



Grouping and fission–fusion dynamics in Australian snubfin and Indo-Pacific humpback dolphins

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Dolphins live in complex social systems with a wide variety of grouping and association patterns. Understanding the spatiotemporal variation of these associations (fission–fusion dynamics) is necessary to investigate the underlying factors and mechanisms shaping mammalian social systems in aquatic environments. We used boat-based surveys, photoidentification, focal observations, association analyses and social network techniques to quantify variation in the grouping patterns and fission–fusion dynamics of small, sympatric populations of Australian snubfin dolphins, *Orcaella heinsohni*, and Indo-Pacific humpback dolphins, *Sousa chinensis*, off the northeast coast of Queensland. Schools of snubfin dolphins were larger and more stable, irrespective of behavioural activity, than those of humpback dolphins. While associations of both species showed nonrandom patterns and structure, the social network of snubfin dolphins was characterized by numerous strong associations, whereas the strength of the humpback dolphin's social network did not differ from random. Modelling of temporal patterns of association indicated long-lasting associations were an important feature of snubfin dolphins' fission–fusion dynamics. In contrast, associations among humpback dolphins over time were best described by short-term relationships. The contrasting grouping and fission–fusion dynamics of snubfin and humpback dolphins appear to be a response to different feeding habits and prey availability. Future studies involving molecular techniques and direct quantification of food availability and predation risk will help elucidate the suite of interacting ecological, social and evolutionary factors shaping their social structures.

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Association patterns among individual animals living in groups vary in space and time (i.e. fission–fusion dynamics, Aureli et al. 2008). This spatiotemporal variation in association patterns has led to a wide variety of animal social structures ranging from highly cohesive with stable associations, to highly fluid with loose relationships (Wrangham & Rubenstein 1986; Connor et al. 1998). Fission–fusion dynamics characterize the social structure of a diversity of vertebrates including fish (Croft et al. 2004), reptiles (While et al. 2009; Leu et al. 2010) and various mammalian species

(e.g. van Schaik 1999; Wittemyer et al. 2005; Sundaresan et al. 2007; Wolf et al. 2007; Smith et al. 2008). Interactions among individuals in these group-living taxa not only affects their social structure, but also influences key population processes, including fitness (Silk 2007), genetic structure (Archie et al. 2008) and the way information and diseases are transmitted (Altizer et al. 2003). Thus, understanding the grouping and fission–fusion dynamics of group-living animals is a key element of their ecology, conservation and management.

Theories on the evolution of group size and social structure in mammals emphasize the influence of ecological factors, particularly resource availability and predation risks, in shaping social systems (Alexander 1974; Rubenstein & Wrangham 1986; van Schaik 1989; Janson 2000; Snaith & Chapman 2007). While several socioecological models have been developed, they all proceed from similar principles, by which it is predicted that animals form groups when the benefits of group living exceed the costs. By forming large groups, animals may benefit from enhanced

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predator detection and avoidance through increased vigilance, dilution and group defence (Pulliam 1973; Alexander 1974; Elgar 1989; Roberts 1996; Lingle 2001). On the other hand, as group size increases, within-group food competition may also increase, especially when food resources are limited and individuals or groups cannot exclude others from them (Chapman et al. 1995; Janson & Goldsmith 1995). As a result, individuals living in groups might adopt distinct grouping and fission–fusion strategies dependent on the trade-offs between the risk of predation and within-group food competition. These theories are supported by a number of studies in terrestrial mammals, which reveal intra- and interspecific differences in sociality with distribution and abundance of food and predators (e.g. Janson & Goldsmith 1995; Kappeler 1997; Brashares & Arceese 2002; Campbell et al. 2006; Ebensperger & Blumstein 2006; Sundaesan et al. 2007). Although the determinants of fission–fusion dynamics and sociality have been extensively investigated in terrestrial mammals, the picture is far from clear for most marine mammals (e.g. Baird & Dill 1996; Heithaus & Dill 2002).

Among cetaceans, the 38 extant species of dolphins (Family: Delphinidae) represent the most widespread and diverse family (Rice 1998). This species-rich family is characterized by marked interspecific variation in ecology and social organization comparable to some of the most well-studied terrestrial mammals (Connor et al. 1998). Theories of social organization in delphinids highlight variation in resource availability and predation risk as important factors underlying intra- and interspecific differences in social structure across populations (Connor et al. 1998; Gowans et al. 2007). For example, the high degree of fission–fusion observed in bottlenose dolphins reflects an adaptation to patchy and irregular distribution of prey resources, with animals spreading out in smaller groups to reduce intraspecific competition for food when resources are limited and aggregating in larger groups when food is abundant and predation risks are high (Connor et al. 2000; Heithaus & Dill 2002). Given dolphins' social plasticity and the diversity of habitats in which they are found, comparative studies of their social structure can provide insights into the adaptive nature and evolution of mammalian social systems in aquatic environments. However, a lack of standardized methodology and differences between study locations in habitat, resource availability and predation risks have made comparisons between species and studies problematic (Baird & Whitehead 2000; Gyax 2002a, b).

Australian snubfin (hereafter 'snubfin dolphins'), *Orcaella heinsohni*, and Indo-Pacific humpback dolphins (hereafter 'humpback dolphins'), *Sousa chinensis*, are medium-sized delphinids (up to 2.6–2.8 m in length) found in shallow, coastal-estuarine waters (Parra et al. 2004; Beasley et al. 2005). The snubfin dolphin was recently described as a new species and it is the only cetacean known to be endemic to Australian/Papua New Guinean waters (Beasley et al. 2005). Humpback dolphins range from the northern coast of Australia to the eastern shores of South Africa (Jefferson & Karczmarski 2001). In Australia, snubfin and humpback dolphins occur in broad sympatry throughout most of the tropical and subtropical coastal waters of Queensland, Northern Territory and Western Australia (Parra et al. 2002, 2004).

In Cleveland Bay (19°13'S, 146°55'E), northeast Queensland, snubfin and humpback dolphins co-occur in direct sympatry and are usually found year-round in coastal and estuarine waters less than 10 m deep (Parra 2006). Their populations in Cleveland Bay are small, numbering 67 (95% confidence interval, CI = 51–88) snubfin dolphins and 54 (95% CI = 38–77) humpback dolphins in 2002 (Parra et al. 2006). Snubfin and humpback dolphin ranging patterns in Cleveland Bay overlap considerably and both species show similar habitat selection and movement patterns (Parra 2006). Both species use shallow, coastal-estuarine waters

extensively, but snubfin dolphins use shallower waters and sea-grass meadows, and occur closer to river mouths than humpback dolphins (Parra 2006). Within these coastal areas there is little predation risk for snubfin and humpback dolphins. Known predators of delphinids such as large (>3 m) tiger sharks, *Galeocerdo cuvier*, and bull sharks, *Carcharhinus leucas* (Heithaus 2001) are fairly uncommon in Cleveland Bay and are caught primarily at beaches close to deep water (>10 m; Simpfendorfer 1992; C. Simpfendorfer, personal communication), away from the core areas of use by snubfin and humpback dolphins (Parra 2006). Additionally, since its inception in 1962, the Queensland Shark Control Program has fished intensively for sharks with gillnets and baited drumlines in coastal areas of Cleveland Bay (Paterson 1990). While scars from nonlethal shark attacks have been observed on individuals of both dolphin species, their similar habitat use and ranging patterns indicate that neither species would be exposed to higher predation risks from sharks than the other.

Stomach contents analysis from humpback and snubfin dolphins from Cleveland Bay and other areas along the east coast of Queensland indicate that both species feed on a wide variety of estuarine fish (Heinsohn 1979; Parra & Jedensjö 2009). Snubfin dolphins, however, also commonly prey upon cephalopods, particularly squid and cuttlefish (Heinsohn 1979; Parra & Jedensjö 2009). Tropical estuarine fishes show significant temporal and spatial variation in Cleveland Bay, (Robertson & Duke 1987, 1990; Kwak & Klumpp 2004), whereas squid and cuttlefish are widespread and abundant with spawning and recruiting occurring throughout the year for some species (Jackson 1991; Moltchanivskyj & Doherty 1994). Squid and cuttlefish are also considered the most gregarious of all cephalopods (Boal 2006). Therefore, as a group, the food resources of snubfin dolphins (i.e. fish and squid) are likely to be more common, abundant and less temporally variable than those of humpback dolphins.

Our study populations thus appear to share key ecological aspects (space use, feeding habits and predation risks) that facilitate interspecific comparisons and the identification of underlying factors and mechanisms shaping grouping and fission–fusion dynamics in delphinids. In this study, we used focal observations, association analyses and social network techniques to investigate the social organization of Australian snubfin and humpback dolphins by quantifying their grouping patterns, fission–fusion dynamics and social network properties. In particular, we addressed four questions: (1) do snubfin and humpback dolphins have different grouping patterns; (2) are snubfin and humpback dolphins' social association patterns nonrandom; (3) do social association patterns change over time; and (4) are populations divided into social units, that is, clusters of individuals that interact more frequently with each other than with members of other clusters? Through these analyses, we aimed to further our understanding of the factors driving fission–fusion dynamics in delphinids, and stimulate the quantification of spatio-temporal grouping patterns in different species to facilitate future comparative research.

METHODS

Field Sampling

Boat-based surveys were conducted in the coastal waters of Cleveland Bay, northeast Queensland, from January 1999 to October 2002. Search effort and direction of travel were limited primarily by sea conditions, as we attempted to remain in areas with sea conditions \leq Beaufort 3 and swell \leq 1 m. Within these constraints, efforts were made to cover all sections of the study area equally. Further details of field techniques are available in Parra et al. (2006) and Parra (2006).

A school was defined as dolphins with relatively close spatial cohesion (i.e. each member within 100 m of any other member) that were involved in similar (often the same) behavioural activities (modified from [Connor et al. 1998](#)). Once a dolphin school was sighted, it was approached to within 10 m to record location, identify the species, estimate school size, assess the age composition of the school, obtain behavioural data, and take photographs of individual animals for photoidentification purposes. For school composition, three age classes (adults, juveniles and calves) were distinguished based on behavioural cues and visual assessment using the average adult size for each species as a reference ([Parra et al. 2006](#)). The predominant behaviour of $\geq 50\%$ of the individuals at the surface on initial approach was recorded. Dolphin schools were classified into different behavioural states: foraging, foraging behind a trawler, travelling, socializing and milling according to standard criteria, detailed in [Parra \(2006\)](#).

Photographs of dolphins were taken for individual identification. All photographs taken on surveys were examined and classified into three grades (excellent, good, poor) depending on focus, contrast between the dorsal fin and background, relative angle to the animal, and the size of the dorsal fin relative to the frame. Photographs classified as excellent and good were used to identify individuals and develop identification catalogues for each species ([Würsig & Jefferson 1990](#)).

Ethical Note

Survey techniques were approved by the Animal Ethics Committee of James Cook University and the Great Barrier Reef Marine Park Authority. Photoidentification is the most commonly used method for recognizing individual dolphins ([Würsig & Jefferson 1990](#)). Both snubfin and humpback dolphins are reliably identified from marks on their dorsal fins ([Corkeron 1990](#); [Parra & Corkeron 2001](#)). Because recognition of individual animals does not require the capture, handling or marking of the animals, it does not entail any risk of injury to the dolphins. To minimize potential disturbance by the presence of the boat we (1) approached dolphin schools slowly and parallel to their direction, (2) avoided sudden turns, and rapid accelerations and decelerations of the boat around dolphin schools, and (3) terminated the photoidentification effort if animals showed signs of disturbance (e.g. dolphins repeatedly tried to avoid the boat).

Data Analysis

School size and behaviour

To test for interspecific differences in the sizes of schools of snubfin and humpback dolphins we performed a two-sample randomization test. This type of randomization compares the difference of the mean school sizes observed with the difference obtained by randomly allocating the observed school sizes among the two species. The randomization test was repeated 5000 times and the significance of the test evaluated by recording the number of times the differences obtained from randomization were greater than the observed value ([Manly 2007](#)).

To determine whether the school sizes of snubfin and humpback dolphins varied with behavioural activity we used Kruskal–Wallis rank-sum tests and Nemenyi post hoc tests, with corrections for multiple testing ([Benjamini & Hochberg 1995](#)), for pairwise comparisons ([Zar 1999](#)). To avoid pseudoreplication of behaviours within a school only the first behavioural sample recorded for each school was used for analysis. All tests were evaluated at $P = 0.05$. Randomization tests were carried out with the POPTOOLS version 2.5 Excel add-in (<http://www.cse.csiro.au/poptools>). The Kruskal–Wallis rank-sum tests and Nemenyi post hoc tests were calculated using R software version 2.8 (R Development Core Team 2008).

Association patterns

Association analyses were carried out in SOCPROG 2.4 ([Whitehead 2009](#)). For the analysis of association patterns, all dolphins identified within the same school at the same time during a single day (the sampling period) were considered associated. In many cases not all individuals in a school were photoidentified leading to a downward bias in association indexes. To minimize this bias, only schools with 50% or more of the individuals identified were included in the analysis. Association analyses were further limited to individuals identified on four occasions or more. This sighting threshold reflects a compromise between including as many individuals as possible and accurately describing their social behaviour ([Bejder et al. 1998](#)). This is consistent with several studies of social structure in dolphins and other vertebrates ([Bräger et al. 1994](#); [Bräger 1999](#); [Chilvers & Corkeron 2002](#); [Ottensmeyer & Whitehead 2003](#); [Vonhof et al. 2004](#)).

We used the half-weight association index (HWI) to estimate the strength of the relationships between dyads ([Cairns & Schwager 1987](#)). Values of the HWI range from 0 (individuals never sighted together) to 1 (individuals always sighted together). [Whitehead \(2008b\)](#) has shown that the true association indexes (the proportion of time that dyads actually do spend together) may differ considerably from the estimated association indexes. As a result matrices of association may not represent real social structures well. To assess whether our association data were sufficient for describing snubfin and humpback dolphins' social structure we calculated: (1) the coefficient of variation of the true association indexes (S), and (2) the correlation between the true association indexes and estimated association indexes (r) following formulas and maximum likelihood procedures described in [Whitehead \(2008a, b\)](#). S is a measure of how much variation there is in the association data within a population: values less than about 0.3 indicate low levels of social differentiation; values around 0.5 and greater indicate a well-differentiated social system. The correlation coefficient r is an indicator of the power of the analysis to detect the true social system with r values close to 1 indicating a good representation of social structure and values around 0.4 a moderate representation ([Whitehead 2008a, b](#)).

We used [Whitehead's \(2009\)](#) modification of the permutation test by [Bejder et al. \(1998\)](#) to assess whether individuals were associating at random or showed preferred/avoidance associations. This test uses a swapping algorithm which ensures equidistribution of the generated matrices and thus deals with known biases of [Bejder et al.'s \(1998\)](#) permutation test ([Miklós & Podani 2004](#); [Krause et al. 2009](#); [Whitehead 2009](#)). To account for nonindependence of school membership, we constrained our randomizations to permute individuals only among schools within each sampling period ([Sundaresan et al. 2009](#)). The test statistic was the standard deviation of the mean association indexes. Simulations and field studies have shown that if some individuals have preferred companionships (i.e. associations occurring more often than expected by chance) over several sampling periods, then the standard deviation of the observed association indexes is significantly higher ($P < 0.05$) than that of the random data, but the means may be the same ([Gowans et al. 2001](#); [Whitehead 2009](#)). Association matrices were randomly permuted 20 000 times. Additional runs of the test showed P values were stable after 20 000 randomizations. Pairs of individuals with an HWI greater than the average association index if individuals associated at random in the population (HWI_{null}) were defined as preferred companionships ([Whitehead 1995](#); [Lusseau et al. 2006](#)):

$$HWI_{\text{null}} = \frac{n_{\text{associates}}}{N - 1}$$

where N is the total number of associates and $n_{\text{associates}}$ is the average school size in which an individual is found.

Network analysis

We used a network approach to investigate in more detail the social association patterns of snubfin and humpback dolphins. In particular we assessed whether their social networks were characterized by a consistent pattern of association among individuals. Social network methods developed in the physical sciences offer simple and powerful tools that can be used in socioecological studies for characterizing patterns of association, at the level of both the individual and the population (Krause et al. 2007). In these social networks, individuals are represented by nodes and the associations between them are represented by edges. Network approaches have been used to characterize social structures and their effects on transmission processes (e.g. information, diseases) in taxa such as delphinids (Lusseau 2003; Guimarães et al. 2007), equids (Sundaresan et al. 2007), otariids (Wolf et al. 2007) and poeciliids (Croft et al. 2006).

Most of the animal social networks that have been studied to date have been characterized by the occurrence of relations; that is, the edges between nodes simply represent the presence or absence of an association, but not the weight (e.g. frequency, strength) of the edge (Lusseau et al. 2008). Social networks are intrinsically weighted, with edges having differing strengths representing stronger or weaker social ties between individuals. Thus, considering the weights of the edges provides a deeper understanding of the dynamic behaviour of a social network (Barrat et al. 2004; Lusseau et al. 2008). We modelled snubfin and humpback dolphins' social networks as weighted networks based on the association matrices defined by the HWIs among individuals. From these networks we calculated the mean of two standard metrics for the characterization of weighted networks: strength (S_i) and clustering coefficient (C_i).

Strength is the sum of the association indexes over the neighbours connected to an individual (Barthélemy et al. 2005; Whitehead 2008a):

$$S_i = \sum_j AI_{ij}$$

where AI_{ij} is the association index between individual i and j . Strength measures an individual's tendency to form associations. High strength values indicate how well connected an individual is to its associates. The clustering coefficient is a measure of the strength of associations among the associates of an individual. A high clustering coefficient indicates that the associates of an individual are strongly associated among themselves. We calculated C_i using Holme's formula (Holme et al. 2007; Whitehead 2008a):

$$C_i = \frac{\sum_{jk} AI_{ij} AI_{ik} AI_{jk}}{\max(AI_{ij}) \sum_{jk} AI_{ij} AI_{jk}}$$

To test the significance of the social network metrics observed, we compared the weighted networks of each species with their expected counterparts (same number of nodes and edges) under random association between individuals. We generated 5000 random social networks of association for each dolphin species using randomization routines in SOCPROG 2.4. For each of the random networks, we calculated the average strength and clustering coefficient and calculated the proportion of these values that were greater than the observed values.

Community structure

Defining local structure within a population can help elucidate the dynamics of individual affiliations and the formation of clusters

of individuals that might correspond to social units (Girvan & Newman 2002). To determine whether the populations of snubfin and humpback dolphins were divided into groups of individuals that were densely connected with each other, but sparsely connected with other groups, we used a modularity coefficient (Newman 2004a, b). The modularity coefficient is simply a numerical index that indicates how well a population can be divided into communities or social units. When using weighted data (i.e. association indexes) the modularity coefficient is the difference between the proportion of the total association among individuals within clusters and the expected proportion if individuals associated at random (Whitehead 2008a):

$$Q = \frac{\sum_{ij} \alpha_{ij} \delta(C_i, C_j)}{\sum_{ij} \alpha_{ij}} - \frac{\sum_{ij} \hat{\alpha}_{ij} \delta(C_i, C_j)}{\sum_{ij} \hat{\alpha}_{ij}}$$

where α_{ij} is the association index between individual i and j , $\hat{\alpha}_{ij}$ is the expected value of α_{ij} if individuals associated at random, $\delta(C_i, C_j) = 1$ if individuals i and j are members of the same cluster, or $\delta(C_i, C_j) = 0$ if i and j are members of different clusters. Modularity values of 0 indicate that the community structure is no stronger than would be expected by random chance and values larger than zero represent deviations from randomness. Values of modularity around 0.3 or higher indicate good divisions of the population (Newman 2004a, b). Ideally, the best partition of the network into different clusters is that which maximizes modularity. To define the most parsimonious clustering step, the social network is iteratively divided into clusters until a peak in the modularity coefficient is reached. We used the clustering algorithm and eigenvector-based approach of Newman (2006a, b) that is implemented in SOCPROG 2.4 to select the community partition that maximizes the modularity coefficient. We used NETDRAW version 2.504 (Borgatti 2002) to display matrices of association and community structure as social network diagrams using a circle layout (i.e. sociogram).

Lagged association rates

Temporal variability in association patterns was investigated by estimating lagged association rates and comparing these to null association rates (Whitehead 1995). The lagged association rate is an estimate of the probability that, if two individuals are associating at a given time, they will still be associated various time lags later. The null association rate is the expected value of the lagged association rate given random association. As not all individuals within a school were identified, lagged and null association rates were standardized (i.e. we considered the number of associates an individual was seen with at specific time lags, Whitehead 1995). Standardized rates are estimates of the probability that if two individuals are associated at any time, the second is a randomly chosen associate of the first after a specified time lag. The temporal association patterns obtained for each species were then compared to four different models of lagged association rates (Table 1; Whitehead 1995) to test whether association patterns among humpback dolphins were temporally less stable than those of snubfin dolphins. These models allow for different levels of temporal association to be evaluated and combinations among them, including: (1) constant companions: stable associations over long periods of time; (2) casual acquaintances: irregular associations that last for some time; (3) two levels of casual acquaintances: where pairs disassociate over time, but at two different rates; and (4) rapid disassociation: associates disassociate within a short time. Model selection was carried out using the quasi-Akaike information criterion (QAIC) which compensates for overdispersed count data

Table 1

Number of sightings, average time lag between sightings, and time lag between first and last sighting of individual snubfin (Oh) and humpback dolphins (Sc) included in association analysis

ID	No. of sightings	Average time lag between sightings (days)	Time lag between first and last sighting (days)
Oh-002	21	68	1352
Oh-003	9	111	889
Oh-004	11	136	1359
Oh-005	18	80	1359
Oh-007	4	166	499
Oh-008	4	196	589
Oh-009	15	89	1250
Oh-010	12	46	503
Oh-011	18	74	1250
Oh-012	14	96	1250
Oh-013	9	54	432
Oh-014	10	79	709
Oh-015	18	66	1125
Oh-018	15	51	710
Oh-019	8	113	792
Oh-025	8	158	1106
Oh-028	5	249	994
Oh-029	5	265	1060
Oh-031	5	265	1060
Oh-032	5	264	1054
Oh-034	14	66	859
Oh-035	5	201	802
Oh-038	4	241	722
Oh-039	6	157	785
Oh-041	4	226	679
Oh-042	5	78	314
Oh-043	4	91	274
Oh-045	4	23	68
Oh-050	4	114	342
Oh-054	4	124	372
Mean±SE	9±0.9	132±13.6	819±66.2
SC-001	12	85	938
SC-002	32	43	1331
SC-003	17	82	1313
SC-005	33	40	1278
SC-009	28	48	1283
SC-010	25	36	858
SC-012	7	210	1263
SC-017	6	155	777
SC-019	8	179	1254
SC-030	7	126	755
SC-033	5	277	1107
SC-034	4	127	382
SC-035	6	94	469
SC-044	9	92	736
Mean±SE	14±2.85	114±19	982±86.9

and performs better for lagged association rates (Whitehead 2007). The model minimizing QAIC was chosen as the best-fitting model. Models differing by two to four units from the model with minimum QAIC were also considered as good descriptors of the data (Burnham & Anderson 2002). When more than one model provided a good description of the data, we followed the principle of parsimony and selected the model with fewer parameters as the most appropriate (Burnham & Anderson 2002).

From the best-fitting model, we estimated the mean number of associates a randomly chosen individual has as the probability that an individual is still with its associates at time zero (probability = 1), divided by the intercept on the Y axis (with lag zero) of the standardized lagged association rate (Whitehead 1995; Ottensmeyer & Whitehead 2003). The proportion of these associates that actually remain with a given individual as long-term companions can be estimated as the lagged association rate when the model curve stabilizes, relative to the maximum rate predicted by the model (Whitehead 1995; Ottensmeyer & Whitehead 2003).

RESULTS

School Size and Behaviour

We encountered 117 schools of snubfin dolphins and 143 schools of humpback dolphins in Cleveland Bay during the study and spent a total of 168 h following focal dolphin schools for data collection. Snubfin dolphins formed larger schools than humpback dolphins (difference = 1.8, 95% CI = 1.1, 2.7, $P < 0.001$). Schools of snubfin dolphins varied in size from one to 15 animals (Fig. 1), with an overall mean school size ± SE of 5.3 ± 0.35 ($N = 101$). The school size of humpback dolphins ranged from one to 12 animals (Fig. 1), with a mean ± SE of 3.5 ± 0.19 ($N = 135$). Schools of both species were composed mainly of adult animals (snubfin = 4.2 ± 0.28 ; humpback = 2.16 ± 0.16) and contained similar numbers of juveniles (snubfin = 0.36 ± 0.07 ; humpback = 0.36 ± 0.05) and calves (snubfin = 0.74 ± 0.10 ; humpback = 0.50 ± 0.06).

School size and behavioural data were available for 202 dolphin schools. As there were too few records of snubfin ($N = 2$) and humpback dolphins ($N = 1$) involved in milling behaviour, this behavioural category was excluded from analyses. Snubfin dolphins were never seen foraging behind trawlers. The mean school sizes of snubfin dolphins did not change significantly with behavioural states and varied from five to six animals ($H_2 = 2.5$, $P = 0.284$; Fig. 2). In contrast, the sizes of humpback dolphin schools varied significantly with behaviour ($H_3 = 23.5$, $P < 0.001$; Fig. 2). Schools of humpback dolphins were larger when socializing than foraging (Nemenyi test: $P < 0.001$) or travelling (Nemenyi test: $P = 0.005$). Additionally, schools foraging behind trawlers were larger than schools foraging independently of trawlers (Nemenyi test: $P = 0.014$).

Association Patterns

Sixty-three snubfin dolphins and 54 humpback dolphins were photoidentified in Cleveland Bay. Analyses of association patterns were carried out on 30 individual snubfin dolphins and 14 humpback dolphins that were sighted on four or more occasions and in schools with 50% or more of animals identified. All individuals in the analyses were adults, except for one snubfin dolphin that was a juvenile (OH-054). Most animals were sighted several times and throughout the study period providing good spatial and temporal data on associations (Table 1). The coefficient of variation of the true association indexes ($S_{\text{snubfin}} = 0.87$; $S_{\text{humpback}} = 0.99$) indicated well-differentiated societies with variable relationships among individuals. The correlation between the true association indexes and estimated association indexes ($r_{\text{snubfin}} = 0.69$; $r_{\text{humpback}} = 0.76$) indicated that our association data had relatively good power to detect the true social system within snubfin and humpback dolphin populations.

The standard deviations (SD) of the mean HWI of snubfin and humpback dolphins were significantly higher than those from random data, indicating that individuals of both species showed a tendency for preferred associations (Table 2). The HWI_{null} was estimated at 0.18 for snubfin dolphins and 0.27 for humpback dolphins. All snubfin and humpback dolphins had preferred companionships. There were 136 preferred companionships ($\text{HWI} > \text{HWI}_{\text{null}}$) among the 30 snubfin dolphins and 17 preferred companionships among the 14 humpback dolphins.

Network Metrics

Comparisons of observed and random weighted networks revealed that the overall strength and clustering coefficients of the humpback dolphins' social network did not differ from random

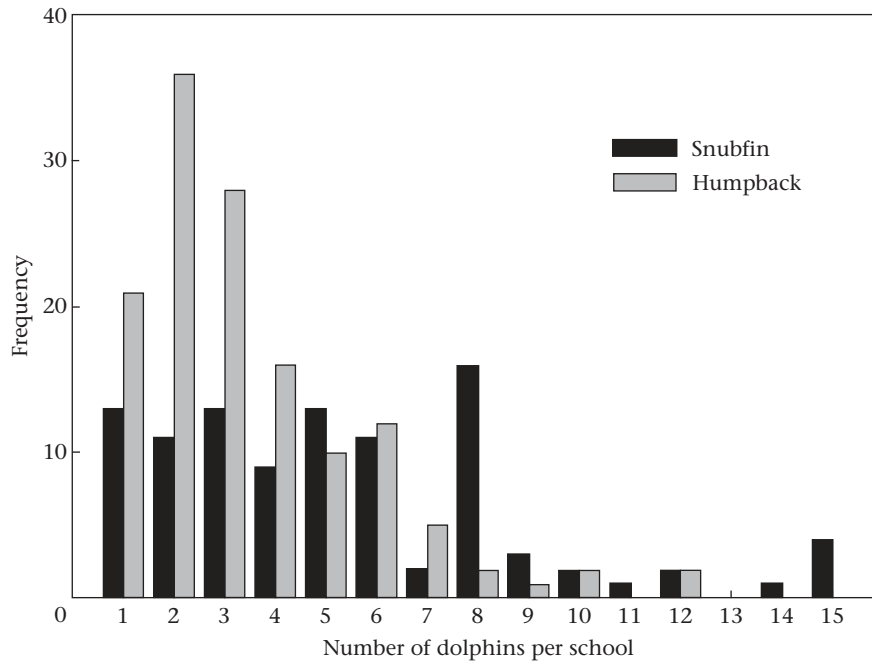


Figure 1. Estimated school sizes of snubfin and humpback dolphins found in Cleveland Bay, northeast Queensland, Australia.

(S_i observed = 1.82, S_i random = 1.83, $P = 0.72$; C_i observed = 0.31, C_i random = 0.31, $P = 0.94$). In contrast, the snubfin dolphins' social network had a higher strength than would be expected by chance (S_i observed = 4.21, S_i random = 4.20, $P = 0.01$). The clustering coefficient of snubfin's social network was higher than that of the random network, but this difference was not statistically significant (C_i observed = 0.29, C_i random = 0.28, $P = 0.14$).

Community Structure

The modularity coefficient indicated important divisions within both snubfin ($Q = 0.36$) and humpback dolphin ($Q = 0.36$) populations. Modularity for snubfin dolphins was maximized at an

HWI of 0.16, resulting in four distinctive clusters composed of 2, 8, 9 and 11 individuals. Three clusters of 3, 4 and 7 individuals were delineated for humpback dolphins, with modularity being maximized at an HWI of 0.12 (Fig. 3).

Temporal Patterns of Association

The standardized lagged association rates of snubfin and humpback dolphins remained higher than the null association rates for the whole study period (Fig. 4), demonstrating the presence of nonrandom associations among individuals of both species. The model that best described the temporal association patterns of snubfin dolphins suggested that an individual snubfin dolphin at any time had two types of associates: 'constant companions' and 'casual acquaintances' (Table 3, Fig. 4a). Therefore the social structure of snubfin dolphins appeared to be driven by a mix of long-term and consistent associations lasting years, and short-term associations that tended to last only a few days.

The value of the standardized lagged association rate at time zero in the best-fitting model was 0.128; thus, the mean number of associates a snubfin dolphin had from one day to the next was approximately eight. The model curve stabilized at an approximate standardized lagged association rate of 0.066, 52% of the maximum (0.128). Thus, each snubfin dolphin had about four 'constant companions' with whom they formed stable associations over long periods of time. These long-lasting bonds among five

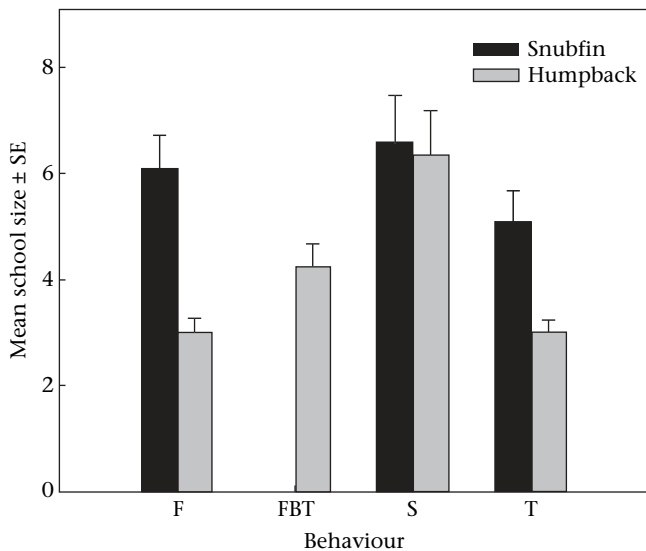


Figure 2. Variation in the mean school sizes of snubfin and humpback dolphins with different behavioural activities (F = foraging, FBT = foraging behind a trawler, S = socializing and T = travelling).

Table 2

Mean and maximum half-weight association indexes (HWI) of snubfin and humpback dolphins

Species	N	Mean HWI ± SD		P
		Observed	Random	
Snubfin dolphins	30	0.15 ± 0.18	0.15 ± 0.17	<0.001
Humpback dolphins	14	0.14 ± 0.18	0.14 ± 0.17	0.003

Observed and random mean HWI ± SD and P values are indicated for the random association test. The test statistic was the SD; P values < 0.05 indicate SD of observed data was significantly higher than that of random data.

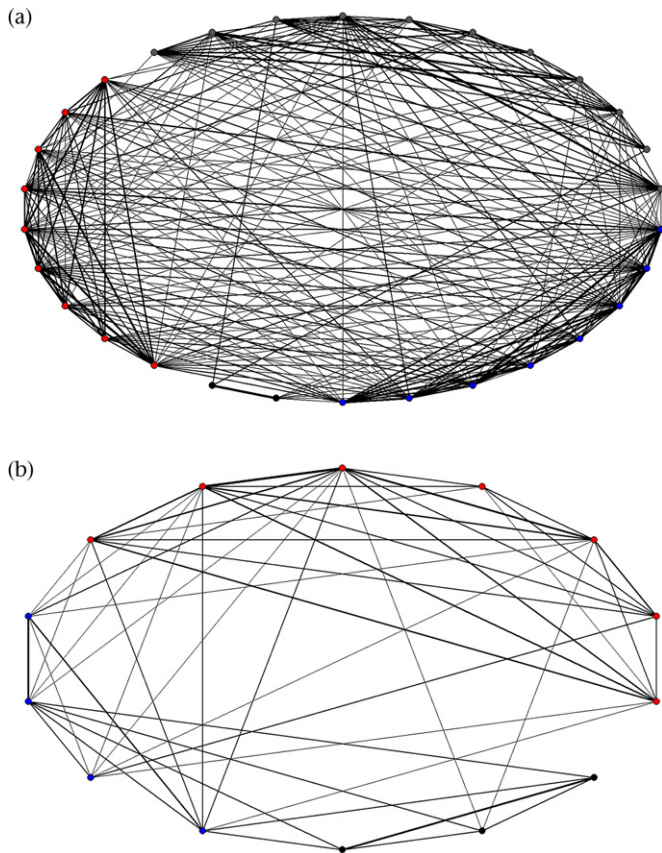


Figure 3. Social networks of (a) snubfin and (b) humpback dolphins in Cleveland Bay. The colour of the nodes represents the clusters identified by the modularity coefficient (Newman 2006b). The thickness of the lines represents the strength of association.

individuals correspond well with the mean school size observed for this species.

For humpback dolphins, the more parsimonious model that best fitted the data was that characterized by ‘casual acquaintances’ (Table 3, Fig. 4b). The model curve suggested that an individual humpback dolphin associates with around five different individuals on a given day. However, the models including ‘two levels of casual acquaintances’ and ‘constant companions + casual acquaintances’ were only 1–4 QAIC units away from the selected model. These closely competing models of social structure for humpback dolphins indicate that associations among individuals displayed different patterns of temporal stability, but that disassociation with time is a key feature of the humpback dolphin’s society. Although long-term bonds between individual humpback dolphins may occur, the variability in school size with behavioural activity and the strength of their social network not differing from random further supports the hypothesis that associations among humpback dolphins are weaker and temporally less stable than those of snubfin dolphins.

DISCUSSION

Dolphins live in complex social systems with a wide variety of grouping and association patterns. Interspecific differences between the grouping and association patterns of delphinids, living under different ecological conditions, indicate that predation risks and resource availability act strongly on their social behaviour (Connor et al. 1998; Gowans et al. 2007). In this study, we used focal observations, association analyses and social network techniques to

quantify variation in the grouping and fission–fusion dynamics of sympatric Australian snubfin and humpback dolphins living under similar ecological conditions. Our analyses show that snubfin and humpback dolphins have contrasting grouping and fission–fusion dynamics, which represent two structurally different societies.

We found schools of snubfin dolphins were larger and more stable in size, irrespective of behavioural activity, than those of humpback dolphins. Analysis of association patterns and community structure demonstrated that individuals of both species formed nonrandom associations and that there were groups of individuals that were densely connected with each other, but sparsely connected with other groups. However, comparisons of observed social networks with their random counterparts revealed that only the snubfin dolphins’ social network was dominated by strong associations between individuals. Modelling of lagged association rates indicated that individuals of both species showed fission–fusion grouping patterns. Nevertheless, long-lasting associations (‘constant companionships’) were a strong feature in the association patterns of snubfin dolphins. In contrast, temporal patterns of association for humpback dolphins were best described by a ‘casual acquaintances’ model indicating associations among individuals were temporally less stable.

Living in groups is often considered to be the result of a trade-off between predation risk and the costs of feeding competition. Since group membership reduces an individual’s risk of predation, the risk of predation is thought to put a lower limit on group size, while within-group food competition sets the upper limit (van Schaik 1989). Current knowledge of the distribution and abundance of large tiger sharks in Cleveland Bay (Simpfendorfer 1992) indicates that predation risks are low and similar for both species. Thus, proximate ecological factors dealing with predation risk seem unlikely to explain the differences in school sizes and fission–fusion dynamics of snubfin and humpback dolphins.

Differences in the feeding ecology of snubfin and humpback dolphins might better explain their contrasting grouping and fission–fusion dynamics. In group-living mammals with relatively low levels of predation risk, high degrees of fission–fusion represent a strategy for coping more efficiently with spatially and temporally varying food sources (Wrangham et al. 1993; Chapman et al. 1995; Janson & Goldsmith 1995). Spotted hyaenas, *Crocuta crocuta*, for example, adjust their grouping patterns in response to feeding competition, forming larger groups when prey is abundant and breaking into smaller subgroups when prey is limited (Smith et al. 2008). Similarly, spider monkeys, *Ateles geoffroyi*, and chimpanzees, *Pan troglodytes*, are more gregarious when food resources are abundant (Chapman et al. 1995). Mammal-eating killer whales, *Orcinus orca*, tend to occur in small groups (usually of three individuals) with members of both sexes dispersing from their natal group, whereas fish-eating killer whales exhibit a wide range of group sizes and no dispersal from their natal group (Baird & Whitehead 2000). Killer whales hunting marine mammals have higher food intake rates in small groups than in larger groups; thus dispersal from natal groups probably occurs as a response to reduced energetic intake associated with foraging in larger groups (Baird & Whitehead 2000). In contrast, the variation in grouping patterns of fish-eating killer whales is related to changes in fish prey availability (Lusseau et al. 2004).

The variable group sizes and high degree of fission–fusion in humpback dolphins documented here may reflect an adaptation to the patchy and irregular distribution of their prey resources (i.e. fish), with animals spreading out in smaller groups when resources are scarce to reduce intraspecific competition for food, and aggregating when resources are abundant. The notion that the upper size limit of schools of humpback dolphins is limited by within-group competition for food is further supported by our

Table 3
Mathematical models fitted to the standard lagged association rates (g'); describing the temporal association patterns of snubfin and humpback dolphins as a function of time lag (td)

	Model	Model formula	No. of parameters	Estimates of parameters (\pm SE)	QAIC _c
Snubfin dolphins	Constant companions	$g' = a1$	1	$a1 = 0.0733 (\pm 0.0130)$	6385
	Casual acquaintances	$g' = a2 \times \exp(-a1 \times t)$	2	$a1 = 0.0005 (\pm 0.0002)$ $a2 = 0.0891 (\pm 0.0166)$	6365
	Constant companions + Casual acquaintances	$g' = a2 + a3 \times \exp(-a1 \times t)$	3	$a1 = 0.0264 (\pm 0.0261)$ $a2 = 0.0659 (\pm 0.0121)$ $a3 = 0.0609 (\pm 0.0218)$	6347
	Two levels of casual acquaintances	$g' = a3 \times \exp(-a1 \times t) + a4 \times \exp(-a2 \times t)$	4	$a1 = 0.0005 (\pm 8.8984)$ $a2 = 0.0005 (\pm 0.0005)$ $a3 = -0.7253 (\pm 6.4214)$ $a4 = -0.8144 (\pm 2.1545)$	6369
Humpback dolphins	Constant companions	$g' = a1$	1	$a1 = 0.1753 (\pm 0.0147)$	11408
	Casual acquaintances	$g' = a2 \times \exp(-a1 \times t)$	2	$a1 = 0.0002 (\pm 0.0001)$ $a2 = 0.1896 (\pm 0.0188)$	11399
	Constant companions + Casual acquaintances	$g' = a2 + a3 \times \exp(-a1 \times t)$	3	$a1 = 0.0234 (\pm 27.6774)$ $a2 = 0.1686 (\pm 1.7802)$ $a3 = 0.0457 (\pm 1450.1249)$	11400
	Two levels of casual acquaintances	$g' = a3 \times \exp(-a1 \times t) + a4 \times \exp(-a2 \times t)$	4	$a1 = 0.0002 (\pm 105.6092)$ $a2 = 0.0002 (\pm 0.0003)$ $a3 = 0.0978 (\pm 242.6253)$ $a4 = 0.0918 (\pm 0.5349)$	11403

Jackknife procedures were used to estimate SEs of parameters (Burnham & Anderson 2002). The model minimizing the quasi-Akaike information criterion (QAIC) was chosen as the best-fitting model (indicated in bold italics). The models are of the exponential form proposed by Whitehead (1995).

behavioural observations. Humpback dolphins forage behind trawlers for extended periods of time, something snubfin dolphins do not do. Trawlers provide a reliable, easily located and large source of food for dolphins through the provision and

concentration of prey while trawler nets are in use and while catches are being sorted (Chilvers & Corkeron 2001). Humpback dolphins joined in larger schools while foraging behind trawlers than when foraging independently of trawlers. This variability in

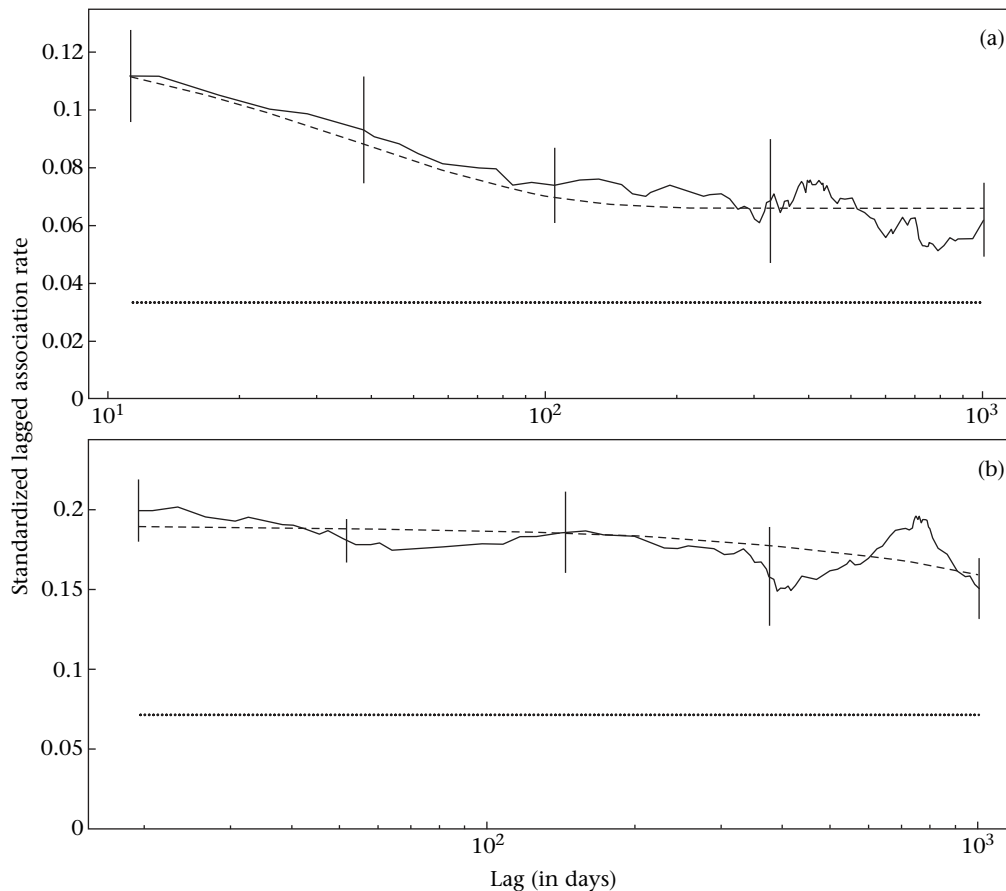


Figure 4. Standardized lagged association rates for (a) snubfin and (b) humpback dolphins, using only individuals sighted on four or more occasions and in schools with $\geq 50\%$ of animals identified. SE bars (vertical lines) were estimated using jackknife procedures implemented in SOCPROG 2.4 (Whitehead 2009). The null association rate (straight dotted line) is the lagged association rate expected if individuals were associating at random. The models that best explained the observed temporal association rates of snubfin dolphins (constant companions + casual acquaintances) and humpback dolphins (casual acquaintances) are shown with a dashed line.

school size in relation to foraging behaviour suggests resource limitation constrains school size.

Snubfin dolphins show a larger dietary breadth than humpback dolphins, feeding on both fish and cephalopods, with the latter found in large quantities in the stomachs of snubfin dolphins. Large prey patches of squid and cuttlefish, in combination with fish prey, may provide enough resources for many snubfin dolphins to share, reducing within-group competition for food and allowing the formation of larger schools. Within-group competition for food may be reduced in large groups by cooperative hunting or foraging (Boesch 1994; Creel & Creel 1995). Within these large schools, coordinated activities and cooperation in gaining access to schooling prey may facilitate the formation of the stable bonds observed among group members as has been suggested for killer whales and Risso's dolphins, *Grampus griseus* (Baird & Dill 1996; Hartman et al. 2008). Our observations of surface behaviour do not provide reliable indications of snubfin dolphins coordinating activities during foraging bouts. Studies involving simultaneous detection of prey and dolphins may help elucidate whether cooperation occurs (e.g. Benoit-Bird & Au 2003).

Various, opposing and synergistic ecological, social and evolutionary pressures influence grouping and fission–fusion dynamics (Aureli et al. 2008). Given their inconspicuous nature and the turbid water snubfin and humpback dolphins inhabit, there are inherent difficulties in studying their fission–fusion dynamics and this study is not without its limitations. The sex and genetic relationships of most individuals in this population are unknown. The interspecific differences observed here could be indicative of important social functions, such as alloparental care, social learning and/or mating strategies, resulting from kin selection or a form of reciprocal altruism between nonkin associates (Hamilton 1964). These social factors, together with ecological pressures, may play important roles in the development of nonrandom and long-term associations among individual snubfin dolphins as has been suggested for killer whales (Baird & Dill 1996; Baird 2000), long-finned pilot whales, *Globicephala melas* (Amos et al. 1993; Ottensmeyer & Whitehead 2003), sperm whales, *Physeter macrocephalus* (Richard et al. 1996; Whitehead 1996; Whitehead & Weilgart 2000) and bottlenose dolphins, *Tursiops* spp. (Parsons et al. 2003). Similarly, the presence of nonrandom associates with temporally loose bonds among humpback dolphins could reflect marked sex differences in association formation (Connor et al. 2000). Our results thus provide a platform for future investigations, involving molecular techniques, into the effects of kinship and sex-specific relationships on the grouping and association patterns of snubfin and humpback dolphins.

Another challenge to the understanding of the pressures shaping the social system of delphinids is the consideration of phylogenetic constraints. Studies on some of the most diverse and widespread primates demonstrate that social structure may be strongly conserved among closely related species, even in the face of considerable environmental, behavioural and morphological variability (Struhsaker 1969; Di Fiore & Rendall 1994; Chan 1996; Thierry et al. 2000; Kerry & Jason 2006). This connection between phylogeny and social structure has also been demonstrated in equids (Linklater 2000) and neotropical birds (Prum 1994) emphasizing the relative importance of phylogeny for social behaviour. Among delphinids the stable long-term association patterns that we have demonstrated in snubfin dolphins appear to be restricted to its closest relatives (Vilstrup et al. 2011): Irrawaddy dolphins, *Orcaella brevirostris* (Kreb 2004; Beasley 2007), killer whales (Bigg et al. 1990; Baird & Whitehead 2000), pilot whales (Ottensmeyer & Whitehead 2003), Risso's dolphins (Hartman et al. 2008), pigmy killer whales, *Feresa attenuata* (McSweeney et al. 2009) and false killer whales, *Pseudorca*

crassidens (Baird et al. 2008). Similarly, most dolphins studied to date that show dynamic fission–fusion social structures with few nonrandom associations between individuals are the ones believed to be closely related to humpback dolphins: bottlenose dolphins (Connor et al. 2000; Rogers et al. 2004), spinner and spotted dolphins, *Stenella* spp. (Norris & Dohl 1980; Norris et al. 1994; but see Karczmarski et al. 2005) and common dolphins, *Delphinus* spp. (Bruno et al. 2004). Comparative phylogenetic approaches of social traits among distant and closely related dolphin species are needed to assess whether social structure in delphinids is correlated with phylogenetic distance.

In conclusion, this study emphasizes the influence of ecological factors on the social structure of delphinids. The dissimilar grouping and fission–fusion dynamics of snubfin and humpback dolphins can be explained by differences in their diets and associated food availability. Future studies involving molecular techniques and fine-scale data on the spatial and temporal distribution of food resources, predation risks and competitive behaviour will help elucidate the suite of interacting ecological, social and evolutionary factors shaping their social structures.

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