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Why do dolphins form mixed-species associations in the Azores?

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Summary

Mixed-species associations are temporary associations between individuals of different species that are often observed in birds, primates and cetaceans. They have been interpreted as a strategy to reduce predation risk, enhance foraging success and/or provide a social advantage. In the archipelago of the Azores, four species of dolphins are commonly involved in mixed-species associations: the common dolphin, *Delphinus delphis*, the bottlenose dolphin, *Tursiops truncatus*, the striped dolphin, *Stenella coeruleoalba*, and the spotted dolphin, *S. frontalis*. In order to understand the reasons why dolphins associate, we analysed field data collected since 1999 by research scientists and trained observers placed onboard fishing vessels. In total, 113 mixed-species groups were observed out of 5720 sightings. The temporal distribution, habitat (water depth, distance to the coast), behaviour (i.e. feeding, travelling, socializing), size and composition of mixed-species groups were compared with those of single-species groups. Results did not support the predation avoidance hypothesis and gave little support to the social advantage hypothesis. The foraging advantage hypothesis was the most convincing. However, the benefits of mixed-species associations appeared to depend on the species. Associations were likely to be opportunistic in the larger bottlenose dolphin, while there seemed to be some evolutionary constraints favouring associations in the rarer striped dolphin. Comparison with previous studies suggests that the formation of mixed-species groups depends on several environmental factors, and therefore may constitute an adaptive response.

Introduction

According to the niche theory, sympatric species with similar ecological requirements compete for resources (Pianka 1974; Roughgarden 1976). Their co-existence requires some degree of resource partitioning, such as habitat segregation or use of different feeding resources. Partial resource partitioning may be achieved through preference for different micro-habitats, temporal variations in habitat use, adoption of different foraging tactics, and preference for different prey items or prey sizes (cf. Bearzi 2005). Sympatric species may also jointly exploit resources through the formation of “mixed-species” associations. Mixed-species or polyspecific associations are temporary aggregations of individuals of different species involved in similar activities for periods ranging from several minutes to hours, days, or even years. They are common in birds, primates and cetaceans (cf. Terborgh 1990 and Stensland et al. 2003 for a review). These functional associations should be distinguished from mere aggregations of animals occurring by chance or due to the gathering of animals of different species around clumped resources (Waser 1982, 1984). Most authors assume that mixed-species associations occur because they give participants some evolutionary benefit over those that do not mix (Whitesides 1989; Heymann & Buchanan-Smith 2000). The main two functional explanations to the formation of mixed-species associations are the predator avoidance and the foraging advantage hypotheses (cf. Stensland et al. 2003). According to the predator avoidance hypothesis, individuals may benefit from the association by increasing their abilities to detect and deter predators. Provided that inter-specific competition is limited, mixed-species groups can be larger than single-species one and allow safety in numbers. According to the foraging advantage hypothesis, individuals may benefit from the association by summing up their capacities to detect and explore patchy food resources (e.g. fruit or fish). In the case of species that hunt collectively, a minimum group size may be necessary to ensure the efficiency of the hunt. A third hypothesis states that participants to the association may gain some social or reproductive advantages, such as exploitation of larger home ranges, use of different habitats, and practise of social behaviour, while enjoying reduced sexual competition (cf. Stensland et al. 2003). These three functional hypotheses are not mutually exclusive. In some taxa, individuals in mixed-species groups increase their detection of predators as well as their foraging efficiency (e.g. in primates: Gautier-Hion et al. 1983; and birds: Sullivan 1984). Independently of the functional explanation that prevails, mixed-species associations may constitute a survival strategy for species present in low numbers and unable to form large groups (e.g. in birds: Morse 1970; and dolphins: Frantzis & Herzing 2002). In some cases, the association may not be beneficial to all the species involved, and some species may benefit from the others (cf. the “social parasitism concept”, Norris & Prescott 1961).

Few studies have focused on the ecology of mixed-species aggregations in the family Delphinidae (cf. Bearzi 2005 for a review) and their function is still not well understood (cf. Stensland et al. 2003). Observations have been carried out on common bottlenose dolphins, *Tursiops truncatus*, and Atlantic spotted dolphins, *Stenella frontalis*, in the Bahamas (Herzing et al. 2003), common dolphins, *Delphinus delphis*, and striped dolphins, *S. coeruleoalba*, in the western Mediterranean Sea (Garcia et al. 2000) and the Gulf of Corinth (Greece, Mediterranean Sea; Frantzis & Herzing 2002), and spinner dolphins, *S. longirostris*, and Pan-tropical spotted dolphins, *S. attenuata*, in the Eastern Pacific (Norris & Dohl 1980; Scott & Cattanach 1998) and Hawaii (Psarakos et al. 2003). While some studies reported a high frequency of social interactions between species (e.g. Garcia et al. 2000; Herzing et al. 2003), others indicated that the frequency of association was influenced by prey distribution and predation pressure (e.g. Norris & Dohl 1980; Scott & Cattanach 1998). In the Mediterranean Sea, the frequency of association of common dolphins was shown to be inversely correlated to their abundance (Frantzis & Herzing 2002).

To better understand the biological significance of mixed-species associations in Delphinidae, we analysed the pattern of occurrence of mixed-species groups around the archipelago of the Azores, in the Northeast Atlantic. The Azores host more than 20 species of Cetaceans (Santos et al. 1995; Gonçalves et al. 1996; Steiner et al. 2007), including at least eight species of Delphinidae. Four species are commonly observed in mixed-species associations: the short-beaked common dolphin, the Atlantic spotted dolphin, the common bottlenose dolphin, and the striped dolphin. While the first three species are very abundant in the archipelago, the fourth one is sighted only occasionally (Silva et al. 2003). Another delphinid species, the Risso’s dolphin, *Grampus griseus*, is also occasionally observed

in association with one or the other of the above mentioned species. These associations are rare and will not be dealt with herein.

Although no data is available on the predation risk in the Azores, this risk can be expected to be low. As a matter of fact, killer whales are rare, big sharks are not very abundant, and bite scars are scarcely observed on dolphins (one single observation in eight years). In any case, calves are much more vulnerable to predation than adults. The feeding ecology of dolphins is poorly studied in the Azores and the pelagic waters of the North Atlantic. Feeding aggregations, involving one or more dolphin species, as well as seabirds and tunas, are common in the Azores (Martin 1986; Clua & Grosvalet 2001), especially around seamounts, where productivity is enhanced (Morato et al. 2008b). Current knowledge and *ad libitum* information show that all focus species feed on blue jack mackerel (*Trachurus picturatus*) and chub mackerel (*Scomber japonicus*) when these preys are abundant. However, in the North Atlantic, the diet of striped dolphins somewhat differs from that of the other three species (cf. Spitz et al. 2006; Doksæter et al. 2008). The social structure of the bottlenose dolphin is based on a fission-fusion social system, where individuals temporarily associate with a number of different individuals, so that group size and composition vary over time (Connor et al. 2000). This kind of social structure is common in small delphinids (Gowans et al. 2007) and is likely to apply to the other three species (Perrin et al. 1994; Bruno et al. 2004).

The aim of the present study was to evaluate the conditions which prevail to the formation of dolphin mixed-species associations in the Azores, and determine which of the “predation avoidance”, “foraging advantage” and “social advantage” hypotheses better explained their formation. Our predictions were that 1/ if associations were primarily driven by the predation avoidance hypothesis, mixed-species groups should include calves relatively more often than single-species ones; 2/ if associations were primarily driven by the foraging advantage hypothesis, mixed-species groups should be observed feeding relatively more often than single-species ones; 3/ if associations were primarily driven by the social advantage hypothesis, mixed-species groups should be observed in social interaction relatively more often than single-species ones, and/or a habitat switch could occur. Independently of the above hypotheses, it can be expected that a minimum group size is required to ensure protection against predators, allow feeding efficiency, and meet social requirements. In that case, and as a consequence of their fission-fusion social system, some species may be facing a strong constraint to associate with heterospecifics in order to maintain this “minimum” group size during periods of low abundance.

To test these hypotheses, we analysed long term data collected within the Exclusive Economic Zone (EEZ) of the Azores since 1999. For each of the four dolphin species that were regularly observed in mixed-species associations, we made comparisons on the temporal patterns of occurrence of single-versus mixed-species groups. We also compared the characteristics of the habitat at sighting location, and the behaviour, size and composition of single- and mixed-species groups.

Material and methods

Study site

The archipelago of the Azores (Portugal) is located between the 37th and 41st northern parallel and the 25th and 31st western meridian, extending more than 480 km along a northwest-southeast axis and crossing the Mid-Atlantic Ridge. It is composed of nine volcanic islands divided into three groups, the eastern, central and western groups, separated by deep waters (*ca.* 2000 m) with scattered seamounts (Santos et al. 1995; Morato et al. 2008a). The Gulf Stream and the North Atlantic and Azorean currents generate a complex and highly variable pattern of ocean circulation around the archipelago, which results in high salinity, high temperature and low nutrient waters (Johnson & Stevens 2000).

Data collection

Data were obtained either during dedicated cetacean surveys or as part of the Azorean Fisheries Observer Program (POPA). The POPA program was implemented in order to guarantee the “dolphin safe” certification to the tuna fishery and its products within the EEZ of the Azores. Trained observers placed aboard tuna-vessels collected extensive data on the presence, abundance and behaviour of cetaceans, seabirds and turtles. Observation sessions usually took place between 8h and 19h, although they could continue until dusk. For each sighting of cetaceans, the following parameters were recorded: the time and geographical position, the species involved, the approximate number of

individuals, group composition and cohesion, and main behaviour. Given that the tuna-vessels did not modify their routes in order to approach the dolphins, we chose not to use the latter four pieces of information. Sightings were checked with binoculars and rated according to visibility conditions and degree of confidence on the identification of species. Dubious sightings were eliminated from the data set. We used only the data recorded during search for tuna schools and travel to or from the harbour, leaving out the data obtained during fishing events. Finally, although the POPA program was initiated in 1998, the data collected prior to 2001 were discarded due to changes in the observation protocol. The temporal distribution of observations was limited by the activity of the tuna vessels, which usually started at the beginning of May and extended until the end of October.

Dedicated surveys (DS) were performed within the scope of several research projects of the Department of Oceanography and Fisheries and Centre of IMAR of the University of the Azores. Surveys started in 1999. Trips were conducted year-round, but most fieldwork was done during summer, due to unfavourable meteorological conditions in winter. Surveys covered the whole archipelago, but they were mostly restricted to the periphery of the islands, within 5 or 10 nautical miles (Nm) from the coast. Trips usually started at 9h and finished around 17-18h. Search for cetaceans was either performed visually from the boat following predefined routes, or guided by land-based observers. At each sighting of cetaceans, the route was modified in order to approach the animals. Recorded data included the time and geographical position, the species involved, group size (minimum, maximum, and average estimates for each species), composition, cohesion and behaviour. Five behavioural categories were defined (following Garcia et al. 2000): foraging, travelling (unidirectional movement), milling (movement with frequent changes of direction), socializing (including play, nurse and courtship), and undetermined (including resting). All major behaviours were recorded, but analyses were restricted to the “main” behaviour, in which the majority of group members was involved prior to the arrival of the boat.

Data analysis

In order to maximize the number of mixed-species observations available for statistical analyses, we decided to analyse all sightings, whether they occurred during active search for cetaceans or not. As a consequence, searching effort, encounter rates and densities could not be calculated, and the data could not be used to describe the spatial distribution and habitat preferences of each species. Statistical analyses were made separately for each species (whenever possible) and for the four species together, using Statistica 6.1 (StatSoft 1984-2002).

We counted the monthly and total number of sightings for each species, and calculated the percentage of sightings in association with other species. We analysed the seasonal and diel patterns of associations. As a preliminary step, we verified the independency of time-series data by means of an auto-correlation analysis between successive measures. The temporal patterns of mixed-species associations were studied in relation to expected patterns based on the occurrence of single-species groups. The seasonality of associations was analysed in two different ways. First, we tried to determine whether the monthly frequency of mixed-species sightings depended on the relative abundance of each species. For each month, we calculated the probability P that two species that meet at random are of different species ($P = f_{DDE}(1-f_{DDE}) + f_{SFR}(1-f_{SFR}) + f_{SCO}(1-f_{SCO}) + f_{TTR}(1-f_{TTR})$), where f is the proportion of sightings attributable to a given species. We then searched for a correlation between this probability and the monthly percentage of sightings of mixed-species groups. Second, for each species, we searched for a correlation between the monthly numbers of sightings in mixed-species groups versus single-species groups, and between the monthly numbers of sightings in mixed-species groups versus the total number of individuals seen (i.e. mean group size x number of sightings). The diel distribution of mixed-species associations was examined using a χ^2 -test. Day time was partitioned into classes of one hour duration, except for observations made after 17h (DS) or 19h (POPA), which were pooled. Class limits were adapted for the purpose of the χ^2 -tests, in such a way that expected frequencies were higher than five (with minor exceptions). For each time interval i , the expected frequencies of occurrence for the mixed-species groups were calculated after the observed frequencies of occurrence of the single-species groups ($n_{i \text{ mixed expected}} = n_{i \text{ single observed}} * n_{\text{total mixed}} / n_{\text{total single}}$).

Statistical tests were performed to determine whether dolphins used the same habitat (depth and distance to the coast) and had the same behaviour while in single-species and in mixed-species groups.

Observed and expected frequencies of occurrence for the mixed-species groups were compared by means of a χ^2 -test, as described above. Distance to the coast (in nautical miles, Nm) and depth (in meters) at sampling location were estimated by means of a Geographic Information System (ArcGis 9.1, ESRI®) using bathymetrical charts from Lourenço et al. (1998). Three distance classes were defined for the DS (0-2 Nm, 2-5 Nm, >5 Nm) and four classes for the POPA (0-5 Nm, 5-10 Nm, 10-30 Nm, >30 Nm). Three depth classes were defined for the DS (0-500 m, 500-1000 m, >1000 m) and four classes for the POPA (0-500 m, 500-1000 m, 1000-1500 m, >1500 m).

Group size and composition were analysed in relation to predictions. First, we tested whether group size differed between species and whether the number of conspecifics as well as the total number of individuals differed between single- and mixed-species groups. We predicted that species facing a strong constraint to associate would be represented by a smaller number of individuals in mixed- than in single-species groups. Group sizes were compared by means of a t-test for unpaired samples with unequal variances, after verifying that variances were significantly different between most samples (Brown-Forsythe test). Second, we intended to determine whether groups involved in foraging activities were larger than groups involved in any other activity. Because group size differed between species and between single- and mixed-species groups, we tested this prediction by means of an ANOVA, with two factors included in the model: group composition (mixed-species, or single-species group of each of the four species) and behaviour (feeding versus any other identified behaviour). Although ANOVA is intended to compare samples with equal variances, it is quite robust to violation of this assumption. Third, we analysed the relative composition of the mixed-species groups in order to determine whether some species were consistently under or over-represented in these groups. We predicted that, although social constraints could favour the formation of balanced groups, species facing a strong pressure to associate would probably be in minority. We calculated the ratio between the number of individuals of one species and the number of individuals of the other species. The proportions of individuals of each species were considered equivalent if the number of individuals of one species was no more than twice the number of individuals of the other species ($0.5 < \text{ratio} < 2$). Because the size of single-species groups differed between species, we simulated the expected distribution of the ratios by a randomisation procedure based on observed single-species group sizes, using R 2.4.1 (2006). Observed and expected distributions of ratios were compared by means of a χ^2 -test. The presence of calves in the mixed-species groups was also analysed by a χ^2 -test.

Results and discussion

Specific patterns of association

Between 2001 and 2004, the POPA observers recorded 4369 sightings involving at least one of the four focus species. There were 4304 single-species and 65 mixed-species sightings, four of which involved more than two species (Table 1). Between 1999 and 2006, the DS produced 1351 sightings involving at least one of the four dolphin species. There were 1303 single-species and 48 mixed-species sightings, three of which involved more than two species (Table 1). The percentage of mixed-species sightings was lower in the POPA (1.5%) than in the DS (3.7%). It is possible that some mixed-species groups were not recognised as such by the POPA observers given that the tuna-vessels did not modify their routes to approach the dolphins. The observed proportion of mixed-species groups was similar to that observed in the oceanic waters of the Gulf of Mexico (about 2 % of small delphinid sightings; Maze-Foley & Mullin 2006), but lower than in the Mediterranean Sea (6-7 %; Garcia et al. 2000; Roussel & Beaubrun 2000) and in the coastal waters of the Bahamas (15 %; Herzing & Johnson 1997; Herzing et al. 2003) and the Gulf of Corinth (35%, Frantzis & Herzing 2002).

In both data sets, the common dolphin was the most sighted species, followed by the spotted and bottlenose dolphins (Table 1). The striped dolphin was rarely seen. All possible kinds of associations were observed, except those involving both the striped and bottlenose dolphins. The percentage of sightings in association was around 2-7% for all species except the striped dolphin, which was observed in association up to 31% of time in the POPA. In this dataset, associations involving striped and spotted dolphins or striped and common dolphins were observed significantly more often than expected based on the relative frequencies of sighting of each species (Fig. 1). Conversely, associations between bottlenose and common dolphins were less frequent than expected. In the DS, as in the POPA, associations between striped and common dolphins were more frequent than expected (Fig. 1). A potential explanation to the higher degree of association of the striped dolphins is that they

associate more because they are less abundant, as already observed in other taxa (e.g. in birds: Morse 1970; and common dolphins in the Mediterranean Sea: Frantzis & Herzing 2002).

Seasonality

The total number of sightings varied between months (Fig. 2A and 2B). It depended on the searching effort, which was not quantified due to the reasons explained in the Material and Methods section. The relative proportion of sightings of each species also varied between months. Common and bottlenose dolphins were observed year-round; while spotted dolphins were observed only between April and October, and striped dolphins primarily between March and October. Mixed-species associations were more frequent between May and September, when all four species were present. There was no auto-correlation in the number of sightings (or individuals) between successive months, except for the bottlenose dolphin in the DS ($p=0.007$ for the number of sightings and the number of individuals).

The monthly number of mixed-species sightings was not proportional to the probability that two groups that meet are of different species (POPA: $R^2=0.558$, $p=0.088$; DS: $R^2=0.001$, $p=0.909$). Thus, mixed-species associations were not a simple consequence of the random meeting of groups of different species.

For each species taken independently, the monthly number of sightings in mixed-species groups was proportional to the number of sightings in single-species groups for the spotted and striped dolphins in the POPA (correlation based on 6 months only) and for all species except the striped dolphins in the DS (Table 2). Similar results were obtained when the number of individuals was taken in consideration (DS only, Table 2). Thus, seasonal trends in mixed-species associations appeared to be mostly influenced by seasonal variations in the occurrence of each species. The dolphins tended to associate more when they were more abundant. However, according to the DS dataset, the striped dolphins appeared not to follow this rule.

Diel pattern

There was no auto-correlation in the number of sightings between successive hour intervals. In the POPA, the diel distribution of mixed-species associations was not significantly different from random between 8h and 22h ($\chi^2=13.96$, $df=11$, $p=0.235$). However, there were significantly more mixed-species observations than expected between 18 and 19h (11 vs 5.0, $\chi^2=6.86$, $df=1$, $p=0.009$). In the DS, the diel distribution of mixed-species associations was not significantly different from random between 9h and 20h ($\chi^2=10.01$, $df=8$, $p=0.264$). However, there were significantly more mixed-species observations than expected between 10 and 11h (15 vs 8.9, $\chi^2=4.19$, $df=1$, $p=0.041$). It is noteworthy that the main periods of mixed-species associations correspond with feeding periods in the Azores. According to the behavioural data recorded during the DS, feeding takes place at any time during the day ($\chi^2=14.25$, $df=9$, $p=0.114$), but is more frequent between 10 and 11h (71 vs 53.5, $\chi^2=5.69$, $df=1$, $p=0.017$). The late afternoon was previously identified as a favoured feeding period in the Azores (cf. Clua & Grosvalet 2001).

Habitat

The distribution of single-species observations in relation to depth and distance to the coast varied between species (as exemplified by the POPA: Fig. 3A and B). The striped dolphins had the most heterogeneous distribution, with most sightings occurring at depth larger than 1000m (DS) or larger than 1500m (POPA) and very few sightings below 500m (DS and POPA). Although the searching effort was not taken into account, the distribution of sightings was in agreement with a previous study conducted in the Azores, which showed that common and bottlenose dolphins had a preference for shallow coastal waters, while spotted and striped dolphins preferred deep pelagic waters (Silva et al. 2003).

In the POPA, there was a significant difference between the predicted and observed distributions of mixed-species sightings with respect to water depth for the striped and spotted dolphins (Fig. 3A). When in association, both species were found more often than expected in shallow waters (<500m), and the striped dolphin was also observed less often in deep waters (>1500m). As for distance to the coast, striped dolphins in mixed-species groups were found more often than predicted in coastal areas (up to 5 Nm from the coast; Fig. 3B). In the DS, there were no significant differences between the predicted and observed distributions of mixed-species sightings with respect to depth or distance to the

coast (data not shown). Discrepancies between data sets may have arisen from the limited range of the DS, which were primarily conducted within 5 Nm from the coast and in waters shallower than 1500m. The fact that striped dolphins were found significantly more often in shallow coastal waters when in mixed-species groups suggests that this species either modified its habits to follow more coastal species or formed mixed groups when coming to shallow waters. Similarly, in the Mediterranean Sea, striped dolphins were more likely to be associated with common dolphins when in relatively shallow waters (Garcia et al. 2000). In the California Bight, shallow waters were shown to attract marine mammal species otherwise favouring deeper waters, due to an abundance of preys in areas of local upwelling (Bearzi 2006).

Behaviour (DS only)

Dolphins in mixed-species groups were not behaving as predicted according to the behaviour of single-species groups ($\chi^2=10.12$, $df=4$, $p=0.038$). Deviation from predictions was due to a significant over-representation of foraging behaviour (Table 3) and concomitant under-representation of travelling ($\chi^2=3.92$, $df=1$, $p=0.048$). The frequency of social interactions (5.4% of mixed-species sightings) and that of other behaviours were not significantly different from predictions. The excess of foraging behaviour in mixed-species groups by comparison to single-species groups was significant for the four species together and for the spotted and bottlenose dolphins (Table 3). On the whole, dolphins in mixed-species groups were observed foraging almost twice as often as dolphins in single-species groups (42.4 vs 23.4%). The bottlenose dolphin was the species that was feeding most often when in mixed-species associations (62.5% of sightings, Table 3). These results suggest that, in the Azores, the main determinant of mixed-species associations is food-related. This situation is different from what has been observed in other locations, where mixed-species encounters seem to be driven by social motivations. In the Alboran Sea, mixed-species groups of striped and common dolphins tend to spend less time feeding and more time socializing than single-species groups (Garcia et al. 2000). In the Bahamas, mixed-species associations between Atlantic spotted dolphins and bottlenose dolphins are often involved in aggressive behaviours and courtship, while they are rarely foraging, playing or nursing (Herzing et al. 2003). A plausible explanation for the high proportion of foraging activities in mixed-species groups in the Azores may be that schooling fish are abundant during the main field season. As observed in other areas, the presence of large schools of fish favours cooperative foraging and the formation of mixed-species associations (e.g. Bearzi 2006; Gowans et al. 2007).

Group size and composition (DS only)

Single-species groups of bottlenose dolphins were the smallest (t-test: $p<0.001$). Groups of common dolphins were significantly smaller than groups of striped and spotted dolphins (t-test: $p=0.002$ and $p<0.001$, respectively), but the difference between the latter two species was not significant. For each species taken independently, the number of individuals was not significantly different in both kinds of groups (Fig. 4), except in the striped dolphin where the number of individuals in mixed-species groups was smaller than in single-species ones ($p=0.05$). Mixed-species groups were significantly larger than single-species ones (t-test: $p=0.005$; Fig. 4). It is likely that they reflected the coalition of single-species groups. Association with heterospecifics appears to allow the formation of large groups, whereas intra-specific competition may impose some ecological or social limits on the number of conspecifics in a group. This situation is similar to the one observed in the western Mediterranean Sea (Garcia et al. 2000) and in the Eastern Pacific (Scott & Cattanch 1998).

The ANOVA confirmed the effect of group composition on group size ($F=26.75$, $df=4$, $p<0.001$), but revealed no effect of behaviour ($F=1.24$, $df=1$, $p=0.265$) nor of the interaction between behaviour and group composition ($F=1.38$, $df=4$, $p=0.239$). Thus, feeding did not appear to occur in larger groups than any other activity.

Mixed-species groups were composed of an equivalent number of individuals of each species significantly more often than if associations occurred at random ($\chi^2=4.62$, $df=1$, $p=0.032$). Bottlenose dolphins were often in lower numbers than the other species involved in the association, striped dolphins were usually in equivalent numbers, and common dolphins in equivalent or higher numbers (Fig. 5). However, all these trends were merely a consequence of the relative group sizes of each species (χ^2 tests, $p>0.05$). When this latter parameter was accounted for, spotted dolphins were found in lower numbers significantly more often than expected ($\chi^2=5.48$, $df=1$, $p=0.019$) and striped dolphins

in higher numbers significantly less than expected ($\chi^2=4.62$, $df=1$, $p=0.032$). In other words, dolphins of the latter two species had a tendency to associate with groups that were larger than expected by chance. In the western Mediterranean Sea, where none of the species is rare, mixed groups of striped and common dolphins tend to be composed of an equal number of individuals of each species (Garcia et al. 2000). In contrast, associations of striped and common dolphins are strongly biased in favour of striped dolphins in the Gulf of Corinth, where common dolphins are in very low numbers (Frantzis & Herzing 2002).

On average, calves were present in 86.6 % of single-species groups and 82.4 % of mixed-species groups. Mixed-species groups did not include calves more often than expected according to the frequency of occurrence in single-species groups ($\chi^2=0.11$, $df=1$, $p=0.744$). This was also true for each of the four species considered independently (data not shown). Thus, the presence of calves did not seem to influence the formation of mixed-species groups. Similar results were reported for striped and common dolphins in the Mediterranean Sea (Garcia et al. 2000).

Conclusion

In the Azores, mixed-species associations involving small delphinids appear to be the exception rather than the rule. The main strategy allowing sympatry between dolphin species in that region of the North Atlantic must be resource partitioning in space and time rather than mixed-species associations. As a matter of fact, our data indicated seasonal variations in the patterns of occurrence of each species and some degree of habitat partitioning (cf. also Silva et al. 2003).

Results did not support the predation avoidance hypothesis as the main explanation for the formation of mixed-species groups, as no influence of the presence of calves was detected. This could be expected given the low predation pressure existing in the Azores. Little support was obtained for the social advantage hypothesis. Dolphins in mixed-species associations were rarely involved in social interactions. On the other hand, it seemed that mixed-species associations gave striped dolphins the opportunity to use unfamiliar habitats. Results suggested that the main determinant of associations was probably food-related. In fact, dolphins in mixed-species associations were involved in foraging activities relatively more often than dolphins in single-species groups, and mixed-species associations were more frequent during preferred feeding periods. To our knowledge, no previous study identified the feeding advantage hypothesis as the main explanation for the formation of mixed-species associations in small delphinids. Differences between studies are likely dependant on several factors such as dolphin densities, habitat and diet overlap between species, prey abundance and distribution, and predation pressure. The distinctiveness of the EEZ of the Azores might be explained by its pelagic environment and complex ocean circulation, which result in abundant and patchily distributed resources (Morato et al. 2008b). According to the foraging advantage hypothesis, these conditions are favourable to the formation of mixed-species associations (cf. Stensland et al. 2003).

It remains to determine whether dolphins actively associate to hunt collectively and thereby enhance their feeding success, or passively associate by gathering around the same schools of preys. Sorting between the two hypotheses is difficult and requires field observations to determine how the hunting groups are formed. In the Azores, Clua and Grosvalet (2001) reported that common and spotted dolphins, and sometimes also striped dolphins, were generally present at the beginning of the hunt, while bottlenose dolphins used to join afterwards. Bottlenose dolphins' behaviour is comparable to that of tunas and seabirds that opportunistically join the hunt to feed on the ball of fish gathered by other delphinids (cf. also Martin 1986). The bottlenose dolphin being the largest of the four dolphin species, it is probably less exposed to predation, and less likely to be deterred by competitors. Its behaviour matches the "social parasitism concept", which has also been invoked to explain associations between sea lions and dolphins in the California Bight (Bearzi 2006).

Reliability on mixed-species associations seemed to be higher in the striped dolphins than in the other three species. Striped dolphins were sighted less frequently and were observed in mixed-species associations relatively more often than the other species. Their frequency of association was not directly proportional to the number of groups or individuals. They were in lower numbers in mixed-species than in single-species groups, and had a tendency to associate with groups that were larger than expected by chance. Thus, striped dolphins probably associated with heterospecifics in order to enlarge group size. Interestingly, although striped dolphins tended to prefer deep waters, they were often observed in shallow waters when in mixed-species groups. Although this could be justified by

the social advantage hypothesis, association with heterospecifics could also be interpreted as a means to enhance feeding success in unfamiliar coastal areas, possibly during periods of food scarcity in preferred areas. It would be worthwhile to investigate further these hypotheses in the future.

In summary, the present study indicates that mixed-species associations are rare in the Azores. When they happen, participants are often involved in foraging activities. It seems that different species may have different motivations for forming mixed-species associations, and that a given species will behave differently in different environments. This diversity of responses illustrates the ability of dolphins to adapt to their environment, an important issue in the face of climate change and growing anthropogenic pressure.

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Table 1. Number of sightings involving common (DDE), spotted (SFR), bottlenose (TTR) and striped (SCO) dolphins in single- (diagonal) or mixed-species groups (upper and lower triangles, and next two lines), total number of sightings (n total) and percentage of sightings in mixed-species associations (% association), for the POPA and dedicated surveys (DS).

	POPA				DS			
	DDE	SFR	TTR	SCO	DDE	SFR	TTR	SCO
DDE	2851	27	5	18	573	9	12	12
SFR	27	899	2	9	9	345	11	1
TTR	5	2	490	0	12	11	321	0
SCO	18	9	0	64	12	1	0	64
(DDE+SFR+TTR)	2	2	2		2	2	2	
(DDE+SFR+SCO)	2	2		2	1	1		1
n total	2905	941	499	93	609	369	346	78
% association	1.9	4.5	1.8	31.2	5.9	6.5	7.2	17.9

Table 2. Correlation between the monthly number of sightings in mixed-species groups versus the number of sightings in single-species groups or versus the number of individuals that were sighted for common (DDE), spotted (SFR), bottlenose (TTR) and striped (SCO) dolphins, in the POPA and dedicated surveys (DS). Significant p-values are in bold ($p < 0.05$).

		DDE		SFR		TTR		SCO	
		R ²	p	R ²	p	R ²	p	R ²	p
POPA	n sightings	0.096	0.550	0.882	0.005	0.388	0.187	0.805	0.015
DS	n sightings	0.882	<0.001	0.999	<0.001	0.809*	<0.001	0.208	0.137
	n individuals	0.943	<0.001	0.991	<0.001	0.889*	<0.001	0.166	0.188

*: significant autocorrelation between time-series data

Table 3. χ^2 -test of observed versus expected numbers of sightings of common (DDE), spotted (SFR), bottlenose (TTR) and striped (SCO) dolphins involved in foraging activities when in mixed-species groups, in the dedicated surveys, and same test for the mixed-species groups independently of the species involved (All). Significant p-values are in bold ($p < 0.05$).

	DDE	SFR	TTR	SCO	All
n observed	13	12	14	2	19
n expected	8.6	5.2	6.3	0.8	11.5
χ^2	2.30	8.76	9.29	-	5.51
p	0.130	0.003	0.002	-	0.019
% foraging	36.4	50.0	62.5	14.3	42.4

-: the expected number of sightings was too low for the test to be performed.

Figure 1. Observed (n obs., left) and expected (n exp., right) numbers of mixed-species sightings involving common (DDE), spotted (SFR), bottlenose (TTR) and striped (SCO) dolphins, for the POPA and dedicated surveys (DS), with results of the χ^2 -test (*: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$).

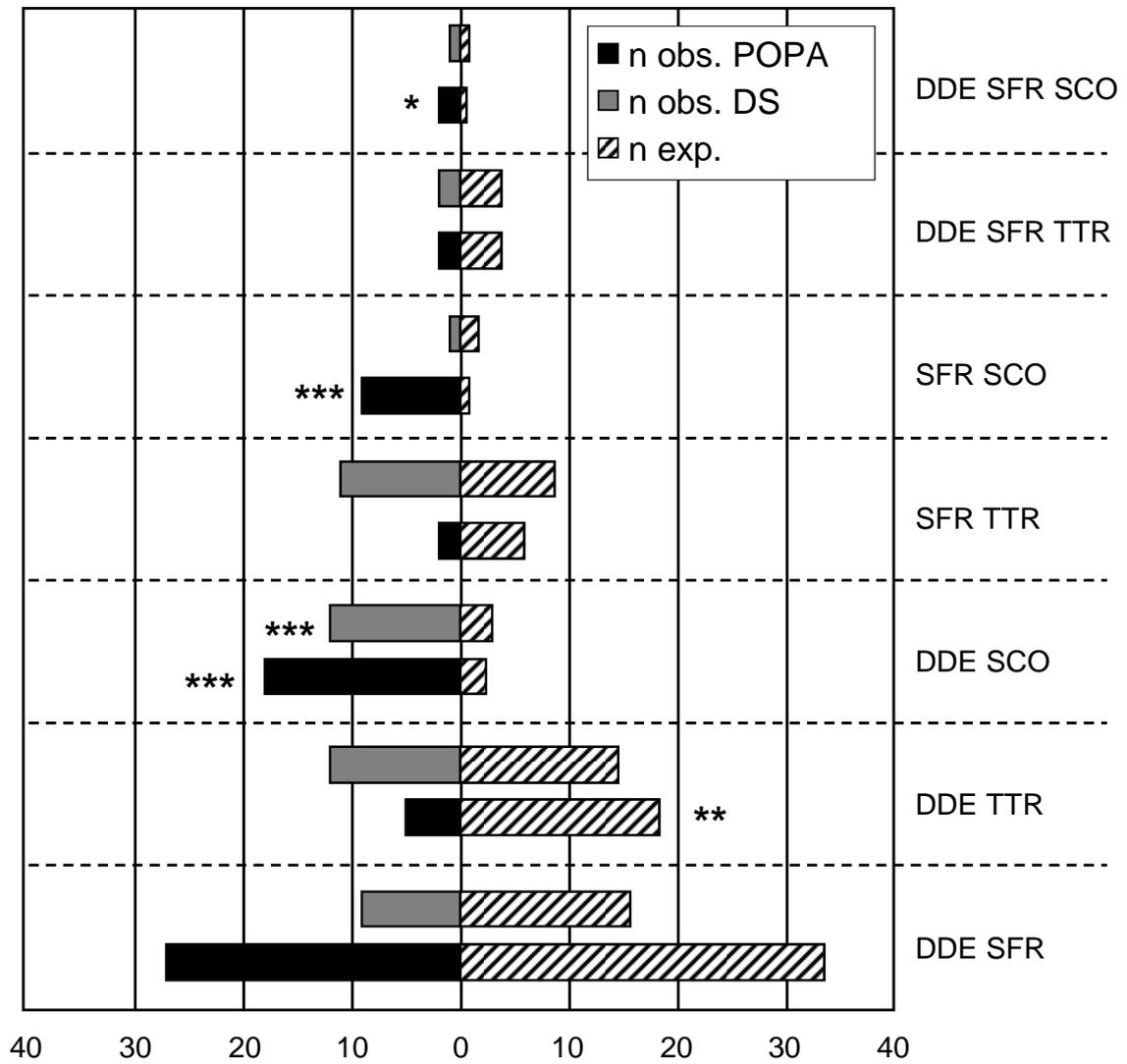


Figure 2. Relative frequency of sightings of single-species groups of common (DDE), spotted (SFR), bottlenose (TTR) and striped (SCO) dolphins, and mixed-species groups (mixed), by months, in the POPA (A) and dedicated surveys (B). Numbers above the bars indicate sample size.

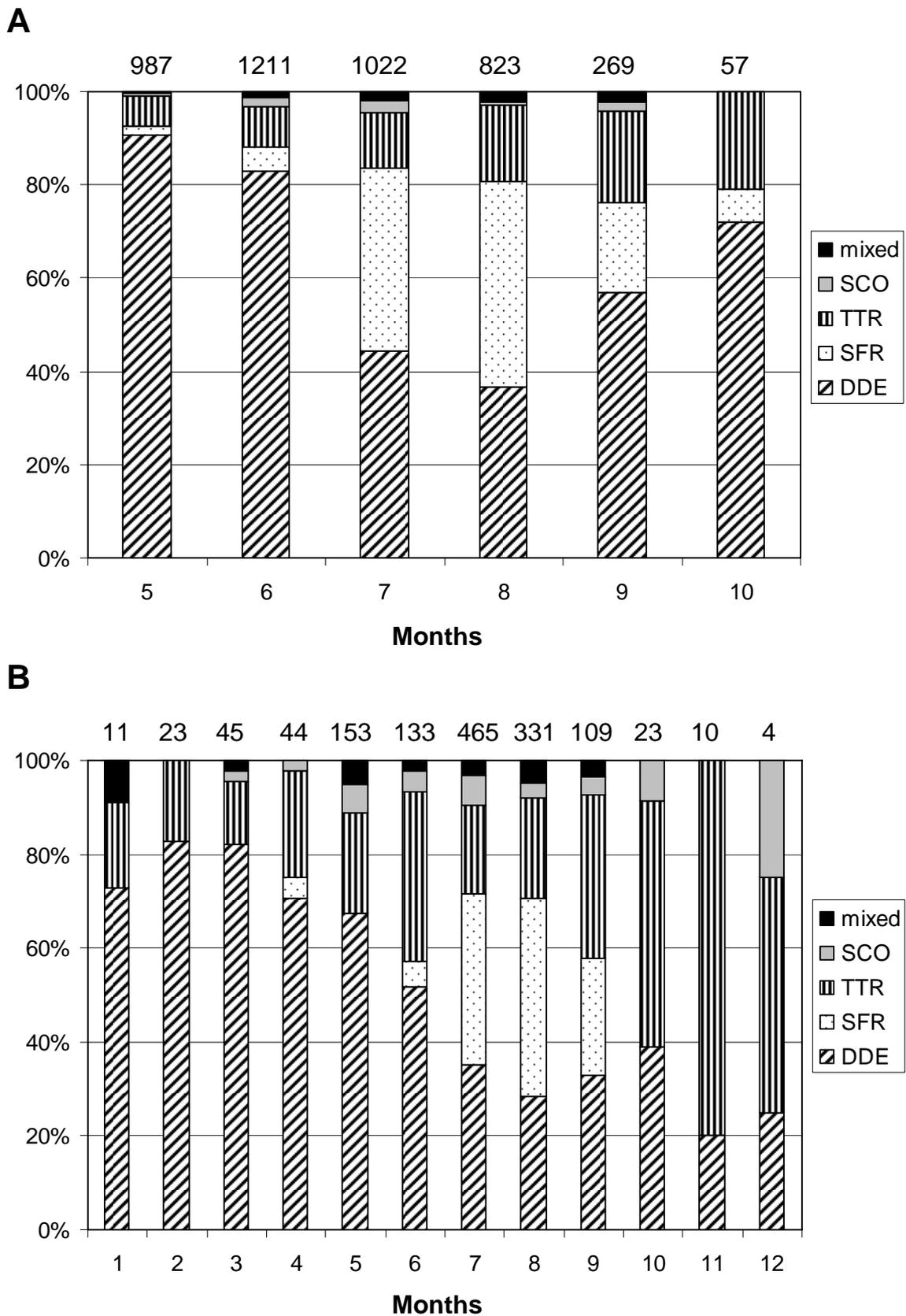
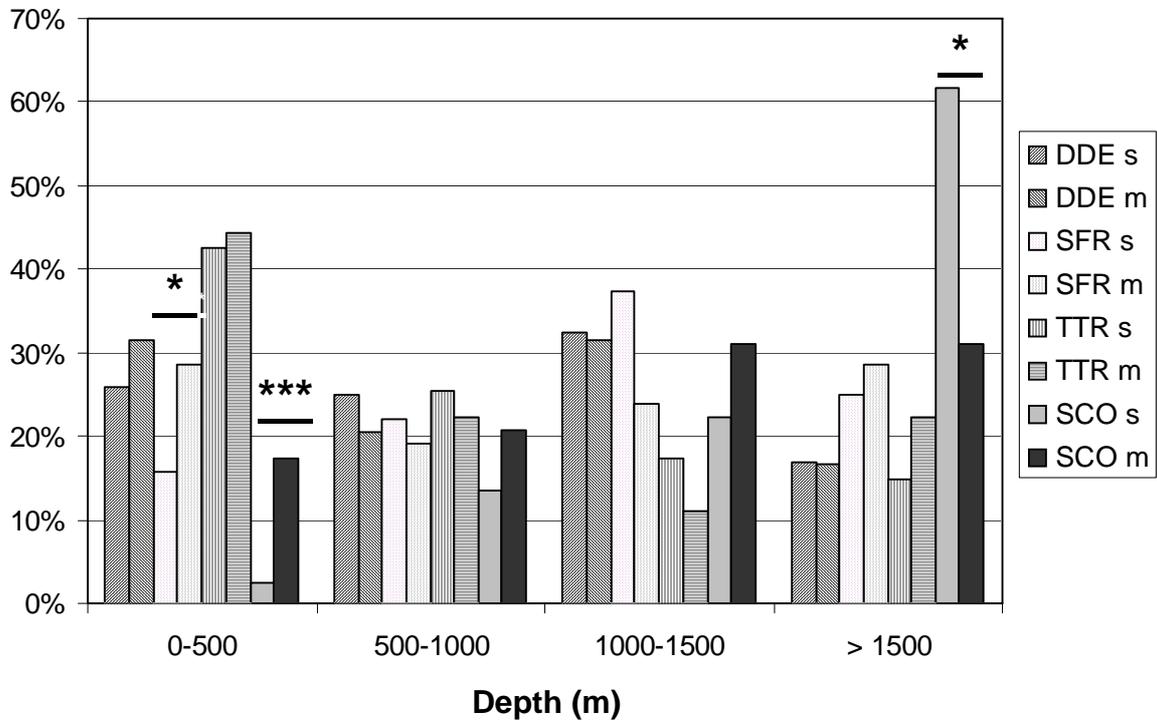


Figure 3. Distribution of sightings of common (DDE), spotted (SFR), bottlenose (TTR) and striped (SCO) dolphins, in single-species groups (s) and mixed-species groups (m) according to water depth (A) and distance to the coast (B), in the POPA data set, with indication of significant differences (χ^2 , *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$).

A



B

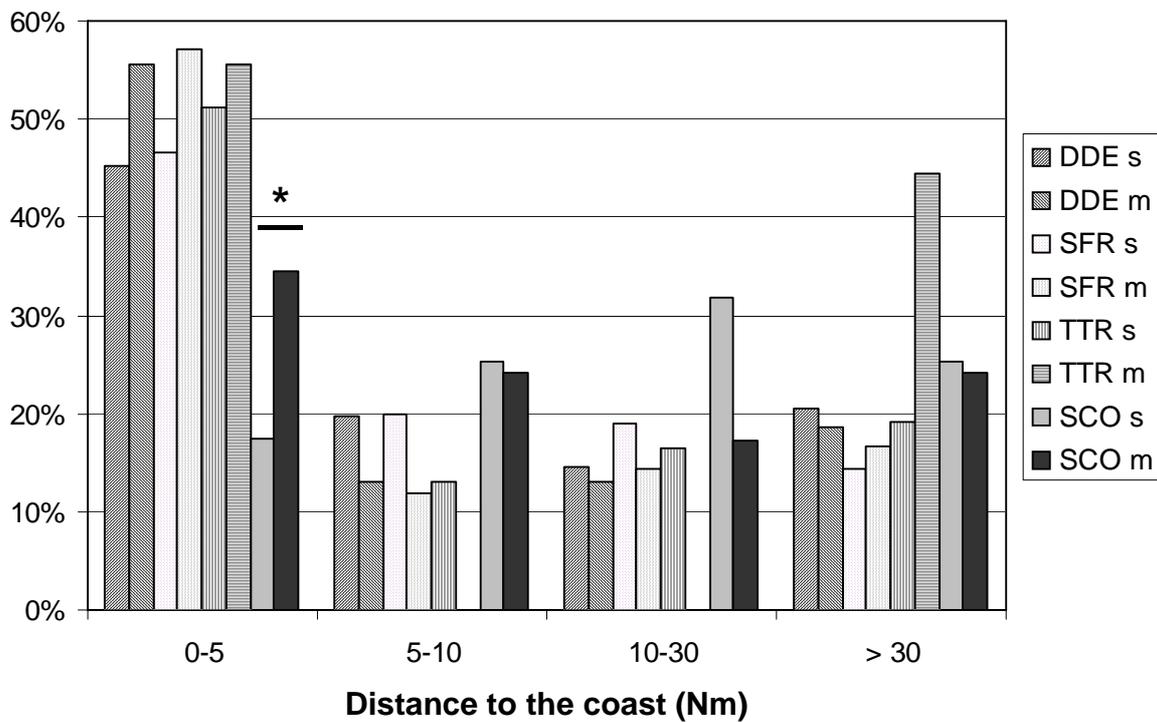


Figure 4. Mean size of single-species (left) and mixed-species (right) groups for common (DDE), spotted (SFR), bottlenose (TTR) and striped (SCO) dolphins, and all species together (All), in the dedicated surveys. The last bar corresponds to the total group size, all species included. Vertical lines indicate standard deviation. Asterisks highlight significant differences (t-test, *: $p=0.05$, **: $p<0.01$).

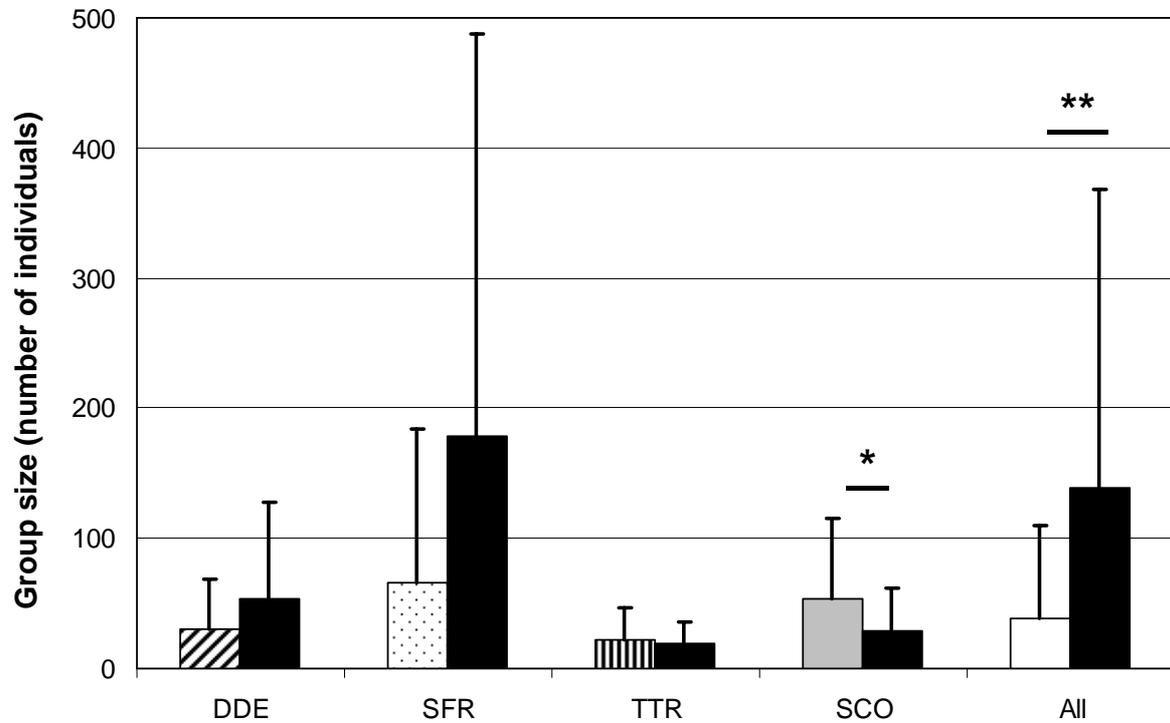


Figure 5. Relative frequency of sightings where common (DDE), spotted (SFR), bottlenose (TTR) and striped (SCO) dolphins were in lower, equivalent or higher numbers to the other species in the association in the dedicated surveys, with indication of significant differences between observed and expected numbers (χ^2 , *: $p < 0.05$).

