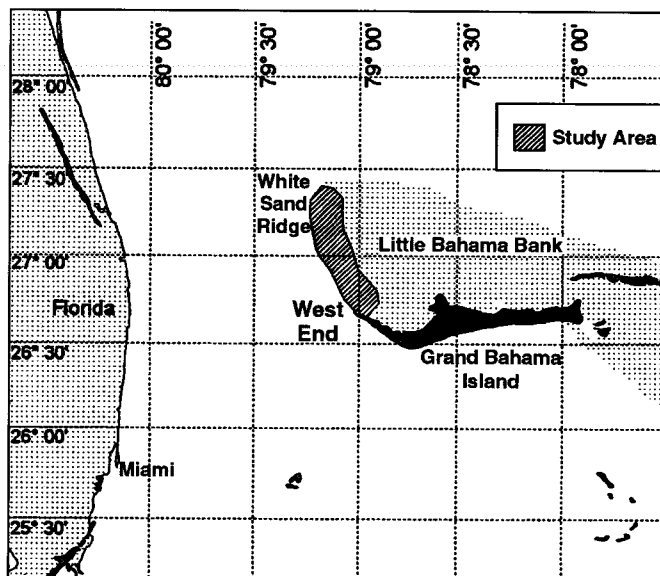
Two ecotypes of the bottlenose dolphin are generally known as coastal and offshore (Hersh and Duffield 1990). However, the coastal ecotype can be found far from shore in locations where the continental shelf extends away from land (Kenney 1990). Bottlenose dolphins occurring coastally are most accessible to researchers, and therefore, their association patterns and movements are best understood. Every study of bottlenose dolphin association patterns has occurred in bays or within a few miles of shore (Wells 1986; Wells et al. 1987; Weller 1991; Smolker et al. 1992; Bräger et al.

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Fig. 1. The study area is located on the western edge of Little Bahama Bank, Bahamas.



1994; Harzen 1995; Wilson 1995; Felix 1997). Little is known about either ecotype, as the species occurs further from shore.

The purpose of this study was to distinguish and describe dolphin communities based on association patterns and ranges of individuals from West End, Grand Bahama Island, due offshore about 56 km along the western edge of Little Bahama Bank, Bahamas. Dolphins in the present study appear to be the coastal ecotype (Hersh and Duffield 1990). They measure about 2.4 m in length and are small compared with dolphins seen in the Gulf Stream just to the west.

Materials and methods

Study area

The study area (Fig. 1) follows the western edge of Little Bahama Bank between West End, Grand Bahama Island (26°42'N, 79°00'W), and the White Sand Ridge (27°15'N, 79°08'W). It is approximately 280 km², spanning 56 km north to south and about 5 km east to west. Water depth varies from <1 to 20 m and generally increases in depth from south to north. The unprotected study area is characterized by a sand bottom with small and large patches of turtle grass (*Thalassia testudinum*) and scattered areas of rock and reef bottom.

Little Bahama Bank extends more than 160 km along the north side of Grand Bahama Island from West End, Grand Bahama Island, to Abaco; and is about 80 km north to south at its widest point. The western border of the study area is a steep drop-off leading to the eastern edge of the Gulf Stream, which is over 500 m deep.

Materials

A 20-m power catamaran (M/V *Stenella*) and a 5.3-m inflatable boat with a 25-hp (1994) or a 75-hp (1995, 1996) motor were primarily used to search for and photograph dolphins (1 hp = 746 W). We used a Canon AE-1 35-mm camera with a 300-mm telephoto lens and Kodachrome 64, Kodachrome 200, or Fuji 100 film to photograph dolphin dorsal fins at the surface. Underwater photos of fin notches, body scars, and genital regions were taken with a Nikonos V 35-mm camera and Kodachrome 200 film.

Search procedure

We divided the study area latitudinally into three sections (southern, central, and northern). The southern section extended from West End (26°42'N) to about 19 km offshore (26°54'N). The northern section (27°03'–27°15'N) was searched in collaboration with the Wild Dolphin Project (WDP), during their ongoing research of spotted dolphins (*Stenella frontalis*). Spotted dolphins are primarily sighted on the bank, north of 27°03'N. The central section (26°54'–27°03'N) was infrequently searched because it was most difficult to reach from the shore-based camp and of less interest to the spotted-dolphin project.

South

Periods of approximately 1–5 weeks were spent searching for dolphins in the southern section of the study area. Most searches were conducted from the inflatable boat under fair to excellent weather conditions (Beaufort Sea states 0–2). Searches started from our base camp at West End and were conducted during all times of the day between dawn and dusk.

Land-based searches were conducted around dawn and during questionable weather conditions. Observers used binoculars from the beach of the Jack Tar Marina, West End, or from the roof of a three-storey building about 100 m east of the marina. When observers sighted dolphins, we followed them with the inflatable boat.

North and central

We searched the northern region of the study area for periods of 1–2 weeks. A dolphin search was conducted continuously from the *Stenella* between 07:00 and 19:00, during all but severe weather conditions. Occasionally, we were able to reach the central section of the study area from the south in the inflatable boat or from the north in the *Stenella*.

Data collection

We collected data at dolphin sightings between May and September, 1994–1996. A dolphin sighting was defined as all dolphins in sight, moving in the same direction, and usually involved in similar activity (termed pod in Shane 1990a). Data were recorded on a tape recorder (transcribed that evening) at each sighting and consisted of date, start time, start location (latitude and longitude from the global positioning system), end time, end location, and the estimated numbers of bottlenose dolphins, young of the year (about half the adult size or smaller, and surfacing in an echelon position with a larger dolphin), and calves (greater than half the adult size, but still with presumed mother). We also recorded water depth, bottom type (sand, rocks, reef, and unknown), vegetation type (turtle grass, other, and absent), dominant benthic features (bottom or vegetation), and the identity of all recognizable dolphins.

Photographs of dorsal fins were used to identify individual dolphins at the surface (Würsig and Würsig 1977; Würsig and Jefferson 1990). After dolphins were photographed, if weather conditions were acceptable and if dolphins were not traveling, we entered the water with snorkel gear to obtain further identification markings, to determine dolphin gender, and to observe behavior. Dolphin gender was determined by direct observation of the genital region. Females were also indicated by regular accompaniment of a smaller animal presumed to be her calf. A concerted effort was made to photograph the genital area when possible. Without a photo, gender confirmation was attempted by a second observer or by the same observer on another occasion.

Photo management and manipulation

We compared and matched dorsal fin photos of each sighting. The number of photoidentified dolphins in a sighting was then

Table 1. Field effort and success of dolphin observations during 1994–1996.

	1994	1995	1996	Total
Workable days* in the field	85	117	54	256
Hours of searching	731	945	486	2162
Days of sightings	49	81	37	167
Number of sightings†	80	123	92	295
Sightings photographed	43	93	67	203
Average minutes spent per sighting	44	96	45	66
Hours of direct dolphin observation	60	197	65	322
Percent of time in direct observation of dolphins	8.2	20.8	13.9	14.9

*Workable days were dry with winds <28 km/h.

†Includes five sightings observed from land (no photos) on days of no searching.

compared with the field estimate. If the number of photoidentified dolphins was equal to or greater than the field estimate (excluding unidentifiable calves), the field estimate was adjusted (if lower) to the number of photoidentified dolphins (plus unidentifiable calves) and the sighting was labeled fully photographed. The term fully photographed was chosen to distinguish sightings in which all individuals were *presumably* photographed from those sightings that we *knew* to be incompletely photographed and from those sightings that we were relatively uncertain about the photographic coverage. Individuals identified in the sighting were then compared with a catalogue of the best photos of previously identified individuals and matched or named as a newly identified dolphin.

Additional photoidentified individuals were recorded when they appeared in photos or videos from WDP, or other reliable sources, and were supplied with at least a date or a location. The field effort for these records is not included in this paper.

Data management, manipulation, and analysis

Dolphin association indices were determined with the use of the simple ratio index (SR) (Ginsberg and Young 1992):

$$\frac{x}{x + Y_A + Y_B}$$

where x is the number of times dolphins A and B were sighted together, Y_A is the number of times dolphin A was seen without dolphin B, and Y_B is the number of times dolphin B was seen without dolphin A. We chose the SR index because it describes associations that were observed without attempting to control for biases in data collection.

Association indices were calculated for all dolphin pairs photographed in each sighting. A dolphin's presence was recorded once each day, unless it was seen with different dolphins >1 h later in the day to justify a separate record. Calves were excluded from all analyses because it was expected that range and association patterns were dependent on those of the mother.

Two data sets were used for the analyses of association patterns. The "All-Associate" data set contained every pair combination of all photoidentified dolphins during 1994–1996. The "Full-Photo Associate" data set was a subset of the All-Associate. It contained pairs of animals in fully photographed sightings only.

The Full-Photo Associate data set was used primarily to distinguish groups. A group was defined as a social unit, somewhat stable over time (Wells et al. 1987). Both multidimensional scaling (MDS; Mardia et al. 1979) and cluster analysis (group average method; Mardia et al. 1979, Manugistics Inc. 1995) were applied to association indices of dolphins photographed ≥ 5 times to distinguish groups. MDS and cluster analysis are multivariate techniques that group interdependent data. The group average method of cluster analysis is a hierarchical method that has been used in many studies of dolphin social systems (Wells et al. 1980; Ballance 1990; Heimlich-Boran 1993; Slooten et al. 1993; Harzen 1995; Wilson

1995). However, cluster analysis is a subjective tool that will group even unrelated data, whereas MDS is an objective tool that will only group data that are related. An agglomeration distance plot (Manugistics Inc. 1995) facilitated the choice of the number of cluster analysis groups. The agglomeration distance plot showed the relative distance between groups when they were combined by cluster analysis.

The All-Associate data set provided information on an individual's total number of associates. Data from the All-Associate data set were also used to distinguish further possible groups in which members were excluded from the full-photo analysis because of an insufficient number of fully photographed sightings. Non-calf dolphins photographed ≥ 5 times in all sightings were used in these analyses.

Results

Effort

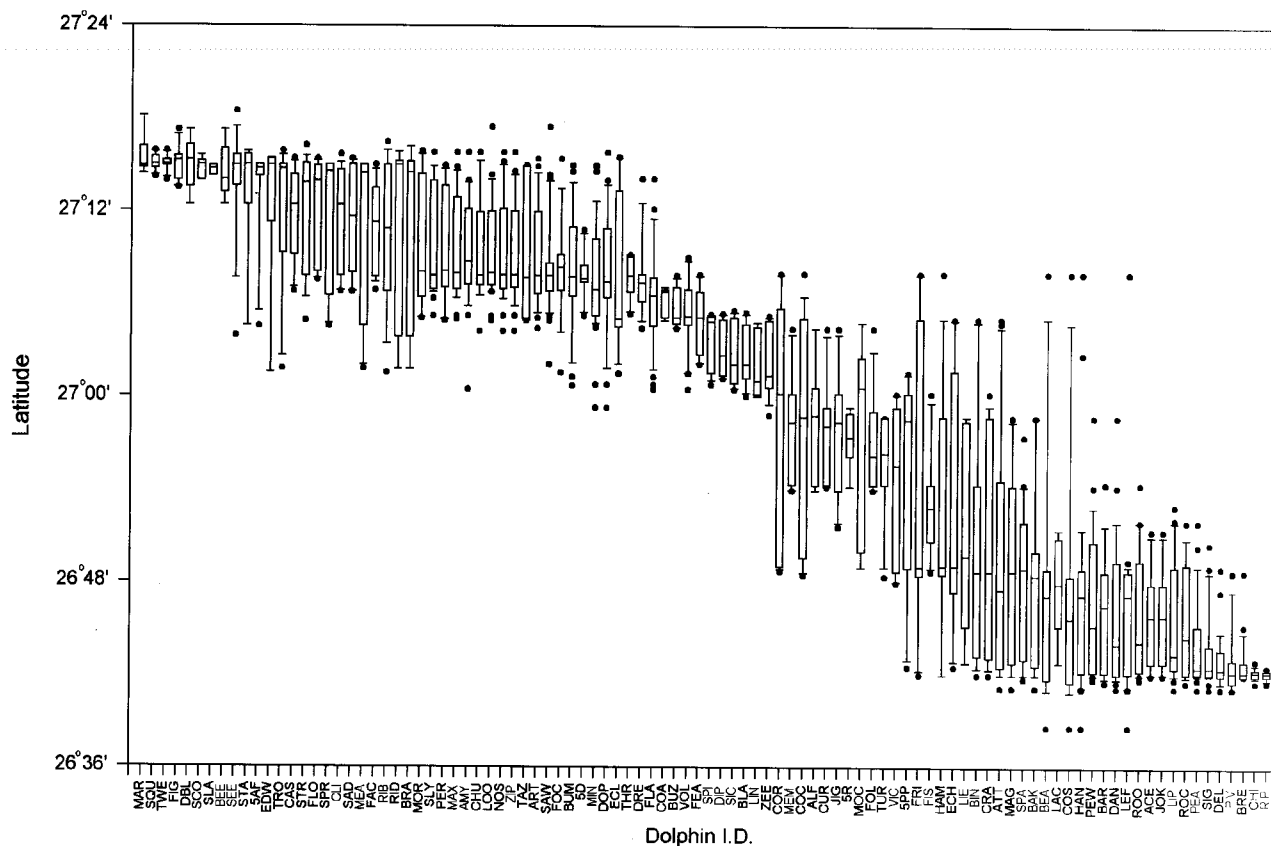
We spent full or partial days searching in the following areas: 86 days in the north, 169 days in the south, and 54 days (50 of which were partial and averaged only 3 h/day) in the central region (Table 1). During 1994–1996, we photographed 203 sightings with 9608 frames of film. We collected 1083 dolphin records (i.e., an identified individual photographed at a unique date, time, and location) including identifiable calves (380 north, 153 central, and 550 south), although not all dolphins were photographed in each sighting.

In addition, over 5300 photos were analyzed from the WDP's collection, dated between 1985–1996. These photos provided 528 additional records. We obtained an additional 103 records during times other than the field season and 37 records were received from other reliable sources. These 668 additional records were located as follows: 522 north, 73 central, 29 south, and 44 unknown locations. Therefore, the number of individual records totaled 1751.

During the study we identified 211 individual dolphins. Of these, 105 were first recorded during 1994. In 1995, 91 new individuals were sighted (48% of 188 individuals identified in 1995), and in 1996, only 15 new dolphins were identified (11.5% of 130 individuals identified in 1996). The substantial decrease in new individuals identified in 1996 suggested that most of the dolphins inhabiting the area between May and September were identified by the end of the study.

Gender was determined for 77 (36%) of the identified dolphins. We directly observed 57 genital regions (37 were photographed) and identified 20 presumed females by regular accompaniment of a calf.

Fig. 2. Latitudinal ranges of 98 noncalves sighted ≥ 5 times (ordered by mean latitude), during 1994–1996. Boxes indicate the 25th–75th percentiles. The solid line inside the boxes represents the median. Whiskers above and below the boxes show the 10th and 90th percentiles. Points indicate outliers.



Site fidelity

Individuals were seen an average of seven times each ($SD = 7$, $n = 211$) during the study. On 35 occasions (2% of 1751 records), a dolphin was counted as present twice in 1 day as result of being photographed with different dolphins in the two sightings. Fifty-four dolphins (205 records) were matched to photos taken opportunistically between 1985 and 1993, many of which were photographed numerous times before 1994 (Rossbach 1997).

All non-calves photographed ≥ 5 times ($n = 98$) showed site fidelity to a specific region of the study area (Fig. 2). Non-calves photographed ≥ 15 times ($n = 28$) during 1994–1996 showed one of two broad-range tendencies, inshore or offshore. Although the 205 pre-1994 dolphin records were not included in these analyses, locations of individuals sighted within the study area were congruent with the 1994–1996 findings (Rossbach 1997), suggesting long-term site fidelity for at least some individuals.

Association patterns

We documented 821 individual records in 158 fully photographed sightings. A total of 148 dolphins was recorded in ≥ 1 fully photographed sightings (dolphin or individual refers to a non-calf dolphin here and for the remainder of results). Association indices showed that $<17\%$ of all possible pairwise interactions between dolphins (1827/10 878 pairs) in these sightings were observed.

Primary groups

Multidimensional scaling of 59 dolphins photographed ≥ 5 times in fully photographed sightings ($n = 1711$ dolphin pairs) indicated three primary groups (Fig. 3). Cluster analysis of the same data suggested four primary groups (Fig. 4) based on a relative distance of 110, which we chose as a divider of groups. The agglomeration distance plot (Fig. 5) suggests that “a sharp jump at some location may indicate that a good choice for the number of groups is just to the left of the jump” (Manugistics Inc. 1995). The resulting cluster analysis groups were also congruent with what we observed in the field and were most similar to the MDS plot.

Members of the same group shared similar ranges. The range of some members of each group overlapped with the range of some or all members of other groups. A large group of 15 dolphins was called the northern dolphins because of the dolphins’ relative range within the study area. Twelve of the 15 individuals were of known sex (6 males; 6 females, 3 with a calf). Northern dolphins were sighted ≥ 27 km from shore and considered offshore relative to a large group of 28 dolphins that was termed the southern dolphins because of members’ inshore range. Nineteen of the southern dolphins were of known sex (9 males; 10 females, 7 with a calf). Members of the two groups were photographed in the same sighting in only 1.3% (2/158) of all fully photographed sightings.

Most dolphins in these two groups were sighted frequently. Northern dolphins were sighted an average of 22

Fig. 3. Multidimensional scaling shows the relative distance between simple ratios of 59 non-calves. Dolphins nearing the center point (0,0) showed no strong affinity to any group or to each other and were not assigned to a group. Some dolphins were moved slightly on the plot for readability.

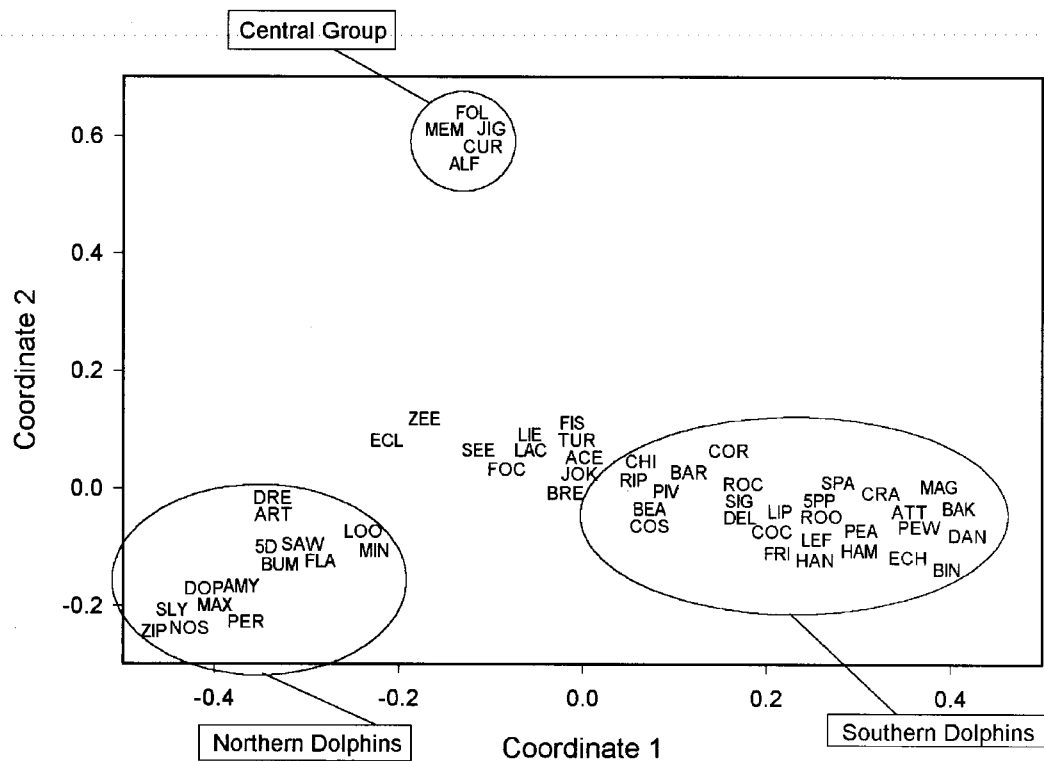


Fig. 4. Cluster analysis (group average method) dendrogram of simple ratios of 59 non-calves shows four groups at a relative distance of 110. In cases where the first association between two dolphins was greater than a distance of 60, the two dolphins were not fit into a new or existing cluster because the indices showed that the two dolphins associated with other dolphins more than with each other.

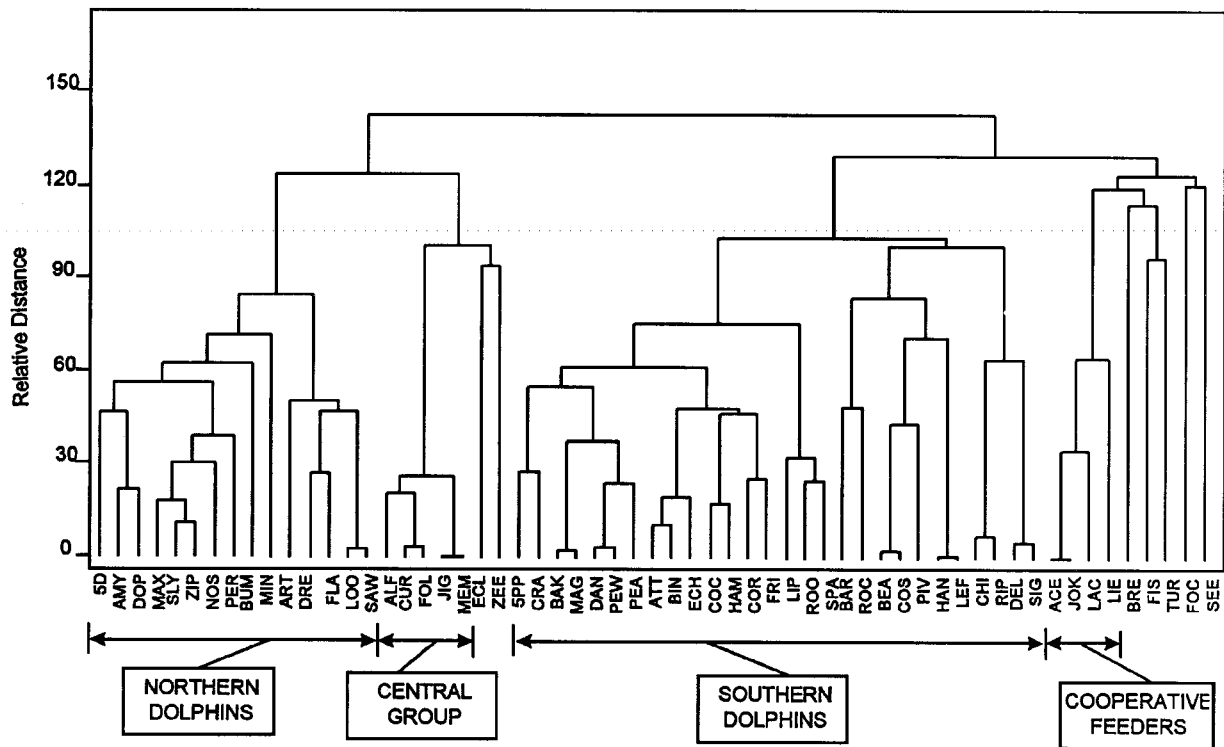
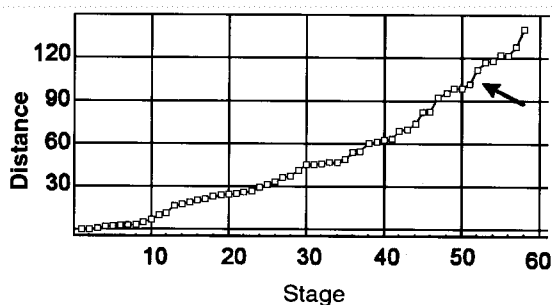


Fig. 5. The agglomeration distance plot shows the relative distance between groups when they were combined by cluster analysis. The arrow indicates the distance of 110, which we chose as a divider of groups.



times each ($SD = 9$, $n = 15$) and southern dolphins were seen an average of 16 times each ($SD = 6$, $n = 28$) between 1994 and 1996, well above the overall average of seven sightings per dolphin ($n = 211$). Also, most sightings of each dolphin were spread over time. Fourteen of the 15 northern members were sighted during all three field seasons and eight dolphins were photographed in the same area between 1986 and 1990. Fifteen of the 28 southern dolphins were sighted during all three seasons and the remaining during two seasons. Four southern dolphins were photographed prior to 1994.

The two large groups of dolphins were considered communities. We defined a community as a group of dolphins that included both genders, showed long-term site fidelity, relatively high association between members, low association with neighboring individuals, and shared similar habitat and feeding habits. The northern and southern members were probably core to larger communities because other probable members were excluded from the analyses simply because of an insufficient number of photographs (i.e., less than five records) in fully photographed sightings.

A smaller group was also shown by both MDS and cluster analysis. It consisted of five dolphins. Three were known females, two with calves. This small group was located between the range of the northern and southern dolphins and was termed the central group. These five dolphins could be a female band (Wells 1991) or clique (Smolker et al. 1992), belonging to the northern or southern communities or could be part of a central community.

Another small group consisted of four dolphins and was suggested only by cluster analysis. These dolphins were rather easily distinguished in the field because of their cooperative feeding method of herding fish, for which they are named cooperative feeders (Rossbach 1999). The cooperative feeders were not distinguished by MDS, probably because of the low number of fully photographed sightings of each individual. Each of the four dolphins was only identified five times in fully photographed sightings. The cooperative feeders were probably part of a larger group; however, other presumed members were photographed an insufficient number of times in fully photographed sightings to be included in the analyses. They were relatively highly associated (SR median = 0.34, $\bar{x} = 0.43$, $SD = 0.29$, $n = 6$ pair combinations), and though overlapping in range, were rarely associated with the southern dolphins.

Table 2. Simple ratio medians, means, and standard deviations within and between dolphin groups.

Group combination	Median	Mean	SD	N
North/north	0.18	0.21	0.13	105
North/south	0	0.01	0.02	420
North/central	0	0.01	0.02	75
North/cooperative	0	0	N/A	60
South/south	0.16	0.19	0.15	378
South/central	0	0.01	0.03	140
South/cooperative	0	0.03	0.04	112
Central/central	0.5	0.57	0.2	10
Central/cooperative	0	0	N/A	20
Cooperative/cooperative	0.34	0.43	0.29	6

Note: Data were taken from the Full-Photo Associate data set. N/A, not applicable.

Simple ratios (SR) were substantially higher between pairs of dolphins within each of the four groups than between pairs of dolphins in different groups (Table 2). All members of the cooperative feeders interacted with each other, as did all members of the central group. A total of 99% of possible associations between pairs of northern dolphins ($n = 105$) was observed and 94% of possible associations were observed within the 28 southern dolphins ($n = 378$). Overall, 95% of possible interactions within groups were observed ($n = 499$ possible pairwise associations) and only 18% were observed between groups ($n = 827$ possible pairwise associations).

Other possible groups

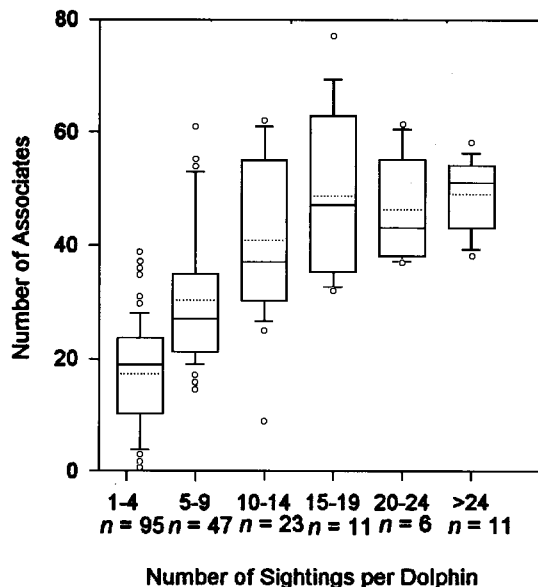
Two range tendencies of dolphins shown in the latitudes of individuals (Fig. 2) (five dolphins found around the latitude $27^{\circ}03'N$ and eight dolphins found only north of $27^{\circ}12'N$) were not distinguished by MDS or cluster analysis. Most dolphins in these two ranges were photographed an insufficient number of times in fully photographed sightings to be included in the previous analyses. However, when noncalves sighted ≥ 5 times in all sightings ($n = 98$ dolphins in the All-Associate data set) were considered, dolphins within each of these two ranges were relatively highly associated.

The five dolphins found near the latitude $27^{\circ}03'N$ were termed the north/central group. This group (DIP, SIC, SPI, VOL, and ZEE) was suggested by overlapping range and high association indices (SR median = 0.21, $\bar{x} = 0.22$, $SD = 0.07$, $n = 10$ pairs in all sightings). All five dolphins were known females (four with calves) and may be a female band belonging to one of the two communities or part of a central community. They interacted more often with the northern dolphins.

Though the central and north/central groups were found in similar ranges, they were rarely sighted together (north/central to central dolphins: SR median = 0, $\bar{x} = 0.02$, $SD = 0.03$, $n = 25$ pairs in all sightings). However, the north/central dolphins may interact with other dolphins more often than shown in the results, because many sightings in which they occurred were not fully photographed.

The eight dolphins found only north of $27^{\circ}12'N$ (>48 km from shore) were named the far north group. This group was

Fig. 6. Number of associates of each dolphin ($n = 193$) based on the number of times the reference dolphin was sighted. The number of associates leveled off when a dolphin was seen about 15 times. All dolphins and associates are non-calves. Boxes indicate 25th–75th percentiles. The solid line inside the boxes represents the median and the dotted line shows the mean. Whiskers above and below the boxes show 10th and 90th percentiles.



sighted only at the northern edge of the study area, although the area just to the south was searched heavily. These eight dolphins (MAR, SQU, TWE, FIG, DBL, SCO, SLA, and BEE) were sighted five to nine times each in all sightings and were associated (SR median = 0.09, $\bar{x} = 0.10$, SD = 0.10, $n = 28$ pairs in all sightings). The far north group rarely interacted with the northern dolphins (SR median = 0, $\bar{x} = 0.01$, SD = 0.02, $n = 120$ pairs in all sightings), although they overlapped somewhat in range. Thirty-two other dolphins sighted one to four times each were seen only at the northern edge of the study area, suggesting that other possible far north members were excluded from analyses because of insufficient photographs. However, this suggestion must be viewed cautiously because not all dolphins were photographed in many of the far north group's sightings.

Long-term associations

Forty-nine percent of dolphin pairs opportunistically photographed in the same sightings between 1990 and 1993 ($n = 97$ different dolphin pairs) were sighted together at least once during the study. Of 12 different dolphin pairs photographed in the same sighting prior to 1990, seven pairs were sighted together at least once during the study. With one exception, all prestudy associations were sighted in the northern section of the study area ≥ 27 km from shore.

Number of associates

The number of associates sighted with an individual dolphin leveled off after the individual was sighted ≥ 15 times (in all sightings; Fig. 6). Overall, dolphins photographed ≥ 15 times averaged 48 associates (SD = 11, range = 32–77, $n =$

28). Southern dolphins sighted ≥ 15 times associated with more dolphins ($\bar{x} = 53$, SD = 12, $n = 14$) than did northern dolphins sighted ≥ 15 times ($\bar{x} = 44$, SD = 9, $n = 12$), but the difference was not significant (Student's t test, $p > 0.05$).

Gender

Association indices of 59 dolphins and their closest associate averaged 0.58 (SD = 0.26, $n = 59$). Forty of the 59 dolphins were of known sex and 31 of the 40 had a closest associate of known sex. Male–male closest pairs averaged a simple ratio (SR) of 0.76 (SD = 0.15, $n = 12$ pair) and the SR of female–female closest pairs averaged 0.68 (SD = 0.22, $n = 11$ pair) (Rossbach 1997). The closest associate for a particular animal was of the same sex 74% of the time (Table 3). Males seen ≥ 15 times associated with slightly more individuals ($\bar{x} = 48$ associates, SD = 9, $n = 12$) than did females ($\bar{x} = 42$ associates, SD = 7, $n = 12$), but the difference was not significant (Student's t test, $p > 0.05$).

Environmental factors

Environmental factors differed between sightings of the northern and southern community members. All dolphins were sighted in water depths typically ranging between 1 and 15 m. Water depth was significantly deeper for northern dolphin sightings (Mann–Whitney U test, $p < 0.01$). Overall, dolphin sightings north of $26^{\circ}59'N$ (the approximate latitudinal halfway point in the study area) typically were in water 5–12 m deep (117/131) and all depths were greater than 4 m ($\bar{x} = 7.6$ m, SD = 2.4 m). In contrast, typical depths south of $26^{\circ}59'N$ ranged between 1 and 3 m (108/121; $\bar{x} = 3.0$ m, SD = 1.8 m).

Benthic characteristics also differed by latitude. Loose sand bottom was the dominant feature in the northern region and grass and patchy grass areas were most common in the southern region (Mann–Whitney U test, $p < 0.01$).

Foraging strategies

Four different foraging strategies were observed. Crater feeding (consisting of individuals echolocating into a sand bottom, searching for prey, and diving into the sand to retrieve prey) was seen primarily around the latitude $27^{\circ}08'N$ and secondarily near Grand Bahama Island at depths averaging 8.5 m (Rossbach and Herzing 1997). A total of 36 individuals (including three identifiable calves) were photographed crater feeding, 20 of which were observed using this method to feed ≥ 4 times between 1994 and 1996. All 15 northern dolphins were found in crater-feeding sightings ≥ 2 times ($\bar{x} = 6$ sightings, SD = 3, $n = 15$).

A variation of crater feeding was seen throughout the study area, mostly in shallower regions (about 2–7 m), sometimes covered with turtle grass. Dolphins' heads circled as they scanned the bottom with rapid clicks from midwater or high in the water column. Little scanning was done directly on the sand (as in crater feeding) until prey was presumably detected. The dolphin then scanned intensely at one spot before digging less vigorously than in crater feeding. Another variation of crater feeding was often seen just north of West End, where water depths average around 2 m. Dolphins fed in holes, sometimes inhabited by squirrel fish (*Holocentrus* sp.), in a similar manner as just described. It is not known what species were taken, but sand tilefish

Table 3. Percentage of closest associates that are same sex versus opposite sex of the partner.

	No. of occurrences	Percentage of <i>N</i>	<i>N</i>
Same sex	23	74	31 dolphins
Male–male	12	92	13 males
Female–female	11	61	18 females
Opposite sex (1 male–female, 7 female–male)	8	26	31 dolphins

Note: Dolphins and their closest associate are non-calves of known sex photographed ≥ 5 times in fully photographed sightings.

(*Malacanthus plumieri*) and small eels frequently inhabit such holes.

Cooperative feeding was observed during six sightings in the southern region. Cooperatively feeding dolphins surrounded fish and herded them into turtle grass to feed (Rossbach 1999). A total of 34 identified dolphins fed cooperatively, 18 of which were observed feeding cooperatively in at least 50% of their total sightings.

A fourth foraging strategy took advantage of what Bahamian fishermen term a snapper run, which occurs near West End in late June and early July when lane snapper (*Lutjanus synagris*) move close to the shore to spawn. Dolphins were occasionally seen fluking up in an area where numerous fishermen were successfully landing lane snapper with a handline from a jetty. Many Bahamians reported dolphins following or feeding on lane snapper during this time of year. This feeding strategy was the only one not observed from underwater.

All of the described foraging strategies (with the exception of crater-feeding variation) occurred in specific and unique regions of the study area. We observed northern dolphins primarily crater feeding in sandy bottoms, whereas southern dolphins were seen bottom feeding in grassy areas or in holes. Seasonally, southern dolphins also fed on lane snapper. No single dolphin was observed using all the above described foraging strategies.

Discussion

More than half of the northern dolphins identified in this study were also photographed between 1986 and 1990. Long-term site fidelity of 6–10 years exists for at least some individuals ≥ 27 km offshore of the Grand Bahama Island. Site fidelity is a typical characteristic of coastal bottlenose dolphins (Leatherwood and Reeves 1982; Connor and Smolker 1985; Shane et al. 1986; Wells 1986; Würsig and Harris 1990; Harzen 1995; Mate et al. 1995) and has also been reported in populations of other cetacean species (e.g., Dorsey et al. 1990; Glockner-Ferrari and Ferrari 1990; Herzing 1997). However, long-term site fidelity has not been previously reported for bottlenose dolphins found far from shore.

Covering a study area over twice the size of most others (Wells et al. 1987; Shane 1990b; Weller 1991; Smolker et al. 1992; Bräger et al. 1994; Harzen 1995; Wilson 1995) allowed the determination of range differences between identified individuals and the distinction of communities. Wells (1978) estimated that with 15 sightings of an individual, a dependable home range estimate could be made for that ani-

mal within the study area. In the present study, 28 non-calves were photographed on 15 or more occasions. Each dolphin's range was characteristic of one of two broad range tendencies, offshore or inshore (Rossbach 1997).

Coastal adjacent communities have been reported by Irvine et al. (1981). They repeatedly observed certain identifiable dolphins only around the edge of the Sarasota study area. Wells et al. (1987) reported that about 17% of sightings contained identifiable residents from adjacent communities. Dolphins found off northern Mexico and southern California also appear to have inshore adjacent home ranges (Hansen 1990; Caldwell 1992). The current study demonstrates that adjacent communities also occur offshore.

A community's range is partially dependent on suitable foraging habitat. Environmental conditions differed between the northern and southern communities' ranges within the study area. The area of overlap between the two communities is an area of transition from shallow to deeper water and from grassy to sand. Foraging strategy may be determined or limited by bottom type. Therefore, benthic environmental factors in the Bahamas probably play a role in the determination of individual range, since many dolphins are bottom feeders.

Previous studies have found that environmental factors influence dolphin range, social structure, and foraging strategy. Bottlenose dolphins inhabiting cold, open, and often deep water tend to migrate (Leatherwood and Reeves 1982; Kenney 1990) and are found in large schools (Saayman and Tayler 1973; Leatherwood and Reeves 1982), presumably to better protect individuals and to provide increased ability to locate prey (Norris and Dohl 1980a). Offshore dolphins often feed on squid (Norris and Dohl 1980b; Leatherwood and Reeves 1982), and dolphins feeding on schooling fish are probably more likely to feed cooperatively (Norris and Dohl 1980a; Leatherwood and Reeves 1982; Würsig 1986). Dolphins found in shallow protected environments are typically year-round residents (Irvine et al. 1981; Wells 1986; Smolker et al. 1992; Bräger 1993) and are usually found in smaller schools (Leatherwood 1979; Irvine et al. 1981; Smolker et al. 1992; Bräger 1993; Herzing and Johnson 1997). Dolphins known to inhabit southern California waters moved north to areas near Monterey Bay during an El Niño period when water temperature increased (Wells et al. 1990).

We used both MDS and cluster analysis (group average method) to distinguish stable dolphin groups. Cluster analysis has been widely utilized in studies of dolphin social systems (Wells et al. 1980; Ballance 1990; Heimlich-Boran 1993; Slooten et al. 1993; Wilson 1995; Harzen 1995). We

demonstrated that MDS is also a useful tool to distinguish stable social groups of dolphins. Multidimensional scaling is an objective tool that groups only related data.

Dolphins tended to associate most closely with dolphins of the same gender. Similarly, coastal dolphins in Sarasota, Florida, and Shark Bay, Australia, form stable social bonds and are organized by sex and age class (Wells et al. 1987; Smolker et al. 1992). Females associate with a network of other females and many adult males form close bonds with one or two other males. In Moray Firth, Scotland, males may associate with a network of dolphins, more similar to the patterns of females (Wilson 1995). Other cetacean species are also known to be organized by gender (Heimlich-Boran 1986; Whitehead and Waters 1990; Heimlich-Boran 1993; Craig and Herman 1997). This study is the first to report social structure parameters of bottlenose dolphins found far from shore.

Dolphins found ≥ 27 km offshore of the Grand Bahama Island showed repeated associations of up to 8 years between individuals. Long-term associations between individuals have been described for coastal bottlenose dolphins in Sarasota Bay, Florida (Wells et al. 1987), Golfo San José, Argentina (Würsig and Harris 1990), and Shark Bay, Australia (Smolker et al. 1992), as well as for other dolphin species (Norris and Dohl 1980b; Würsig and Bastida 1986; Bigg et al. 1990; Herzing and Brunnick 1997). This study provides the first record of long-term associations of bottlenose dolphins found far from shore.

Bottlenose dolphin studies on association patterns report a wide range of mean and median levels of association (Wells et al. 1987; Weller 1991; Smolker et al. 1992; Bräger et al. 1994; Harzen 1995; Wilson 1995; Felix 1997). The variation of association index values between studies may be due to real differences in social structure or could be due to differences in data collection, manipulation, analyses, and interpretation.

Association analyses of dolphins are not currently standardized and the methods used by researchers vary considerably. At least five factors can seriously affect the meaning and interpretation of results: (i) the association index applied, (ii) choice of data applied to the index (e.g., which sightings were used and the minimum number of sightings per dolphin used), (iii) sampling method of data, (iv) method used to identify dolphins, and (v) the location of the sampled area in relation to the range of the dolphins.

Index choice

The two indices most commonly used to measure association patterns in dolphins are the simple ratio (SR) and the half-weight index (HWI; Dice 1945):

$$\frac{2j}{a + b}$$

where a is the number of times dolphin A was sighted, b is the number of times dolphin B was sighted, and j is the number of times dolphins A and B were seen together, scored once for each occurrence of both individuals together.

According to Cairns and Schwager (1987), the choice of formula should be based on the sampling method used. They recommend that HWI is the most appropriate when a pair is

more likely to be sighted when apart than when together, because it controls for this sampling bias. All photographic identification studies have this bias because it is more difficult to record the presence of two dolphins in a sighting than one. Further, when two dolphins are separate, only one of the two schools needs to be sighted, whereas when they are together, only one school can provide the necessary data (Slooten et al. 1993). Cairns and Schwager (1987) state that SR describes the associations that were actually observed and that it is the least biased when the sample is random. Ginsberg and Young (1992) argue that HWI controls for the direction of the bias, but is not able to control for the extent of the bias. Therefore, they recommend that SR be used in all cases (except where a maximum-likelihood estimator can be used) and for the researcher to detail biases in the data.

Previous to the findings of Ginsberg and Young (1992), dolphin association studies used HWI (Wells et al. 1987; Weller 1991; Smolker et al. 1992). Although HWI continues to be used in dolphin studies (Bräger et al. 1994; Felix 1997; Herzing and Brunnick 1997), SR has been increasingly utilized (Heimlich-Boran 1993; Wilson 1995; Dudzinski 1996) and two studies conducted analyses using both indices (Slooten et al. 1993; Harzen 1995). Most recently, Whitehead (1997) developed a system that includes the dimension of time to analyze association patterns.

Data choice

The choice of data applied to the index formula affects the association analyses. Were data used from all sightings or some? In Australia, all sightings of single individuals (and lone mother-calf pairs) were excluded from association analyses (Smolker et al. 1992). This exclusion biases association indices upward for dolphins that are sighted alone.

It is also important to know if a subset of the entire data set was used for analyses. Were only fully photographed sightings used? How was fully photographed defined? Würsig (1978) and Ballance (1987, 1990) used a quantitative approach to determine if all identifiable dolphins in a sighting were photographed. The technique requires a minimum of four photos of each dolphin photographed in a sighting. Other researchers have not used this method probably because of its relative unfeasibility (i.e., the large effort required and presumably the lower sample size). This method aside, it is impossible to know if a sighting is fully photographed. However, many times it is fairly clear that all dolphins in a sighting are not photographed (in the current study, at least 61% of dolphin records in the northern half of the study area and 27% of dolphin records in southern half were not fully photographed). We used data from fully photographed sightings (a subset of the whole, as defined in the methods) for the primary analyses of association patterns. We used data from all sightings to distinguish possible groups in which dolphins were excluded from the previous analyses owing to insufficient numbers of fully photographed sightings. A few studies state their photographic success rate of dolphin sightings (Ballance 1990; Wilson 1995; Dudzinski 1996). It is unclear in many studies whether selective criteria were used to create a subset of the data to perform association analysis, and other studies did not report photographic success rates of dolphin sightings.

A second important aspect in the choice of data applied to the index is how many sightings of an individual were necessary for that dolphin to be included in the analysis. For example, some studies included all identified dolphins in their analyses (Heimlich-Boran 1993; Harzen 1995; Dudzinski 1996; Herzing and Brunnick 1997). Bräger et al. (1994) used dolphins photographed ≥ 4 times. Others used individuals photographed ≥ 5 times (Wells et al. 1987; Weller 1991; Felix 1997), and Smolker et al. (1992) reported association patterns of dolphins of known sex photographed ≥ 10 times. Wilson (1995) used dolphin pairs in which, when combined, the two dolphins were seen a total of ≥ 7 times. Choosing a minimum number of sightings may depend on the research question. Descriptive information may include all individuals, whereas distinguishing long-term or important associates requires more sightings per dolphin. The lower the number of sightings per dolphin, the increased chance of a bias in either direction owing to the smaller sample size. A larger sample size lessens the weight of two dolphins reported as found together when they are actually usually found apart (and *visa versa*). Additionally, less weight is given to errors (i.e., a sighting that may actually include a dolphin thought to be absent).

Sampling method

The method of defining which dolphins are associates varies. For example, how was a sighting defined; were the data (i.e., presence or absence of a dolphin) taken once during an observation period, each time that the school composition changed, or periodically over time? We defined a dolphin sighting as all dolphins in sight, moving in the same direction, and usually involved in similar activity (termed pod in Shane 1990a). On only a few occasions did it appear clear that two separate sightings were present at the same time. In these instances, the dolphins in each sighting either never interacted or only briefly interacted and then separated again. This definition of sighting is similar to that used in many other association studies (Bräger et al. 1994; Harzen 1995; Wilson 1995; Felix 1997). Wells et al. (1987) and Smolker et al. (1992) use a more spatial definition. However, most variability between studies may occur in cases where dolphins join and separate from a school during the observation period. Biases in the data may be present depending on how these subgroups are manipulated with regard to the association between individuals. In the present study, a sighting included the maximum number of dolphins seen between the time that they were approached by the vessel and the time that they were left or were lost. One disadvantage to this method is that in cases when some dolphins leave a sighting before new dolphins arrive, the two subgroups could be considered associated when in fact they were not. This bias possibly occurred on at least one occasion during the current study.

We recorded a dolphin's presence once each day, unless it was found >1 h later in another sighting with different dolphins when it was recorded again (2% of all dolphin records). However, our association analyses did not include dolphins that associated twice in 1 day because we were unable to fully photograph two sightings that contained the same dolphin in 1 day. Only Wells et al. (1987) and Smolker et al. (1992) discussed challenges brought on by changing

school composition. In Sarasota, a dolphin's presence was re-counted if the two sightings were greater than 1 h apart or if school composition changed during the observations. In Shark Bay, a dolphin's presence was recounted when the second sighting was greater than 1 h from the first and the school changed by at least 30% of its original composition.

Identification technique

The method used to positively identify dolphins varies between studies. Many researchers use photographs to make a positive identification (Wells et al. 1987; Weller 1991; Heimlich-Boran 1993; Slooten et al. 1993; Harzen 1995), whereas photos are not required in other studies to positively identify an individual (Smolker et al. 1992; Dudzinski 1996; Herzing and Brunnick 1997). The method of identifying dolphins may produce differing results. First, if or when a less experienced observer identifies dolphins without a photo, the risk of a wrong identification and the chance of missing dolphins present increases. In contrast, an experienced observer may be able to identify a greater percentage of animals in schools, if it requires less time to observe dolphins than to photograph them.

Area sampled

The area sampled in relation to the sampled dolphins' ranges can play a role in determining the outcome of the association values. Are all dolphins part of the same community? If sampling occurs in an area that is between communities, the resulting index may show how the dolphins of different communities interact, which results in a different meaning than if sampling was done in the middle of a community's range.

Mean association values have a range of meanings and interpretations depending on the factors discussed above. As much detail as possible should be used in describing methods used to calculate association indices (Ginsberg and Young 1992). Each factor should be clearly defined and explained. Straight comparisons between studies should be avoided, and when done, must be viewed with caution (Ginsberg and Young 1992). Analyses of association patterns will differ depending on the circumstances of the study (time frame, vessel, observers, and equipment), the environment, the dolphins, and the study questions.

We distinguished and described adjacent, stable social groups of bottlenose dolphins found inshore and offshore. Long-term site fidelity of up to 10 years and repeated dolphin associations of up to 8 years occurred ≥ 27 km from shore, demonstrating long-term, stable social behavior of dolphins found far from shore. Further long-term studies will add to the understanding of the benefits of complex dolphin social structure.

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