

Resighting and association patterns of bottlenose dolphins (*Tursiops truncatus*) in the Cedar Keys, Florida: insights into social organization

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Abstract: Little is known about the social organization of bottlenose dolphins (*Tursiops truncatus*) inhabiting open estuarine systems. Our purpose was to identify and quantify the resightings of bottlenose dolphins and associations formed among them to provide insights into the social organization of the species in the open estuarine system of the Cedar Keys, Florida. We conducted monthly photographic-identification surveys from June 1996 through May 1997. We identified a total of 233 dolphins of which 217 (93%) were classified into one of four categories based on the number of months in which they were sighted. "Rare" dolphins (sighted during 1–2 months) constituted more than half of these individuals (61%), followed by "occasional" (3–5 months; 20%), "common" (>8 months; 12%), and "frequent" (5–6 months; 7%) dolphins. We quantified the associations for dolphins sighted 10 times (26 common, 12 frequent, and 8 occasional) and found that individuals with different resighting patterns associate with each other but the association is mostly at a low level. The level of association among common dolphins, however, was higher within than between the sexes. Association patterns of common dolphins in the Cedar Keys resemble the associations of resident bottlenose dolphins inhabiting closed estuarine bays, suggesting that the selective pressures which induce such associations are the same in these aquatic systems.

Résumé : On connaît peu de choses au sujet de l'organisation sociale des Dauphins à gros nez (*Tursiops truncatus*) dans les systèmes estuariens ouverts. Nous avons tenté d'identifier et de quantifier les observations de dauphins déjà vus et leurs associations afin de pouvoir mieux comprendre l'organisation sociale de cette espèce dans le système estuarien ouvert des Cedar Keys, en Floride. Nous avons procédé à des inventaires photographiques de dauphins de juin 1996 à mai 1997. Nous avons pu reconnaître au total 233 dauphins dont 217 (93 %) ont été assignés à l'une de quatre catégories en fonction du nombre de mois où ils ont été vus. Les animaux « rares » (aperçus 1–2 mois) constituaient plus de la moitié des individus (61 %), suivis des dauphins « occasionnels » (3–5 mois; 20 %), des dauphins « communs » (>8 mois; 12 %), et « fréquents » (5–6 mois; 7 %). Nous avons quantifié les associations des dauphins aperçus 10 fois (26 communs, 12 fréquents et 8 occasionnels) et constaté que des individus dont les repérages suivent des patrons différents s'associent mais à un degré faible. Le degré d'association de dauphins communs s'est avérée plus forte entre individus de même sexe qu'entre mâles et femelles. Les patrons d'association à Cedar Keys sont comparables à ceux des dauphins qui habitent les systèmes estuariens clos, ce qui indique que les pressions de sélection qui déclenchent de telles associations sont les mêmes dans ces systèmes aquatiques.

[Traduit par la Rédaction]

Introduction

The evolution and maintenance of mammalian social organization have been of great interest to evolutionary biologists and behavioral ecologists for many decades (Eisenberg 1966; Crook et al. 1976; Rubenstein and Wrangham 1986). Intraspecific variation in social factors such as associations,

group stability, group composition, and reproductive strategies has been interpreted as representing adaptive responses to variation in environmental parameters. Individuals are considered to display behaviors that maximize their fitness under a particular set of ecological conditions (Hirth 1977; Rubenstein and Wrangham 1986).

Resighting of individuals in order to assess association patterns is an important tool for understanding this variation in social organization. Information obtained on individuals over time elucidates spatial and temporal changes in the community composition by identifying individuals that stay in or move out of an area. Resighting patterns are commonly used by researchers to monitor long-term associations among birds and mammals (Wrangham and Rubenstein 1986; Wells et al. 1987; Whitehead 1995; Bejder et al. 1998).

This study examines the resighting and association patterns of the bottlenose dolphin (*Tursiops truncatus*), a species with a social organization that is both variable and complex. Bottlenose dolphins, like other species that have a fission–fusion social organization (e.g., chimpanzee, *Pan troglodytes*,

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Wrangham et al. 1993; spider monkey, *Ateles paniscus*, McFarland 1986), exhibit associations that change frequently in composition and size over small spatial and temporal scales, and exhibit others that are remarkably stable over many years (Wells et al. 1987; Wells 1991; Connor et al. 1992; Smolker et al. 1992). Additionally, bottlenose dolphins exhibit various levels of association and variable numbers of close associates in areas with different ecological conditions (Wells et al. 1987; Wells 1991; Smolker et al. 1992; Wilson 1995). For example, in some closed estuarine systems (estuaries with waters protected from open-water winds and currents by a parallel obstruction or bar along the coastline; Sumich 1992) males form long-term associations at a high level (Wells et al. 1987; Wells 1991), while in open-sea embayments this type of association appears to be absent (Wilson 1995). In some areas, high-level associations between two males are common (Wells et al. 1987; Wells 1991), whereas in other locations alliances of two or three males exist (Smolker et al. 1992). Associations of bottlenose dolphins are also complex because they are influenced by movement patterns (e.g., residency, migration, and nomadism). For example, when dolphins that have been in an area for some time leave, associations of the remaining residents shift (Bräger et al. 1994).

Since the nature of the physical environment affects the operation of ecological pressures on social systems (Lott 1991; Rubenstein and Wrangham 1986), the observed intra-specific variation in social behavior of bottlenose dolphins may be due to differences in predation risk and food availability and distribution among areas (Wilson 1995; Connor et al. 2000). Our objective was to determine the resighting and association patterns of bottlenose dolphins under a set of ecological conditions that has received little research attention, that of the open estuarine system. Open estuarine systems, common along coasts, are characterized by unbarred coastlines exposed to direct weather conditions and by waters that connect directly to an open body of water (Sumich 1992). Because the instability of estuaries (Sumich 1992) may influence the occurrence and distribution of prey and predators and because open habitats may provide less protection from predators (Lott 1991), it is possible that bottlenose dolphins develop different association patterns, and yield different resighting patterns, in open estuaries than in other areas.

We quantified the resightings and associations of bottlenose dolphins in the open estuarine system of the Cedar Keys, Florida, to provide insights into the social organization of the species in this type of system. Little is known about the ecology and behavior of bottlenose dolphins using these waters. The only existing information is an anecdotal description of the resighting pattern for one dolphin (Caldwell 1955). We examined association patterns of identified dolphins of different genders and the same gender and compared them with those exhibited by bottlenose dolphins living under other ecological conditions. We examined resightings of identified dolphins to distinguish between individuals that are possible residents of the area and individuals that are present only briefly. This identification was important because theories on the evolution of animal movements (Baker 1978; Sinclair 1983; Swingland 1983) propose that species with a widespread distribution, such as bottlenose dolphins, commonly

exhibit a mixed strategy involving residents and nonresidents. We searched for origins and destinations of nonresidents by examining records of identified bottlenose dolphins in other inshore locations in the eastern Gulf of Mexico, which provided a novel opportunity to examine potential long-distance movements of bottlenose dolphins over a range of ecological conditions.

Materials and methods

Study area

The Cedar Keys (29°05'49"N, 83°03'8"W) form an archipelago of five major and numerous smaller islands that partially enclose estuarine waters connecting with the Gulf of Mexico by an open system of shallow flats and channels (Kilby 1949). The study area extends from the western side of Corrigan Reef to the southern end of Derrick Key and 2 km into the offshore Gulf waters off the Cedar Keys, an area of approximately 67 km² (Fig. 1).

Field and laboratory methods

Photographic-identification surveys of bottlenose dolphins, hereafter referred to as surveys, were conducted each month from June 1996 through May 1997 to cover the major habitats in the Cedar Keys (Quintana-Rizzo 1999). Daily surveys were planned according to tidal state and weather, and survey routes were standardized and used throughout the study to preclude heterogeneous sampling of habitats among surveys. During the first half of the study (summer and fall), surveys were conducted on 15–17 days each month. During the second half (winter and spring), the survey period was reduced to 3–5 days each month because of poor weather. Surveys were conducted from a 4.8-m outboard motorboat driven at idling speed, and effort was measured as the number of linear kilometres traveled by the boat. A daily survey or combination of surveys was (were) defined as complete when it (they) covered the entire study area. The entire study area refers to all the habitats identified within the Cedar Keys (Kilby 1949; Quintana-Rizzo 1999). Complete surveys ranged from 1 to 11 per month and required 1–3 days to complete.

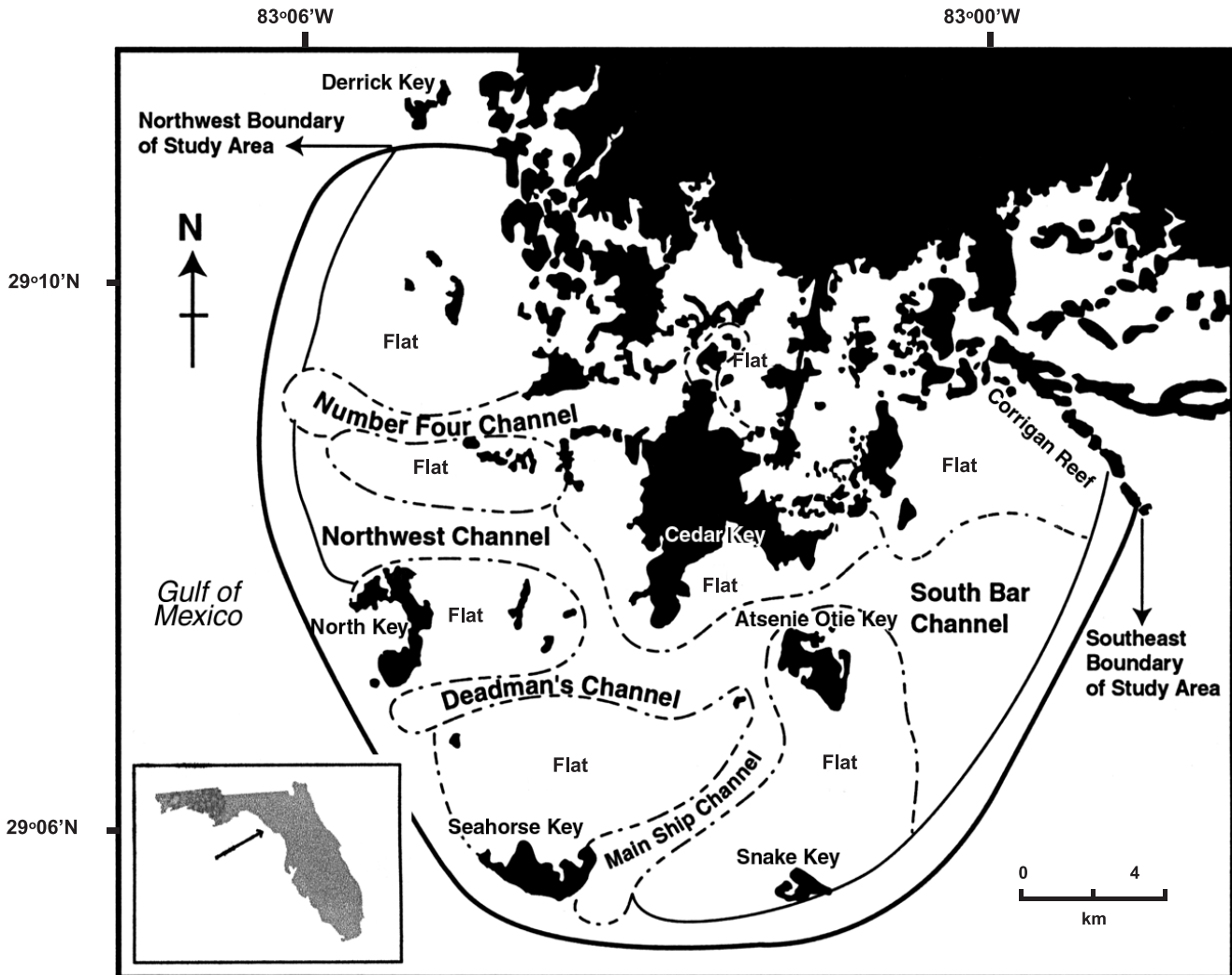
Once an individual was sighted, we followed it or stopped the boat to photograph natural marks on the dorsal fin (Irvine et al. 1981; Scott et al. 1990; Wells and Scott 1990). Photographs were taken with a Canon Elan IIEQD 35-mm camera fitted with a 75- to 300-mm lens, databack, and Kodachrome (K-64) color slide film. This fine-grain film provides good resolution of fin features (Wells et al. 1996).

Gender was determined from photographs of the genital area or from regular association with a calf. Dolphins were identified as females if they were observed on at least 3 days with a calf alongside, and as males only if their penis was observed.

Dolphins were placed into one of three relative age categories: (1) Young of the year (YOY): a dolphin that is approximately less than one-half the body length of an adult, and that typically surfaces in close proximity to the presumed mother (baby position; Cockcroft and Ross 1990). YOYs less than 3 months old have darker coloration than adults, characteristic head-up surfacing patterns, and fetal folds that remain evident for several weeks as neonatal stripes (Urian and Wells 1996). (2) Calves: small dolphins larger than YOYs and up to about 75% of the presumed mother's length (Urian and Wells 1996). Calves consistently travel alongside their presumed mothers, in the baby position (Wells et al. 1987; Smolker et al. 1992). (3) Non-calves: large dolphins that exceed approximately 2 m in length.

A group was defined as the number of dolphins sighted within an approximate 100-m radius (school; Wells et al. 1987; Wells et al. 1999) from the boat. We stayed with a group until photo-identification data were collected (usually for 10 min), until weather

Fig. 1. Location of the study area, including habitats, at the Cedar Keys on the west coast of Florida. “Flat” denotes shallow-flat regions (water <2 m deep).



conditions made this impossible, or a dolphin could no longer be found. Each group of dolphins encountered was considered a sighting. For each sighting, standard data forms were completed, with information about time, location, environmental conditions, individual markings, dolphin behavior, and minimum, maximum, and best field estimates of group size, number of calves, and number of YOYs (Urian and Wells 1996). Standard photoidentification techniques were used to identify dolphins (Urian and Wells 1996).

Data analysis

Resighting patterns

In examining resighting patterns, we only included identifiable dolphins sighted during complete surveys, and months with at least three complete surveys. Thus, we excluded data from December 1996 and February 1997, months in which no new dolphins were identified.

Preliminary observations suggested that some dolphins were sighted more often than others. Because this trend could affect resighting patterns, we examined the frequency distribution of dolphin sightings during complete surveys on the assumption that the distribution of individuals was random. We assigned a random number to each dolphin identification and used these numbers to divide the data in half. We then compared the frequency distribu-

tions of the number of sightings in the two halves (Wilson et al. 1997). We expected that if the trend was not random, the two halves would be correlated (Wilson et al. 1997). In contrast, we expected that if the trend was random, the two halves would not be correlated, and it would not be appropriate to use the number of times a dolphin was seen in examining resighting patterns.

We performed this analysis on two sets of data: frequency distributions for all months and for a particular month. The purpose of the first analysis was to examine the frequency distribution of dolphin sightings during the entire study. However, since a positive correlation of the two data halves may result from differential identifiabilities of dolphins (the more identifiable ones having high numbers in both data halves), identification rates that differ among surveys (those appearing in the most intensive surveys having high numbers in both halves), and numbers of surveys that differ among seasons (those appearing in the high-intensity months having higher numbers of sightings in both data halves), we also examined the frequency distributions of dolphins in a particular calendar month to reduce the effect of these factors. We expected that if both analyses showed a positive correlation, this would indicate that the trend in heterogeneity of sightings was not random. Conversely, if the tests produced different results, this would indicate that the trend was random and it would not be appropriate to use the number of times a dolphin was seen in examining resighting patterns.

Both tests showed that the frequency with which identified dolphins were seen was not random (Spearman's rank correlation, for all months, $r_s = 0.18$, $p < 0.05$; for a particular month, $r_s = 0.38$, $p = 0.05$). Hence, we examined resighting patterns using the temporal distribution of individual dolphin sightings during 10 months.

Dolphins were classified into one of four arbitrary categories (modified from Wilson et al. 1997): (1) "common": dolphins sighted during ≥ 8 months, (2) "frequent": dolphins sighted during 6 or 7 months, (3) "occasional": dolphins sighted during 3–5 months, and (4) "rare": dolphins sighted during 1–2 months.

Resighting patterns were quantified using a residence index, which is the proportion of sightings of an identifiable dolphin relative to the total number of complete surveys carried out in a month (Koelsh 1997). Multiple sightings of a dolphin during a complete survey were counted as a single sighting. Since the number of complete surveys varied among months, we calculated an average residence index (ARI) for each dolphin included in the analysis.

Association patterns

To quantify the level of association among dolphins, we calculated the half-weight index (HWI). This index is commonly used to describe associations of bottlenose dolphins (Wells et al. 1987; Smolker et al. 1992; Bräger et al. 1994; Félix 1997), hence facilitating comparison with other studies. Additionally, this index is the least biased estimator in cases where individuals of a pair are more likely to be observed separately than together (Cairns and Schwager 1987), which we believe is the case for the dolphins examined in this study.

To calculate HWI, we included only those identified dolphins with at least 10 sightings. The resulting indices were grouped into five association categories: low (0.01–0.20), moderate–low (0.21–0.40), moderate (0.41–0.60), moderate–high (0.61–0.80), and high (0.81–1.00). We studied the patterns of association among individuals that exhibited different levels of association. To examine whether associations were the result of social preferences or overlapping ranges, we compared the ranges, or geographical areas within which individuals were sighted (Ballance 1992), of females and males with similar and different association patterns (Wilson 1995).

Movement patterns

Possible long-distance movements of dolphins between study sites were evaluated by attempting to match dolphins from the Cedar Keys catalog with existing and outgoing catalogs from the west coast of Florida. Fins were compared with those from Clearwater (catalog developed by Mark Allen of the University of North Carolina at Wilmington), Boca Ciega Bay (catalog developed by Dr. John E. Reynolds III and his students from Eckerd College in St. Petersburg, Florida), and Tampa Bay, Sarasota Bay, Charlotte Harbor, and Pine Island Sound (catalogs developed by the Dolphin Biology Research Institute, Sarasota, Florida). In total, these catalogs covered waters from 120 to 300 km south of the Cedar Keys.

Results

Survey effort and identified dolphins

One hundred and five surveys, with approximately 911 h of search time and 423 h of direct observation, were conducted in the Cedar Keys (Table 1). Of these surveys, 88 were considered complete. Two hundred and thirty-three individual dolphins were identified. Photoidentification focused on 852 groups composed of 3517 dolphins (including marked and unmarked animals). Photoidentification data from 353 groups (41%) with complete photographic coverage (sightings in which all dolphins in a group were positively identified, and in which the total of positively identified dolphins

Table 1. Summary of photoidentification-survey effort.

	1997											
	June	July	August	September	October	November	December	January	February	March	April	May
No. of days of surveying	16	17	16	16	15	5	2	3	2	5	3	6
No. of hours of surveying	139.22	143.06	136.54	158.48	125.00	39.32	18.18	18.59	13.42	36.41	33.54	47.10
No. of sightings	131	106	134	159	91	45	11	18	12	36	30	41
No. of dolphins sighted	451	504	591	796	314	143	39	87	86	167	104	235
No. of complete surveys	11	6	11	14	9	4	1	3	0	3	3	3

Table 2. Number of identifiable bottlenose dolphins (*Tursiops truncatus*) sighted in a given number of months (only months with at least 3 complete surveys), including the number of sightings in these months, in the Cedar Keys, Florida, 1996–1997.

No. of sightings	Number of months dolphins seen										Total no. of dolphins seen
	1	2	3	4	5	6	7	8	9	10	
1	85										85
2	17	18									35
3	1	6	7								14
4		4	9	2	1						16
5		2	5	3							10
6			3	1							4
7				2	1	1					4
8			1	1		2					4
9					1	2	1				4
10				1	1	2					4
11					1	1					2
12					2						2
13								1	1		2
14								2			2
15								1			1
16								1			1
17							1		1	1	3
18				1						1	2
19								2	1		3
20							1			1	2
21							1	1	2	1	5
22						2					2
23									1		1
24							1	1	1		3
25									1		1
26									1	1	2
28									2	1	3
Total	103	30	25	11	7	10	5	9	11	6	217

Note: Dolphins are categorized as “rare” when sighted in only 1–2 months, “occasional” when sighted in 3–5 months, “frequent” when sighted in 6–7 months, and “common” when sighted in 8–10 months. A blank indicates a value of zero.

and unmarked dolphins distinguished from high-quality photographs accounted for each dolphin scored in the best field estimates) indicated that about 76% of the dolphins sighted had natural markings on their dorsal fins, 21% were unmarked adults or juveniles, and 3% were unmarked calves.

A high percentage of the dolphins with markings were identified at the beginning of the study: 40% in the first month and 72% in the first 4 months. Although the percentage of new animals identified each month decreased over time, from 40% (94 animals) in the first month to 3% (8 animals) in the last month, the size of the catalog increased gradually.

Of the 233 dolphins cataloged, the sex of 36 animals was determined (27 females and 9 males). Two females had new calves in 1996 and four females had new calves in 1997. One female was observed with an old calf in 1996 and a new calf in 1997.

Resighting patterns

The frequency with which identified dolphins were seen in the Cedar Keys varied greatly. Of the 217 (93%) identified dolphins included in the resighting-pattern analysis, more

than half (61%) were seen in only 1–2 months (47% seen in 1 month and 14% seen in 2 months; Table 2). These 133 dolphins that had 1–3 resightings were categorized as rare. Of the remaining 84 dolphins, 43 were sighted in 3–5 months and 41 were sighted during at least 6 months. Of these 84 dolphins, 43 (51%) were classified as occasional, 15 (18%) as frequent, and 26 (31%) as common. Each month we sighted an average of 22 common (range 14–26), 10 frequent (range 5–15), 16 occasional (range 3–33), and 16 rare (range 6–25) dolphins (Table 3).

Sixty-nine dolphins (occasional and rare) displayed three resighting patterns. The “continuous” pattern was displayed by dolphins that were sighted during only one block of time (an interval of 2–4 consecutive months) after which they were not seen again. The “interval” pattern was displayed by dolphins that were sighted during two blocks of time. Each block represented an interval of between 1 and 3 consecutive months. The number of months between blocks of time ranged from 1 to 8. The “intermittent” pattern was displayed by dolphins that were sighted during three to five blocks of time. Each block of time represented an interval of 1 or 2 consecutive months. The number of months between sight-

Table 3. Numbers of individual bottlenose dolphins categorized as rare, occasional, frequent, and common that were sighted during months with at least three complete surveys in the Cedar Keys, 1996–1997.

Year and month	Dolphin category				Total
	Rare	Occasional	Frequent	Common	
1996					
June	23	16	14	24	77
July	6	16	8	23	53
August	20	30	12	26	88
September	25	33	15	26	100
October	7	16	10	24	57
November	13	14	8	22	57
1997					
January	23	11	6	22	62
March	17	13	5	14	49
April	7	3	9	18	37
May	18	12	8	24	62

ings ranged between 2 and 5. Of these 69 dolphins, 45 and 42% showed the continuous and interval pattern, respectively, while only 13% showed the intermittent pattern.

ARI values (the proportion of surveys in which an identified dolphin was observed, averaged over months) differed significantly among the four categories of dolphins (Kruskal–Wallis test, $KW = 144$, $p < 0.05$). ARI values were high for common (median = 0.35, $\bar{x} = 0.34$, $SD = 0.08$, range = 0.29–0.50), moderate–high for frequent (median = 0.20, $\bar{x} = 0.21$, $SD = 0.07$, range = 0.09–0.32), moderate–low for occasional (median = 0.09, $\bar{x} = 0.09$, $SD = 0.04$, range = 0.04–0.25), and low for rare individuals (median = 0.03, $\bar{x} = 0.03$, $SD = 0.02$, range = 0.01–0.11).

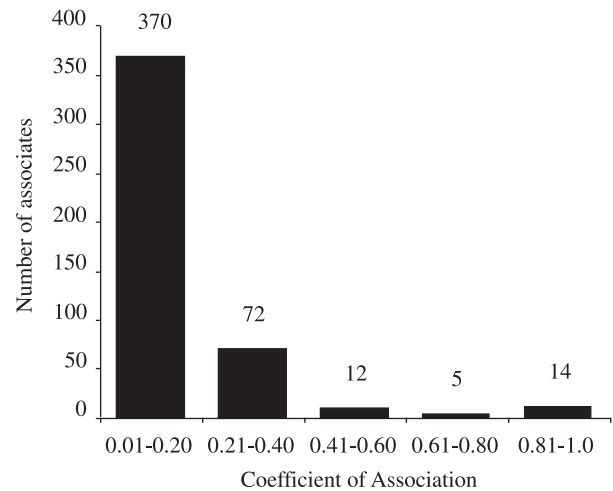
Movement patterns

The possibility of long-distance movements of more than 120 km to the south of the Cedar Keys was examined for all identified dolphins. No positive matches were found between the Cedar Keys dolphin catalog and the Clearwater catalog ($n = 151$ identified dolphins) or the combined Tampa Bay, Boca Ciega Bay, Charlotte Harbor, Pine Island Sound, and Sarasota Bay ($n = 2579$ identified dolphins) catalogs. These findings suggest that movements of inshore dolphins are infrequent over the approximately 120 km from the Cedar Keys to Clearwater, 160 km from the Cedar Keys to Sarasota Bay, or 240–300 km from the Cedar Keys to Charlotte Harbor and Pine Island Sound.

Association patterns

We examined associations for 46 individuals (26 common, 12 frequent, and 8 occasional) sighted at least 10 times. The average number of identifiable associates per individual was 55 (range = 10–85, $SD = 15.17$). Dolphins had few high-level associations and many low-level associations. Only 30% (all common individuals) of the 46 dolphins had high-level associations ($\bar{x}_{HWI} = 0.94$, $n = 14$; Fig. 2). Of these, 50% were female–calf associations, 14% were male–male associations, and the remaining 36% were associations among individuals of unknown gender.

Fig. 2. Distribution of coefficient of associations for 46 bottlenose dolphins (*Tursiops truncatus*) (26 “common”, 12 “frequent”, and 8 “occasional”) sighted at least 10 times during surveys carried out at the Cedar Keys, 1996–1997.



Both females and males had low-level associations ($HWI = 0.10$ – 0.20), which accounted for a large proportion of the total associations for any given dolphin ($n = 2438$ associations). For this type of association the mean number of identifiable associates per dolphin was 53 (range = 9–85, $SD = 14.83$).

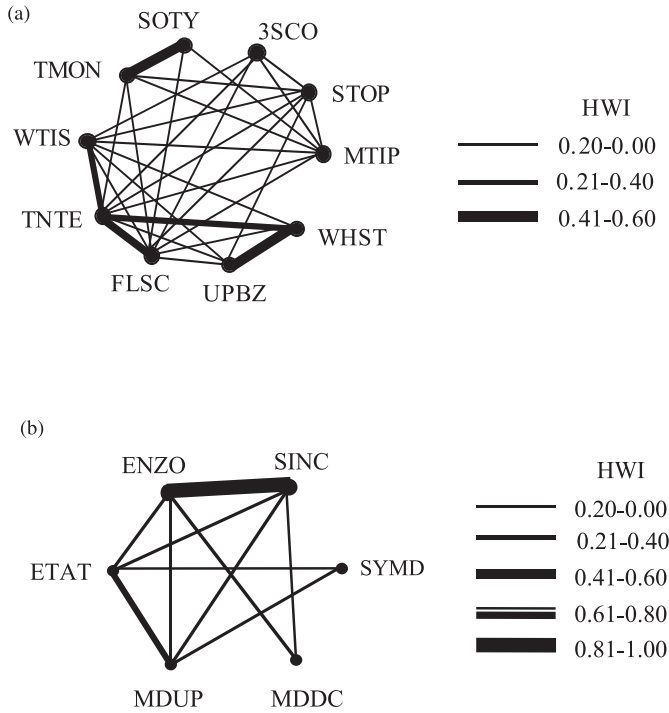
We observed that dolphins with different resighting patterns do associate with each other. Associations between frequent and occasional individuals were mostly (83%) low level ($HWI = 0.03$ – 0.18 ; $n = 5$). However, we recorded one association of moderate–high level ($HWI = 0.69$). Between common and frequent individuals, we recorded only two associations and they were of moderate–low level ($HWI = 0.23$ – 0.32).

We observed variation in the number of associations and number of associates among common individuals whose sex was determined. Females and their young calves had the highest associations ($\bar{x}_{HWI} = 0.90$; $n = 8$). They had moderate- to low-level associations with an average of 64 other associates (excluding calves; range = 49–84, $SD = 12.78$). Females whose new calves were born in 1996 had a very high coefficient of association with their calves ($HWI = 0.94$ – 1.00). Females with older calves had a coefficient of association with their calves that ranged from 0.24 to 0.97.

The second type of association observed was among multiple females with calves. Of the 10 females with calves considered for this analysis, 4 had their highest coefficient of association with 1 of these 10 females ($HWI = 0.47$ and 0.57 ; Fig. 3a). Six females with calves did not have high- or moderate-level associations except with their calves. Overall, a large proportion of the female–female associations fell into the lowest coefficient range ($HWI = 0.01$ – 0.20).

The third type of association pattern observed was between males. Only one pair of males had a high level of association ($HWI = 0.92$; Fig. 3b). The remaining associations were lower level ($HWI = 0.24$ and 0.35). The mean number of associates of the six males was 54 (range = 35–73, $SD = 14.38$). However, the pair of males with a high level of association had the lowest number of other associates (range = 36–38; Table 4).

Fig. 3. Sociogram representing female–female (a) and male–male (b) association coefficients for common individuals, Cedar Keys, 1996–1997. Four-letter codes denote individual bottlenose dolphins. Lines of increasing thickness represent increasing pairwise association coefficients.



The fourth type of association observed was between a female with a calf and a male, and all associations occurred at a low level. The coefficients of association ranged from 0.01 to 0.17. The extent and number of associations between females and males appeared to be related to the level of association of males with other males. Among the six males, the one pair with a high level of association had the lowest coefficient of association with females ($\bar{x}_{HWI} = 0.02$, $SD = 0.02$, $n = 20$). A single male had the highest mean coefficient of association ($\bar{x}_{HWI} = 0.08$, $SD = 0.03$, $n = 10$) with females. Among females, however, no significant difference was found in their coefficients of association with males (Kruskal–Wallis test, $KW = 11.80$, $p > 0.05$).

The associations among the 10 common females with calves and among the six common males included in the association analyses were also studied by examining group size. Females with calves and associated males were found in groups that varied from 1 to 28 individuals. Groups containing females tended to be larger than those containing males ($z = 7.02$, $p < 0.001$; groups containing females: $\bar{x} = 8.07$, $SD = 5.04$, $n = 331$, mode = 5; groups containing males: $\bar{x} = 5.64$, $SD = 4.80$, $n = 196$, mode = 2).

Range patterns

Comparisons of the ranges of the 10 common females with calves included in the association analysis showed that some ranges overlap. Within the study area, the range of one pair with a moderate level of association covered the north-west side of the Cedar Keys, and the range of the other pair

Table 4. Number of identified associates of each known common male bottlenose dolphin in the Cedar Keys, 1996–1997.

	Type of association					
	Pair of males (HWI = 0.92)		Single male			
Total no. of associates	38	35	63	69	49	73

with a moderate level of association covered the southeast side. The ranges of these two pairs overlapped approximately 1%. The ranges of the single females with calves overlapped 20–25% of the ranges of the pairs. However, the ranges of the single females extended farther from the coastline on the Gulf side of these Keys. The ranges of the trio of females with a moderate–low level of association extended along the entire coastline and overlapped the ranges of all other females.

A comparison of the sightings between one pair of males with a high level of association and one pair with a moderate–low level of association showed that their ranges within the study area were the same. However, the level of association between these two pairs of common males was low. Single males also had a similar range to one of the pairs of males.

Discussion

Resighting patterns

The estimated ARI values confirm that the categorization of common, frequent, occasional, and rare dolphins that was based initially on monthly sighting patterns is a useful tool for identifying resighting patterns. However, since this categorization depends on the number of months during which a dolphin was sighted, future research can determine whether particular dolphins maintain their categories. The high ARI values and high number of months during which common and frequent individuals were resighted suggest that they are residents of the Cedar Keys. This speculation is supported by reports from local fishermen and photographs of some common individuals taken in the mid-1990s by other visiting scientists. The lack of sightings of frequent individuals for weeks or months suggests that their home range (a well-defined area of regular usage that typically provides all or most of an animal’s needs; Wells et al. 1999) extends outside of the Cedar Keys. Patterns of disappearance of some residents have been reported in other areas (Würsig 1978; Shane 1980; Wells et al. 1990; Wells 1991).

The low ARI values and numbers of resightings of rare and occasional individuals suggest that they are nonresidents. Rare and occasional individuals could either be wide-ranging, have home ranges that overlap in the Cedar Keys, or inhabit the deeper waters of the Gulf of Mexico. The frequency of occurrence of individuals in the two categories, however, may vary between rare and occasional. For instance, the greater frequency of visits in the intermittent and interval patterns and the significantly longer visits (inferred from moderate–low ARI values) of occasional individuals suggest that their home ranges overlap in the Cedar Keys more than those of rare individuals. Short visits to some parts of a home range have been reported among nonterritorial species

(Mace et al. 1983). Similarly short visits and overlapping ranges have been reported for nonresident and resident dolphins in other areas (Wells 1978; Wells et al. 1987; Scott et al. 1990; Bearzi et al. 1997; Félix 1997; Rossbach and Herzing 1999).

The possible wide-ranging movements of rare and occasional individuals may also differ. Some rare individuals may enter and leave the Cedar Keys on their migration route, as is suggested by their short visits and long periods between sightings of up to 7 months. Wide-ranging movements of bottlenose dolphins have been documented for some areas of the Gulf of Mexico (Shane 1980). However, movements of dolphins between the Cedar Keys and five study areas 120–300 km to the south appear to be infrequent, as no positive dolphin matches were found. In the case of occasional individuals, their continuous pattern of resightings suggests that they remain in the area for several months. These individuals could be called “seasonal residents” because their continuous resighting pattern closely resembles the “seasonal residence” documented for bottlenose dolphins elsewhere (Würsig 1978; Shane 1980; Barco 1995).

Association patterns and social organization

Associations between dolphins sighted regularly (common and frequent) and those sighted sporadically (rare and occasional) were infrequent in the Cedar Keys. Mixed groups of these individuals were observed to participate in such activities as feeding, socializing, and on one occasion, an interaction that appeared to be a forced copulation (Quintana-Rizzo 1999). Mixed groups were noted in only 20% of sightings in which all possible photoidentifications were made. This percentage is comparable to that reported for mixed groups of resident and nonresidents in the open waters of Sarasota Bay in the Gulf of Mexico (17%, Wells et al. 1987).

As has been reported from studies conducted in closed systems (Wells et al. 1987; Smolker et al. 1992) and semi-closed systems (Wilson 1995; Félix 1997), identified female dolphins and their young calves exhibited some of the strongest associations in the Cedar Keys. The level of association between a female and her young calf was highly predictable because newborn calves are very dependent on their mothers and associate consistently with them (Wells 1991). Association was loose between mothers and older, more independent calves.

Common females with calves were observed with a variety of associates. However, they had two general patterns of association: either they were single individuals or they formed groups of two or three female members. Two of the female groups, referred to as bands, showed characteristics resembling those of the female bands described by Wells et al. (1987), i.e., ranges similar to those of other group members, a coefficient of association of at least 0.31 with one or more group members, and a mean coefficient of association with all group members that was within 1 standard deviation of the overall mean coefficient of association for all group members with each other male, and those of the female cliques described by Smolker et al. (1992), i.e., a mean coefficient of association among females of 0.45. A third group of females did not meet the criterion of the minimum coefficient of association (Wells et al. 1987). However, since they

did share ranges within the Cedar Keys and had an indirect-link association (two individuals share a common associate but are not themselves associates; Smolker et al. 1992) of a moderate–low level, they were called the indirect-link group because of their apparent role in the indirect association between female bands and single females.

Females with calves formed a network of associations with most other females. However, they were never seen all together in a single group. In fact, one of the female bands never associated directly with any of the single females or with the other band during the study. The other band only associated with one single female, whereas the indirect-link group associated with all single females and both female bands. These patterns of association appear to be related in part to the degree of overlap among their ranges. Within the Cedar Keys, the ranges of the two bands overlapped slightly in the center of the Keys. The range of the indirect-link group overlapped the ranges of the two bands and extended along areas close to the shore. The ranges of solitary females overlapped the range of the indirect-link group and to some degree the range of the two bands, covering most of the central inshore habitats. Although no information is available about home ranges and past associations, the observed patterns suggest that the associations among identified females with calves are in part the result of overlapping ranges (Wilson 1995).

The day-to-day activities of the female bands and the indirect-link group were concentrated in different areas than those of single females. The female bands and the indirect-link group were more restricted than single females to close-shore areas. This restricted range could be a strategy to decrease the chance of encountering predators (Vaughan 1986) or an influence of habitat characteristics that affect the extent to which individuals concentrate in particular areas (Waser 1988). These factors may be important in open systems, where females with calves may be less protected from open-water predators. In the Cedar Keys, the open waters of the Gulf are approximately 2.5 km from the nearshore areas that female bands and females in the indirect-link group use most. Females may provide more protection for their calves by staying within 80 m of the coastline (where predators may be uncommon), far from the open Gulf waters.

Home ranges of common females and males probably extend beyond the study area. However, the repeated presence of these dolphins suggests that the Cedar Keys are a very important part of a possibly larger home range. Within these Keys, male ranges extended from the close-shore areas to the Gulf side of the Keys. However, the two male pairs and two single males did not associate very frequently, even though they had similar ranges.

Male ranges covered wider areas than female ranges within the Cedar Keys, especially those of the female bands and the indirect-link group. Among mammals (Mace et al. 1983), including bottlenose dolphins (Wells 1986; Wells et al. 1987; Smolker et al. 1992; Wilson 1995; Bearzi et al. 1997; Félix 1997), males generally have larger home ranges than females. The large male ranges are usually attributed to breeding patterns and increased access to females (Eisenberg 1966; Wells et al. 1987; Wells 1991). Interestingly, however, the pair of males with the highest level of association tended to

associate mostly with similarly ranging females with calves. Nevertheless, since associations between males are not statistically independent, these results should be interpreted with caution.

Like bottlenose dolphins inhabiting closed estuarine systems (Wells et al. 1987; Smolker et al. 1992), identified males commonly sighted in the Cedar Keys formed close pair associations with other males, or were single individuals. Pairs of males associated with each other at a low level, and each of them only associated with one of the solitary males, also at a low level. We did not observe among the identified common males the associations of trios of males described for the dolphins in Shark Bay, Australia (Connor et al. 1992; Smolker et al. 1992).

It is remarkable that in spite of differences in the types of system, certain aspects of bottlenose dolphin social organization are rather uniform. The association patterns of commonly sighted dolphins between and within the sexes vary little among open, semiclosed, and closed systems. Similar patterns of little intraspecific variation in social organization have been observed in other mammal species such as the chimpanzee (Wrangham 1986). Differences in habitat and predation pressure have little influence on overall association patterns and group composition among chimpanzees, whereas the number of individuals involved in the associations is relatively more variable (Wrangham 1986). The pattern appears to be the same for the bottlenose dolphin. For example, in all types of systems, both females and males form close associations with individuals of the same sex or are solitary. However, the number of individuals that form such associations or are solitary appears to vary among systems, suggesting that the selective pressures which induce such associations are the same but the intensity of the pressures varies among systems.

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