SOCIAL AND BEHAVIOURAL CHARACTERISTICS OF INDO-PACIFIC BOTTLENOSE DOLPHINS (*TURSIOPS ADUNCUS*) IN NORTHERN NEW SOUTH WALES, AUSTRALIA

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Bottlenose dolphins (*Tursiops spp.*) are one of the most common genera of cetacea encountered throughout the world's tropical and temperate regions. However, there is relatively little knowledge on the populations of bottlenose dolphins in Australia. The present study assessed the pod characteristics, behaviour, movement patterns and social structure of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in coastal inshore waters off northern New South Wales, Australia, using vessel-based and land-based surveys. Dolphins spent most time travelling (38%), followed by milling (31%), feeding (19%), and socialising (12%). The mean pod size of dolphins in Byron Bay was 13 (S.D. = 12). The social foundation of this population was characterised by sexual segregation. Significant variations were found between the mean size of mother-calf pods (21; S.D. = 15) and adult-only pods (5; S.D. = 5). Two 'resident' groups of females were identified that occupied adjacent territories of between 177 km² and 320 km². 'Resident' females appeared to maintain loose associations with other 'resident' females (HWI = 0.28; S.D. = 0.66). Despite the large differences in environmental conditions, habitats and prey species, it appeared that the social organisation, movement patterns and behaviour of *T. aduncus* populations in coastal regions is similar. The Byron Bay population of dolphins is not presently heavily impacted by interactions with humans, compared to populations with regular commercial dolphin-watching operations. This means the population may provide important base-line data for assessment of potential human impacts on dolphin populations.

Key words: behaviour, bottlenose dolphin, conservation, group dynamics, photo-identification, social structure, *Tursiops aduncus*,

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Bottlenose dolphins (*Tursiops* spp.) occur throughout the world's temperate and tropical regions. Recent studies suggest that there are at least two species of *Tursiops* in Australian waters. An 'inshore' ecotype has been identified as *Tursiops aduncus* and an 'offshore' ecotype as *Tursiops truncatus* (Ross and Cockcroft 1990; Hale *et al.* 2000; Moller and Beheregaray 2001). These species show morphological, physiological and genetic differences (Cockcroft and Ross 1990; Gao *et al.* 1995; Hale *et al.* 2000; Moller and Beheregaray 2001).

Population characteristics of each *Tursiops* species differ between geographic regions and habitat types (Weigle 1990; Barco *et al.* 1999; Moller *et al.* 2002). Some dolphins migrate seasonally, while others display high site fidelity and occupy discrete home ranges within coastal regions (Shane *et al.* 1986; Scott *et al.* 1990; Wells *et al.* 1990).

Bottlenose dolphins live in complex fission-fusion societies where the composition of groups or pods may change within an hour or over a number of days, and may depend on the abundance and distribution of prey, foraging techniques, habitat type, behaviour, reproductive state, time of day and season (Shane *et al.* 1986; Bearzi 2005; Wells *et al.* 1990; Constantine and Baker 1997; Connor *et al.* 2000; Moller *et al.* 2002). Bottlenose dolphin societies are usually sexually segregated with long-term bonds more likely to be established between individuals of the same sex (Smolker *et al.* 1992; Sayigh *et al.* 1998; Connor *et al.* 2000). Females of *Tursiops* spp. frequently maintain complex social networks, which can include several discrete bands of individuals with relatively high rates of association, shared core areas and limited home ranges (Wells 1991; Scott *et al.* 1990).

Because of their iconic status, wide geographic distribution and coastal habitats, bottlenose dolphins are one of the most studied groups of cetaceans. However, there have been few detailed studies in Australia so much of their social biology and conservation status are unknown (DEH 2006). With growing human pressures in coastal regions, it is imperative that the social, ecology and biology of dolphins is understood to reduce any threats to their survival. The present study is the first that describes the social and ecological characteristics of a relatively undisturbed population of Indo-Pacific bottlenose dolphins (*T. aduncus*) in Australia, and can serve as a baseline for comparing the impacts of humans on dolphins in other studies.

METHODOLOGY

Study Site

Surveys were conducted in an area of 229 km² along a 55 km stretch of exposed coastal waters in the Byron Bay region (28º27’60”S; 28º55’50”N) of northern New South Wales, Australia (Fig. 1). Waters to five nautical miles east of the coastline were surveyed in the Cape Byron Marine Park, a biologically significant area with high biodiversity of temperate and tropical marine species (MPA 2004). The survey area was typified by frequent large swells and surf conditions. The estuaries to two rivers, the Richmond and Brunswick, were also included in the survey area. The Richmond River estuary was larger than the Brunswick and both are characterised by shallow, often treacherous sand bars across their entrances and man-made seawalls. Genetic studies have confirmed that the population of coastal bottlenose dolphins occurring in the study area are *T. aduncus* (Wiszniewski *et al.* 2005).

Data Collection

Both land-based and vessel-based surveys were conducted during intensive seasonal surveys between autumn 2003 and summer 2006. Recordings of dolphin behaviour from four land-based vantage points were conducted along the coastline during five hour observation periods between 0700 and 1300. The vantage points were at the Cape Byron Lighthouse, Broken Head, Lennox Headland and the Ballina break-water. To assist in recording data, the area of sea observed from each vantage point was divided into grids so that the location of dolphins and vessels could be recorded more

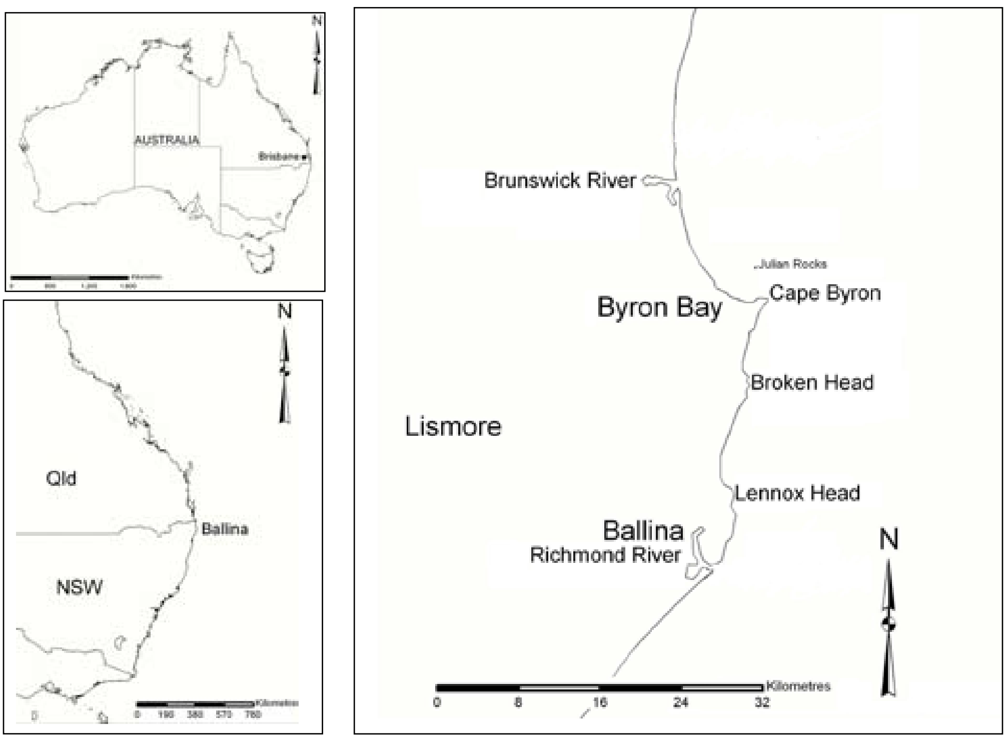

Fig. 1. Byron Bay, New South Wales, Australia survey area (Map courtesy of Greg Luker, Southern Cross University, 2006)

precisely. Landmarks and cues such as rock bommies and outcrops were used as grid boundary markers.

Two boats were used at different times to conduct vessel-based surveys: a 6 m aluminium hull motor vessel and a 12 m Caribbean van-der-stat sailing yacht. Surveys using the motor vessel were conducted between 0700 and 1500. Survey times conducted from the yacht were dependent on tidal conditions to enable the crossing of the Richmond River bar. Yacht surveys were carried out over periods of three to eight hours between 0700 and 1700. During survey periods the vessels moved along pre-set transects within the study area. When a pod of dolphins was sighted, the vessel diverted from the transect and began a one-hour 'focal follow', that is, the vessel followed one pod for one hour. Individual dolphins were photographed to provide a visual identification system based on physical characteristics during pod focal follows. Photographs were taken with a Nikon SLR D100 digital camera with 70–300 mm lens, except during the 2003 season where photographs were taken using a Minolta SLR camera with 400 iso film with 70–300 mm lens.

Land-based and vessel-based surveys were only conducted in weather conditions where the wind did not exceed 25 knots, swell was <2 m and Beaufort (sea state) conditions were three or less (on a scale of 12). Observations of time, pod location, pod composition, behaviour of dolphins, weather conditions and behaviour of the research vessel were manually recorded onto data sheets. When a pod of dolphins was sighted, dolphin behaviour was continuously recorded during one-hour focal follows on the vessels and for the duration a pod could be seen from land-based sites.

A pod or 'focal group' was defined as – *'any group of dolphins (of the same species) observed in association, moving in the same direction and usually engaged in the same activity'* (Shane 1990a). This definition was extended to encompass all dolphins within a 100 m radius which included all dolphins that may have been engaged in different behaviours but were in the same pod. For example, a group of juveniles may have been socializing and the rest of the group may have been feeding within a 20 m radius. The pod composition was described by the number of adults, sub-adults, juveniles, calves and unknowns. Adults were identified by their relative length, ventral speckling (if present) or presence of a calf in proximity. Sub-adults were identified by their size relative to an adult and by their behaviour. Juveniles and calves were identified by their relative size and close proximity to their mothers. Calves and juveniles were frequently observed in infant (i.e. when the calf swims between the dorsal fin and the tail of its mother) or echelon position (i.e. when the calf swims between the dorsal fin and the eye of its mother). Individuals of unidentified age class were included in the unknown category.

Data Analysis

Behaviour

Four behavioural states (Altmann 1974) were identified and defined as milling, travelling, socialising and feeding (Table 1). The percentage of time dolphins were engaged in the four behaviour states - feeding, milling, socialising and travelling, on a daily basis were estimated using land-based survey data. Statistical tests were conducted using SPSS v. 11.0 (SPSS Inc. 1989-2002).

Home Ranges and Social Structure

Capture histories (number of times an individual dolphin was identified) from photo-identification data were used to estimate the home ranges of 'resident' dolphins. Dolphins 'captured' between two and 10 or more occasions were labelled 'residents' within the survey area and were the only individuals included in this analysis. Sighting locations of 'resident' individuals were considered to define the home ranges of their social groups or communities. The home ranges of

BEHAVIOUR STATE	DESCRIPTION
TRAVELLING	Dolphin moves consistently in a defined direction; often with consistent dive times
SOCIALISING	When two or more dolphins clearly interact with each other; making frequent physical contact and are surface active.
MILLING	Dolphins frequently change travel direction, slowly swim and rest whilst remaining within a particular area.
FEEDING/FORAGING	Dolphins are clearly involved in the pursuit of prey and feeding; behaviour events will vary depending on the techniques being used; deep dives, fast swims and porpoising may be observed.

Table 1: Ethogram of behaviour states.

these 'residents' were estimated using Kernel Analysis in Home Range Tools for ArcGIS 9.0 (Rodgers and Carr 1998).

The social dynamics and association patterns of 'resident' individuals were modelled using SocProg v 2.2 (Whitehead 2005b). Only individuals from waters adjacent to Cape Byron were used in this analysis because no individuals from the Ballina area were captured on ≥5 or more occasions.

Examination of the social dynamics and association patterns of individuals within the 'resident' Cape Byron group were expressed as association indices: an expression of the proportion of time individuals were seen together (Whitehead 1997). Values of association indices vary between 0 (individuals never observed associating) and 1 (individuals always observed together). Therefore, the higher the association index value, the higher the association level or proportions of time two individuals spent together (Cairns and Schwager 1987).

The Half Weight Index (HWI) (Cairns and Schwager 1987) is the most commonly used method for expressing association indices in biological studies. To ensure compatibility with other research on *Tursiops spp.* and reduce bias, the HWI method also was used to test the association patterns of resident dolphins in the Byron Bay area. The HWI may be expressed as:

$$HWI = \frac{X}{X + Yab + \frac{1}{2}(Ya + Yb)}$$

Where *X* is the number of pods in which individual *a* and *b* were observed together; *Ya* is the number of pods individual *a* was not sighted with *b*; *Yb* is the number of pods individual *b* was not sighted with *a*; and *Yab* is the number of pods in which dolphins *a* and *b* were seen together.

In HWI calculations, the numbers of sightings of individuals are averaged, unlike simple ratio analysis where values are summed. Therefore in HWI analysis, values for association tend to be overestimates and caution must be exercised in interpretation (Ginsberg and Young 1992).

In order to test if the association rates calculated by HWI analysis were due to random association or preferred/avoided association between individuals, further examination of the data was conducted (Whitehead 1999). Tests for preferred/avoided associations in SocProg v. 2.2 were used to assess if there was an equal probability of association between all individuals (Whitehead 2005a). These tests used random permutations to test the hypothesis that there were no preferred companions between sampling periods (Whitehead 2005a). For this analysis, 1000 permutations of associations within samples were conducted. SocProg's preferred/avoided tests were also used to test if the variation of real association indices was no greater than would be expected from random association between dyads or pairs of individuals.

RESULTS

Survey Effort

The total duration of vessel-based and land-based surveys in the study was 821 hrs 19 mins, comprising of 507 hrs 23 mins of land-based observations and 313 hrs 56 mins vessel-based observations. A total of 9975 sightings of individual dolphins and 779 sightings of pods were observed.

Pod Sizes and Characteristics

Pod sizes varied between one and approximately 200 individuals. The mean pod size was 13 individuals (total number of individuals = 9975; total number of pods = 779; S.D. = 12). Spring 2004 and summer 2004/5 had the largest pod sizes (mean = 22, S.D. = 8.4; mean = 14, S.D. = 5.5 respectively) and the lowest size was observed during autumn 2004 (mean = 4; S.D. = 3.7).

The number of dolphins sighted per day varied between seasons with the largest number per day observed during summer 2004/05 (77 dolphins/day; S.D. = 12.7) and the lowest during autumn 2003 (18 dolphins/day; S. D. = 8.6). The mean number of dolphins sighted per day during the study was 60 (S.D. = 33.2).

The mean number of pods sighted per day during the study was four (S.D. = 0.7). The highest mean number of pods per day was observed during summer 2003/4 (6 pods/day; S.D. = 2.7) and the lowest was observed during spring 2004 (3 pods/day; S.D. = 1.2).

Throughout this study, 219 pods were composed of mothers and calves. Mean mother-calf pod sizes were 21 individuals (N = 4691; Npods = 219; S.D. = 15.1) and were significantly larger ($p < 0.01$), than adult-only pods that had a mean of around five individuals (N = 693; Npods = 123; S.D. = 5.5). Pod sizes varied between seasons and years. During the warmer seasons of summer 2003/4 and summer 2005, the mean mother-calf pod size was largest (mean 28 individuals, S.D. = 9.8; mean 25 individuals, S.D. = 9.5 respectively) whereas autumn 2003 and spring 2004 had the smallest mother-calf pod sizes (mean 6 individuals, S.D. = 4.4; mean 10 individuals, S.D. = 10.2 respectively) (Fig. 2). Conversely, adult pod sizes showed little variation between seasons. The largest adult only pods were observed during autumn 2003 (mean 6 individuals; S.D. = 5.1) and the lowest was observed during winter 2004 (mean 4; S.D. = 2.5).

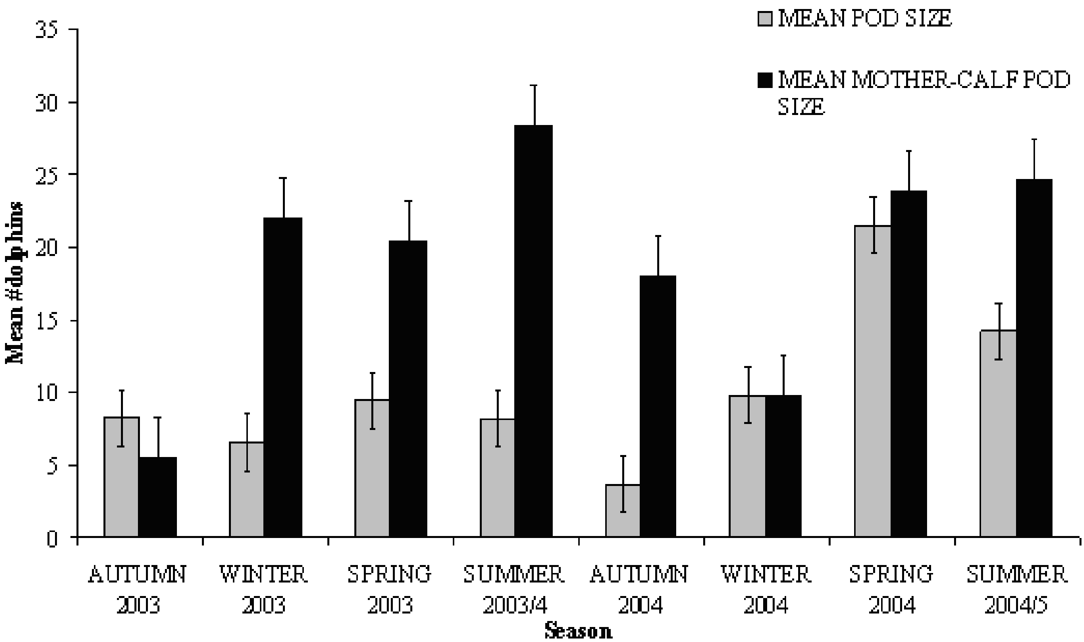

Fig. 2: Mean pod sizes and mother-calf pod sizes observed per season with standard error bars.

Behaviour

During land-based surveys conducted between 0700 and 1300, travelling (38%) and milling (31%) were the most frequently observed behaviour states followed by feeding (19%) and socialising (12%). Ten land-based surveys were conducted in the afternoon between 1200 and 1800 during 2003. During these afternoon surveys, 25 pods were observed. Feeding was observed most frequently (37%) during afternoon surveys, followed by travelling (31%), milling (25%) and socialising (7%). Observations conducted during the afternoon were made difficult by increased wind and poor lighting conditions creating increased difficulty in accurate dolphin sightings. Because of these factors, no further

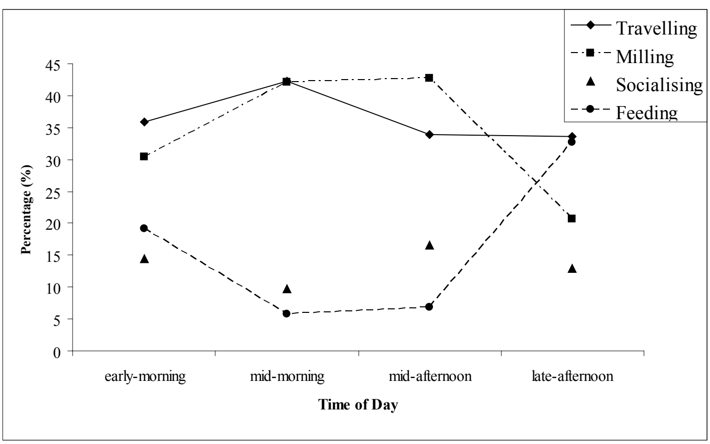

Fig. 3: Percent occurrence of behaviour states during four time periods; early-morning (7.00 am-10.00 am), mid-morning (10.01 am-12.00 pm), mid-afternoon (12.01 pm-2.00 pm) and late-afternoon (2.01 pm-5.0 pm).

land observations were made during the afternoon for the remainder of the study.

Using data from all land site observations it was apparent that the occurrences of different behaviour states varied throughout daylight hours (Fig. 3). Pearson's Chi-Square tests indicated that there were significant differences between the occurrences of behaviour states at different times of day ($P < 0.0001$). There were two daily peaks in feeding behaviours: during early-morning ($N = 283$; 19%) and during late-afternoon ($N = 38$; 33%). Milling was more likely to occur mid-morning ($N = 565$; 42%) and mid-afternoon ($N = 213$; 42%) dropping in the early-morning ($N = 449$; 30%) and late-afternoon ($N = 24$; 21%). A peak in socialising was observed during mid-afternoon ($N = 83$; 17%). A peak in travelling behaviours was observed during the mid-morning ($N = 567$; 42%).

The occurrence of behaviour states varied between seasons and years. Regression analysis indicated there was a strong relationship between the occurrence of feeding between seasons ($R = 0.89$, $df = 6$, $\alpha = 0.05$) with the highest percentage observed during winter 2003 (47%). There was a weak relationship between the occurrence of milling and seasons ($R = 0.09$, $df = 6$) with the highest percentage observed during autumn 2004 and summer 2004/05 (40% and 36% respectively). There was a strong relationship between the occurrence of socialising ($R = 0.93$, $df = 6$) and travelling behaviours between seasons ($R = 0.98$, $df = 6$). The highest percentage of socialising was observed during summer 2004/5 (26%). A peak in travelling behaviours was observed during summer 2003/4 (47%). These results suggested that there is a general change in the occurrence of different behaviour states between seasons.

Home Ranges of 'resident' Dolphins

Twenty-six individual dolphins were photographed between two and 10 occasions. All of these were adults and were assumed to be females as they were observed in the company of calves on ≥1 occasion. Two distinct ranges of two adjacent 'resident' groups were identified around Cape Byron and Ballina (Fig. 4). Dark toning within the contours of the estimated home range indicated 'core' areas of usage which was determined by the area where the highest number of sightings was made. Six individuals were identified as Ballina 'residents' and 17 as Cape Byron 'residents'. There appears to be an overlap in the ranges of the two resident groups south of Lennox Head. Three individuals were sighted at both Ballina and Cape Byron. These individuals were eliminated from this section of the analysis because they could not be assigned to one or other group. One individual was 'captured' on four occasions in Byron Bay and twice in the Ballina area. Another individual was 'captured' on four occasions in Ballina and once in Byron Bay. This suggests that there is likely to be some intermixing by a few individuals between the Cape Byron and Ballina 'resident' groups.

The home range area of Ballina residents is estimated to be 177 km² while the Cape Byron resident home range is around 320 km², so it appears that the home range of Cape Byron's resident dolphins' is much larger than for Ballina. This may be due to the arbitrary boundaries of the survey area (it is probable that the Ballina residents are travelling south outside the survey area boundary) and the low number of dolphins 'captured' five or more times in Ballina (all Ballina residents were observed between two and five occasions compared to Cape Byron where all residents were observed on more than five occasions). Because of these methodological restrictions, home ranges are likely to be larger than those estimated here.

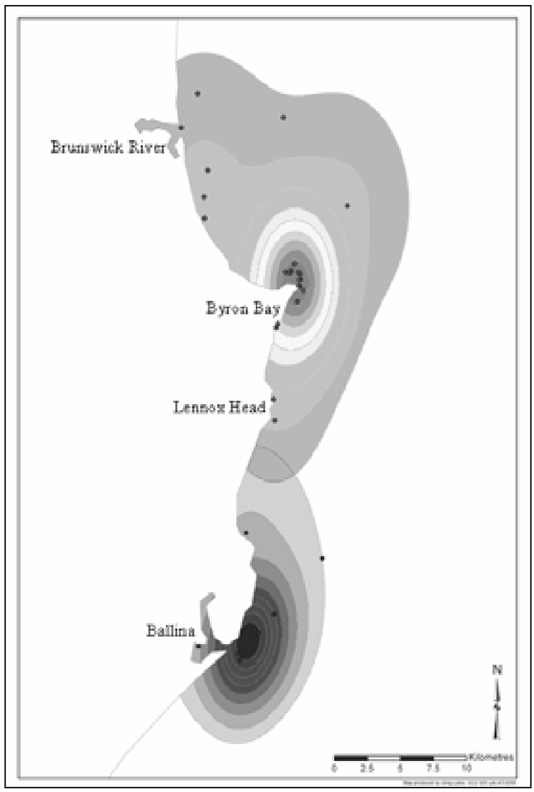

Fig. 4: Map of Cape Byron and Ballina residents estimated home ranges (Note: Ballina 'residents' are represented the circular contours shaded in the south and Cape Byron 'residents' by circular contours of shading in the north). The dots ($N = 95$) represent locations where resident individuals were sighted during vessel surveys (some of which were in the same location)).

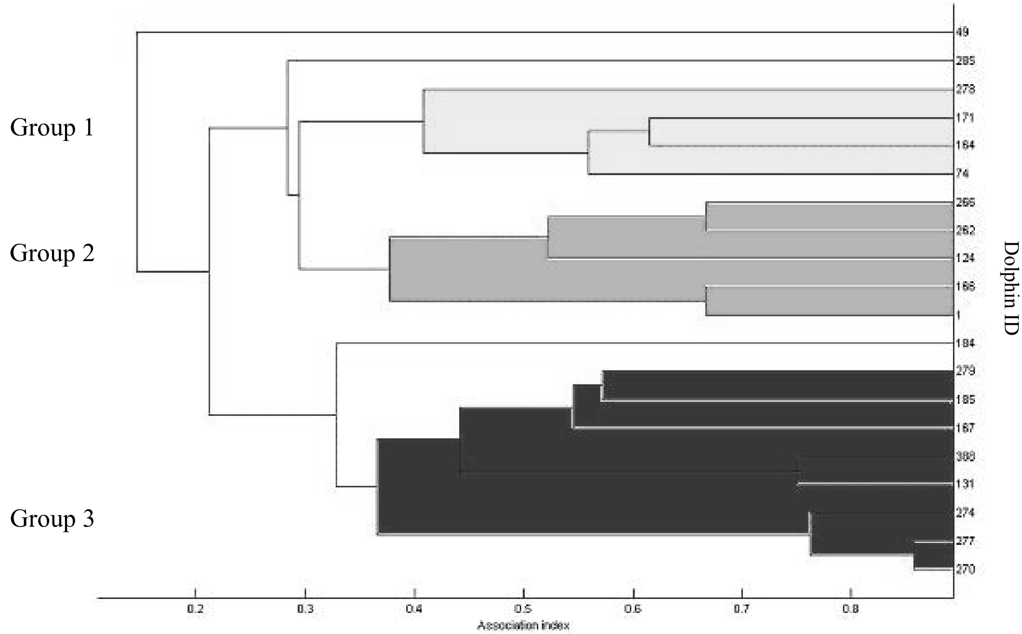

Fig. 5. A Hierarchical Cluster analysis of Half Weight Index of association between resident Cape Byron dolphins (Note: shading represents groups with higher association values).

Social Structure

Twenty individuals were identified on five or more occasions (range: 5–13) in waters adjacent to Cape Byron (as determined from home range analysis). All of these individuals were adult females as all were observed in association with calves on ≥1 occasions.

The mean Half Weight Index (HWI) of individual association is 0.28 (S.D. = 0.06). Hierarchical cluster analysis shows three distinct groups of close associations (HWI ≥ 0.45) (Fig. 5). Dolphins 49 and 285 appear to have loose associations with numerous individuals from multiple groups. This is indicated by their low HWI and separation from the clustered groups in the statistical analysis. Dolphin 49 was observed associating with individuals from social groups one and three. Dolphin 285 was observed associating with individuals from one and two. Dolphin 184 also had loose associations with individuals from group one and dolphin 49. Dolphin 184 had been observed in the Ballina survey area on two (of six) occasions. No other individuals included in this analysis were observed at Ballina.

Tests of preferred/avoided associations (using 1000 permutations) show that differences between the real and random association indices values is small, indicating that preferred associations are not significant and social bonds between most individuals appear to be weak (Table 2). Real and random non-zero elements of preferred/avoided association tests indicate that most individuals do not avoid others. Results of two-sided significance tests between dyads indicated that the number of significant dyadic associations (one) was lower than the expected number of associations (9.5) and therefore the results of these tests are not reliable and are inconclusive. In this analysis, dyads with significant associations, whether preferred or avoided are those

	Mean	S.D.	C.V.
Real A.I.	0.28	0.19	0.69
Real Non-zero elements	0.35	0.15	0.44
Random A.I.	0.28	0.2	0.7
Random Non-zero elements	0.34	0.16	0.46
p-value	0.82	0.36	0.35
p-value Non-zero elements	0.72	0.18	0.14

Table 2. Results of preferred/avoided association tests between resident Cape Byron dolphins. Note: A.I. = Association Index; S.D. = Standard Deviation; C.V. = Coefficient of Variation.

with real association levels of less than 2.5% or greater than 97.5% of the random association indices. Preferred associations are those with less than 2.5% significance and avoidance associations are those with more than 97.5% significance. The p-value in this test represents the structure of the data and reliability of the index value. The significant dyadic association between dolphins 184 and 74 (HWI = 0.33; p-value = 0.99) indicates that these individuals are not preferred associates and are more likely to avoid association. Results from dyadic relationship tests are inconclusive due to the small data set used in this analysis. More sightings of individuals would be required to improve statistical inference from these results. Due to these inconclusive results, rates of lagged association were not modelled as it was thought the results would not be an accurate representation of the true patterns of association over time.

Analysis of social organisation suggests that association patterns of resident female groups are weak and that the individuals within this group are highly gregarious, although there were several individuals that were seen in association on numerous occasions suggesting that several smaller, more tightly bonded social groups exist within the female network. Several individuals appear to maintain loose associations with numerous individuals of several social groups.

DISCUSSION

Pod Sizes and Characteristics

Geographic variation in the pod sizes of *Tursiops spp.* may be attributed to climatic or environmental conditions (Wells *et al.*, 1980; Weigle 1990; Hubard *et al.*, 2004; Bearzi 2005). The mean pod size observed in Byron Bay (13) was similar to those found in two other studies of populations of *T. aduncus* in Australia; Jervis Bay, New South Wales (Moller *et al.* 2002) and Shark Bay, Western Australia (Preen *et al.* 1997). In contrast, a study conducted in Port Stephens, New South Wales, a small protected bay, reported a much smaller mean pod size (seven) (Moller *et al.* 2002). This pattern appears consistent with the trend in the *Tursiops* genus where smaller pod sizes are found in more protected habitats such as estuaries and sheltered embayments, while dolphins occupying open coastal waters generally have intermediate group sizes (<50 individuals). Occasional large aggregations of several hundred dolphins seen in this study are also characteristic of coastal *Tursiop* spp. populations which have been observed to occasionally congregate in large numbers at other locations around the world (Scott and Chivers 1990; Wells *et al.* 1980).

Some studies have reported that pods containing calves tend to be larger on average than non-calf pods (Moller *et al.* 2002; Rogers *et al.* 2004). A similar pattern of pod sizes was observed in the Byron Bay study, although the mean pod sizes of 21 individuals observed were much larger than those observed in the Bahamas, U.S.A. (Rogers *et al.* 2004), Port Stephens and Jervis Bay, New South Wales (Moller *et al.* 2002). This observation may be linked to the exposed environment of the Byron Bay population, where the predatory threat may be much higher than in sheltered or shallow waters such as those in the Jervis Bay and the Bahamas studies.

The sizes of mother-calf pods were observed to vary between seasons in the *T. aduncus* population of Byron Bay with larger pod sizes observed during the warmer seasons of spring and summer. A similar pattern was observed in the population of *T. truncatus* in the Bay of Islands, New Zealand (Constantine and Baker 1997). Observations of changes in mother-calf pod sizes are likely to be directly related to an increase in calving during this time of the year. In previous studies, pods with young calves were found to be larger than pods with older calves. Observations in Shark Bay, Western Australia and Sarasota, Florida, suggest that a decline in pod size occurs as the calves get older (Mann 2000; Wells *et al.*, 1987).

Behaviour

In common with the bottlenose dolphins (both *T. truncatus* and *T. aduncus*) of several other regions including the *T. truncatus* of Florida (Jones and Sayigh 2002; Odell and Asper 1982; Shane 1990b) and Southport, North Carolina (Jones and Sayigh 2002) as well as the *T. aduncus* of Moreton Bay, Queensland (Chilvers 2001), on a daily basis *T. aduncus* of Byron Bay were observed to spend the greatest amount of their time travelling. Percentages varied with geographic location and may be related to the spatial distribution and availability of food and to differences in the methodologies used by researchers.

T. aduncus in Byron Bay were observed to mill and rest for 31% of daylight hours. Similarly, bottlenose dolphins (*T. truncatus*) in eastern Florida (Chilvers 2001; Odell and Asper 1982), North Carolina and Sarosota Bay, Florida (Jones and Sayigh 2002) were also engaged in milling behaviours for 26–33% of daylight hours. The occurrence of milling behaviours of bottlenose dolphins observed from Byron Bay, eastern Florida and North Carolina, appeared to be much higher than in many other geographic regions. Low percentages of milling behaviours have been reported for *Tursiops spp.* of Moreton Bay, Queensland (Chilvers 2001), San Diego, California (Hanson and Defran 1993), Southport, North Carolina (Jones and Sayigh 2002) and Santa Monica Bay, California (Bearzi *et al.* 2005). In these reports, bottlenose dolphins were observed to display milling or resting behaviours between 0.5% in Santa Monica and

2–3% in Moreton Bay and San Diego. Some bottlenose dolphin (*Tursiops sp.*) populations such as those of Port Phillip Bay, Victoria, have reportedly never been observed milling (Scarpaci *et al.* 2000). Differences in the occurrence of milling behaviours may be due to different methodologies used and the size of the areas surveyed which may not have encompassed areas that the dolphins used for resting or milling activities. Milling behaviours may also be easily misidentified as foraging behaviours, particularly if the dolphins are resting while submerged rather than at the surface.

The times spent on feeding behaviours vary between geographic locations. In Santa Monica Bay, California, *T. truncatus* were observed to feed for 9% of daylight hours (Bearzi *et al.* 2005) whilst in the North Adriatic Sea, *T. truncatus* were observed to feed for 82% of daylight hours (Bearzi *et al.* 1999). The daily percentage of time *T. truncatus* of Byron Bay spent feeding was similar to that for bottlenose dolphins (*Tursiops spp.*) of Port Phillip Bay, Victoria (Scarpaci *et al.* 2000), Moreton Bay, Queensland (Chilvers 2001), San Diego, California (Hanson and Defran 1993), Texas (Shane 1990b), and eastern Florida (Odell and Asper 1982). All these dolphin populations spent between 15–29% of the day feeding. Differences in the availability of prey may cause differences in the percentage time spent feeding or foraging (Bearzi *et al.* 1999; Shane 1990b). In theory the time that dolphins spend on feeding behaviour is a reflection of the availability of prey: dolphins have to feed for longer periods of time when prey are scarce.

As in the findings of other research (Saayman *et al.* 1973; Hanson and Defran 1993; Shane 1990b), the time of day appears to influence the occurrence of certain activities. In the bottlenose dolphins of Byron Bay, feeding activities were more likely to occur during the early morning and late afternoon. Following the feeding peak in the early morning, the *T. aduncus* at Byron Bay typically engaged in milling behaviours for several hours until mid-afternoon when an increase in social and feeding behaviours occurred. Localised environmental and ecological conditions such as water and prey movements may influence behaviour patterns and may be an important cue for the commencement of certain activities, particularly feeding. Seasonal peaks in behaviours were also evident in this study. These changes in behaviours are likely to be attributed to influxes of prey species and reproductive cycles (Acevedo 1991; Bearzi 2005).

Home Ranges and Movement Patterns

The movement patterns and home ranges of *Tursiops* spp. vary greatly between different sexes, social groupings and individuals. In Port Stephens, New South Wales, *T. aduncus* were found to range between 2 km² and 267 km² (Allen and Moller 1999). Many *Tursiops spp.* appear to be site specific, typically occupying core habitat areas where they remain resident throughout the year (Scott *et al.* 1990). The population had some female groups that were resident throughout the year and occupied defined areas adjacent to other female groups (Moller *et al.* 2002).

Female *Tursiops* spp. reportedly prefers protected shallow bays and estuaries, rather than exposed oceanic waters. Bottlenose dolphins of Palma Sola Bay, Florida were found to use sheltered areas more during the peak birthing seasons of spring and summer (Scott *et al.* 1990). Core areas of usage of both resident female groups in the Byron Bay area were typified by large swells, frequently rough surf conditions and large tidal currents. However, these areas were still the most protected positions within the apparent home range of these dolphins, indicating consistency in this characteristic of bottlenose dolphins.

Social Structure

The social organisation of *Tursiops* spp. is highly complex with most being sexually segregated. Typically, females form loose bonds between many individuals and males maintain strong bonds with only a few individuals (Connor *et al.* 1992; Scott *et al.* 1990; Smolker *et al.* 1992). The overall Half Weight Indices (HWI) between 'resident' females identified in this study (0.28) indicates that females did not have preferences for long-term associates and are highly fluid in their associations with other females, a trend consistent with other populations of *T. aduncus* (Moller and Beheregaray 2004; Smolker et al. 1992). However, the HWI of subgroups identified in the 'resident' female group were higher than the average (≥0.45). This finding may indicate, as in other populations (Scott *et a*l. 1990), that the sub-grouping arrangement within female networks is based on the reproductive status of individuals: between females on the basis of individuals with similar reproductive status. Over time, the arrangement of sub-groupings may be altered as the reproductive status of the individuals change. It is therefore likely that social structure of females within the Byron Bay population is based on the formation of an associative network composed of relatively loose bonds between individuals, similar to other populations of *Tursiops* spp. reported in the literature such as Scott *et al.* (1990), Smolker *et al.* (1992) and Wells (1991).

Lusseau and Newman (2004) found that the population of *T. truncatus* of Doubtful Sound, New Zealand consisted of several distinct social groups. These researchers identified 'brokers' in the population which they defined as: 'individuals that remain on the outskirts of communities and maintained loose bonds between different social groups' (Lusseau and Newman 2004). It was suggested that these individual dolphins may have had a crucial role in maintaining cohesiveness between social groups. Several individuals of *T. aduncus* in the 'resident' female groups of Cape Byron were found to have low levels of association. These individuals appeared to associate on some level with at least two of the three tightly associated female sub-groups identified. Several other females were also observed to associate with both Cape Byron and Ballina 'resident' female groups. These individuals may have a similar role to the 'brokers', described by Lusseau and Newman (2004) and increase social cohesiveness between adjacent female groups.

Conclusions

Despite the geographic isolation, the large differences in environmental conditions, habitats and prey species, it appears that the basic social foundation and structure of both *T. truncatus* and *T. aduncus* are similar. This study has provided additional evidence to suggest there is a general structure emerging in *Tursiops* spp. societies throughout their geographic ranges: the majority of *Tursiops* spp. societies are sexually segregated, females maintain large networks of loose associations between other females, some female groups tend to occupy defined territories often adjacent to other female groups, with particular areas within these territorial boundaries utilised for specific purposes and the pod sizes of *Tursiops* spp. appear to be influenced by the sex of individuals and the presence of calves. In addition, the present study also found that, in general, *Tursiops* spp. from different geographic regions spend similar proportions of time engaged in different behaviour states.

This study has provided information that may be relevant for conservation management. The Byron Bay population of *T. aduncus* may be considered a single unit for management purposes with known localised movement, social structure and behaviour characteristics. This knowledge may assist in the design and application of a management plan to conserve this population that is facing increasing interaction with humans and particularly with commercial operations. It would be desirable to have information on other attributes of the population, these include; population size, sex ratios, the impact of short and long term threats to their survival, and which if any of these threats can be mitigated by management or conservation measures.

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