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### Moving in concert: Social and migratory behaviour of dolphins and whales in the North Atlantic Ocean

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## Chapter 4

# Social structure of Risso's dolphin (*Grampus griseus*) at the Azores: A stratified community based on highly associated social units

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## Chapter 4. Social structure of Risso's dolphin (*Grampus griseus*) at the Azores: a stratified community based on highly associated social units

Karin L Hartman, Fleur Visser & Arthur JE Hendriks

### Abstract

In this study, we present for the first time a model for the social structure of Risso's dolphin (*Grampus griseus*). Over the period 2004-2006, 1028 Risso's dolphins were identified at Pico Island, Azores. Individuals sighted on 10 or more occasions were included in analysis of social structure ( $n = 183$ ). High resighting rates indicate strong site-fidelity of at least part of the population. We found that individuals form stable, long-term bonds, organised in pairs or in clusters of 3 - 12 individuals. Social structure is stratified based on age- and sex-classes, with strong associations between adult males and between adult females. We suggest that clusters form the basic units of Risso's dolphin society. Thirteen pods consisting solely of adults, likely males, and 3 pods consisting of mother-calf pairs were identified. Males are organised in stable, long-term associations of varying size that occur throughout the complete range of behavioural states observed. For females, associations can be of similar strength, but the time scale may vary depending on the presence of nursing calves. As sub-adults, associations also occur (pair-formation), but are less stable than those observed for adults. We propose a new model for Risso's dolphin societies known as a stratified social organisation, which differs from fission-fusion and matrilineal society models.

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## Introduction

The social organisation and group stability of wild ranging cetaceans have been studied intensively in several odontocete species, including the sperm whale (*Physeter macrocephalus*, e.g. Letteval et al. 2002; Whitehead 2003), bottlenose dolphin (*Tursiops* spp., e.g., Wells 1991; Connor et al. 2001; Chilvers and Corkeron 2002; Gero et al. 2005), killer whale (*Orcinus orca*, e.g., Baird and Whitehead 2000), and pilot whale (*Globicephala* spp. e.g., Heimlich-Boran 1993; Ottensmeyer and Whitehead 2003). In all these species, individuals can be identified on the basis of morphological characteristics (e.g., distinctive markings on body and flukes, shape of the dorsal fin and the presence of scars).

In general, group stability shows a negative correlation with body size, becoming more fluid in smaller odontocetes (Bräger 1999). The larger ones in particular form highly stable, lifelong bonds. In the case of sperm whales, pilot whales and fish-eating killer whales, females (and in the latter, males) may never leave their natal pod, forming matrilineal societies (Bigg et al. 1990; Whitehead and Weilgart 1990; Amos et al. 1993). For the bottlenose dolphin, long-term research in several areas has shown a fission-fusion society. Here, individuals associate in subgroups that often change in size and composition. Additionally, associations are formed, ranging from long-term stable alliances of male pairs and trios to larger, less-associated networks of males (Shane et al. 1986; Connor et al. 1992, 2000).

For the Risso's dolphin (*Grampus griseus*), social structure has not yet been determined. Risso's dolphins are present worldwide in temperate and tropical waters (Ross 1984; Baumgartner 1997; Balance and Pitman 1998; Gannier 1998; Kruse et al. 1999). Some evidence of summer inshore movements and site-fidelity of individuals has been reported (Leatherwood et al. 1980; Evans 1987; Olavarria et al. 2001). Recent research, comparing genetic material from Risso's dolphins in UK waters and the Mediterranean Sea, has shown no evidence of exchange between these two populations, indicating little long-range dispersal between them (Gaspari et al. 2007). Reported group size ranges from 1 to several hundreds of individuals, with a mean of 10-30 animals (Leatherwood et al. 1980; Kruse et al. 1991; Kruse et al. 1999). The diet of Risso's dolphin is mainly composed of deep-water cephalopods (Clark and Pascoe 1985; Pauly et al. 1998), resulting in a distribution in deep, offshore waters (350 to >1000 m) or over the continental-shelf edge (Ross 1984; Baumgartner 1997; Davis et al.

1998). Some preliminary data were reported on the social organisation of the species. During a study along the southeast coast of Spain (1992-1995), in which 281 individuals were identified and 29% of identified individuals were resighted, preliminary results indicate fluid structures, along with some evidence of stable associations (A. Cañadas, personal communication (2007)).

The Azorean archipelago, where we conducted the present study, is characterized by steep submarine walls (Mortan et al. 1998); hence Risso's dolphins are found close to shore, creating a unique research opportunity. The protective status of Risso's dolphins is listed as data-deficient (IUCN 2006). Here, we studied group stability and association patterns of Risso's dolphins to develop a social organisation model for this species. We report the results of photo-identification studies carried out in the coastal waters of Pico Island, Azores over a 3-year period (2004-2006).

## Materials and Methods

### *Field observations*

During April – October of three consecutive years (2004-2006), shore- and boat-based surveys were conducted mainly off the south coast of Pico island (Fig. 1). More than 20 species of whales and dolphins are regularly recorded near Pico and other islands of the archipelago, including species with a seasonal presence, (e.g., blue whale (*Balaenoptera musculus*), fin whale (*Balaenoptera physalus*), sei whale (*Balaenoptera borealis*), minke whale (*Balaenoptera acutorostrata*), humpback whale (*Megaptera novaeangliae*), pilot whale, Atlantic spotted dolphin (*Stenella frontalis*), and several beaked whale species (family Ziphiidae) as well as species that are sighted throughout the year (sperm whale, Risso's dolphin, common dolphin (*Delphinus delphis*), striped dolphin (*Stenella coeruleoalba*) and bottlenose dolphin).

Daily land-based surveys were made from a lookout in Santa Cruz das Ribeiras at 30 m above sea level to detect Risso's dolphin presence in the study area. Land-based surveys were extended with regular observations from look outs placed along the island's coast, which together cover the total coastal waters off Pico (Fig. 1). Land-based surveys were made using 25 mm x 80 mm Observer binoculars (Steiner Binoculars, Bayreuth, Germany). During observations at sea, the research vessel was guided by the observers from land. The simultaneous



Therefore, complete coverage of Risso's dolphin groups in the study area was generally possible from photo-identification data. Variation between the two measures of group size was low (mean  $\pm 1.5$  individuals). Group composition was based on age classes of individuals, determined by patterns of body colouration and body size.

#### *Photo identification*

Risso's dolphins show a range of colouration patterns. Individuals can be recognized by the distinctive scarification patterns and the shape of their dorsal fin. The dark body colouration of subadults lightens with age and adult individuals may become almost white. This is possibly caused by a scarcity or loss of pigment. Scarification is mainly caused by the teeth of other Risso's dolphins, during inter-specific interactions, as well as by their cephalopod prey and predators (Macleod 1998). Therefore, photo-identification technique is a good tool for individual identification of Risso's dolphins that can be used in the study of patterns of association and social structure of this species (Würsig and Jefferson 1990).

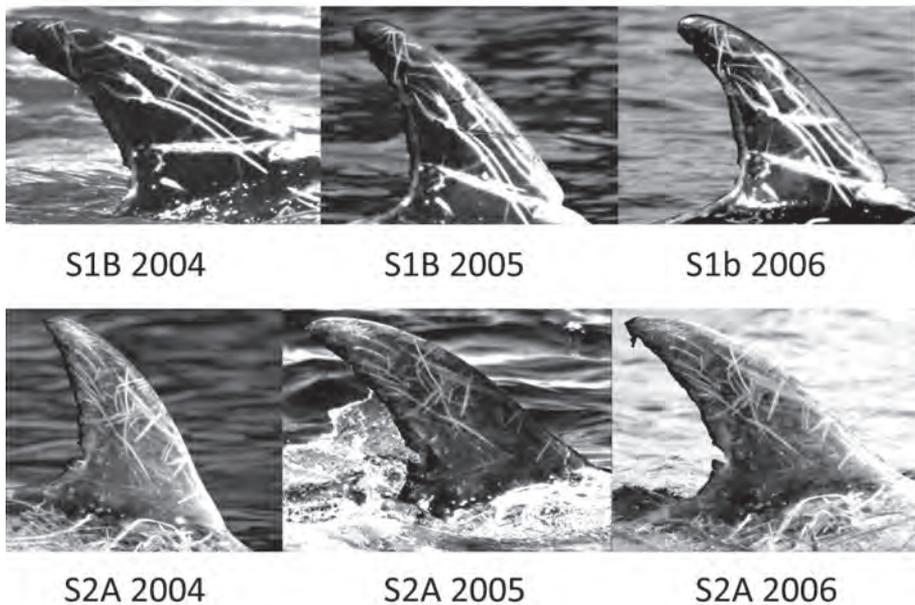


Figure 2. Long-term identification of Risso's dolphins (*Grampus griseus*): individuals S1b "Pointer" and S2a "Blunt", photographed over three consecutive years (2004-2006). The figure is a composite of cropped colour pictures converted to black-and-white images.

Dorsal fins (left and right) were photographed for individual identification (Fig. 2). On average, over 400 pictures were taken per sampled group. Only high-quality pictures ( $Q \geq 3$ ; Arnborn 1987) were used in analysis. Dorsal fins in the high-quality pictures were cropped and the contrast of the fins was enhanced using the autocolor function in Adobe Photoshop CS2 (version 9.0). For identification purposes, the degree of scarification was determined for all high-quality crops. Six categories of scarification were identified based on the ratio of black skin versus the white scars on the dorsal fin (Fig. 3). For example, the density of white scars is  $>75\%$  for the “very severe” category (Table 1). Group observations lasting  $<15$  min, as well as groups in which  $<100\%$  of the estimated individuals could be photographed, were excluded from data analysis. For the determination of association patterns and resightings of identified individuals, a group ID database was set up next to the ID catalogue, listing the composition of individuals of all groups by time and date of observation. Identified individuals were categorized in several age classes: adult (A; male or female), adult female (AF), subadult (SA), and calf (C). Adults were defined as individuals with moderate to very high scarification or white body colouration and mature body size. Adults with at least one identified calf during the study period were defined as females. Sexual size dimorphism in Risso’s dolphin is low; on average, males are slightly larger than females (sexual size dimorphism ratio of 1.04;  $\sim 12$  cm) (Perrin and Reilly 1984). Unambiguous determination of individual sex without a clear view of the genital area is therefore difficult. Older, mature males can often be distinguished from mature females because of their more muscular, robust body build and the relative presences of more scars. However, females can also become largely white making them difficult to distinguish from adolescent males. Subadults were defined as dark brown individuals with limited scarification, not accompanied by calves. Calves were defined as individuals maximally 75% of the size of adults and were accompanied by adults.

#### *Analysis of associations*

For the analysis of association coefficients we used the simple ratio, which is deemed the best for this type of analysis (Cairns and Schwäger 1987). Patterns of social structure were determined using cluster analysis (Appendix Fig. A1). To minimize possible autocorrelation of sightings, resightings of identified individuals needed to be separated by at least 1 day to be included in the

analysis. All dolphins photographed in the same group were recorded as being associated. An association index (AI)  $\geq 0.5$  was chosen as the threshold for stable associations (Bigg et al. 1990). Three types of association were recognized for individuals: clustered, paired, and not-associated. Clusters were defined as samples of  $>2$  individuals, all with intercluster AI  $\geq 0.5$ . Stable, long-term clusters were used to define pods (Bigg et al. 1990). Pairs were defined as a dyad of individuals with AI  $\geq 0.5$ , i.e., not associated in clusters. Not-associated individuals did not form any associations with AI  $\geq 0.5$ . Due to their tight bond, mother-calf pairs were not considered associated dyads, but were treated as a single "individual". Only individuals sighted on 10 or more observation days during the research period were included in the analysis. The relatively high number of 10 sightings was chosen to obtain a robust data set (individuals with low resightings may skew observations). This threshold still left sufficient individuals for the analysis of social structure. Also, it only included individuals identified from both the left and the right sides. To test whether the relatively high standard for sighting, excluding most individuals from the data set, affected the results, a second analysis was conducted that included all individuals sighted  $\geq 5$  times. Permutation tests, permuting groups within samples, were conducted to determine whether the observed patterns of association were different than would be expected from random using the method as described by Beider et al.

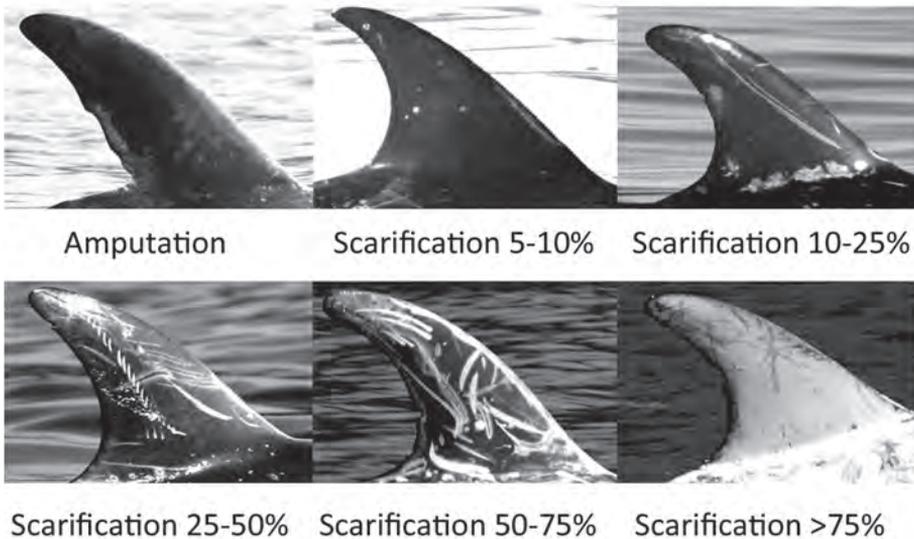


Figure 3. Categories of dorsal fin scarification for Risso's dolphins (*Grampus griseus*). The figure is a composite of cropped colour pictures converted to black-and-white images.

## Results

During 230 days of fieldwork, we encountered Risso's dolphins 595 times at sea. For each group, on average, 60 minutes were spent on focal follow observations. Group size of Risso's dolphins ranged from 1 to 61 individuals, with a median group size of 13 animals. Over 150 000 identification photographs were taken, resulting in 34 000 high quality ID photographs ( $Q \geq 3$ ). During 553 encounters (93%), 100% identification was achieved.

### *Individual identification and sightings*

We sighted a total of 7332 individuals, of which 752 individuals were identified from both sides, 152 individuals were identified from the right side and 124 individuals were identified from the left side, resulting in a minimum of 876 (both sides + left side) and 904 (both sides + right side) identifications and a maximum of 1028 (both sides + left side + right side) identifications.

Table 1. Percentage of individuals per category of dorsal fin scarification (over all left and all right sides) of the total identified population ( $n = 1028$ ) of Risso's dolphins (*Grampus griseus*) and the population used in the analyses ( $n = 183$ ).

Scarification category	Scarification (%)	All individuals (%)	Analysed individuals (%)
Very severe	>75	7	18
Severe	50-75	24	31
Moderate	25-50	30	24
Limited	10-25	23	18
Very limited	5-10	5	4
Amputation	Variable	11	5
Total (%)		100	100

Repeated matching of single left and single right sides and cross-matches between individuals in the catalogue by three researchers indicated only a small number of possible unmatched pairs of left and right identifications, missed matches (double counts) and mismatches (underestimation). Additionally, the fraction of the identified population with very limited scarification, was low: 5% for the total population and 4% for the analysed population (Table 1). Moreover, calves, with the least scarification, were identified unambiguously

as a result of their mothers' presence. Therefore, the chance for mismatches and missed matches were deemed low and analyses were conducted using the 1028 identified individuals. The number of sightings per individual ranged from 1 to 61 (median (SD) sightings of  $2 \pm 10.4$ ; median (SD) resightings of  $4 \pm 12.0$ ). Sixty-three percent of individuals were resighted, of which 50 individuals were sighted 30 times or more, indicating strong site fidelity by these individuals (Fig. 4). Almost half of the population (47.2%) was identified in 2004, followed by 28.3% in 2005, and 24.5% in 2006. During all three research years, between 47.2% and 51.8% of the identified population were sighted.

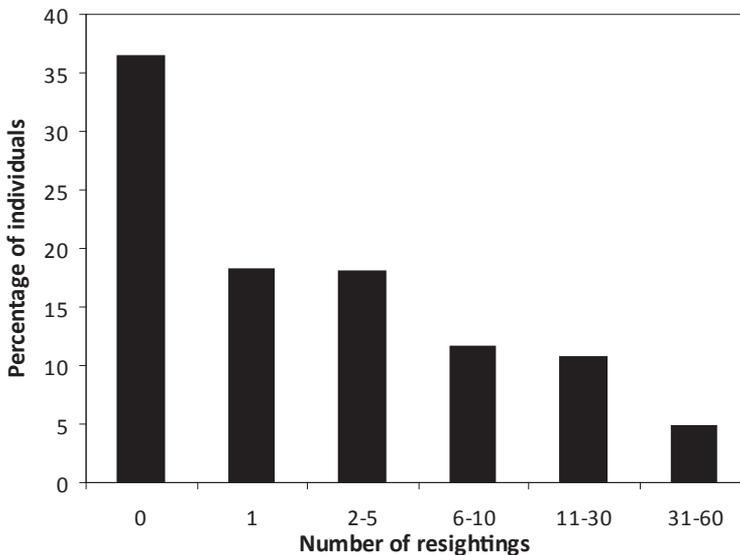


Figure 4. Frequency distribution of resightings of Risso's dolphins (*Grampus griseus*).

#### *Population size and structure*

Analyses of the rate at which new individuals enter the data set suggest a population size >1028 individuals (Fig. 5). Forty-three percent of the population were adult, of which 13% could be identified as adult females (Table 2). A large part of the population consisted of sub-adults. Calves comprised >15% of the population. We found it interesting that identifications over the years showed strong variation between the age classes. Adult females and their calves were resighted fewer times between years than other adults, while subadults had the highest chance of being resighted between years.

Table 2. Age class composition (number and percentage) of the identified population and the percentage of individual Risso's dolphins (*Grampus griseus*) that were sighted during all three research years.

Age class	Number of individuals	Percentage of total	Percentage of individuals sighted from 2004 to 2006
Adult (male or female)	305	30	26.2
Adult female (AF)	135	13	8.8
Calf (C)	158	15.5	6.4
Subadult (SA)	425	41.5	48.9
Total	1023	-	29.9

Note: For 5 individuals, the age class could not be determined from photo-identification photographs.

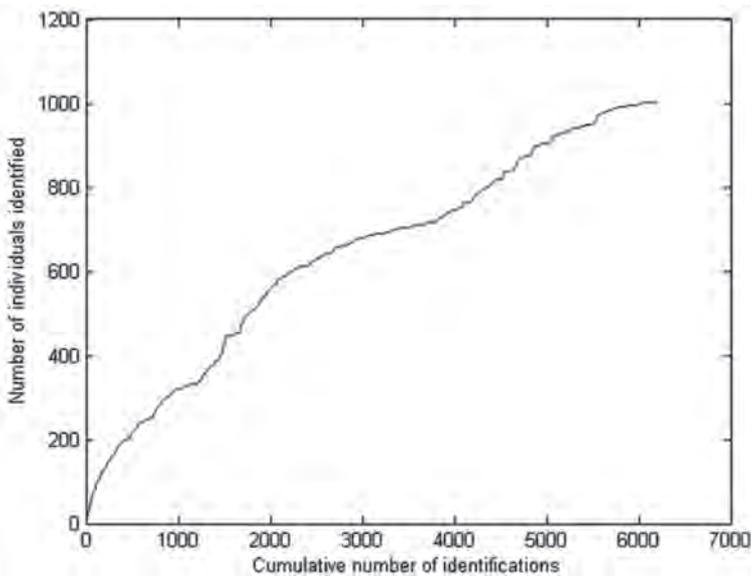


Figure 5. Number of identified individuals as a function of the cumulative number of identifications for all identified individual Risso's dolphins (*Grampus griseus*).

### Associations

In total 447 encounters of Risso's dolphin groups (6446 sightings of individuals) were used in further analysis of social structure (focal follow  $\geq 15$  min; 100% identification). A total of 183 individuals (4290 sightings; 18% of individuals) were sighted on  $\geq 10$  sampling days. In total, 22% of all possible associations were observed, with a mean AI of 0.04 (SD = 0.02). Permutation tests showed that the observed associations differ significantly from random ( $p < 0.00001$ ). Cluster analysis revealed several clear patterns of association. Table 3 shows the characteristics of association for the different age classes, which is summarized

by the dendrogram in Fig. 6. It appears that 50% of the individuals form strong associations that were organised either in pairs or clusters. A large portion of our sample (38%) was organised in long-term, stable clusters or pods. Pair-formation (outside clusters) was less prominent and constituted 12% of the individual associations. What became apparent is that patterns of association varied widely between age classes as well as possibly between sex classes. Adults that have never been observed with calves are predominantly organised in clusters. In contrast, adult females and their calves are either organised in pairs (37%) or form singleton units (58%). Calf association was analysed by the mother-calf pair unit. No lone calves were present in the population. Not-associated calves were mother-calf pairs without stable associations. The  $\geq 10$ -sighting criterion "splits" several mother-calf pairs by excluding only the calf from the analysis, which left 14 calves compared with 19 adult females. This breaking up of mother-calf pairs was fixed by using the  $\geq 5$ -sighting criterion (see below). For subadults, identified by a low degree of scarification and dark body colouration, yet another pattern emerges: most subadults (83%) lack strong associations.

Using the  $\geq 5$ -sighting criterion rather than the  $\geq 10$ -sighting criterion did not substantially alter the results for the adults (males or females) and subadults (Table 3). However, the pattern did change for the adult females and their calves, which showed an increase in the degree of cluster formation for adult females (5% - 30%). This cluster formation apparently was based on pairs, because the relative percentage of pairs decreased (37% - 10%), while the percentage of not-associated females remained similar (58% - 60%) when using the  $\geq 5$ -sighting criterion. The highest number of mother-calf pairs was sighted between 5 and 15 times, a significant number of which was removed from the data set when the  $\geq 10$ -sighting criterion was used. By removing part of the cluster associates (sighted  $< 10$  times), clusters are broken up into pairs of individuals (sighted  $\geq 10$  times). Therefore, association patterns of adult females and their calves were further analysed based on the  $\geq 5$ -sighting criterion.

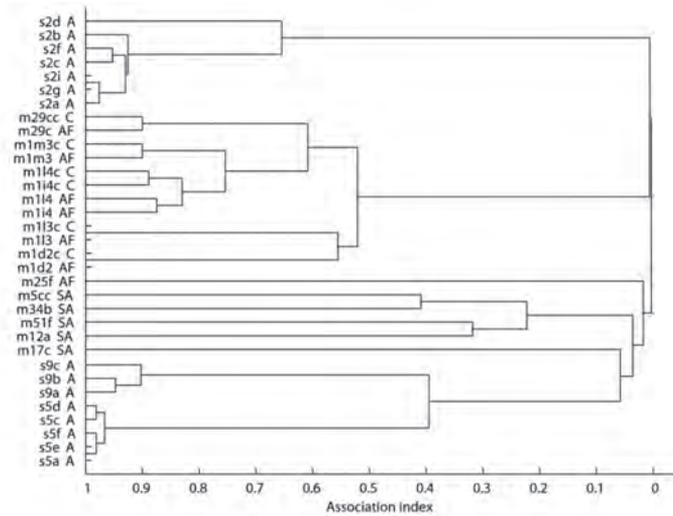


Figure 6. Detail from the dendrogram from cluster analysis (sightings  $\geq 10$  and sightings  $\geq 5$  for adult female and calf), showing four clusters (S2, S5, S9 and M1-3) and 6 not-associated individual Risso's dolphins (*Grampus griseus*). Individuals are denoted by their specific individual code and their age class. A = adult (male or female), AF = adult female, C = calf and SA = subadult.

Table 3. Social organisation of individuals per age class of Risso's dolphins.

Age class	Individuals sighted $\geq 10$ times				Individuals sighted $\geq 5$ times			
	No. of individuals	Pairs (%)	Clusters (%)	Not associated (%)	No. of individuals	Pairs (%)	Clusters (%)	Not associated (%)
Adult (male or female)	97	6	67	27	131	8	54	38
Adult female (AF)	19	37	5	58	43	10	30	60
Calf (C)	14	29	0	71	40	5	35	60
Subadult (SA)	53	11	6	83	114	16	4	80
Total	183	12	38	50	328	11	31	58

### Clusters

We identified a total of 16 clusters that were composed of stable associations (AI  $\geq 0.5$ ) of  $>2$  individuals (Table 4). Cluster size ranged from 3 to 12 individuals, with a mean of 6. Individuals found in clusters were among the animals with the highest sighting rates. This is especially true for clusters 1-6, which showed a high degree of site-fidelity in the area. Two types of clusters emerged, both of uniform composition: clusters composed of adults (1 - 13) and clusters composed of adult females with their calves (14 - 16). A small number of adult clusters contained subadults and one contained a single adult female.

Table 4. Characteristics of all clusters, using the criteria of sightings  $\geq 10$  times (nos. 1-13) and sightings  $\geq 5$  times (nos. 1-16), showing the mean number of sightings, number of years sighted, cluster size, and age class composition, as well as the mean association index (AI) and the range of maximum AIs between all cluster members of Risso's dolphins (*Grampus griseus*). A = adult (male or female), AF = adult female, C = calf and SA = subadult.

No.	Name	Mean no. of sightings	No. of years sighted	Size	Composition*	Mean (SD) AI	Maximum AI range
1	S9	58.3	3	3	A	0.92 (0.01)	0.91–0.95
2	S5	57.6	3	5	A	0.97 (0.01)	0.98–1.00
3	S6	51.8	3	6	A + SA (2)	0.63 (0.02)	0.71–0.80
4	S8a	47.4	3	5	A	0.69 (0.07)	0.64–0.79
5	S8b	41.8	3	4	A	0.53 (0.03)	0.53–0.60
6	S2	39.6	3	7	A	0.94 (0.01)	(0.67) 0.95–1.00
7	S29	19.3	3	3	A	0.83 (0.03)	0.80–0.90
8	S1	18.4	3	7	A	0.73 (0.04)	0.81–0.91
9	S33	16	2	5	A + SA (1)	0.77 (0.07)	0.71–0.94
10	S21+	14.4	2	5	A + AF (1)	0.65 (0.09)	0.61–1.00
11	S16	13.4	3	5	A	0.93 (0.03)	0.92–1.00
12	S31	12.3	2	3	A	0.95 (0.02)	0.92–1.00
13	S4 and S19	12.1	3	11	A	0.66 (0.08)	0.69–1.00
14	MI-1	9.5	2	6	AF + C	0.68 (0.06)	0.64–0.82
15	MI-2	9.2	1	10	AF + C	0.73 (0.06)	0.73–0.82
16	MI-3	8.2	1/2	12	AF + C	0.59 (0.07)	0.63–0.88

\*A, adult (male or female); AF, adult female; C, calf; SA, subadult.

This suggests that associations within age and sex classes are favoured over those between classes. The mean AI between cluster members ranged from 0.53 to 0.97. Clusters are further broken down into pairs and triplets. A large portion of the clusters had extremely high within-cluster associations, differing between pairs and reaching maximum AI of 1.0. Pods S9, S5, S2, S16 and S31, which were all composed entirely of adults, had high mean association indices ( $>0.9$ ). Pods S1, S2, and S4 have been observed as of 2000 and pods S5 and S9 were observed as of 2002. During these two periods, none of these adults, or any of the other adults that formed stable clusters, were ever observed with a calf. Therefore, we assumed that these individuals are all males. Five adults, from pods S4, S5, S8 and S19 were sexed as males, as we had a clear view of their genital area, were all males. In addition, behavioural observations of active participation in mating behaviour corroborate these findings, as well as the white, heavily scarred colouration patterns and robust body build of these individuals. Cluster association was not limited to certain behavioural contexts: pod members are observed resting, travelling and socialising together as a group. The clusters formed basic units that were part of larger groups for short periods of time ( $< 1$  day); we left these groups in their original compositional state. One individual of the S2 pod (S2d "Skinny") was not sighted during the

entire season of 2006, although this individual was observed since 2000 within the S2 pod. Therefore, he was assumed to have died, which resulted in a low mean AI (0.67) with his pod's members during the 2004-2006 period.

## Discussion

The present study has yielded the largest identified population of Risso's dolphin known to date, with 1028 individuals recorded during the 3-year period. In addition, a high number of encounters and high resighting rates of individuals allowed us to make strong inferences on the social organisation of this population.

### *Site-fidelity*

The highest number of the individuals (63%) was resighted during the study period, with a third of the identified dolphins being sighted each year. The high number of resightings, ranging up to 60, indicated strong site-fidelity by individuals to our study area, which is a relatively small research area that probably covers only part of their range. If the research area was increased and stable or increased resighting rate of individuals within and between years were found, then one could conclude that a resident population of Risso's dolphins was present in the Azorean waters.

The Risso's dolphins identified in this study likely formed a single social network. Although interanimal differences existed in the number of (stable) associates and possibly in the range patterns of individuals, the population showed a dense network of associations (22% of all possible relations were observed) that lacked outliers. It is possible for two distinct cetacean populations to use the same area; for example, separate populations of killer whales have been characterized by differences in behaviour, habitat-use, morphology, diet and (or) social organisation (Bigg et al. 1990; Baird and Whitehead 2002). We found no evidence of these types of differentiation in our population of Risso's dolphins population, but instead, found individual differences that were largely based on age and sex classes. Such differences in sperm whales in Azorean waters could indicate that females and their calves have different residential patterns compared with males (Lyrholm et al. 1999; Matthews et al. 2001). However, since both male and female Risso's dolphins, as well as individuals of all age classes, were recorded year-round, it is unlikely that this separation also exists at the population level.

*Social Structure: stratified social units*

Adult Risso's dolphins are predominantly organised in pairs. However, apparently one strong association was not enough, as a high number of pairs was further associated into stable clusters composed of 3-12 individuals. Remarkably, these clusters have a highly uniform structure, which is composed of either adults (never observed with calf) or mother-calf pairs. At cluster-level, association patterns among males and among females, as well as associations between the sexes, appear to diverge.

Our study showed stratification based on age and sex classes in a Risso's dolphin population. A degree of food-source partitioning, seen between males and females and between age classes of Risso's dolphins off the east coast of South Africa (Cockroft et al. 1993), also pointed towards the possibility of social stratification based on these characteristics. In addition, Amano and Miyazaki (2004) reported the absence of mature males in one school of 79 Risso's dolphins caught in Japanese waters. They suggested that mature females of similar reproductive condition associate together, whereas young animals leave their natal group around puberty.

Similar patterns in group stability of cetacean species of similar size were found (Bräger 1999). Our findings showed basic characteristics of the fission-fusion model, as noted in similar-sized odontocetes; i.e., part of the identified population had no stable associations ( $AI \geq 0.5$ ) and females showed various patterns of association that were possibly based on their reproductive stage. In addition, both male and female subadults left their natal pods. Also, it can be profitable to form male alliances in fission-fusion societies as seen in bottlenose dolphin populations.

However, in contrast with fission-fusion societies, the majority of adult Risso's dolphins were organised in pods, which are basic and easily discernible units of the population. Additionally, the social organisation of Risso's dolphins was strongly stratified based on age and sex classes. The loose formations observed were mainly seen in subadults. These features do not comply with a fluid society, but bear more resemblance to the lifelong, stable groups seen in matrilineal societies as reported for several other deep-diving cetaceans (pilot whale, sperm whale) and killer whales. In contrast, however, the pods of Risso's dolphins pods were first formed during subadulthood and were uniformly composed of either adult males or mother-calf pairs; i.e., they were not composed of matrilineal.

Risso's dolphin, sized between the fission-fusion bottlenose dolphins and the matrilineal pilot whales, also showed characteristics of social structure that placed them in between these two species. Here, we believe diet to play a key role in the evolution of Risso's dolphin society. The fission-fusion society, generally displayed by small fish-eating cetaceans appears to form the basis of the organisation of Risso's dolphins. We hypothesize that their diet of deep-sea cephalopods (instead of fish) has driven the evolution of stable patterns, rather than to more fluid structures. All teuthophagous cetaceans of which social structure has been revealed form stable pods. For deep-diving cetaceans, this stability apparently imposes substantial benefits in social support (calf care) and possibly foraging benefits. Thus, we suggest a new model for the social organisation of Risso's dolphin that is based on a stratified community of highly associated social units grouped by age and sex classes.

#### *Stratification based on age and sex classes*

The benefits of living in groups have been addressed by a number of authors (for an overview see Connor 2000). Social benefits of group living include predator defense, foraging benefits and social support. Risso's dolphins around the Azores face predation from sharks and killer whales. Several observations were made of wounded animals, especially calves. Cooperation during foraging dives in deep-diving cetaceans has been suggested (*e.g.*, sperm whale, Whitehead 2003), whereby individuals benefit from each other by searching a larger area for food than would be possible alone. Dietary studies from other areas have shown that Risso's dolphin feeds primarily on solitary, evenly and widely distributed species of cephalopods (*e.g.*, Cockroft et al. 1993). As dive duration is limited and their prey-species dwell in deep waters, collective searching of an area might prove beneficial over solitary hunting. During foraging dives, teuthophagous cetaceans have to leave their calves at the surface for at least several minutes. The females partly overcome this problem by reciprocal social support, which involves alloparental care (*e.g.*, sperm whale, Whitehead 1996).

#### *Adult Females and Calves*

As for all other cetaceans, the mother-calf bond is very strong and forms the base of female social organisation (Whitehead and Mann 2000). Adult females showed several patterns of associations; they can either be organised in pairs or clusters or are not associated (according to the  $AI \geq 0.5$  criterion). The

stable associations in pairs and clusters are formed with other females and are composed of aggregations of mother-calf pairs. However, we were unable to recognize with certainty adult females with no calves, so our inferences for adult females should be treated with caution.

Resightings between years varied between the age classes and were lowest for adult females and their calves. This could indicate age- and sex-differentiated ranges of dispersal. If so, and counter-intuitively, inferred ranges of females with calves would be larger than that of other individuals. A possible explanation could be that female Risso's dolphins with calves have to be more selective and dynamic in their choice of feeding grounds. To minimize dive duration (during which the calf is most vulnerable), feeding locations with shallow depths may be preferred over deeper depths. Also, the grouping of females with calves has the drawback of being more noticeable to predators. Perhaps, this problem is overcome by the females moving between patches of good feeding grounds. As they have to be relatively more selective than other individuals and cannot stay put at one good location, the relative range of dispersal range of females with calves will be higher than that of individuals who do not have care for young.

### *Adult Males*

Based on the long-term absence of calves, corroborated by behavioural (and genital area) observations, severity of scarification patterns, and body-build of its members, we suggest that adult pods are uniformly composed of males. This would be the first time that large, stable units consisting only of adult males have been documented in odontocetes. Stable, long-term male associations were first reported for bottlenose dolphins. However, these consisted of a maximum of three males. Larger alliances occur, but are less stable and seem to function predominantly to access females (Connor et al. 1992, 2001). In contrast, the male pods observed in our study form a basic unit of Risso's dolphin society, with males cooperating throughout the entire range of behavioural contexts (Gero et al. 2005). Also, more often than not, pods are encountered as a distinct group and not as part of a larger congregation of individuals. Based on body colouration, stability of male clusters seems to increase as individuals age; i.e., strongest bonds occur between animals of whitest colouration. The strength of stability varies between clusters. Male formations seem stronger than female formations, as females may adapt their patterns of association towards depending calves.

Our results indicate a strong selection towards alliance formation and cooperation in male Risso's dolphins. As for bottlenose dolphins, stable associations may lead to reproductive benefits through cooperation. Inferences on Risso's dolphin mating strategy derived from relative testis size suggests a multiple male breeding system for this species (Perrin and Reilly 1984), which would be consistent with the high competition between males. The individual S5a "Chicco" was clearly observed mating with a known female in the presence of all four of his S5-cluster members. Additionally, teuthophagous cetaceans likely gain feeding benefits from cooperative foraging. Primarily, in order to form large, stable groups, feeding conditions have to be sufficient to sustain these groups. This is especially true for groups with a high site fidelity, as we found in our study. In contrast with male sperm whales, who migrate to high latitude feeding grounds and lead a largely solitary life (Lyrholm et al. 1999), group living might be a strategy adopted by male Risso's dolphins to increase foraging success.

#### *Subadults*

Apparently, ageing calves, i.e., becoming subadults, do not maintain the association patterns of their mothers. Instead, subadults leave their natal pods and show a lower degree of stable associations (pair-formation) with other subadults. Higher levels of association do occur, but are less stable than those observed in adults (e.g., at  $AI \geq 0.3$ ). The associations between subadults again points at stratification between age and sex classes. Future patterns of association remain uncertain, as it appears that young adults form new pods. Alternatively, individuals (or possibly pairs) could join existing pods. However, the present study did not support the latter hypothesis, as pod composition was highly stable.

#### *Regulation of pod size*

The pod size of Risso's dolphins ranged from 3 to 12 individuals. In the light of optimizing foraging and reproductive benefits, this range appears to be rather wide. The presence of foraging benefits by cooperative hunting in teuthophagous cetaceans is still uncertain. However, the group tendency of teuthophagous cetaceans is to hunt simultaneously in the same area. Sperm whales are even known to dive "lined-up" (Whitehead 2003). As such, foraging benefits are likely influence group size. Characteristics of reproductive benefits are expected to vary between males and females. For male bottlenose dolphins,

the optimal stable group size is three (Connor et al 1992, 2001). Apparently, for three males, the balance of access to females which have to be shared with alliances, is optimized. The same could be true for Risso's dolphins. In this case, reproductive benefits would drive down male pod size (group size of three is the smallest pod found). For females, reproductive benefits are primarily related to calf survival (Whitehead and Mann 2000). Here, the benefits of social support will effect an increase in group size. Hence, female pod size will be positively influenced by both forces, while male pod size will be a trade-off between foraging and reproductive benefits (Fig. 7). The data indeed show that most large pods are composed of females and their calves. Male pods are highly variable in size. We propose a third force that effects the group size of Risso's dolphin, that of "habitat defence". As male Risso's dolphins do not seem to disperse from the population, males will constantly share the same area. As such, it may prove beneficial to be organised in larger groups, in order to outcompete other male alliances for access to females and possibly foraging grounds. Temporary and unstable large alliances of male bottlenose dolphins have been found, in relation to competition for females (Connor et al. 1992, 2001). Active intermale and interpod competition was regularly observed during this study. Also, pods of Risso's dolphins, generally males, were observed several times harassing pilot whales, sperm whales and (on one occasion) false killer whales (*Pseudorca crassidens*).

In conclusion, we found that Risso's dolphins off Pico island have a complex social structure where individuals may belong to stable, long-term units, to a strongly associated pair, or have no long-term associations. Association patterns varied between age classes, being most stable in adult males and most fluid in subadults. The society was structurally based on preferred associations between individuals of the same age and sex class. Highly stable pods of 3 to 12 individuals were formed both by adult males and by adult females, forming basic units of Risso's dolphin society. Large, stable groups of males have not been reported for cetacean species until now. Their teuthophagous diet was probably a primary force in the evolution of these pods. However, stability was not found for all life stages (young adults, females without calves), and therefore cannot be the only, or dominant driving force. For females, additional driving forces behind pod formation most likely included social support for calf care, while for male Risso's dolphins, the largest benefits are likely gained by access to females. It seems that males did not disperse from their natal grounds,

suggesting that some strategy to avoid inbreeding should be present in the mating strategy of Risso's dolphins. As such, Risso's dolphin society differs from all models of cetacean society described to date, thus providing new insights in the structuring of social organisation of mammals in the marine environment.

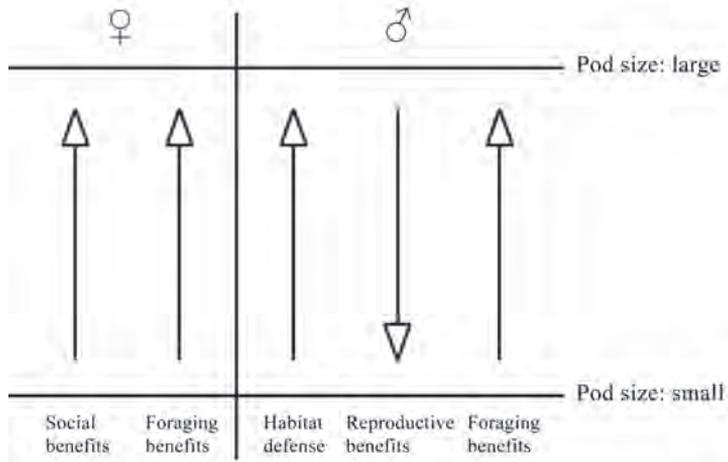


Figure 7. Proposed driving forces for optimum male and female pod size in Risso's dolphins (*Grampus griseus*). Strength of the driving forces is not static and will depend on male and female life stages, as well as external factors such as food supply and the presence of competitors and predators.

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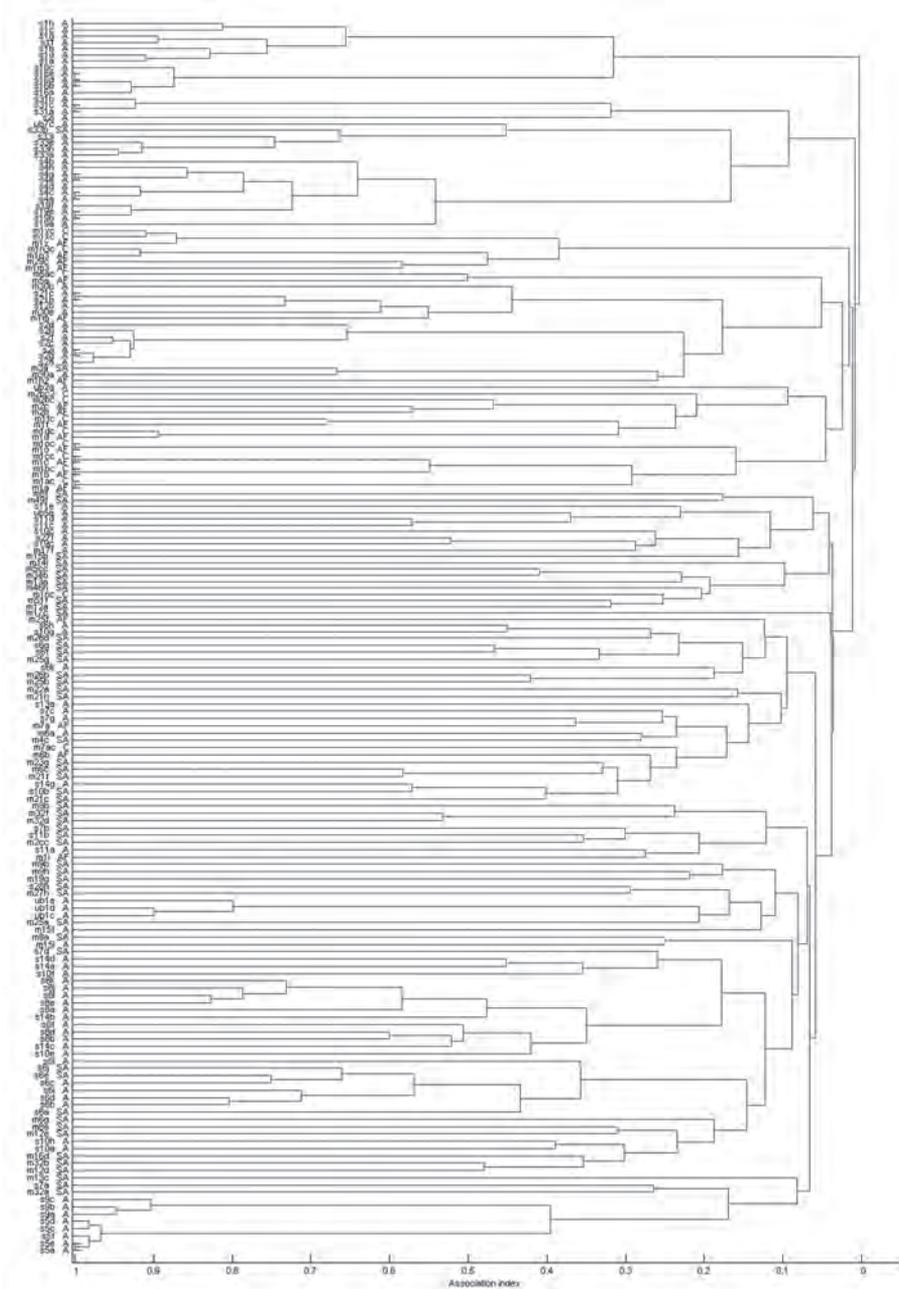


Figure A1. Dendrogram from the cluster analysis showing all individuals Risso's dolphins (*Grampus griseus*) sighted  $\geq 10$  times. Individuals are denoted by their specific individual code and their age-class. A = adult (male or female), AF = adult female, C = calf and SA = subadult.