

What drives island-associated tropical dolphins to form mixed-species associations in the southwest Indian Ocean?

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Mixed-species associations are temporary aggregations of individuals of different species involved in similar activities. Such associations form for foraging, protection against predators, and social advantage. Mixed-species groups in delphinids are frequent in the wild. We aimed to understand the ecological significance of mixed-species group formation by 2 tropical delphinids, the spinner dolphin (*Stenella longirostris*) and the pantropical spotted dolphin (*Stenella attenuata*), in waters surrounding the island of Mayotte in the southwestern Indian Ocean. We used sighting data collected year-round from 2004 to 2009. We encountered a total of 67 mixed-species groups (comprising 21% of all groups observed) of spinner and pantropical spotted dolphins around Mayotte. No daily or seasonal variability in the occurrence of associations was detected. Behavioral activities of single- and mixed-species groups differed significantly. Foraging was observed only in single-species groups of pantropical spotted dolphins. Mixed-species groups were larger than single-species groups. When in association, spinner dolphins used deeper waters than while in single-species groups. No evidence of association for social advantage was observed. We suggest that spinner dolphins associate with spotted dolphins for protection against predators when transiting between resting areas.

Key words: antipredator strategy, mixed-species associations, pantropical spotted dolphin, spinner dolphin, *Stenella attenuata*, *Stenella longirostris*

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Mixed-species associations—also called interspecific, poly-specific, or heterospecific groups—are temporary aggregations of individuals of different species involved in similar activities for periods of variable duration, from minutes to days and even years (Stensland et al. 2003; Terborgh 1990). Mixed-species associations have been described in many animal species, including birds, fishes, and mammals (Terborgh 1990). In mammals they have been reported in ungulates, primates, and cetaceans. Mixed-species associations should be distinguished from aggregations occurring by chance, when 2 or more species move independently and mix when responding in a similar way to environmental stimuli, such as a common resource or habitat (Stensland et al. 2003; Waser 1982). In this case associations might not have a functional explanation. Mixed-species associations occur because they provide evolutionary benefit over

populations or species that do not mix (Heymann and Buchanan-Smith 2000; Whitesides 1989).

Three main functional explanations for the formation of mixed-species associations have been proposed: improved foraging, protection against predators, and social advantage. According to the foraging-advantage hypothesis, mixed groups can locate and use resources more efficiently than either species alone. The 2nd hypothesis is that mixed-species groups could enhance protection against predators, because such groups could reduce predation due to their larger size than single-species groups, by improved detection and deterrence of



predators. The social advantage hypothesis contends that mixed-species groups provide social, ecological, or reproductive advantages, such as exploitation of larger home ranges, use of different habitats, and facilitated social behavior (Stensland et al. 2003).

The function of mixed-species groups in delphinids has been documented in various places. For example, common (*Delphinus delphis*), striped (*Stenella coeruleoalba*), and Atlantic spotted (*Stenella frontalis*) dolphins form mixed-species aggregations in the Azores, putatively for foraging advantage (Qu  rouil et al. 2008). Because the hypothesized functional explanations are not mutually exclusive, ≥ 2 species might associate for both antipredator and foraging advantage, as suggested for common bottlenose dolphins (*Tursiops truncatus*) and short-finned pilot whales (*Globicephala macrorhynchus*) in the eastern tropical Pacific (Scott and Chivers 1990). Interspecific associations between spinner (*Stenella longirostris*) and pantropical spotted dolphins (*Stenella attenuata*; hereafter, spotted dolphins) have been documented in the eastern tropical Pacific and western Indian Ocean (Ballance and Pitman 1998; Perrin et al. 1973), and spinner and spotted dolphins there form mixed-species association for protection against predators (Norris and Dohl 1980; Scott and Cattanaach 1998). Associations between these 2 species might not be food-related, because their diets and feeding depths differ significantly. Both spinner and spotted dolphins feed primarily at night, with spinner dolphins likely feeding deeper and spotted dolphins feeding more frequently than spinner dolphins on larger epipelagic prey during the day (Galv  n Maga  a 1999; Perrin et al. 1973, 2008). Spinner dolphins are relatively deep feeders, foraging to at least 400 m in the Sulu Sea (Dolar et al. 2003). Spinner dolphins, while resting during the day, can seek out more-alert spotted dolphins to get protection against predators (Norris and Dohl 1980). This strategy also is supported by behavioral studies of insular spinner dolphins around Hawaii, which feed at night and rest during the day in shallow waters with open, sandy bottoms where predators are easily detected (Norris and Dohl 1980; W  rsig et al. 1994). In the open ocean, where spinner and spotted dolphins occur in sympatry and frequently in association, no such safe resting areas are available, and spotted dolphin schools can serve as surrogate "bays."

Around the island of Mayotte (Comoro Islands, Mozambique Channel) spinner and spotted dolphins occur in such close sympatry along the outer slope of the barrier reef that identifying mechanisms allowing ecological partitioning between the 2 species was challenging (Gross et al. 2009). Habitat partitioning could not be demonstrated from the analyses of either daytime visual observations or from $\delta^{13}\text{C}$ signatures in skin and blubber biopsies, but some degree of ecological partitioning was found in terms of trophic level as revealed by $\delta^{15}\text{N}$ signatures (Gross et al. 2009). Such associations have been documented only rarely around islands; for example, off Oahu, Hawaii, where social interactions between the 2 species have been observed (Psarakos et al. 2003). However, very little is known of other insular populations of spotted and spinner dolphins, particularly in the Indian Ocean.

We aimed 1st to characterize mixed-species associations in terms of occurrence, group size, and habitats as compared to single-species groups and 2nd to determine whether mixed-species associations likely occurred for protection against predators, enhanced foraging, or social advantage on the basis of activity budgets. In other taxa group size increases when mixed-species groups form, and individual vigilance against predators decreases as a result (Bshary and No   1997; Cords 1987; FitzGibbon 1990; Hardie and Buchanan-Smith 1997). Thus, if the mixed-species dolphin schools are larger than single-species schools, one might expect some benefit in terms of protection against predators. Finally, if spinner dolphins use the higher vigilance of spotted dolphins while resting, we might observe a higher occurrence of resting behavior in spinner dolphins when associated with spotted dolphins. Alternatively, if mixed-species groups are related to enhanced social opportunities, one might expect a higher proportion of social activities in mixed-species groups than in single-species ones. Similarly, if these associations provide foraging benefits to either species involved, one should observe more foraging activity in mixed-species groups than in single-species groups.

MATERIALS AND METHODS

Study area.—Mayotte (12  50'S, 45  10'E) is located in the northern Mozambique Channel in the Comoro Islands Archipelago (Fig. 1). The island is almost entirely surrounded by a 197-km barrier reef. The lagoon and surrounding reef complexes have an area of 1,500 km², with an average depth of 20 m and a maximum depth of 80 m in the western lagoon. The peri-insular slope off the barrier reef is very steep and contains many submarine canyons and volcanoes. Mayotte is characterized by high delphinid diversity (12 species—Kiszka et al. 2010). The most common and abundant species are the spinner dolphin and the spotted dolphin (Kiszka et al. 2010). Preliminary abundance estimates obtained from aerial surveys suggest a total of 703 spinner dolphins (95% confidence interval [95% CI] = 643–1,046) and 375 spotted dolphins (95% CI = 342–557—Pusineri et al. 2009).

Data collection.—From July 2004 to April 2009 small-boat surveys were undertaken around Mayotte. Surveys were conducted throughout the study period during daylight hours between 0700 and 1800 h in sea conditions not exceeding Beaufort 3. Survey vessels did not follow predefined transects, but every attempt was made to sample the entire daylight period and each habitat type within the surrounding waters of Mayotte (inner lagoon, outer slope of the barrier reef, and oceanic waters deeper than 500 m).

When dolphins were encountered, sighting data were recorded: species, and for each species, group size (maximum, minimum, and best estimate), geographic position (using a handheld global positioning system [Garmin Gecko 201; Garmin Ltd., Olathe, Kansas]), and behavioral activity. Group size was defined as the number of animals at the surface within 5 body lengths of each other (Smolker et al. 1992). However spinner and spotted dolphins also occurred in "super groups," consisting of several tight aggregations (typically of

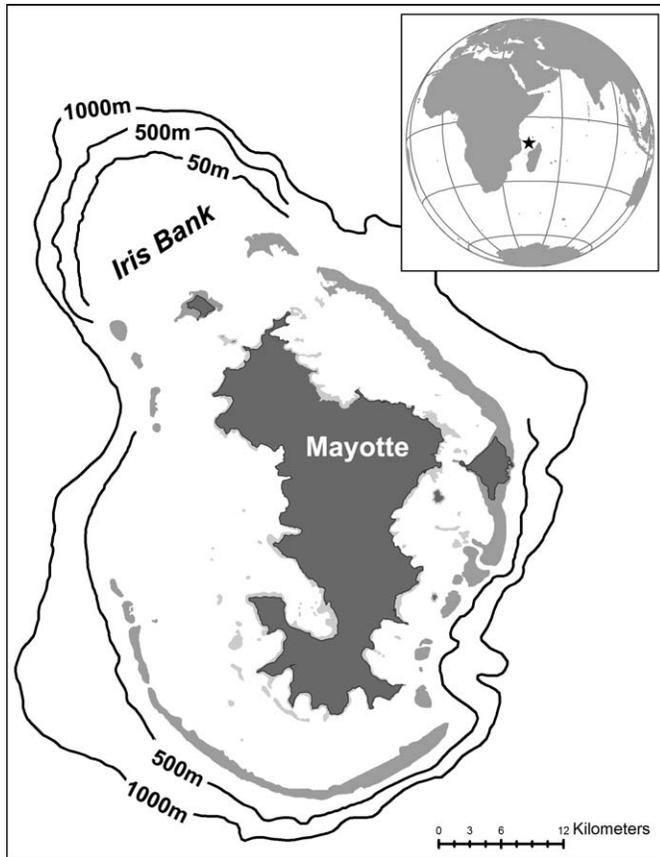


FIG. 1.—Mayotte, the study area (Comoros, northeastern Mozambique Channel) for observations on mixed-species associations of spinner (*Stenella longirostris*) and pantropical spotted (*Stenella attenuata*) dolphins.

2–10 individuals) spaced at a few tens of meters, moving in the same direction, and exhibiting similar patterns of behavior. These associated aggregations were considered collectively as an individual group for purposes of estimating group size.

The predominant activity, defined when a group was encountered, was considered as the behavioral state in which most animals (>50%) of the group were involved. Typically, >90% of the animals in a group were engaged in the same activity. Five categories of behavioral state were defined: milling, resting, traveling, feeding/foraging (hereafter, foraging), and socializing, as used in previous studies (Bearzi 2005; Degradi et al. 2008; Neumann and Orams 2006; Norris and Dohl 1980). Milling was characterized by nondirectional movements of the dolphins, with frequent changes in heading. Resting was characterized by low level of activity, with groups in tight formations and little evidence of forward propulsion. Surfacing in this mode was slow and relatively predictable. Traveling consisted of persistent and directional movements of all individuals in a group. Foraging was characterized by loose to dispersed group formation, with dolphins swimming in circles and pursuing fish. Prey was frequently seen at the surface during foraging activity. Socializing consisted of frequent interactions between individuals in the form of body contacts, high-speed movements, frequent changes in direction, and aerial displays.

A mixed-species group was defined as a group that included at least 1 individual of both species. We considered that the 2 species were in association when they were observed for >15 min moving in the same direction and exhibiting similar patterns of activity. Shorter occurrences with noncoordinated activity were considered in our analysis to have happened by chance.

Data analysis.—Nonparametric tests (Mann–Whitney *U*-test and Kruskal–Wallis *H*-test) were selected because assumptions regarding normality and homogeneity of variance were not met. Seasonal and daily variations of the occurrence of mixed-species groups were tested using Kruskal–Wallis tests. Four seasons were considered: summer (December–February), fall (March–May), winter (June–August), and spring (September–November). To analyze diel patterns of associations we defined 3 time blocks: morning (between 0700 and 1000 h), noon (between 1001 and 1400 h), and evening (between 1401 and 1800 h). We also tested whether spinner and spotted dolphins had different group size in single- compared to mixed-species aggregations using Mann–Whitney *U*-tests. To infer the function of mixed-species groups we tested whether the behavioral activities of spinner and spotted dolphins were different when they were in association compared to when they were not. We compared the frequencies of activities between single- and mixed-species groups using chi-square (χ^2) contingency-table analysis. We also compared the frequencies of activities between single- and mixed-species groups using contingency-table analysis. Finally, we used Mann–Whitney *U*-tests to assess whether habitat characteristics (especially water depth at encounter) were different between the 2 species when they were observed in mixed-species groups and when they were not. We constituted a database in which every dolphin observation was associated with depth corresponding to the global positioning system fixes of the observation. Bathymetric data were obtained from the Service Hydrographique et Océanographique de la Marine (www.shom.fr). Statistical analyses were made in Microsoft XLStat 5.1 (Addinsoft, Paris, France) with the significance level set at $\alpha = 0.05$.

RESULTS

Occurrence of mixed-species associations and group characteristics.—From July 2004 to March 2009 data were collected during 224 daily small-boat surveys. From a total of 315 sightings of single-species and mixed-species groups we recorded 67 sightings (21% of the total) of mixed-species associations of spinner and spotted dolphins. Single-species groups were encountered on 195 occasions for spinner dolphins (62%) and on 53 occasions for spotted dolphins (17%). Spotted dolphins were encountered more frequently in association with spinner dolphins than in single-species groups. When associated, spinner and spotted dolphins comprised equal percentages of the total group size, ranging from 7% to 97% for spinner dolphins and from 3% to 93% for spotted dolphins.

No daily ($H_2 = 3.714$, $P > 0.05$) or seasonal ($H_3 = 3.837$, $P > 0.05$) variability in occurrence of mixed-species groups

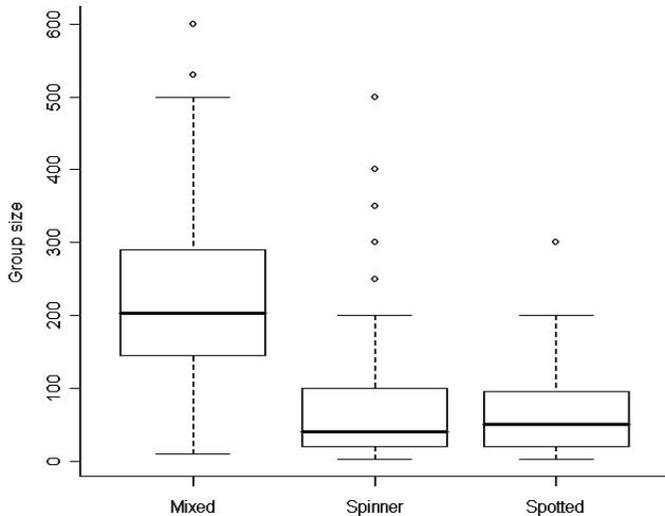


FIG. 2.—Box plot (black bar: median; box: quartiles 1–3; whiskers: 1.5 times the interquartile range of the data; white dots: outliers) of group size of single-species and mixed-species groups of spinner dolphins and pantropical spotted dolphins around Mayotte from 2004 to 2009.

was detected. No difference in group size was observed between spinner and spotted dolphins when associated ($U = 2,102$, $n_1 = 66$, $n_2 = 66$, $P > 0.05$). In single-species groups numbers of spinner and spotted dolphins were not statistically different ($U = 3,967$, $n_1 = 66$, $n_2 = 170$, $P > 0.05$; Fig. 2). However, group size differed between single and mixed-species groups, because both spinner and spotted dolphins were present in larger aggregations when associated (spinner dolphin: $U = 5,571$, $n_1 = 66$, $n_2 = 170$, $P < 0.0001$; spotted dolphin: $U = 2,652$, $n_1 = 66$, $n_2 = 47$, $P < 0.0001$; Fig. 2).

Effect of habitat.—Depth preference differed between mixed-species groups and single-species spinner dolphin groups ($U = 4,340$, $n_1 = 66$, $n_2 = 170$, $P = 0.02$; Fig. 3). When compared to spotted dolphins, spinner dolphins occurred in shallower waters; spinner dolphin single-species median depth was 230 m (quartiles 1–3: 73–285 m), and spinner dolphin mixed-species median depth was 262 m (quartiles 1–3: 98–364 m). Spotted dolphins were seen in depths that did not differ when associated with spinner dolphins or when in single-species schools ($U = 1,327$, $n_1 = 66$, $n_2 = 44$, $P = 0.49$; Fig. 3).

Effect of behavior.—Behavioral activities of single- and mixed-species groups differed significantly ($\chi^2_6 = 26.41$, $P < 0.001$). Only the spotted dolphin was seen foraging in single-species groups, and no foraging events were observed for mixed-species groups (Fig. 4). When in association with spotted dolphins, spinner dolphins increased their travel activity and decreased their social and resting behaviors (Fig. 4). No direct interactions between spinner and spotted dolphins other than close association were observed.

DISCUSSION

As for most field studies of dolphin behavior, this study suffers from limited sample size and the difficulty of inferring underwater activities from surface observations only.

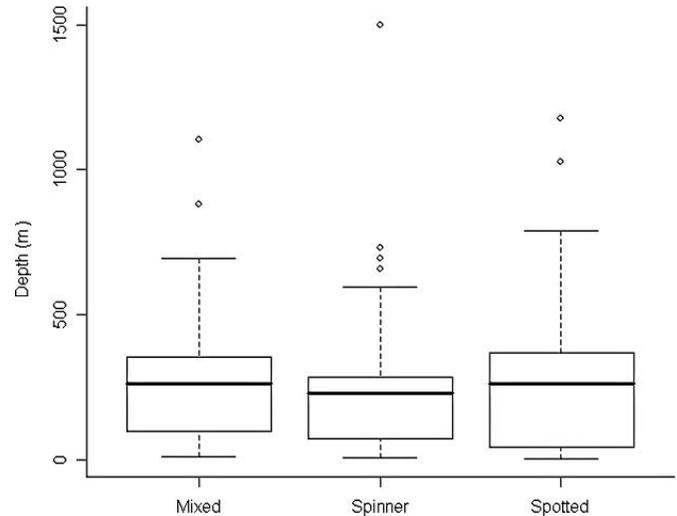


FIG. 3.—Box plot (black bar: median; box: quartiles 1–3; whiskers: 1.5 times the interquartile range of the data; white dots: outliers) of depth preference of single-species and mixed-species groups of spinner dolphins and pantropical spotted dolphins around Mayotte from 2004 to 2009.

Nonetheless, it provides new insights on the characteristics and circumstances in which mixed-species associations of small delphinids occur. Spinner and spotted dolphin regularly formed mixed-species groups (which constituted 21% of all groups involving either species) around the island of Mayotte. Such associations are rare in other locations, such as off Hawaii, where the 2 species also co-occur (Psarakos et al. 2003). Conversely, a relatively similar occurrence (15%) of mixed-species groups of Atlantic spotted and common bottlenose dolphins has been observed in the Bahamas (Herzing and Johnson 1997). Around Mayotte spotted dolphins were encountered more frequently in association with spinner dolphins than in single-species groups. Spotted dolphins also were encountered more frequently in mixed-species groups than spinner dolphins, and an opposite situation occurs in the open waters of the eastern tropical Pacific (Scott and Cattanach 1998). No diel pattern of mixed-species group formation was observed around Mayotte, whereas in the eastern tropical Pacific mixed-species groups were encountered more frequently in the early afternoon (Scott and Cattanach 1998).

Around Mayotte group sizes were larger and traveling was a more predominant activity in mixed-species groups than in single-species groups of spinner dolphins. In addition, water depth used by mixed-species groups was greater than by spinner dolphin single-species groups. Behavioral activities other than traveling and milling were observed infrequently, and foraging behaviors were absent for spinner dolphins. Conversely, single-species groups of spotted dolphins were regularly seen foraging.

The present observations speak against the foraging-advantage hypothesis, because foraging was not observed for mixed-species aggregations. Moreover, previous studies on the comparative feeding ecology of spotted dolphins and spinner dolphins, such as in the oceanic eastern tropical Pacific,

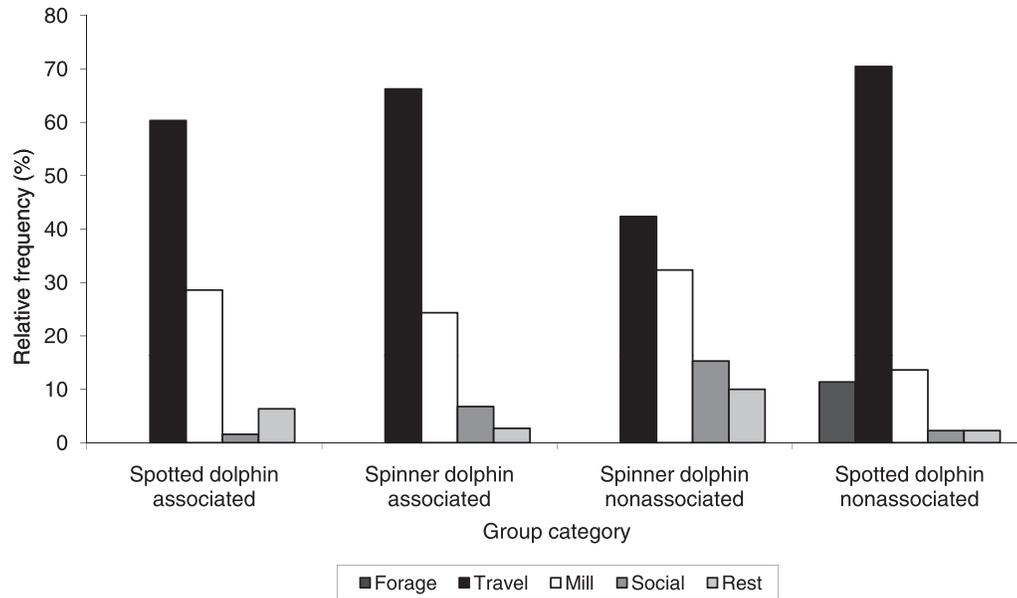


FIG. 4.—Occurrence of behavioral states observed in single-species (nonassociated) and mixed-species (associated) groups of spinner dolphins and pantropical spotted dolphins around Mayotte from 2004 to 2009.

showed that the 2 species use distinct feeding niches (Perrin et al. 1973, 2008) and therefore are unlikely to forage jointly. In the same study area Scott and Cattanch (1998) discounted the hypothesis that mixed-species groups of spinner and spotted dolphins formed for foraging advantage, because the associations were most prevalent during the afternoon when neither species fed. The pattern of mixed-species group formation in the eastern tropical Pacific seems to be produced by an interaction between predator pressure and prey distribution (Scott and Cattanch 1998).

Among the 5 activity categories, traveling and to a lesser extent milling were markedly higher in mixed-species groups (66%) than in single-species (42%) groups of spinner dolphins. Therefore, we propose that around Mayotte spinner dolphins that usually rest in shallow waters during the day associate with spotted dolphins when moving offshore between resting and socializing sites. Hence, the heterospecific aggregation observed between spotted and spinner dolphins might provide some antipredator benefits for the spinner dolphin. Group sizes support this hypothesis. Mixed-species groups were significantly larger than single-species groups, suggesting that 1 or both species could decrease individual vigilance when associated. Benefits would be greater for the spinner dolphin than for the spotted dolphin because the former species is smaller and thus possibly more vulnerable to shark attack. In addition, because spinner dolphins forage at night offshore, they might be less alert during the day when resting and, consequently, more vulnerable to shark attacks (Norris and Dohl 1980).

The formation of mixed-species groups could decrease predation risk for spinner dolphins. Species of large sharks that are known to prey on small delphinids and that occur around Mayotte include the tiger shark (*Galeocerdo cuvier*), hammerhead shark (*Sphyrna* sp.), short-fin mako shark (*Isurus oxyrinchus*), bull shark (*Carcharhinus leucas*), and oceanic

whitetip shark (*Carcharhinus longimanus*—Heithaus 2001; Jamon et al. 2010). Several cases of severe injuries inflicted by sharks on dolphins have been observed around Mayotte, especially in Indo-Pacific bottlenose dolphins (*Tursiops aduncus*—Kiszka et al. 2008), which highlights the importance of the predation risk for dolphins in this area. Large delphinids, such as killer whales (*Orcinus orca*), false killer whales (*Pseudorca crassidens*), short-finned pilot whales, and pygmy killer whales (*Feresa attenuata*) also are potential predators of spinner and spotted dolphins (Norris and Dohl 1980; Perryman and Foster 1980; Scott and Cattanch 1998). These species occur in the deeper-water areas around Mayotte (Kiszka et al. 2010). Oceanic populations of spinner and spotted dolphins might associate to gain antipredator advantages because of the higher predation risk in offshore waters of the eastern tropical Pacific (Norris and Dohl 1980). However, several large predatory sharks are abundant in shallow waters (over sea-grass beds and coral reefs), such as the tiger shark in Shark Bay in Western Australia (Heithaus and Dill 2002). Spinner dolphins could face predation risk and deal with it similarly around other islands in the Indian Ocean. Around Réunion Island, in the Mascarenes, spinner dolphins frequently associate with another delphinid, the Indo-Pacific bottlenose dolphin, which occurs mainly in coastal waters. Associations between spinner and bottlenose dolphins around Réunion Island might be due to the closer proximity of spinner and bottlenose dolphin habitat because no lagoon exists there (Dulau-Drouot et al. 2008). Around Mayotte spinner dolphins live outside the lagoon, whereas bottlenose dolphins occur inside. Spinner dolphins at Mayotte live in close sympatry with spotted dolphins, which could influence mixed-species association patterns between these 2 species.

No direct interactions between spinner and spotted dolphins were observed in mixed-species groups around Mayotte.

Hence, it is difficult to speculate about the social advantage hypothesis. However, spinner dolphins might use larger home ranges and different habitats when associated with spotted dolphins. Around Hawaii, during rare associations between spinner and spotted dolphins, mating between the 2 species has been observed, and potential hybridization has been recorded (Psarakos et al. 2003). This could occur around Mayotte, but no evidence exists so far. In the Bahamas Atlantic spotted and bottlenose dolphins form regular mixed-species aggregations (Herzing and Johnson 1997), and the function of mixed-species groups seems primarily social. Affiliation behavior, such as play, social, and traveling behavior, occurred in >60% of all observations. However, anti-predator behaviors have been observed on a regular basis, including chasing sharks and repelling bottlenose dolphins (Herzing and Johnson 1997). This means that social advantage is not mutually exclusive of antipredator behavior. In the case of spinner and spotted dolphins around Mayotte, the formation of mixed-species groups also might include some social advantages that were not visible during boat-based observations. In the Bahamas underwater observations were made and social activity also was noted in surface observation (Herzing and Johnson 1997). Therefore, this situation does not support the social advantage hypothesis of mixed-species groups of spinner and spotted dolphins around Mayotte, because no social interactions were observed between spinner and spotted dolphins.

In conclusion, spinner dolphins seem to associate with spotted dolphins for antipredator advantage, but the social advantage hypothesis is not excluded, because the 2 functions are not mutually exclusive. Although some differences are seen between mixed-species group formation in the oceanic waters of the eastern tropical Pacific (Scott and Cattanaach 1998) and around Mayotte (this study), patterns of mixed-species group formation appear similar; that is, for antipredator advantage. When associated with spotted dolphins, spinner dolphins use deeper waters where spotted dolphins preferentially occur, which could constitute a strategy to detect and deter predators such as large sharks. In mixed-species groups spotted dolphins are not seen foraging, and both species are observed mostly traveling. Therefore, we suggest that spinner dolphins associate with spotted dolphins when transiting between resting or socializing areas.

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