



Dolphins restructure social system after reduction of commercial fisheries

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Although human activities are known to affect the social behaviour of group-living animals, the resilience of animals' social structure to disturbance is poorly understood. In the 1990s, bottlenose dolphins, *Tursiops aduncus*, in Moreton Bay, Australia, formed two distinct social communities ('trawler' and 'nontrawler dolphins') based on foraging interactions (or lack thereof) with commercial prawn trawlers. Members of the two communities almost never associated, despite overlapping home ranges. Since then, changes to fisheries legislation have substantially reduced trawling in Moreton Bay. We used association analyses and social network metrics to compare patterns of sociality among bottlenose dolphins across two periods: 1997–1999 (during trawling) and 2008–2010 (post trawling). Over this decade, their social network became less differentiated and more compact (average geodesic distance between individuals decreased), with significantly more and stronger associations between individuals (mean and maximum half-weight indices increased). The previously described partitioning into two communities has disappeared, with former 'trawler' and 'nontrawler dolphins' now dispersed over the entire social network and associating with each other. This restructuring suggests that although fisheries can influence the social behaviour of bottlenose dolphins, their social structure represents a complex adaptive system that is resilient to disturbance.

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Anthropogenic activities can alter the structure of animal societies (Chilvers & Corkeron 2001; Díaz López & Shirai 2008; Rutledge et al. 2010), which in turn can have direct effects on population fitness (Silk 2007), reproductive success (Sterck 1998), genetic population structure (Altmann et al. 1996), transfer of learned behaviour and culture (Whitehead 2010) and disease transmission (Cross et al. 2004). These disturbances can impact the viability of the target populations, thus understanding the resilience (how fast a system returns towards its equilibrium following a perturbation; Pimm 1984) of animals' social behaviour to human disturbance provides us with means to predict the likelihood that those disturbances will result in behavioural alterations and develop management strategies to reduce or eliminate those impacts.

Bottlenose dolphins (*Tursiops* spp.) are highly social mammals that form complex and diverse fission–fusion societies characterized by dynamic associations of varying strength and temporal stability (Wells et al. 1987; Connor et al. 2000b; Gero et al. 2005; Foley et al. 2010). Despite their flexible and dynamic group

structure, bottlenose dolphin societies contain certain stable elements such as long-term associations between individuals (e.g. Lusseau et al. 2003; Wiszniewski et al. 2009). Moreover, despite their fluid fission–fusion dynamics, the intrapopulation structure of their social systems appears to be stable over time (Gowans et al. 2007). An estimated 600–800 Indo-Pacific bottlenose dolphins, *Tursiops aduncus*, live in Moreton Bay, southeast Queensland, Australia, where they are exposed to a number of anthropogenic activities including important commercial and recreational fisheries (Lukoschek & Chilvers 2008). A study in the late 1990s (Chilvers & Corkeron 2001) found that bottlenose dolphins in southern Moreton Bay grouped into two distinct social communities: that is, behaviourally discrete sets of individuals that were associating with most others within their community but rarely between communities (Whitehead 2008a). This structuring was based on whether or not they interacted with commercial prawn trawl fisheries. 'Trawler dolphins' were frequently observed following trawler vessels and foraging on discarded trawl by-catch while 'nontrawler dolphins' never exhibited this behaviour (Chilvers & Corkeron 2001). 'Trawler' and 'nontrawler' dolphins were almost never observed associating even though their core spatial habitats overlapped substantially (Chilvers & Corkeron 2001).

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Since then, there have been significant changes to the management and fisheries legislation of Moreton Bay, owing to the implementation of the 1999 Trawl Management Plan (TMP; [State of Queensland 2008a](#)) and the 1997 Moreton Bay Marine Park Zoning Plan (MBMP Zoning Plan; [State of Queensland 2008b](#)). The TMP applied protected area and seasonal and weekend closures, limited entry to the fishery and restricted numbers of fishing days/nights per vessel ([State of Queensland 2008a](#)), which has led to an almost 50% reduction of fishing effort. In 1999, 1253 tonnes of seafood were caught by 182 trawling vessels on 17 471 effort days in Moreton Bay, but by 2005, trawl effort had nearly halved to 9390 days, with 103 boats catching 742 tonnes ([DAFF 2012](#)). Furthermore, the MBMP Zoning Plan divided the bay into a series of general use and protected zones ([State of Queensland 2008b](#)). Trawling is now banned in all but the general use zones, which are mostly situated in the central/northern and offshore areas of the marine park. Most of the area included in [Chilvers & Corkeron's \(2001\)](#) study, which covered only the southern bay, is now protected ([State of Queensland 2008b](#)).

Using association and social network analyses, we investigated the social structure of bottlenose dolphins during trawling (1997–1999) and after reduction of trawling activities (2008–2010) in Moreton Bay. We addressed the question of whether changes in trawling activities had an effect on the dolphins' association patterns and social network connectivity and structure. In particular, we compared the level of associations between individuals, and connectedness across the social network for each of the two study periods (1997–1999 and 2008–2010), by calculating association indices and social network metrics. Structuring and potential clustering into communities were assessed and compared between the study periods using modularity analysis and network diagrams. We further analysed how the association patterns of any individuals identified in both study periods changed over the 11-year interval.

METHODS

Social analyses were conducted for two data sets of sighting records of photographically identified ([Würsig & Jefferson 1990](#)) individual bottlenose dolphins in southern Moreton Bay: one collected in 1997–1999 ([Chilvers & Corkeron 2001](#)) and a more recent one collected over the period July 2008–March 2010. Both data sets were collected in daylight hours during regular systematic boat-based surveys over 2 years covering both summer and winter seasons. In 2008–2010, boat-based surveys of bottlenose dolphins in Moreton Bay (27°00'–27°35'S, 153°00'–153°27'E) were conducted over a total of 86 survey days throughout four field seasons, each of 3 months duration (24 days in winter 2008, 21 in summer 2009, 26 in winter 2009, 15 in summer 2010). Surveys followed predetermined zigzag line transects designed to optimize sampling coverage of all areas and habitat types throughout all of Moreton Bay (ca. 1300 km²). Each dolphin group encountered was followed for a maximum of 2 h. During this time we attempted to identify each individual dolphin photographically using a Canon EOS 400D digital SLR camera with a Canon 90–300 mm zoom lens. In comparison, the previous study was conducted over 89 days between July 1997 and August 1999 and covered a smaller area of ca. 350 km² in southeastern Moreton Bay ([Chilvers & Corkeron 2001](#); [Fig. 1](#)). Identification photographs were obtained using a Nikon FM2 camera with 300 mm lens or a Minolta 500i camera with 100–400 mm zoom lens and Ektachrome 100 slide film ([Chilvers 2001](#)). Only high-quality photographs (based on focus, contrast, angle and distance to animal) from both studies were used to identify individuals based on the size, shape, location and pattern of notches on the trailing and leading edges of the dorsal

fin, and dorsal and lateral body markings ([Würsig & Jefferson 1990](#)). Sex of identified individuals was determined genetically if a biopsy skin sample of the individual was available (for 2008–2010 data set only), by screening DNA against ZFX and SRY primers ([Gilson et al. 1998](#)). In addition, adults continuously and closely accompanied by a calf were classed as female (for both data sets).

Both data sets (1997–1999 and 2008–2010) were restricted to include only adult individuals seen on at least five different occasions to reduce bias introduced by low resighting rates ([Whitehead 2008b](#)). These restrictions resulted in the 1997–1999 data set comprising 50 individual adults: 13 'nontrawler' and 37 'trawler' dolphins. The 2008–2010 data set included 42 adults. The mean number of sightings per individual was higher for the 1997–1999 data set, during which individuals were seen a mean \pm SD of 10.5 ± 5.1 times compared to 6.5 ± 1.7 sightings per individual for the 2008–2010 data set. Despite the much larger study area surveyed in 2008–2010, sightings of individuals seen at least five times were all in the southeastern parts of the bay and, since this overlapped for the most part with the 1997–1999 study area ([Fig. 1](#)), the data sets were considered comparable.

Bottlenose dolphins were recorded as 'associated' with others based on school membership, which was defined as individuals clustered within an area of approximately 100 m radius, showing similar and/or coordinated behaviour ([Wells et al. 1987](#)). If new individuals joined the group during sampling, these were also considered as 'associated' with the original group members. The sampling period was set as 1 day, that is, resightings of the same group on the same day were counted only once. We used the half-weight association index (HWI; [Cairns & Schwager 1987](#)) to estimate the strength of the relationship for each pair of individuals. HWI ranges from 0 to 1 indicating the proportion of time a pair of individuals is associated (0 = never, 1 = always). To test whether our data accurately described the social structure of the dolphins, we calculated the social differentiation (*S*) as the variation among pairs of individuals in terms of time actually spent together, and the correlation between true and estimated association indices (*r*; [Whitehead 2008b](#)) using SOCPROG 2.4 ([Whitehead 2009](#)). *S* is calculated as the coefficient of variation of estimated association indices minus an estimate of the sampling variance, where values of less than 0.3 indicate a homogeneous society, greater than 0.5 a variable society and greater than 2.0 an extremely differentiated society ([Whitehead 2008b](#)). The Pearson correlation coefficient *r* indicates the power of the analysis to detect the true social system, with *r* values approaching 1 indicating a good representation, and values around 0.4 a moderate representation of social structure ([Whitehead 2008b](#)).

Association Patterns and Network Metrics

To assess whether association patterns and network connectedness changed with changes in trawl activities, we compared the mean and maximum individual HWI during trawling (1997–1999) and after reduction of trawling (2008–2010) using SOCPROG 2.4 ([Whitehead 2009](#)). The social network measures of Strength, Reach, Clustering Coefficient and Affinity were calculated in SOCPROG 2.4 ([Whitehead 2009](#)). Geodesic Distance was calculated using UCINET 6 ([Borgatti et al. 2002](#)). These measures describe different aspects of connectedness across the network. Strength is a measure of the connections (or gregariousness) of an individual calculated as the sum of all of its HWI. Reach takes into account indirect connections of an individual through intermediate associations. The Clustering Coefficient describes how well associates of one individual are themselves associated. Affinity measures how strongly an individual is associated to others with high strength ([Whitehead 2008a](#)). Geodesic Distance provides an indication of how closely

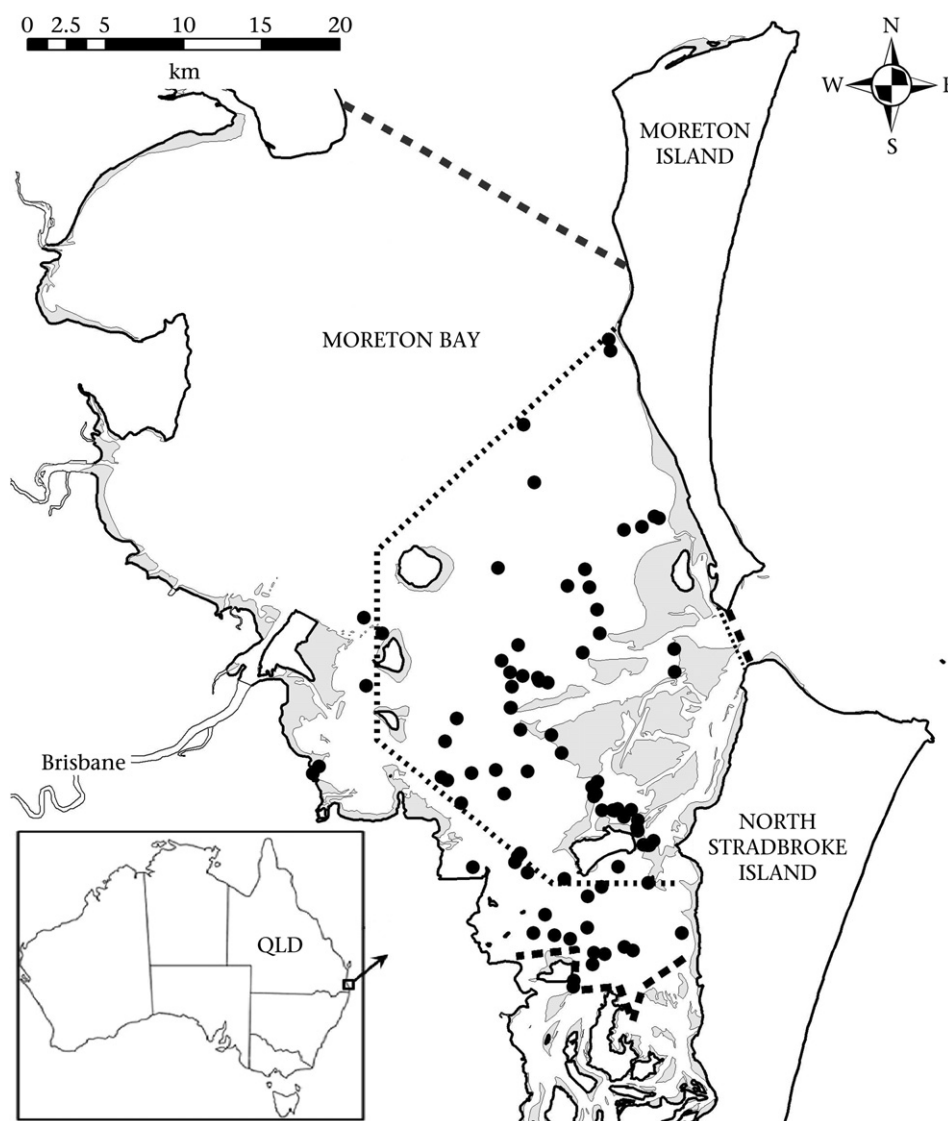


Figure 1. Map of Moreton Bay, Queensland (QLD), Australia (inset) showing study area (dashed lines) and sightings (black dots) of individuals seen on at least five occasions in 2008–2010, as well as the smaller study site (dotted lines) of the 1997–1999 study (after Chilvers & Corkeron 2001).

connected all members of the social network are, or in other words, how long it would take for information to spread from one individual throughout the entire network, and is calculated as the number of associations in the shortest path between two individuals (Croft et al. 2008). The means of these measures were compared between the two data sets using two-sample permutation tests (Good 2005) with 1000 permutations in R (R Development Core Team 2010), to assess and compare levels of associations and connectedness between individuals.

Social Network Structure

For the 1997–1999 data set, mean association rates were calculated for members of each community ('trawler' and 'non-trawler') and a two-tailed Mantel test was used to assess whether association rates were similar between and within communities. Potential subgrouping within the 2008–2010 network was explored using analyses of modularity (in SOCPROG 2.4; Whitehead 2009), which divide the population into communities (clusters) that have higher association indices between members of the same

cluster than expected by chance using the eigenvector-based method of Newman (2004). This method aims to optimize values of modularity (Q) over possible divisions of the network, where Q is the number of associations within communities minus the number of such associations expected by chance. Q values above 0.3 are generally considered to present a meaningful description of the data (Newman 2004). The distribution of associations was also examined within and between sex classes (excluding individuals of unknown sex) and a two-tailed Mantel test was used to test whether association rates were similar between and within sexes. Social network diagrams were drawn using a spring embedding layout showing all associations with HWI > 0.1, in the program NetDraw (included in UCINET 6; Borgatti et al. 2002).

Resighted Individuals

We compared the photoidentification catalogues of the two study periods to investigate whether any of the 242 individuals identified by Chilvers & Corkeron (2001) in 1997–1999 were still present in the study area in 2008–2010 and, if so, how their social

associations had changed and, consequently, their current positions in the social network. To investigate whether these dolphins still associated more with members of their own former community than members of the other community, another association analysis of the 2008–2010 data set was conducted, restricted to all matched former 'trawler' and 'nontrawler dolphins' seen at least twice in the 2008–2010 study. The minimum number of resightings was reduced to two for this analysis to increase sample size of matched individuals. A Mantel test was used to test for differences in association rates between and within communities, using SOC-PROG 2.4 (Whitehead 2009).

Ethical Note

This study uses data previously published (Chilvers & Corkeron 2001) as well as a newly collected data set. The latter data were collected under permits from the Queensland Government Environmental Protection Agency (WITK04729707), the Queensland Parks and Wildlife Service (QS2008/CVL1413) and under approval by the University of Queensland Animal Ethics Committee (SVS/622/08/OPCF and SVS/350/10/WV SCOTT FOUNDATION). Research was conducted on wild, free-ranging bottlenose dolphins. Each dolphin group encountered was approached slowly and followed for a maximum of 2 h to reduce disturbance. During this time, attempts were made to obtain identity photographs of all members of the group. If dolphins displayed boat avoidance behaviour (repeatedly changing direction away from the research vessel upon approach), follows were terminated. Biopsy samples used for sex determination were collected employing a remote biopsy system specifically designed for small cetaceans (PAXARMS, Krützen et al. 2002). This system uses a modified 0.22 calibre rifle with a detachable barrel and a valve to adjust pressure in the chamber, and a floating plastic biopsy dart with a stainless steel cutting head. It is arguably the safest, most straightforward, cost-effective and commonly used method of obtaining small skin and blubber samples from wild dolphins. It has been shown to cause only mild short-term reactions by the animals and biopsy wounds heal quickly and without complications (Krützen et al. 2002). To reduce stress to the animals, any individual was followed for a maximum of 20 min while attempting to obtain a biopsy sample. Samples were not collected from mothers or dependent calves.

RESULTS

Association Patterns and Network Metrics

School sizes of bottlenose dolphins encountered during surveys in 2008–2010 ranged from one to 35 individuals (mean \pm SE = 6.4 ± 0.51). This average school size falls between observed school sizes of 'trawler' (range 1–45, 11.5 ± 0.95) and 'nontrawler dolphins' (1–20, 4.5 ± 0.20) in 1997–1999 (Chilvers 2001).

Estimates of the correlation between true and estimated association indices indicated reasonably good representations of the true social systems for both sampling periods (1997–1999: $r \pm$ SE = 0.83 ± 0.02 ; 2008–2010: $r \pm$ SE = 0.67 ± 0.06). The social structure of bottlenose dolphins was more highly differentiated in the 1990s than a decade later (1997–1999: $S \pm$ SE = 1.58 ± 0.22 ; 2008–2010: $S \pm$ SE = 0.95 ± 0.19).

Associations between individuals were stronger in 2008–2010 than in 1997–1999: both the overall mean individual HWI and the mean maximum individual HWI increased significantly over this period (Table 1). Mean Strength, Reach, Clustering Coefficient and Affinity were all significantly higher in the 2008–2010 social network than in 1997–1999 (Table 1). The Geodesic Distance

Table 1

Social network metrics of bottlenose dolphins in 1997–1999 (during trawl fishery) and 2008–2010 (after cessation of trawl fishery)

Metric	1997–1999 N=50	2008–2010 N=42	P
Mean individual HWI	0.09 \pm 0.06	0.16 \pm 0.07	<0.001
Maximum individual HWI	0.53 \pm 0.22	0.72 \pm 0.22	<0.001
Strength	4.52 \pm 2.92	6.37 \pm 3.03	0.002
Reach	28.83 \pm 22.14	49.57 \pm 30.42	<0.001
Clustering Coefficient	0.26 \pm 0.10	0.33 \pm 0.06	<0.001
Affinity	5.47 \pm 2.07	7.12 \pm 1.83	<0.001
Geodesic Distance	2.15 \pm 0.54	1.84 \pm 0.28	<0.001

N = number of individuals; HWI = half-weight association index. Data are presented as mean \pm SD. P values are from a two-sample permutation test.

between individuals decreased significantly (Table 1), indicating a more compact social network in 2008–2010.

Social Network Structure

Associations among dolphins within the two communities identified in 1997–1999 had a mean \pm SD HWI of 0.15 ± 0.08 within 'trawler dolphins' and 0.14 ± 0.08 within 'nontrawler dolphins'. However, mean HWI between the two communities was only 0.004 ± 0.01 , supporting the observation that associations between members of the two communities were almost nonexistent, that is, dolphins associated significantly more within than between communities (two-tailed Mantel test: $t = 8.83$, $P = 1.0$). The network diagram for 1997–1999 (Fig. 2a) shows distinct clustering into 'nontrawler' and 'trawler' communities with very few connections between the two.

The 2008–2010 social network did not show conclusive partitioning into separate communities (Fig. 2b). Modularity analysis assigned individuals to four clusters with significantly higher associations within than between clusters (two-tailed Mantel test: $t = 16.88$, $P = 1.0$). However, the modularity (Q) of this assignment was only 0.298 indicating only a marginally useful community division (Newman 2004). Thus, while some substructuring was present, the marked partition of the network into two communities ('trawler' and 'nontrawler') was no longer apparent. Associations were also not significantly different between and within sexes (Mantel test: $t = 0.58$, $P = 0.72$). Mean HWI \pm SD was 0.14 ± 0.08 between females ($N = 18$), 0.17 ± 0.09 between males ($N = 11$) and 0.11 ± 0.07 between members of opposite sexes.

Resighted Individuals

In total, 39 individuals were common to both photo-identification catalogues compiled in 1997–1999 and 2008–2010, comprising 20 former 'trawler dolphins' and 19 former 'nontrawler dolphins'. Eight of these individuals (three 'trawler' and five 'nontrawler dolphins') were seen on at least five occasions in the recent study; and thus were included in the analysis of the 2008–2010 social network. From the position of these individuals (indicated as larger nodes) in the network diagram (Fig. 2b), it was apparent that both former 'trawler' as well as former 'nontrawler' dolphins were spread out over the entire 2008–2010 network and associating with each other, rather than clustering together. Of these eight, two individuals (highlighted with arrows in Fig. 2) had also been sighted at least five times in the earlier study and were thus present in both social network analyses. These were a female former 'nontrawler' dolphin (dark grey arrow) and a male former 'trawler' dolphin (light grey arrow). The 'trawler' male's social behaviour had undergone substantial changes over the intervening decade

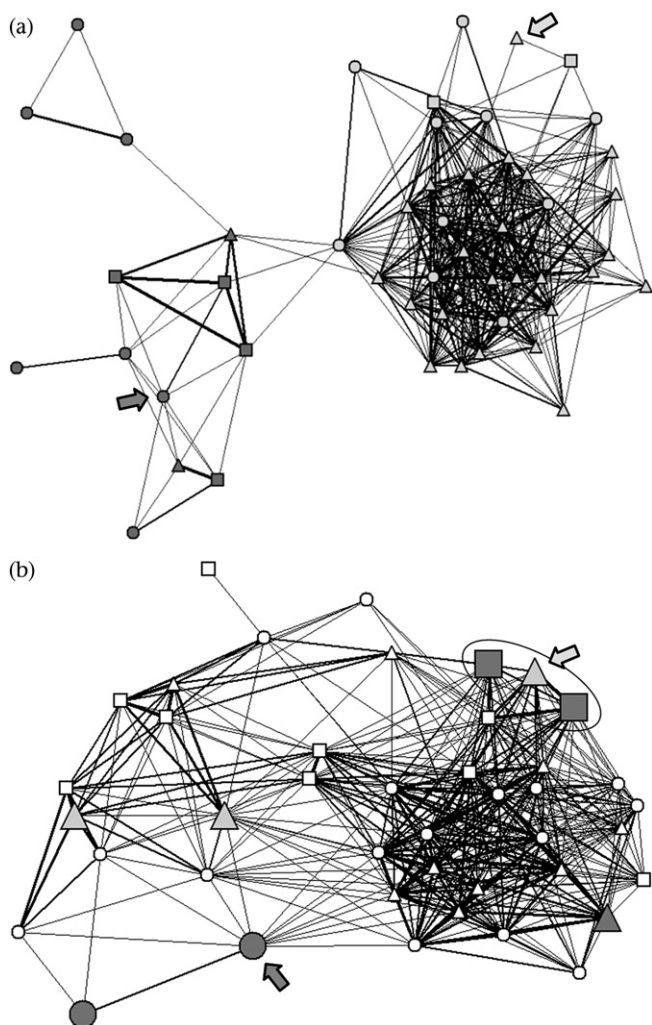


Figure 2. Social networks of bottlenose dolphins in southern Moreton Bay (a) during trawl fishery, 1997–1999 and (b) after cessation of trawl fishery, 2008–2010. Symbol indicates sex (■ = male, ● = female, ▲ = unknown). The thickness of the line between pairs of individuals indicates the strength of their association (HWI). ‘Trawler dolphins’ are represented by light grey, ‘nontrawler dolphins’ by dark grey symbols. Eight resighted former ‘trawler’ and ‘nontrawler dolphins’ are represented by enlarged nodes in (b) and shaded light or dark grey according to former community membership. Of these eight, two individuals (highlighted with arrows) had been sighted at least five times in both studies and were thus included in both social network analyses. The encircled individuals in (b) highlights a case of closely associated former ‘trawler’ and ‘nontrawler dolphins’.

(Fig. 2). He had 21 direct associates in 2008–2010, compared to only two in 1997–1999, his HWI rose from a mean \pm SD of 0.01 ± 0.03 with maximum association strength of 0.20 in 1997–1999 to a more than 10-fold higher mean of 0.18 ± 0.23 with a maximum of 0.91 in 2008–2010. He had also formed strong bonds (with HWI of 0.55 and 0.83) with two former ‘nontrawler dolphins’ (circled in Fig. 2b).

Furthermore, we found that the 12 former ‘trawler’ and 16 former ‘nontrawler dolphins’ seen at least twice in 2008–2010 did not associate significantly more with members of their own former community than with members of the other community: mean association indices were not significantly different within or between former communities (two-tailed Mantel test: $t = 0.18$, $P = 0.57$); mean HWI \pm SD was 0.06 ± 0.03 within the ‘trawler’ community, 0.06 ± 0.04 within the ‘nontrawler’ community and 0.06 ± 0.05 between the two communities.

Of the 20 former ‘trawler dolphins’ resighted during the 2008–2010 study, only one appeared to have shifted its distribution to the current trawl area and was observed following a prawn trawler in northwestern Moreton Bay. In contrast, the majority (14 of 20) of resighted ‘trawler dolphins’ were still only found in the southern bay where trawling no longer occurs.

DISCUSSION

In the late 1990s, the bottlenose dolphins in southern Moreton Bay were structured into two discrete social communities (‘trawler’ and ‘nontrawler’ dolphins), with almost all associations occurring within rather than between these communities. Significant changes have subsequently occurred in the management and fisheries legislation of Moreton Bay, resulting in a substantial reduction (ca. 50%) of the trawling effort in the bay during the last decade. Our comparative analysis of association patterns and social networks of bottlenose dolphins in Moreton Bay (11 years apart) shows that their social structure changed significantly after the reduction of trawling. The society has become less differentiated (lower social differentiation S) with no marked division into two separate communities, but more compact (lower average distance between individuals) with more and stronger associations (significantly higher association indices). Network metrics including Strength, Clustering Coefficient, Reach and Affinity were all significantly higher in the 2008–2010 network, which is consistent with the merging of the two communities into one more well-connected network: former members of different communities were now interacting, which increased the number of each individual’s associates and thus Strength, Reach and Affinity. These results are not merely an artefact of different mean resighting rates per individual between the two data sets. The average number of sightings per individual was higher for the 1997–1999 data set than in 2008–2010, thus one might expect higher network measures (such as Strength) in the 1990s because animals were seen more often, increasing the potential number of associates they could have been seen with. However, the opposite was observed here, with higher network measures in 2008–2010 despite lower sighting numbers. These current (2008–2010) association and social network patterns are similar to those described for bottlenose dolphin (*Tursiops* spp.) populations elsewhere, which are typically characterized as highly connected and dynamic fission–fusion societies (Wells et al. 1987; Connor et al. 2000b; Gero et al. 2005; Foley et al. 2010).

Animal social systems are thought to be shaped by the trade-off between the advantages gained from group living (such as cooperating to acquire resources or predator defence) and the costs incurred (such as competition for resources between group members; Wrangham 1980). The specific costs and benefits shaping any given animal society are largely dependent on the ecological environment, including predation risks, and resource availability and distribution (Wrangham 1980; Isbell 1991; Van Schaik 1999). 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 (Corkeron et al. 1990). With the loss of this artificial food source, individual dolphins who foraged in association with trawlers possibly faced a more patchy and irregular distribution of prey. When resources are spatially and temporally variable, theory predicts that dolphins should not remain resident but must instead range widely to find sufficient resources (Gowans et al. 2007). Thus, reductions in the availability of trawler by-catch might have led ‘trawler dolphins’ to range more widely within Moreton Bay and forage in areas where ‘nontrawler dolphins’ traditionally feed. These changes in resource availability and ranging patterns of

'trawler dolphins' may have resulted in (1) the formation of a larger more connected community of bottlenose dolphins in Moreton Bay and (2) animals spreading out into smaller groups to reduce intraspecific competition for food (Connor et al. 2000b).

When resources are abundant, many mammal species living in fission–fusion societies form highly clustered social networks. In contrast, scarcely distributed resources have been found to lead to the formation of one large highly connected network that may facilitate cooperation and information sharing (Cross et al. 2004; Sundaresan et al. 2007; Chaverri 2010). Higher Strength and Reach and lower Geodesic Distance as observed for the 2008–2010 dolphin network may facilitate improved flow of information (e.g. communication/social learning/cooperation) among individuals (Wey et al. 2008). The more compact and well-connected bottlenose dolphin society of 2008–2010 in Moreton Bay may benefit from increased cooperation, learning and information sharing to forage on natural food sources that are spatially and temporally variable. In contrast, the presence of trawler by-catch as an easy and readily available opportunistic source of food may have made it less necessary for dolphins to cooperate with (or learn from) a large number of conspecifics (Díaz López & Shirai 2008), resulting in a less compact and connected social network in the late 1990s.

Bottlenose dolphins are known for their wide range of foraging strategies including distinct specialized techniques (e.g. Smolker et al. 1997; Connor et al. 2000a; Torres & Read 2009). This ability to develop novel foraging techniques allowed dolphins in Moreton Bay to utilize a novel food source (trawler by-catch), which in turn may have artificially increased the carrying capacity of the population, as has been suggested for killer whales, *Orcinus orca*, scavenging on whale carcasses produced by whaling (Whitehead & Reeves 2005). Otter trawling for prawns commenced in Moreton Bay in 1952 and reached a peak in the mid-1960s (Quinn 1992). If reproductive rates and survival and consequently population size of bottlenose dolphins in Moreton Bay increased in response to the availability of trawler by-catch and subsequently decreased again when this artificial food source was reduced in the late 1990s, these changes in population size may also have affected the social structure of these animals. However, accurate and comparable estimates of population size before, during and after trawling times are unavailable, and carrying capacity has never been assessed. Thus it is difficult to assess whether and how trawling and/or its subsequent reduction may have impacted on the carrying capacity and population size of dolphins in Moreton Bay.

An alternative scenario is that the reduction of commercial fisheries may have led to increasing fish stocks and thus a greater availability of 'natural' prey for dolphins. As more prey becomes available, individuals are less likely to compete for resources, thus reducing one of the major disadvantages of group living (Wrangham 1980). Recovering fish stocks after reduction of the trawl fishery in Moreton Bay may have allowed dolphins to socialize more, as the benefits of sociality outweighed the reduced cost of competition for food.

As a fission–fusion species, bottlenose dolphins have social systems that are typically characterized by many weak and some strong associations. Subgroupings may exist, often related to sex and reproductive status (e.g. Wells et al. 1987; Lusseau et al. 2003) or individual ranging patterns (e.g. Lusseau et al. 2005; Wiszniewski et al. 2009). However, communities as distinctly segregated and apparently influenced by a single anthropogenic factor (trawling), such as the 'trawler' and 'nontrawler dolphins' present in Moreton Bay in the 1990s, have not been described elsewhere (Chilvers & Corkeron 2001). While trawling and aquaculture have also been found to influence social structure of bottlenose dolphins, *Tursiops truncatus*, off the coast of Italy, the communities of dolphins that did or did not feed on these

anthropogenic food sources were not as distinctly segregated and still associated regularly (Pace et al. 2012).

Management of human activities that impact wild animal populations has proven successful at restoring natural social systems in some instances. For example, culling of wolves, *Canis lycaon*, at the borders of Algonquin Park in Canada had led to increasing inclusion of unrelated animals in packs. However, after culling was banned, the social system of wolves returned to its natural state, characterized by packs of closely related individuals (Rutledge et al. 2010). The reduction of trawling in Moreton Bay appears to have led to a restructuring of the bottlenose dolphins' society into a more interconnected social network, which may increase information sharing and mating interactions (and thus gene flow) across the dolphin population. This is likely to be beneficial for the conservation of the bottlenose dolphins in Moreton Bay because social learning and information sharing facilitate the spread of new behaviours, allowing animals to adapt to changing environments (Whitehead 2010). Furthermore, increased gene flow makes a population more resilient than if it is fragmented into smaller subpopulations with reduced fitness owing to genetic drift and loss of heterozygosity (Allendorf 1986).

Delphinids display high behavioural and social plasticity (Connor et al. 1998). This study suggests that plasticity in behaviour and social structure is an important factor in bottlenose dolphins' ability to adapt to and exploit a wide range of environmental conditions, ranging from shallow coastal, estuarine waters (e.g. Irvine et al. 1981) to deep offshore habitats (e.g. Klatsky et al. 2007) and from tropical (e.g. Bahamas, Parsons et al. 2006) to temperate waters (e.g. Scotland, Wilson et al. 1997). At the same time, social structuring of mammalian populations may influence their rate of speciation (Bush et al. 1977). The dynamic social structure reported here, where completely segregated social groups may resume interactions as environmental conditions change, may represent one of the evolutionary processes preventing speciation. Our results support the view that social barriers to gene flow do not appear to accelerate speciation in social mammals (Storz 1999).

Complex adaptive systems can have several stable solutions, and systems that are more diverse tend to be more stable and more resilient to perturbations (Ives & Carpenter 2007). Our findings indicate that bottlenose dolphins' social structure represents such a system, making them adaptable and resilient to certain anthropogenic activities and changes in local environmental conditions.

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