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The bottlenose dolphin community of Doubtful Sound features a large proportion of long-lasting associations

Can geographic isolation explain this unique trait?

Abstract More than 12 studies of different bottlenose dolphin populations, spanning from tropical to cold temperate waters, have shown that the species typically lives in societies in which relationships among individuals are predominantly fluid. In all cases dolphins lived in small groups characterised by fluid and dynamic interactions and some degree of dispersal from the natal group by both sexes. We describe a small, closed population of bottlenose dolphins living at the southern extreme of the species' range. Individuals live in large, mixed-sex groups in which no permanent emigration/immigration has been observed over the past 7 years. All members within the community are relatively closely associated (average half-weight index>0.4). Both male–male and female–female networks of preferred associates are present, as are long-lasting associations across sexes. The community structure is temporally stable, compared to other bottlenose dolphin populations, and constant companionship seems to be prevalent in the temporal association pattern. Such high degrees of stability are unprecedented in studies of bottlenose dolphins and may be related to the ecological constraints of Doubtful Sound. Fjords are low-productivity systems in which survival may easily require a greater level of co-operation, and hence group stability. These conditions are also present in other cetacean populations forming stable groups. We therefore hypothesise that ecological constraints are important factors shaping social interactions within cetacean societies.

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Introduction

Observing the association pattern of individuals allows inference about the social organisation of animal populations (Whitehead 1995). From such studies bottlenose dolphin (*Tursiops* spp.) communities around the world have been described as fission–fusion societies (Connor et al. 2000). In a fission–fusion society individuals associate in small groups in which composition changes very dynamically several times per day (White 1992). Most information available on bottlenose dolphin social organisation originates from three long-term studies in Sarasota Bay, Fla. (Wells 1991), Shark Bay, Western Australia (Smolker et al. 1992) and Moray Firth, Scotland (Wilson 1995). There is a large variability in the association patterns of female bottlenose dolphins. Some females live in bands, while others have few or no strong associates with most females living on a continuum between these two extremes (Connor et al. 2000). The formation of female bands largely depends on the reproductive state of individuals. Males seem to form strong alliances that last for many years (Connor et al. 2000). In Shark Bay, these alliances of two to three dolphins form second-order alliances (Connor et al. 1992a) where several alliances team up to consort females and/or attack other alliances. Such long-term associations were not detected in the Moray Firth (Wilson 1995). Associations between males and females are related to the reproductive state of the females (Connor et al. 2000) and seem to be mainly linked to a reproductive goal. However mixed-sex groups are not uncommon in Shark Bay (50%

of focal groups) and in Sarasota Bay (31%) (Connor et al. 2000). Finally, these three bottlenose dolphin populations do not seem to be closed to other communities (Connor et al. 2000). For example in Sarasota Bay, 17% of sightings included individuals that were not community members (Wells et al. 1987).

The social organisation of animal communities is influenced by environmental variables such as predation and prey resources (Wrangham and Rubenstein 1986). Female grouping pattern tends to be more directly related to these parameters, while male social strategies are more related to mate access (Trivers 1972; Bradbury and Vehrencamp 1977; Wrangham 1980; Connor et al. 2000). However, a recent comparative study of two deep-water foraging species, sperm whale (*Physeter macrocephalus*) and bottlenose whale (*Hyperoodon ampullatus*), showed that their social organisation could not be related to their common foraging strategy (Gowans et al. 2001). Sperm whales live in a matrilineal social organisation, which is thought to minimise predation pressure on juveniles via communal care (Whitehead and Arnbom 1987). In contrast, bottlenose whales present in the Gully off Nova Scotia, Canada, live in a fission–fusion society (Gowan et al. 2001). Communal care of juveniles does not seem to occur in bottlenose whales and therefore different association strategies are available for deep-diving cetaceans (Gowans et al. 2001). Prey availability affects the social organisation of killer whales (*Orcinus orca*). Two sympatric forms of this species, with different foraging ecology, inhabit the Pacific Northeast. This difference in diet influences the social organisation of both groups (Baird and Whitehead 2000).

With the exceptions of this study and Rossbach and Herzing's (1997) study of bottlenose dolphins in a shallow open ocean habitat, all other studies have taken place in shallow estuaries or bays (Würsig and Würsig 1977; dos Santos and Lacerda 1987; Ballance 1990; Corkeron 1990; Hansen 1990; Shane 1990; Wells 1991; Smolker et al. 1992; Felix 1994; Bräger et al. 1994; Wilson 1995; Bearzi et al. 1997). These studies covered the temperature range in which the species occurs, from cold temperate (Moray Firth) to tropical (Ecuador), and a wide range of other environmental factors. All these populations are relatively open and have some degree of mixture with individuals outside their community. All these populations seem to be fluid and dominated by short-term associations between individuals, typical of a fission–fusion social organisation. The population of Doubtful Sound is similar to the population of the Moray Firth in that it lives at the extreme range of the species. It is also unique as it lives in a deep environment and does not mix with adjacent communities. The population, composed of 65 dolphins, is essentially closed (Williams et al. 1993). At least two other populations of bottlenose dolphins are present in Fiordland, yet no mixing or temporary immigration has been observed since 1991 (Williams et al. 1993; Schneider 1999; Haase and Schneider 2001). Doubtful Sound (Fig. 1) is the second largest fjord (83.7 km^2) of the 14 fjords that compose Fiordland in New Zealand (Stanton and Pickard 1981). Mean depth is about 200 m (maximum=434 m; Stanton and Pickard 1981). Annual rainfall in the area reaches 6,747 mm (Stanton and Pickard 1981). This heavy rainfall, combined with a low water circulation typical of fjords, results in a freshwater layer present on top of the marine layer ranging in depth from 0 to 10 m (Gibbs et al. 2001). Temperature of the marine layer ranges between 13°C and 17°C, while the freshwater layer ranges between 0 and 19°C. The layer freezes over in certain locations during winter (Gibbs et al. 2001).

We describe the social organisation of a population of bottlenose dolphins living in a fjord, a deep coastal environment, geographically isolated, located at the southern extreme of the species' range. This is the first description of a dolphin society in such an unusual environment.

Methods

Field techniques

From November 1994 to November 2001 we conducted systematic surveys in Doubtful Sound, Fiordland, New Zealand (Fig. 1) from a 4.5-m vessel powered with a 50 hp, four-stroke outboard engine. The survey route has remained constant over the 7-year period and covered the entire home range of the Doubtful Sound population. We spent 594 days (3,284 h) looking for dolphins and 2,301 h photo-identifying focal schools. All years but 1998 were sampled (Table 1). A school was defined as an aggregation of dolphins that operated in a coordinated fashion. Individuals in a school followed the same direction and were cohesive in their movement (Baird and Whitehead 2000). Because of the nature of the dolphins' distribution in Doubtful Sound (Schneider 1999), this corresponded to all dolphins that were within visual range of the observers as well as all dolphins swimming within 10 m of one another (Connor et al. 2000). Identifying schools was not difficult because the distance between schools was wide and measurable most of the times in kilometres while the distance between individuals within schools was small and measurable in metres (to a maximum of 50–100 m). All members of a school were assumed associated. Once a school of dolphins was encountered, individuals were photo-identified

Table 1 Sampling effort from 1995 to 2001

Year	Days in the field	Time on effort (h)	Time spent with dolphins (h)
1995	133	621	418
1996	94	414	288
1997	78	415	256
1998	0	0	0
1999	107	759	533
2000	78	489	360
2001	56	319	275

Fig. 1 Location of the study area
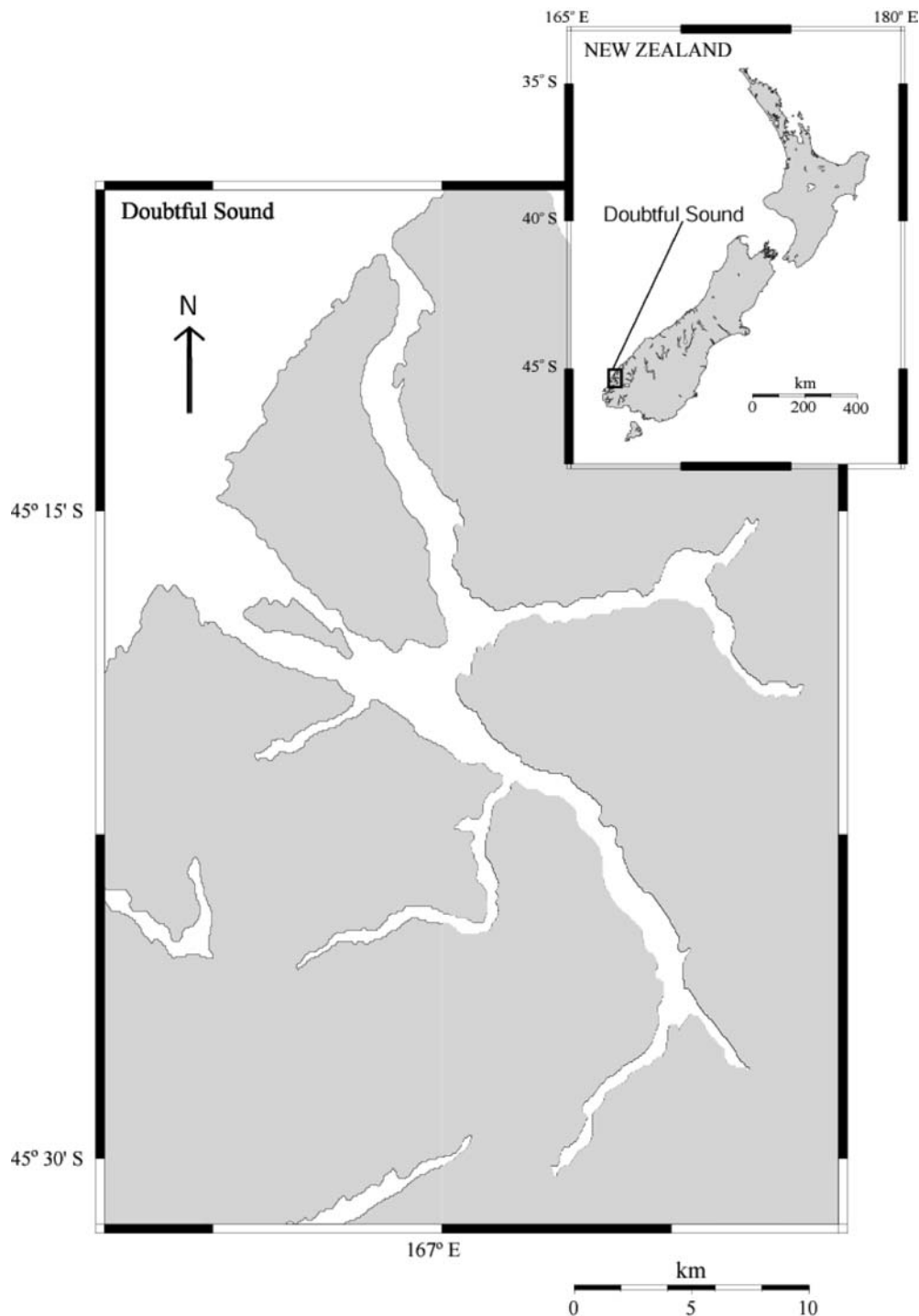
using natural markings on their dorsal fins (Würsig and Würsig 1977; Whitehead 1990; Dufault and Whitehead 1995). Some especially distinctive individuals were identified visually. Only schools in which all animals were identified were considered in this analysis; other schools constituted a small fraction of the total number of schools observed (<5%). A school was considered 'new' when individual(s) left or joined the focal school. These fusions/fissions were rare (less than 1/day) and therefore considering a school new after such an event did not bias the sampling towards schools that were followed for longer periods. Dolphin sex was determined by direct observations of the genital area, either visually

or via an underwater video camera mounted on a pole. Any dolphin that was constantly accompanied by a small calf was assumed to be a mother and therefore female.

Defining associations

For reasons of minimising bias (Cairns and Schwager 1987) and to enhance comparability within studies (e.g. Wells et al. 1987; Smolker et al. 1992), the half-weight index (HWI) was used to quantify the frequency of association among individuals.

$$\mathrm{HWI} = \frac{X}{X + 0.5(Y_a + Y_b)}$$

where: X is the number of schools where dolphin a and dolphin b were seen together, Y_a is the number of schools where dolphin a was sighted but not dolphin b, and Y_b is the number of schools where dolphin b was sighted but not dolphin a. HWIs were calculated only for animals sighted in more than 20% of the focal schools. This truncation of the dataset restricted the analysis to animals known to be present over most of the study period, removing individuals that died early in the study. Moreover, sample size can bias association indices (Chilvers and Corkeron 2002). Juvenile animals were not included in the association matrices.

Social organisation

The dataset was analysed using SOCPROG 1.3, a program developed for Matlab 5.1 by Hal Whitehead to analyse the social organisation of animal communities (Whitehead 1999a). The social organisation of the population was graphically represented for the entire study period using a hierarchical cluster analysis (average linkage method) of the HWI matrices. This technique clusters individuals not only by preferred partnerships, but also using least preferred partners. Therefore two individuals can be members of a cluster because they are seen more often together, or because they both do not associate with individuals outside their clusters (without being preferred partners themselves). The significance of all possible dyads in the population, and therefore the significance of the groups discriminated by the cluster analyses, was assessed using a Monte Carlo randomisation approach (Manly 1995; Bejder et al. 1998; Whitehead 1999b). Individuals within focal schools were randomly permuted, keeping school size and the number of times each individual was seen the same as in the original dataset (Whitehead 1999a). HWIs were then calculated for each dyad after each random simulation of the data. The expected HWI for each dyad was the average HWI of all permutations and was compared to the observed HWI. The observed value was significantly higher or lower than the expected value at the $P \leq 0.05$ level if it was within either 0.025 tail of the randomised frequency distribution (Whitehead 1999a). Associations significantly higher than expected were plotted in a sociogram. A Mantel test, using 1,000 permutations, was utilised to assess differences in association depending on sex.

To determine the stability of associations among individuals, variations in lagged association rates (e.g. average association rates with time lag) were calculated for all associations and for each sex-class of association (male–male, female–female, and male–female) (Whitehead 1995). For each individual the program SOCPROG calculated the proportion of companions the individual had at time t that remained companion at time $t + d$ where d is the time lag and averaged this proportion over all individuals in the study. Precision was estimated by jackknifing over a typical sampling trip (30 days) (Efron and Stein 1981). All individuals in the population were considered for this analysis in order not to positively bias the lagged association rates (Baird and Whitehead 2000). Lagged association rates were then compared to the null association rate (Whitehead 1995) to determine whether preferred associations were present in the population. The null association rate represents the lagged association rate of the dataset if individuals were associating at random. The temporal pattern of association of the population was compared to models of social organisation developed by Whitehead (1995). Two types of associates are taken into consideration by these models: constant companions that stay associated until death and casual acquaintances that dissociate over time. Each model possesses a combination of different levels of associate. The best model was selected using maximum likelihood and binomial loss techniques (Whitehead 1995, 1999a). The standard error of each model term was obtained by jackknifing.

Results

School size and sex ratio

Average school size was 17.2 individuals (median=14, mode=8) for the 1,292 schools followed between 1995 and 2001. The frequency distribution of school size is skewed towards smaller schools (Fig. 2), yet more than 65% of the schools were larger than 10 individuals, explaining the discrepancy between the mean and the mode school size.

During the study period 83 individuals were identified. During this period animals disappeared, presumed dead, and young individuals became identifiable photographically as they became older. This explains the discrepancy between the reported population size and the number of photographed individuals. Of these 83 individuals, 12% of them remained unsexed, 43.4% were females and 44.6% were males. Most focal schools (90.5%, n=1292) were of mixed sex (Fig. 3). Sexes were not segregated in this population.

Association pattern

After frequency of occurrence of individuals in focal schools was taken into consideration, 40 dolphins were retained for association analyses (21 males, 18 females and 1 unknown sex). Associations between and within sex classes were significantly different (Mantel test, $t=3.96$, $P<0.001$). Intersexual associations were less strong that intrasexual associations (Table 2). There was a non-significant tendency for male–male associations to be strongest. Maximum and average HWIs within the
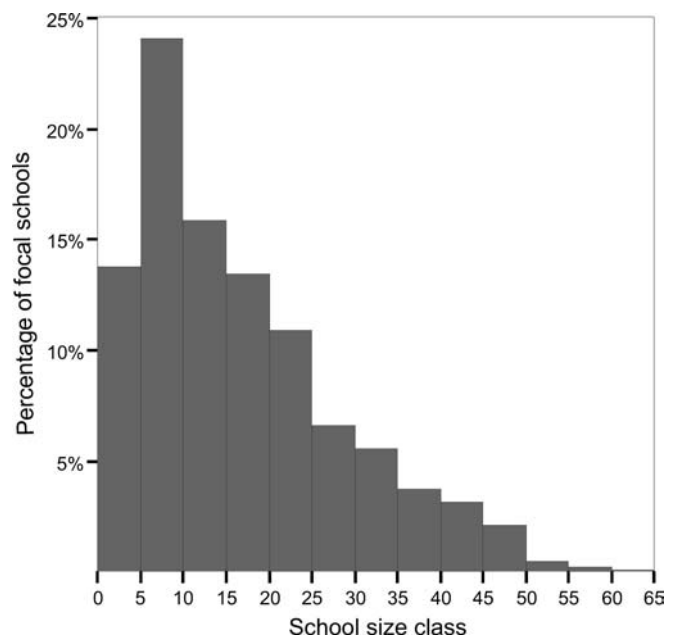
Fig. 2 Frequency distribution of focal group size from 1995 to 2001 (n=1292 groups)
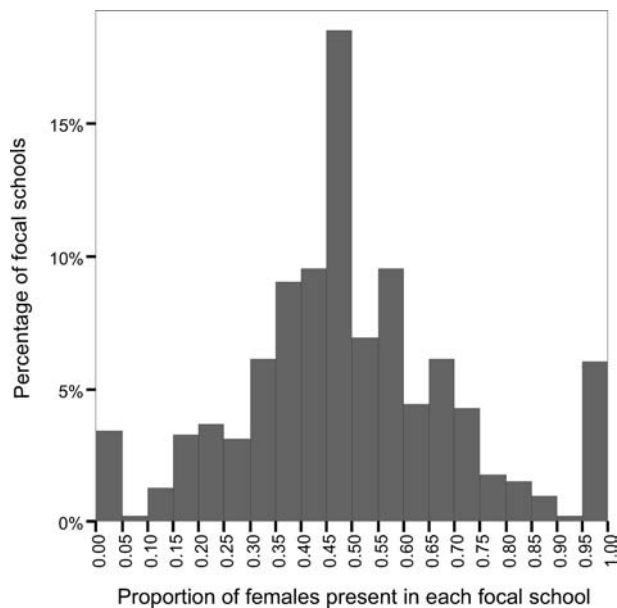
Fig. 3 Frequency distribution of the percentage of females present in each focal group between 1995 and 2001 (*n*=1292)

Table 2 Average and maximum half-weight indices between and within sex classes

	Average HWI (SD)	Maximum HWI (SD)
All individuals	0.47 (0.04)	0.63 (0.08)
Female–female	0.47 (0.05)	0.60 (0.08)
Male–male	0.49 (0.04)	0.65 (0.07)
Female–male	0.45 (0.04)	0.57 (0.07)

than the random one (observed SD=0.089, random SD=0.077, *P*>0.999) demonstrating a wider range of associations than expected if dolphins associated at random (i.e. dyads with higher HWI than expected and dyads with HWI lower than expected). This demonstrates the presence of preferential associations in the community (Gowans et al. 2001). Two hundred and seventy-one dyads were significantly different from random (Table 3). Preferred and non-preferred associates existed among and between sex classes over the 7-year study period. Most dyads lower than expected were between individuals of different sex, while most associations higher than expected were between males (Table 3).

different sex groups followed the same trend, and low variation indicates consistency of HWIs among individuals within these sex groups (Table 2).

The association dataset was randomly permuted 50,000 times. The observed mean association index was significantly lower than the random mean (observed mean=0.47, random mean=0.48, *P*<0.001) establishing that individuals showed significant preferential associations over the 7 years of the study. Additionally the observed standard deviation was also significantly higher

Social organisation

The cluster analysis shows no clear division in the community (Fig. 4). However, three mixed-sex groups spent more time together than all individuals did on average (HWI>0.47, Table 2 and Fig. 4). All individuals were associated at a HWI of 0.4. One female, Trigger, seemed to have a central position between groups 2 and 3. Individuals of group 1 were less often seen than other ones and this group is an artefact of the similar likelihood

Fig. 4 Average linkage dendrogram of the Doubtful Sound community for associations observed between 1995 and 2001. Females are represented in *italics*. The three groups described in the text are outlined
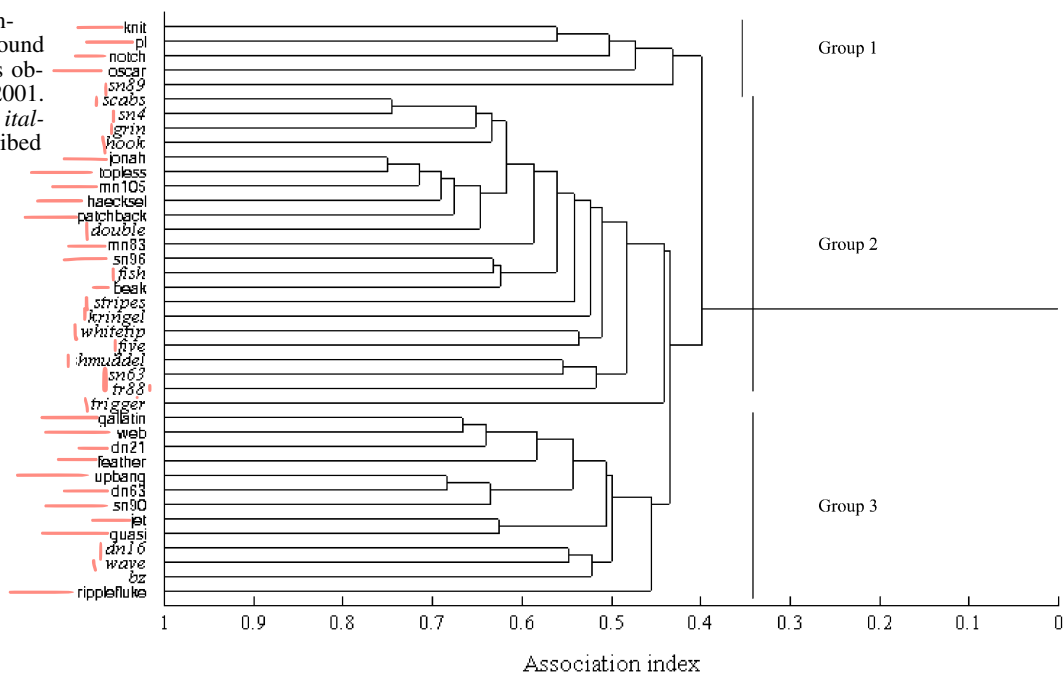
Table 3 Number of dyads significantly different from random depending on sex classes; the total number of possible dyads is given for each dyad category

	Fewer than expected (P<0.025)	More than expected (P>0.975)	Total number of possible dyads
Male–male	52	40	210
Female–female	27	20	153
Male–female	120	12	378
Totals	202	74	780
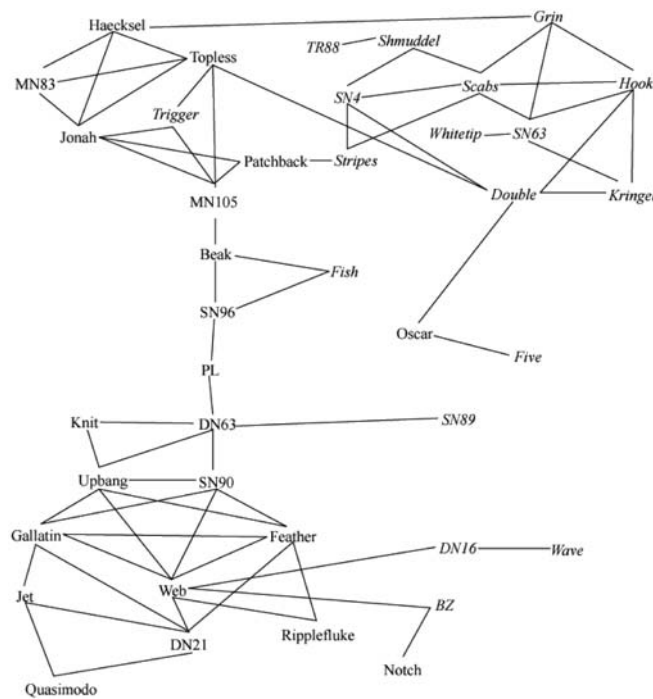
Fig. 5 Sociogram of the community for groups followed between 1995 and 2001. *Solid lines* are dyads likely to occur more often than expected at *P*<0.05 (2-tailed). Females are in *italics*

to encounter these individuals in the study area (White-head and Dufault 1999). Groups 2 and 3 both contain a male network and a female network. The male network of group 3 is a group of nine males linked at different degrees of associations. The structure of group 2 is more complex with an echelon pattern expressing no clear architecture within the group, except for dyads, triads, and the networks. In all but one case sub-groups of group 2 were unisex, the exception being the Fish/SN96/Beak triad.

The sociogram showing only the significant associations from the permutation test shows three complex networks of association. The first (top left) is composed of six males and one female with Jonah and Topless as the central individuals (Fig. 5). At the bottom left of the sociogram a male band is composed of eight males and one unknown sex individual (Ripplefluke), in which Gallatin has the central position (i.e. individual with the most associates). Finally, a female band is at the top right consisting of nine individuals. Since this dataset spans over 7 years, this female association cannot be related to individuals calving simultaneously and clustering for the protection of the calves (cf. Wells et al. 1987) because the significance of the associations is calculated over seven reproductive and seven non-reproductive periods. During these periods some of these females had calves but did not seem to leave this band to associate with other mothers. Scabs seems to hold a central position in this female group. The female Trigger only had significant associations with members of the Jonah/Topless network. The structure of the three unisex groups is complex, individuals forming associations with associates of associates (Fig. 5). The female group from group 3 (Fig. 4, Wave, DN16 and BZ) is not as tightly linked as the Scabs group. Only Wave and DN16 are associates (Fig. 5). Fifty percent of the male–female associations are between the

Table 4 Models describing temporal association patterns among all individuals and within and between sexes. The association rate between individuals, $g(d)$, is given as a function of the time lag, d. Each model is defined by the proportion of constant companions (p_{ct}) and the proportion of casual acquaintances (p_{cas}) individuals have and the length of these casual acquaintances (τ_{cas}) given in days. Male–male associations were defined by two levels of acquaintances: a casual level defined by p_{cas} and τ_{cas} and a more permanent one defined by p_{perm} and τ_{perm}. The standard error (SE) of each parameter was defined by jackknifing. The SE for the time lags is given as a ±1SE interval around the mean. For a full description of each model refer to Whitehead (1995)

Model of association	p_{ct} (SE)	p_{cas} (SE)	τ_{cas} (SE)	p_{perm} (SE)	τ_{perm} (SE)
All–all associations: $g(d) = p_{ct} + p_{cas}e^{-\frac{d}{\tau_{cas}}}$	0.41 (0.021)	0.16 (0.038)	180 (139–255)		
Female–female associations: $g(d) = p_{ct} + p_{cas}e^{-\frac{d}{\tau_{cas}}}$	0.43 (0.020)	0.15 (0.039)	135 (108–181)		
Male–female associations: $g(d) = p_{ct} + p_{cas}e^{-\frac{d}{\tau_{cas}}}$	0.43 (0.019)	0.13 (0.033)	123 (96–171)		
Male–male associations: $g(d) = p_{perm}e^{-\frac{d}{\tau_{perm}}} + p_{cas}e^{-\frac{d}{\tau_{cas}}}$		0.18 (0.050)	2.2 (2.24–2.28)	0.52 (0.026)	5249 (4211–6969)
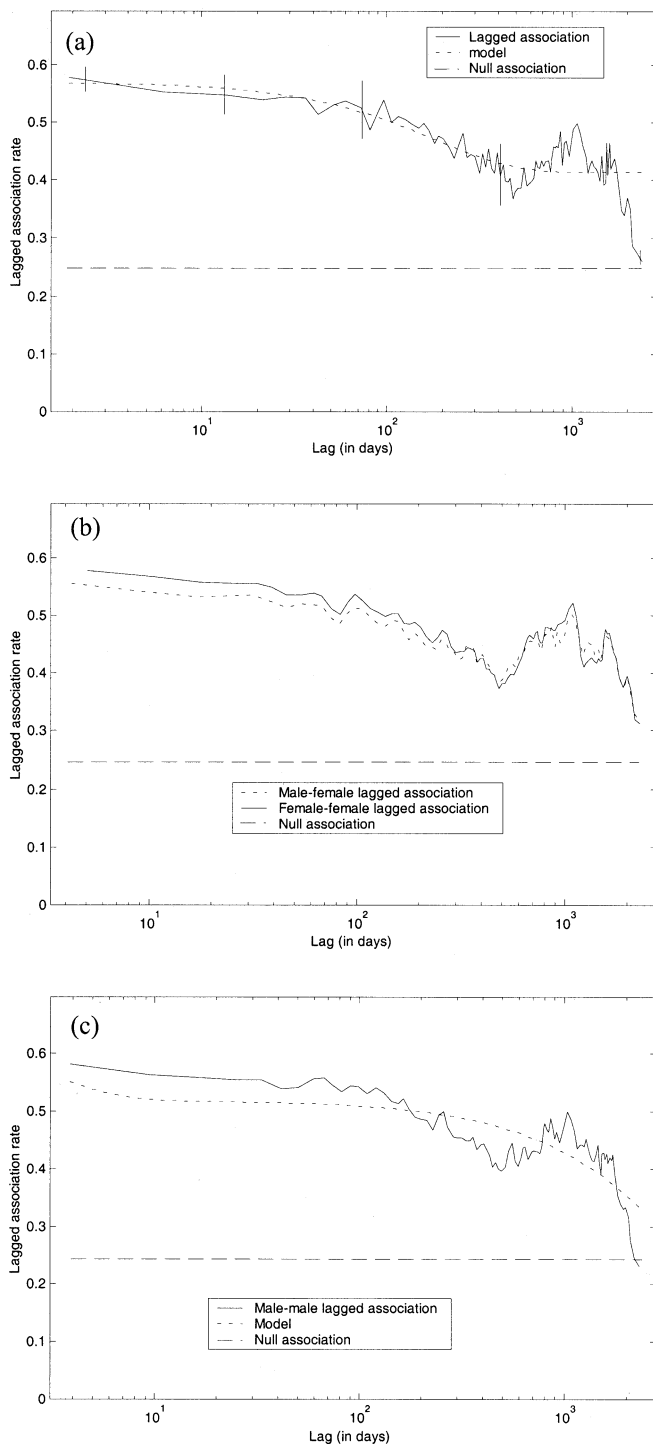
Fig. 6 Lagged association rates for all individuals (**a**), among females and between males and females (**b**) and among males (**c**). Each lagged association rate is compared to the null association rate. *Error bars* were obtained by jackknifing. Best models explaining the observed association rates are displayed for figures **a** and **c**

Jonah and Scabs groups and 17% between the Web and Wave groups.

Temporal pattern

Associations were quite stable and were best described if constant companionship was considered as an important feature of the community (Fig. 6, Table 4). Individuals had 40% of constant companions and 15% of acquaintances that lasted 6 months (Fig. 6a, Table 4 length of casual acquaintances is 180 days). Female–female and male–female associations demonstrated a similar association rate pattern but casual acquaintances were shorter (length of casual acquaintances is 96–180 days, 3–6 months, Fig. 6b, Table 4). Male–male associations were more complex and fell to a random level after 7 years (Fig. 6c). Males mostly had long-lasting associates (predicted to last for 14 years from the best fitting model, Table 4) and 18% of short casual acquaintances (for 2 days). More males disappeared than females during the study period. These deaths can explain the difference in association rate displayed by males (Whitehead 1995).

Discussion

The Doubtful Sound community has a unique social structure

The organisation of the bottlenose dolphin community in Doubtful Sound is dissimilar to that seen in other bottlenose dolphin populations. This small society lives in large mixed-sex schools. Strong associations occur within and between the sexes. No clear sub-units exist in the community, yet three groups of individuals tend to spend more time together than with others. Long-lasting associations are a strong feature of the community structure and are more prevalent than in previously studied bottlenose dolphin populations. This stability in the dynamics of association was observed within and between sexes. Seasonal factors such as mating behaviour and care of the young that affects other bottlenose dolphin populations (Connor et al. 2000) do not play a major role in the association structure of the Doubtful Sound population. Only 15–18% of associates were casual acquaintances. Interestingly the length of casual acquaintances observed between males and females and among females corresponds to the length of the breeding season (Haase and Schneider 2001). Still, a large portion of associations lasted less than 2 days (Fig. 6). The Doubtful Sound population can be therefore regarded as a fission–fusion social system with an extraordinarily large number of strong and long-lasting bonds underlying this dynamic organisation. In contrast the average HWI of other studied bottlenose dolphin populations range from 0.1 to 0.2, underlying the predominantly fluid nature of these societies (Wells et al. 1987; Smolker et al. 1992; Bräger

et al. 1994; Connor et al. 2000; Quintana-Rizzo and Wells 2001; Chilvers and Corkeron 2002).

At the level of the population, females did display a similar association pattern to that observed in other populations. Some females did not have any close associates, a few females had one associate, and a band of females was present with the formation of a complex network. This network was unique in that it was temporally stable and the level of associations within this network was high, presenting transitivity in association only previously observed in male networks before for the species (Connor et al. 2000). The behavioural basis of these associations is still not well understood, as at this stage it is not possible to tease apart reproductive, foraging, and defence advantages of associations. Since some female associations have remained stable over 7 years (Fig. 6), during which births have occurred, it suggests that females do not change their association pattern to maximise the protection of their calves as in Sarasota Bay (Wells et al. 1987).

Interestingly sexes were not as segregated as in other described populations. Some male–female associations were stable over the 7 years of the study (Fig. 6), eliminating mating behaviour as an explanation for these associations. Several hypotheses can be constructed from these male–female relationships. A parsimonious hypothesis would liken these associations to mother–son relationships in which close association increases their inclusive fitness. However male–female associations are heterogeneous: two males (Topless and Web) have 33% of male–female significant associations and two females (BZ and Double) also have 33% of female–male associations. If these relationships were mother–son we would expect a more homogeneous distribution and males should only have one permanent female associate. It is possible that these significant male–female associations represent an increased involvement of both sexes in reproductive strategies. Many behavioural mechanisms could play a role in the maintenance of these female–male associations, for example male and female dominance structures (Datta 1992), which would explain the presence of both female and male complex networks. In Shark Bay mating seemed to dictate male–male long-term association patterns (Connor et al. 1992a). Seasonal mating strategies did not seem to be of importance in the social organisation of the Doubtful Sound community. It is therefore possible that similarly to Shark Bay, long-term relationships, not only among males, but also both among females and between males and females, may be dictating reproductive strategies.

The bottlenose dolphin community of Doubtful Sound is uniquely organised. Long-lasting associations, within and between sexes, are a clear feature of this organisation and are more predominant than in other populations. In addition the large average size of the focal schools in Doubtful Sound has rarely been observed in other locations (Connor et al. 2000).

A different social organisation caused by isolation

No immigration or emigration has been observed since 1995 (Williams et al. 1993; Schneider 1999; Haase and Schneider 2001). If both males and females do not disperse from the natal group, they have much more opportunity to form alliances with siblings and/or other related animals if the incentive is present. Isolation from other communities therefore favours the stable social organisation observed in Doubtful Sound. The costs and benefits of such an extreme philopatry are numerous (Perrin and Lehmann 2001) and difficult to tease apart.

It seems likely to us that ecological constraints are an important driving feature in the social organisation observed in Doubtful Sound. The productivity of fjord systems is highly variable temporally and spatially (Matthews and Heimdal 1979). This high variation seems to be related to low ecological efficiency (Matthews and Heimdal 1979). A top predator may therefore need to possess information on the location of food resources in time and space that can only be gathered over several generations in order to successfully forage in this environment. If food acquisition drove the social organisation of this community it would explain why both sexes have similar association dynamics and that male–female associations do not seem to be related to mating behaviour. If the members of the community rely on information transfer, it is necessary for the social organisation to stabilise to allow for reciprocity of information exchange and maximisation of fitness (Barta and Szep 1995; Barta and Giraldeau 2001; Crowley 2001). This hypothesis is very similar to the Information Center Foraging model described for breeding colonies of seabirds (Allchin 1992; Barta and Szep 1995; Buckley 1997; Barta and Giraldeau 2001). Perrin and Lehmann's (2001) modelling approach showed that the proportion of philopatric individuals and the level of reciprocal interactions in pairs increased as ecological constraints increase. Bottlenose dolphin sociality in Doubtful Sound certainly fits this hypothesis. The geographic complexity of the Fiordland environment increases the difficulty for neighbouring communities to meet. Moreover the high variability of the system's productivity coupled with the energy requirement of this population living at the southern extreme of the species' range stresses the need for individuals to maximise energy input and maximise energy acquisition for their relatives. These factors are likely to decrease the likelihood that a dispersing individual will be ecologically successful and increases reciprocal interactions within the community, thereby stabilising the social organisation. The possibility of inbreeding though must be overpowering the dispersal cost at some stage, but a very low dispersal level (one individual every generation), that could not be detected over a 7-year period, would allow to keep a diverse gene pool in the population (Perrin and Mazalov 1999).

Isolation seems to be a common denominator of other cetacean populations in which a stable social organisation has been described (killer whales, long-finned pilot

whales and sperm whales; all matrilineal societies). In resident killer whales and long-finned pilot whales both males and females exhibit philopatry (Bigg et al. 1990; Amos et al. 1993). Upon reaching physical maturity male sperm whales do disperse from their natal groups, but female social units are defined as matrilineal (Christal and Whitehead 2001). Likewise, the heterogeneity of the environment in which these three species live necessitates information exchange among group members in order to find resources.

We therefore conclude that the most parsimonious explanation for the stable social organisation observed in Doubtful Sound is the population isolation from other communities. It seems that this isolation is a by-product of the intrinsic oceanographic factors of fjords, which decrease the survival likelihood of a dispersing individual. In addition, these constraining ecological factors resulted in an increase of group stability in order to increase inclusive fitness. Bottlenose dolphins are one of the most widely distributed cetaceans. This study suggests that social plasticity is an important factor in this species' ability to exploit an extraordinary variety of habitats.

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