

Resource partitioning in sympatric delphinids: space use and habitat preferences of Australian snubfin and Indo-Pacific humpback dolphins

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Summary

1. Many species of delphinids co-occur in space and time. However, little is known of their ecological interactions and the underlying mechanisms that mediate their coexistence.

2. Snubfin *Orcaella heinsohni*, and Indo-Pacific humpback dolphins *Sousa chinensis*, live in sympatry throughout most of their range in Australian waters. I conducted boat-based surveys in Cleveland Bay, north-east Queensland, to collect data on the space and habitat use of both species. Using Geographic Information Systems, kernel methods and Euclidean distances I investigated interspecific differences in their space use patterns, behaviour and habitat preferences.

3. Core areas of use (50% kernel range) for both species were located close to river mouths and modified habitat such as dredged channels and breakwaters close to the Port of Townsville. Foraging and travelling activities were the dominant behavioural activities of snubfin and humpback dolphins within and outside their core areas.

4. Their representative ranges (95% kernel range) overlapped considerably, with shared areas showing strong concordance in the space use by both species. Nevertheless, snubfin dolphins preferred slightly shallower (1–2 m) waters than humpback dolphins (2–5 m). Additionally, shallow areas with seagrass ranked high in the habitat preferences of snubfin dolphins, whereas humpback dolphins favoured dredged channels.

5. Slight differences in habitat preferences appear to be one of the principal factors maintaining the coexistence of snubfin and humpback dolphins. I suggest diet partitioning and interspecific aggression as the major forces determining habitat selection in these sympatric species.

Key-words: coexistence, Delphinidae, habitat selection, *Orcaella heinsohni*, *Sousa chinensis*.

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Introduction

Many species of delphinids co-occur in the same immediate habitat (i.e. direct sympatry, *sensu* Bearzi 2005) and may even occur in mixed-species schools (see reviews in Stensland, Angerbjorn & Berggren 2003; Bearzi 2005). Despite the acknowledgement of these coexisting communities few studies have gone beyond recording their occurrence. Questions such as ‘To what extent do coexisting delphinids differ in their resource use?’ remain unanswered. Thus, little is known about the mechanisms that allow sympatric dolphins to coexist. Understanding

the spatial dynamics and habitat preferences of coexisting species is also necessary to determine species-specific requirements, and thus provides valuable information on how to manage areas effectively for the conservation of different species (e.g. Durant 1998; Sachot, Perrin & Neet 2003; Sergio, Marchesi & Pedrini 2003).

Coastal dolphins are among the most threatened species of cetaceans because of their close proximity to anthropogenic activities (Thompson *et al.* 2000; DeMaster *et al.* 2001). In Australia, Snubfin dolphins *Orcaella heinsohni* Beasley, Robertson & Arnold (2005) and Indo-Pacific humpback dolphins *Sousa chinensis* (Osbeck 1765, hereafter humpback dolphins), co-occur in broad sympatry (*sensu* Bearzi 2005) along most of the northern tropical coast (Parra *et al.* 2002; Parra, Corkeron & Marsh 2004). Little is known of their

ecology and their population status is uncertain (Parra, Corkeron & Marsh 2006). Reviews of aerial survey sightings indicated both species occur mainly in shallow coastal waters (Corkeron *et al.* 1997; Parra *et al.* 2002). The space use patterns and habitat preference of snubfin and humpback dolphins for particular environmental conditions or resource patches within these areas has not been quantified.

In this study, I use data collected during boat-based surveys in Cleveland Bay, north-east Queensland, Australia to: (1) determine the space use patterns of snubfin and humpback dolphins occurring in direct sympatry; (2) assess whether their space use patterns relate to behaviour; (3) measure the spatial overlap and concordance in space use between both species; and (4) determine their habitat preferences. Based on these findings, I discuss how habitat selection appears to be a major resource partitioning mechanism between these sympatric coastal dolphins.

Methods

DATA COLLECTION

This study was conducted from January 1999 to October 2002 in the coastal waters of Cleveland Bay Dugong Protected Area (hereafter referred to as Cleveland Bay, Fig. 1a), a tropical embayment located in north-east Queensland, Australia (Fig. 1a). Boat-based surveys were carried out between 06:00 h and 14:00 h (wind almost invariably increased in the afternoon, making fieldwork impossible). The study area was divided into four sections (A, B, C, D) of similar length (Fig. 1a). Surveys followed a predetermined route from Townsville Harbour to Black River mouth (covering sections A and B) or to Cape Cleveland and back (covering sections C and D). The outward and return legs of the survey were spaced at least 1 km apart to: (1) avoid resampling the same area; (2) minimize repeated sightings of the same dolphin school within a single survey; and (3) sample all major coastal habitat types. Search effort and direction of travel were limited primarily by sea conditions, attempting to remain in areas with calm sea conditions \leq Beaufort 3 and swell \leq 1 m. Within these constraints, efforts were made to give equal coverage to all sections within the study area. Further details of survey procedures are given in Parra *et al.* 2006).

A school was defined as an aggregation of dolphins with relatively close spatial cohesion (i.e. each member within 100 m of any other member) that were involved in similar (often the same) behavioural activities (modified from Connor *et al.* 1998). Once a dolphin school was sighted, it was approached slowly to within 10 m to record its location, identify the species and obtain behavioural data. Dolphin school position was recorded using a handheld 12-channel Global Positioning System (GPS, position accuracy = ± 15 m).

Using the sequential positions of the same school close in time may lead to serial autocorrelation in the data

compromising statistical tests (increase in Type I error) and habitat selection analyses (Aebischer, Robertson & Kenward 1993). I minimized dependency in the data by: (1) taking out of the analysis schools that were sighted close in time and had the same school size and age composition, and (2) based all hypothesis tests on randomizations of the data (e.g. Conner, Smith & Burger 2003).

As dolphin schools were approached during surveys, I scanned the school from front to back and the predominant behaviour of $\geq 50\%$ of the individuals at the surface was recorded. Dolphin schools were classified into different behavioural states according to the following criteria:

- *Foraging*: individuals move in various directions without an obvious pattern. Dolphins dive frequently and steeply downwards [often preceded by fluke (tail fin) up or peduncle (tail stock) arches], with extended submergence times. Rapid accelerations and erratic movement at the surface, indicative of animals chasing fish. Animals seen directly pursuing a fish (e.g. fish jumping at surface) or with fish in their mouth.
- *Foraging behind trawler*: repeated dives in varying directions around the side or behind the stern of a trawler boat while the boat is fishing for prawns.
- *Travelling*: movement persistent and directional with a regular pattern of surfacing and diving. Dive angles are shallow. Animals are not underwater for extended lengths of time.
- *Socializing*: localized movement. Dive direction is unpredictable. Dolphins in close proximity showing high levels of interaction (animals touching each other, rubbing their bodies). Fins and flukes often break the surface of the water. Frequent aerial behaviour such as leaps and summersaults.
- *Milling*: movement slow and with no apparent direction. Dolphins swim in close proximity, but without interaction. No aerial behaviour, activity levels are low. Dolphins surface in a synchronized manner and most of the time is spent at the water's surface. Dive angles are shallow.

I considered foraging behind trawler as a separate behavioural state from foraging because this behaviour appears to be a specialized feeding technique that humpback dolphins engage in for long periods of time (Corkeron 1990; Jefferson 2000). I have observed humpback dolphins in Cleveland Bay engage in this behaviour for over 2 h without leaving the trawler while actively fishing, and dolphins foraging independently of trawlers stop to forage behind active trawlers. Thus, these two behaviours appear to be mutually exclusive.

Any indication of animals interacting with the research boat as they were approached (e.g. animals being attracted to the boat or actively avoiding it) were recorded, but not used in the analysis, as these were not indicative of undisturbed behaviour of the school. Schools for which behaviour could not be determined because animals were lost after initial sighting were also excluded from analysis.

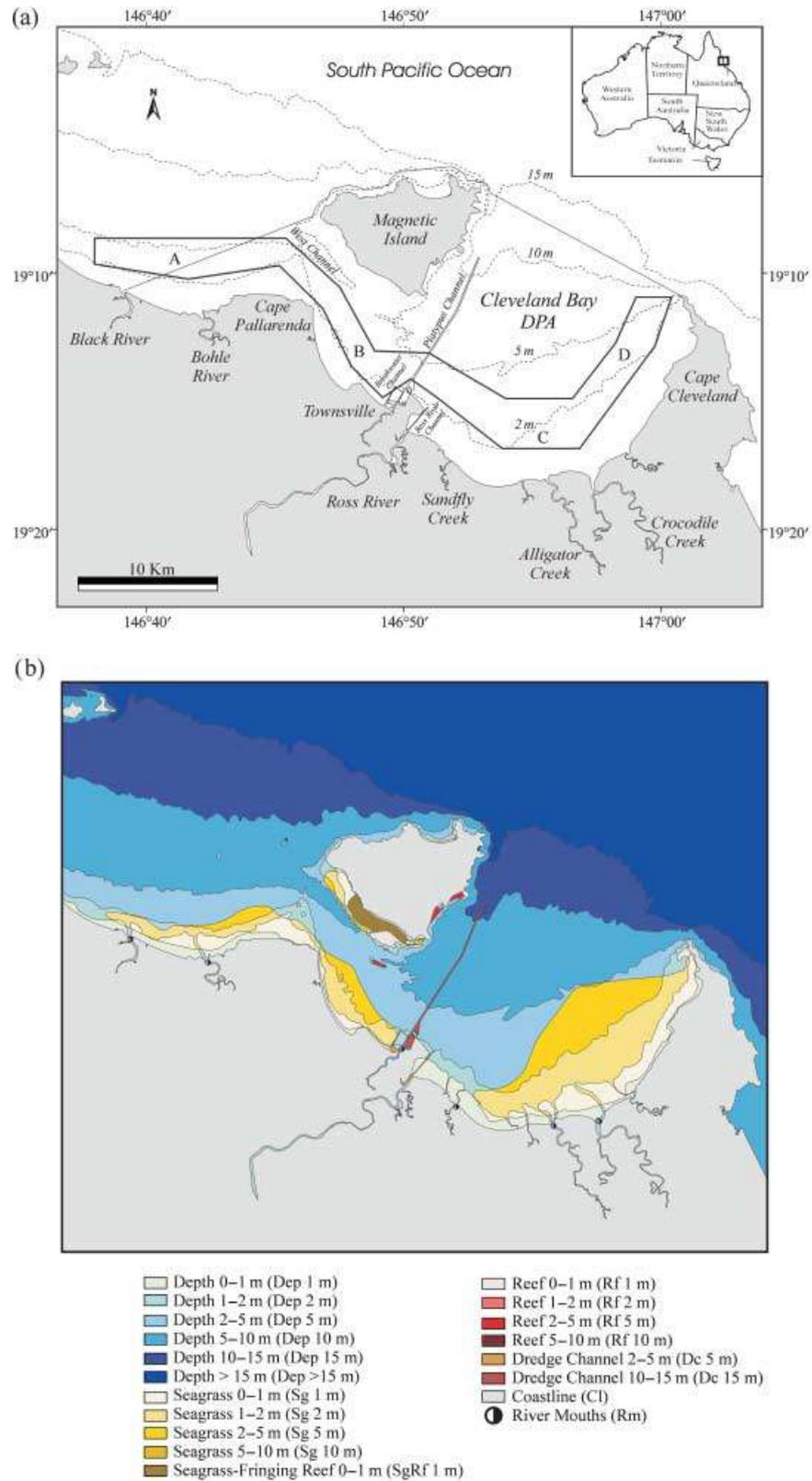


Fig. 1. Study area: (a) Map of Cleveland Bay indicating survey route (—), limits of Dugong Protected Area (---), and principal locations named in text, (b) ArcView GIS coverage of the different habitat types found in the Cleveland Bay region. See Table 1 for description of habitat types and abbreviations used in figures and tables.

DATA ANALYSIS

Space use patterns and behaviour

The Utilization Distribution (UD) is a probability density function that describes the relative use of space by an animal, within a defined area based on a sample of animal locations (Van Winkle 1975). To estimate the UD of snubfin and humpback dolphins, I converted all school sightings into an ArcView GIS point coverage and used the ArcView-Animal Movement Analyst extension to estimate a fixed kernel UD for each species (Hooge & Eichenlaub 2000). Kernel ranges of 50% (core area) and 95% (representative range) probability of occurrence were calculated using smoothing parameters calculated via the least squares cross-validation procedure (Seaman *et al.* 1999).

Individual animals were tracked by means of photo-identification (e.g. Parra & Corkeron 2001), but the number of relocations for most animals was insufficient to use true probabilistic methods (i.e. kernel methods) to estimate UDs reliably for each individual. Therefore, I have calculated UDs for snubfin and humpback dolphins using locations of schools of animals rather than of individuals, an approach similar to Wilson, Thompson & Hammond (1997) and Ingram & Rogan (2002). Therefore, the space use and habitat preference analysis presented here follows the 'Design I' of (Thomas & Taylor 1990): inferences on space use and habitat preferences are made at the population level (i.e. dolphin schools recorded in the study area).

The 50% and 95% kernel ranges were selected as they are generally considered the most robust estimators of animals' core areas and home ranges, respectively (Worton 1989). Because my data were restricted to the inshore waters of Cleveland Bay, and dolphin schools instead of individual animals were used for analysis, I considered the 50% and the 95% kernel ranges as the core areas and representative ranges of both species at the population level within the study area. The 95% kernel range of each species also defined the area for the analysis of habitat preferences.

To investigate whether behavioural states varied spatially (i.e. inside and outside 50% core areas) and with time of day for each species, I used Chi-square homogeneity tests (Zar 1999). As some behaviours were only observed a few times per location or per time of day (i.e. milling, socializing) comparisons were made only across the main behavioural states.

SPATIAL OVERLAP AND CONCORDANCE IN
SPACE USE

To measure the extent of space sharing between snubfin and humpback dolphins, I computed the per cent area overlap (PAO) between the representative ranges (i.e. 95% kernel range) (Atwood & Weeks 2003) of both species as:



where $A_{Oh,Sc}$ is the area of overlap between the two species, A_{Oh} is the area of snubfin dolphins 95% kernel range, and A_{Sc} the area of humpback dolphins 95% kernel range. Although this index provides a first approximation of the space use sharing by both species, it does not take into account the UD (i.e. probability of use) within these shared parts (Doncaster 1990). For example, the ranges of two species may overlap by over 50% but contain the least utilized parts of both ranges. Alternatively, a shared area may contain a region used intensively by one species and less by the other. To account for this problem and measure the similarity in relative use of shared areas (i.e. concordance in space use); I tested for correlation (Spearman's coefficient of rank correlation r_s) between the UDs of snubfin and humpback dolphins. A Spearman's coefficient was calculated on the pairs of probability of use estimates obtained from all grid cells (100×100 m) frequented by one or both species. Species with perfectly matched utilization distributions will show a r_s of 1, while species with complete discordance will have a r_s of -1 (Doncaster 1990).

HABITAT DELINEATION AND ANALYSES OF
HABITAT USE

A habitat map of Cleveland Bay including areal (e.g. seagrass, reefs), linear (i.e. coastline) and point features (i.e. river mouths) was developed for analysis of habitat use (Fig. 1b, Table 1). Areal habitat types were defined based on water depth, presence of seagrass, coral reefs, and dredged channels (Table 1). Bathymetry, coral reefs, dredged channels, and coastline were digitized into an ArcView Geographic Information System (ESRI 1996)

Table 1. Descriptions of the different habitat types and abbreviations used in figures and tables

Water depth (m)	Seagrass present?	Reef present?	Dredged channel present?	Habitat type
0–1	No	No	No	Depth 1 m
1–2	No	No	No	Depth 2 m
2–5	No	No	No	Depth 5 m
5–10	No	No	No	Depth 10 m
0–1	Yes	No	No	Sg 1 m
1–2	Yes	No	No	Sg 2 m
2–5	Yes	No	No	Sg 5 m
0–1	Yes	Yes	No	SgRf 1 m
0–1	No	Yes	No	Rf 1 m
2–5	No	Yes	No	Rf 5 m
2–5	No	No	Yes	Dc 5 m
10–15	No	No	Yes	Dc 15 m
NA	NA	NA	NA	Cl
NA	NA	NA	NA	Rm

NA, not applicable; Cl, coastline; Rm, river mouths; Sg, seagrass; Rf, reef.

from a 1:50 000 scale navigation chart of Cleveland Bay provided by the Australian Hydrographic Service.

The bathymetry of the study area was digitized using the isobaths (i.e. 1 m, 2 m, 5 m, 10 m and 15 m) in the navigation chart, which represent the lowest level of astronomical tide. As a result, all areal habitats (i.e. coral reefs, dredged channels, and seagrass) are represented at the minimum depth they are found.

The seagrass coverage for the region was provided by the Seagrass Ecology Group, Queensland Department of Primary Industries (Lee Long *et al.* 1998). Point locations of major river mouths were obtained from the Australian National Mapping Agency. All spatial layers were sampled at a cell resolution of 100×100 m, and projected into Universal Transverse Mercator (UTM) Zone 55 for distance and area calculations. Only the habitat types that fell within the representative range of each species were considered available to the animals and included in subsequent analyses of habitat use.

Habitat selection was defined as the difference between observed habitat utilization and expected habitat utilization as determined from a null model (Johnson 1980). To assess habitat selection, I used a distance-based analytical approach (Conner *et al.* 2003), modified for use with locations of groups of animals (i.e. dolphin schools). The distance-based approach I used compares the average Euclidean distance between the locations of dolphin schools and the nearest representative of each habitat type to expected distances obtained from random dolphin school locations. Random locations, equalling the number of schools observed for each species, were generated within the respective representative ranges. The vectors of distances from observed locations and random locations to habitat types were then used to derive a habitat use/habitat availability ratio (following Conner *et al.* 2003). This procedure was repeated 2000 times and an average habitat use ratio ρ calculated for each habitat type. Under the null hypothesis of no habitat selection the expected value of ρ is 1 (i.e. mean dolphin distance to habitat = mean random distance to habitat). If ρ is < 1 the corresponding habitat was preferred (i.e. mean dolphin distance to habitat $<$ mean random distance to habitat) and the opposite if ρ is > 1 . To determine which habitat types were used more frequently in relation to their availability, I used a randomization test to evaluate the number of times the ratio obtained from 2000 randomizations exceeded or was equal to the expected ratio of 1. A thousand randomizations is a reasonable minimum for tests at the 5% level (Manly 1997), I chose 2000 randomizations to provide balance between precision and calculation time.

The habitat use/habitat availability ratio ρ provides a ranking matrix of habitat use relative to habitat availability (which habitat type animals occurred closer to relative to random points), but it does not assess which habitat types were selected significantly more than others (Conner *et al.* 2003). I defined 'preferred' habitats as the ones that were used most relative to expectation and 'least preferred' as the habitat that were used least

relative to expectation (Conner *et al.* 2003). To test for preferences in habitat selection, I carried out a pairwise *t*-test among the different habitats and adjusted *P*-values with the False Discovery Rate (FDR) method (Benjamini & Hochberg 1995).

To evaluate if there were any significant interspecific differences in habitat use, I carried out a two-sample randomization test between the distances to habitat types that were common to both species (i.e. found within the representative ranges of both species). The test compared the observed difference between mean distances to a habitat type with the difference obtained by randomly allocating the observed values between the two species multiple times (2000 times in these analyses).

Randomization tests were carried out with the POP-TOOLS version 2.6 Excel add-in (Hood 2005). POPTOOLS uses the robust Mersenne Twister algorithm for the generation of pseudo-random numbers solving problems with built-in functions of Excel (e.g. Knüsel 1998). The Spearman rank correlations, pairwise *t*-test, and confidence intervals around effect sizes (i.e. differences between means) were calculated with the R software version 2.1.1 for statistical computing and graphics (Ihaka & Gentleman 1996). Confidence intervals around the effect sizes were obtained by nonparametric bootstrapping using the bias corrected and accelerated method (BCa) (Efron & Tibshirani 1993). Interpretations of results are based on the examination of *P*-values evaluated at $\alpha = 0.05$.

Results

SURVEY EFFORT

I spent 630 h looking for snubfin and humpback dolphins and a total of 168 h following focal dolphin schools for data collection between 1999 and 2002. In total, 117 schools of snubfin dolphins and 143 schools of humpback dolphins were sighted in Cleveland Bay during this period. Survey effort was not uniformly distributed across the study area because of environmental constraints. Survey effort was similar across sections A (201 h), B (191 h) and C (179 h); however, section D (59 h) was surveyed less than the other sections because of its exposure to strong south-easterly winds (Fig. 1a).

SPACE USE PATTERNS AND BEHAVIOUR

The kernel UD analysis revealed that snubfin and humpback dolphins did not use Cleveland Bay uniformly (Fig. 2). The representative ranges (95% kernel range) of snubfin and humpback dolphins were similar in size covering a total area of about 197 km² and 190 km², respectively. The representative range of snubfin dolphins concentrated in two areas: north-west of Cape Pallarenda (93 km²), and south towards Townsville's Port (104 km²). Within these two areas there were also two core areas (50% kernel range): 16 km² around the Port of Townsville, and 27 km² between the mouths of the Bohle and Black rivers. Humpback dolphins

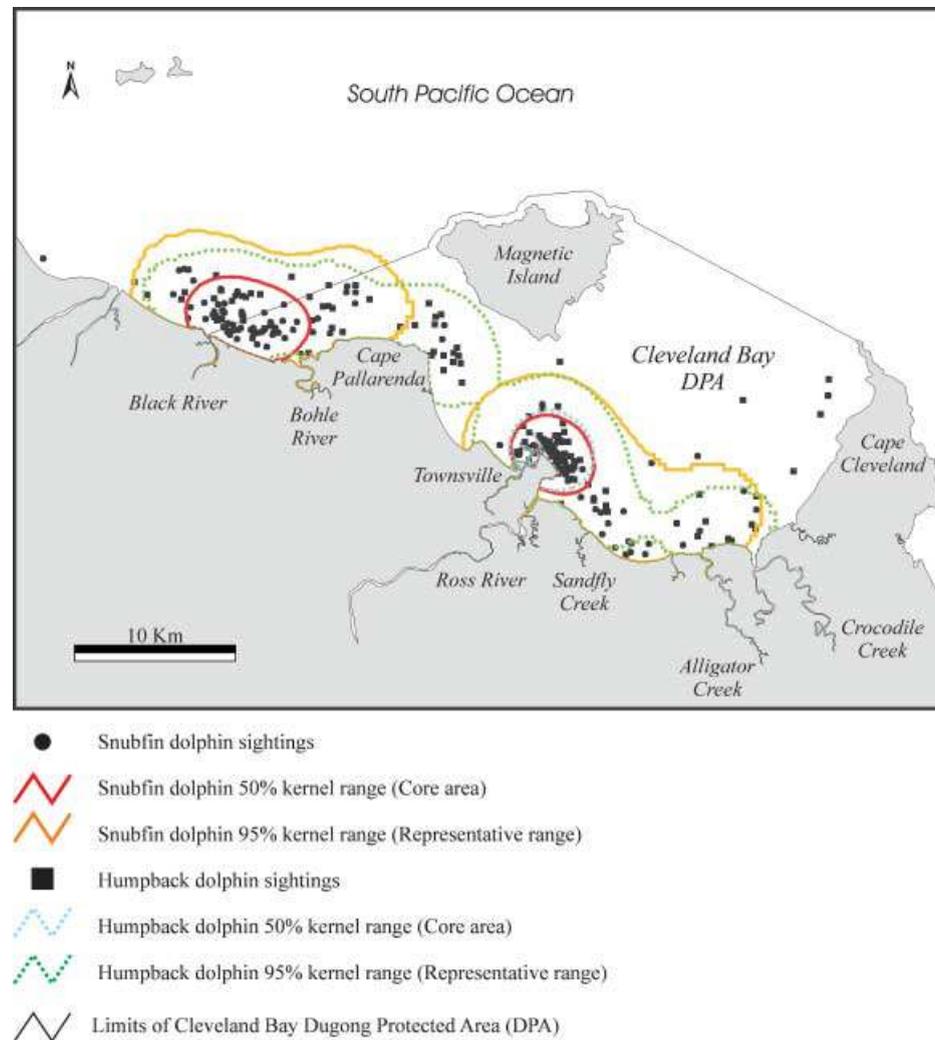


Fig. 2. Core areas (50% kernel range) and representative ranges (95% kernel range) of snubfin and humpback dolphins in Cleveland Bay.

showed a continuous representative range extending from Crocodile Creek in the south-east to Black River in the north-west. Inside this range, a core area of approximately 17 km² was located around the Port of Townsville.

The discontinuity in the representative range of snubfin dolphins does not demonstrate the presence of two distinct populations. Photo-identification data show that animals did move between these two areas (Parra 2005). Hence, these data were pooled for analysis of behaviour and habitat use.

Snubfin dolphins were mainly seen foraging and travelling. In combination, these behaviours contributed over 50% of the behaviours observed at any time (Fig. 3a). Snubfin dolphins were never seen foraging behind trawlers and milling was observed only once outside their core areas. Overall, there was no difference in the occurrence of foraging, socializing or travelling between core and non-core areas ($\chi^2_{0.05,3} = 0.024$, $P = 0.987$). Similarly no differences were detected for foraging and travelling between core and noncore areas according to time (Foraging: $\chi^2_{0.05,3} = 2.4$, $P = 0.501$, Travelling: $\chi^2_{0.05,3} = 1.7$, $P = 0.642$).

The behaviour of humpback dolphins was dominated by foraging (Fig. 3b). There were differences in the behaviour of humpback dolphins according to location ($\chi^2_{0.05,3} = 12.9$, $P = 0.005$) with animals observed travelling more often outside their core area, and foraging behind trawlers inside their core area (Fig. 3b). The frequency of the behaviours foraging, and foraging behind trawler varied according to time and location (Foraging: $\chi^2_{0.05,3} = 23.5$, $P < 0.001$, Foraging Behind Trawlers: $\chi^2_{0.05,3} = 10.1$, $P = 0.018$). Foraging in the early morning hours (i.e. 06:00–08:00 h) took place mainly inside the core area. Between 08:00 and 10:00 h foraging activities appeared to shift to locations outside the core area (Fig. 3b). Foraging behind trawlers occurred mainly inside the core area throughout the hours surveyed (Fig. 3b).

SPATIAL OVERLAP AND CONCORDANCE IN SPACE USE PATTERNS

The 95% representative ranges of snubfin and humpback dolphins showed considerable spatial overlap (Fig. 2). The area shared between both species was 156 km²

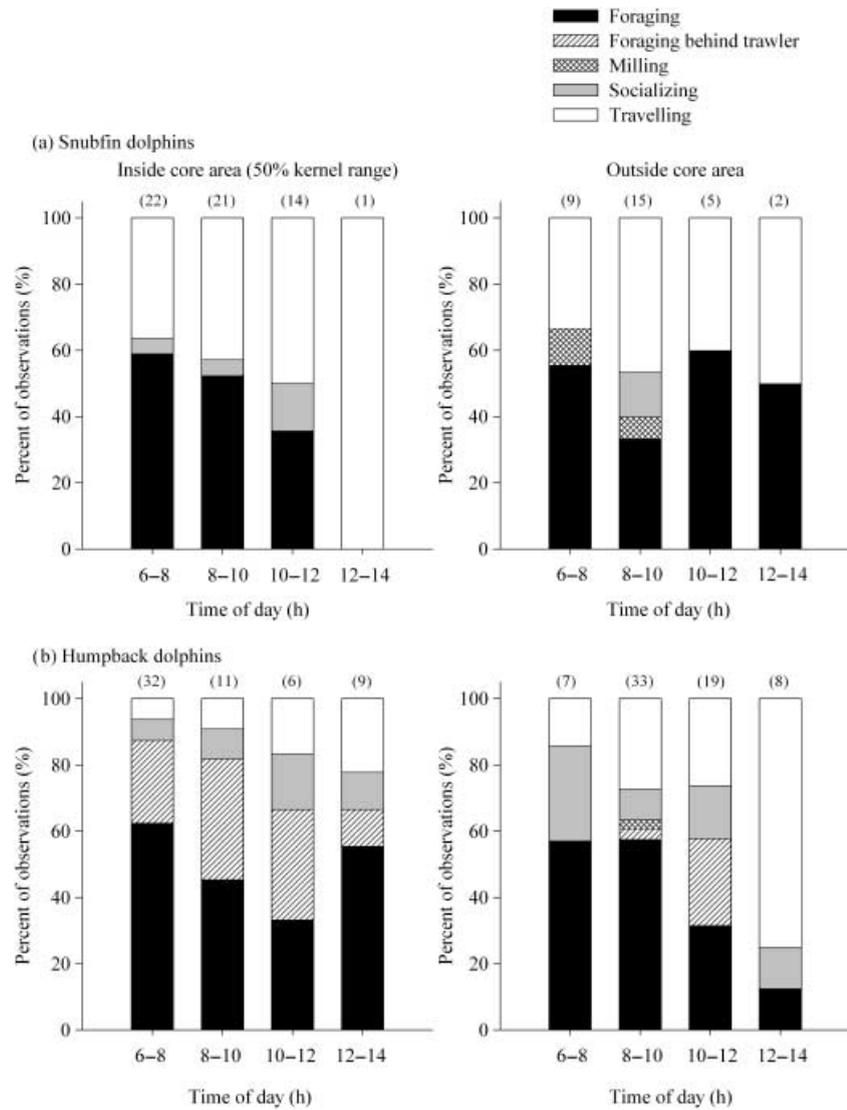


Fig. 3. Differences in the proportions of various behavioural states observed according to time within and outside core areas (50% kernel range) of (a) snubfin, and (b) humpback dolphins. Numbers in parenthesis on top of each bar indicate the total number of schools observed for which known behaviour was known for that time.

with a per cent area overlap of 81%. Almost all of the two core areas of snubfin dolphins (99%) and all of the humpback dolphin's core area were contained within this shared area. The Spearman rank correlation between the UDs of snubfin and humpback dolphins ($r_s = 0.55$, $P < 0.05$) indicated strong concordance in the utilization patterns of these shared areas by both species.

HABITAT USE

Overall, the representative ranges of snubfin and humpback dolphins comprised the same habitat types in similar proportions (Fig. 4). However, coral reefs and fringing reefs with seagrass (between Cape Pallarenda and southern coast of Magnetic Island) occurred within the representative range of humpback dolphins only.

The analysis of distance ratios (ρ) indicated that habitat use within the representative range of each species was

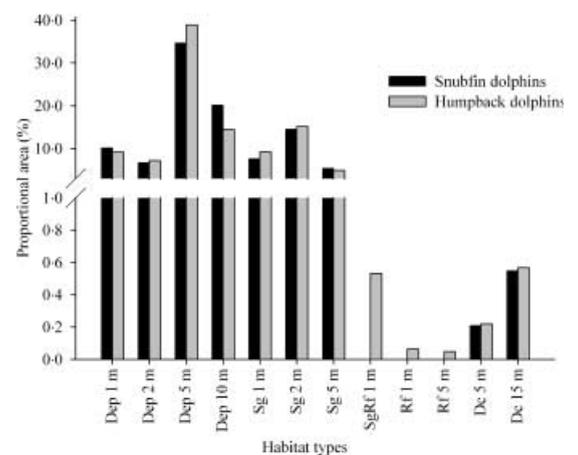


Fig. 4. Relative proportion of various habitat types within the representative range (95% kernel range) of snubfin and humpback dolphins in Cleveland Bay. See Table 1 for descriptions of habitat types and abbreviations.

Table 2. Mean ratios (ρ) of the distance between dolphin school locations and habitat types to the distance between random locations and habitat types after 2000 randomizations. Associated P -values of randomization test are shown in parenthesis. Values for $\rho < 1$ indicate that animal locations were closer to habitat than expected by chance. Significant values ($P < 0.05$) are indicated in bold italics. P -values for multiple pairwise comparisons were adjusted with the False Discovery Rate (FDR) correction method (Benjamini & Hochberg 1995). See Table 1 for description of habitat types and abbreviations

	Snubfin dolphins	Humpback dolphins
Habitat*	ρ (P -value)	ρ (P -value)
Depth 1 m	<i>0.60 (< 0.0001)</i>	<i>0.87 (0.033)</i>
Depth 2 m	<i>0.47 (< 0.0001)</i>	<i>0.66 (< 0.0001)</i>
Depth 5 m	<i>0.64 (0.001)</i>	<i>0.65 (0.002)</i>
Depth 10 m	1.11 (0.890)	0.99 (0.557)
Sg 1 m	<i>0.66 (< 0.0001)</i>	1.06 (0.799)
Sg 2 m	<i>0.60 (< 0.0001)</i>	1.03 (0.706)
Sg 5 m	<i>0.77 (< 0.0001)</i>	1.02 (0.706)
SgRf 1 m	NA†	0.96 (0.274)
Rf 1 m	NA	0.95 (0.184)
Rf 5 m	NA	<i>0.89 (0.014)</i>
Dc 5 m	1.02 (0.664)	<i>0.72 (< 0.0001)</i>
Dc 15 m	1.02 (0.664)	<i>0.69 (< 0.0001)</i>
Cl	<i>0.58 (< 0.0001)</i>	<i>0.65 (< 0.0001)</i>
Rm	<i>0.68 (< 0.0001)</i>	<i>0.81 (< 0.0001)</i>

*Habitat types available within 95% kernel range of each species.

†Habitat types not available (NA) within 95% kernel range of snubfin dolphins.

not random (Table 2). Snubfin dolphins occurred closer to most habitat types than would be expected under the null hypothesis of no habitat selection. The only habitats showing no selection were dredged channels and waters 5–10 m deep. Humpback dolphins selected most habitat types including dredged channels, except: (1) areas with seagrass present; (2) reefs at 0–1 m depth; and (3) waters 5–10 m deep.

Table 3. Ranking matrix of the habitat preferences of snubfin dolphins (most preferred {Ranking = 1} to least preferred {Ranking = 9}). Numbers indicate differences associated with pairwise comparison of mean ratios (ρ) to habitat types. Negative differences indicate preference of habitat above over habitat to the left, positive differences indicate underutilization of habitat above over habitat to the left. Significant differences (pairwise t -test, $P < 0.05$) are indicated in bold italics. Habitats with the same ranking did not differ significantly in relative preference. P -values for multiple pairwise comparisons were adjusted with the False Discovery Rate (FDR) correction method (Benjamini & Hochberg 1995). See Table 1 for description of habitat types and abbreviations

Habitat	Habitat ranking										
	3	1	4	9	5	3	7	8	8	2	6
Depth 1 m	–										
Depth 2 m	<i>0.128</i>	–									
Depth 5 m	<i>–0.043</i>	<i>–0.171</i>	–								
Depth 10 m	<i>–0.509</i>	<i>–0.636</i>	<i>–0.466</i>	–							
Sg 1 m	<i>–0.055</i>	<i>–0.182</i>	<i>–0.012</i>	<i>0.454</i>	–						
Sg 2 m	0.000	<i>–0.127</i>	<i>0.043</i>	<i>0.509</i>	<i>0.055</i>	–					
Sg 5 m	<i>–0.168</i>	<i>–0.296</i>	<i>–0.125</i>	<i>0.341</i>	<i>–0.113</i>	<i>–0.168</i>	–				
Dc 5 m	<i>–0.414</i>	<i>–0.542</i>	<i>–0.371</i>	<i>0.095</i>	<i>–0.359</i>	<i>–0.414</i>	<i>–0.246</i>	–			
Dc 15 m	<i>–0.415</i>	<i>–0.542</i>	<i>–0.371</i>	<i>0.094</i>	<i>–0.360</i>	<i>–0.415</i>	<i>–0.246</i>	0.000	–		
Cl	<i>0.019</i>	<i>–0.109</i>	<i>0.062</i>	<i>0.528</i>	<i>0.074</i>	<i>0.019</i>	<i>0.187</i>	<i>0.433</i>	<i>0.433</i>	–	
Rm	<i>–0.078</i>	<i>–0.205</i>	<i>–0.035</i>	<i>0.431</i>	<i>–0.023</i>	<i>–0.078</i>	<i>0.090</i>	<i>0.336</i>	<i>0.337</i>	<i>–0.097</i>	–

The ranking of habitats based on pairwise comparisons of ρ indicated that snubfin dolphins used waters 1–2 m deep, followed by waters close to the coast, and waters 0–1 m deep and 1–2 m deep with seagrass, proportionally more than any other habitats (Table 3). Humpback dolphins preferred waters close to the coast and 2–5 m deep, followed by waters 1–2 m deep over all other habitat types (Table 4).

Examination of the difference between the mean distances to habitat types common to both species (Table 5) revealed that snubfin dolphins occurred closer to waters 0–1 m deep, closer to waters 0–2 m deep with seagrass, and closer to river mouths than humpback dolphins. Humpback dolphins occurred closer to the dredged channels than snubfin dolphins. Both species occurred at similar distances to waters 5–10 m deep, and waters close to the coast.

Discussion

SPACE USE AND HABITAT PREFERENCES

I found that sympatric snubfin and humpback dolphins have a high degree of interspecific spatial overlap in Cleveland Bay, with shared areas used heavily and similarly by both species. The predominance of foraging activity throughout the core areas and representative ranges of both species suggests that coastal waters of Cleveland Bay represent an important feeding area for local snubfin and humpback dolphins.

Despite the high spatial overlap and concordance in space use, there were differences in the habitats selected by both species and their preferences. Snubfin dolphins preferred slightly shallower (1–2 m) waters than humpback dolphins (2–5 m). Shallow areas with seagrass ranked high in the habitat preferences of snubfin dolphins, whereas humpback dolphins favoured dredged channels. Analysis of interspecific differences in selection

Table 4. Ranking matrix of the habitat preferences of humpback dolphins (most preferred {Ranking = 1} to least preferred {Ranking = 13}). Numbers indicate differences associated with pairwise comparison of mean ratios (ρ) to habitat types. Negative differences indicate preference of habitat above over habitat to the left, positive differences indicate underutilization of habitat above over habitat to the left. Significant differences (pairwise t -test, $P < 0.05$) are indicated in bold italics. Habitats with the same ranking did not differ significantly in relative preference. P -values for multiple pairwise comparisons were adjusted with the False Discovery Rate (FDR) correction method (Benjamini & Hochberg 1995). See Table 1 for description of habitat types and abbreviations

Habitat	Habitat ranking														
	6	2	1	10	13	12	11	9	8	7	4	3	1	5	
Depth 1 m	Depth 1 m	Depth 2 m	Depth 5 m	Depth 10 m		Sg 1 m	Sg 2 m	Sg 5 m	SgRf 1 m	Rf 1 m	Rf 5 m	Dc 5 m	Dc 15 m	Cl	Rm
Depth 1 m	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Depth 2 m	<i>0.209</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Depth 5 m	<i>0.227</i>	<i>0.018</i>	–	–	–	–	–	–	–	–	–	–	–	–	–
Depth 10 m	<i>–0.118</i>	<i>–0.327</i>	<i>–0.345</i>	–	–	–	–	–	–	–	–	–	–	–	–
Sg 1 m	<i>–0.184</i>	<i>–0.393</i>	<i>–0.411</i>	<i>–0.066</i>	–	–	–	–	–	–	–	–	–	–	–
Sg 2 m	<i>–0.155</i>	<i>–0.364</i>	<i>–0.382</i>	<i>–0.037</i>	<i>0.029</i>	–	–	–	–	–	–	–	–	–	–
Sg 5 m	<i>–0.144</i>	<i>–0.353</i>	<i>–0.371</i>	<i>–0.026</i>	<i>0.040</i>	<i>0.011</i>	–	–	–	–	–	–	–	–	–
SgRf 1 m	<i>–0.086</i>	<i>–0.296</i>	<i>–0.314</i>	<i>0.031</i>	<i>0.097</i>	<i>0.069</i>	<i>0.057</i>	–	–	–	–	–	–	–	–
Rf 1 m	<i>–0.073</i>	<i>–0.282</i>	<i>–0.300</i>	<i>0.045</i>	<i>0.111</i>	<i>0.082</i>	<i>0.071</i>	<i>0.013</i>	–	–	–	–	–	–	–
Rf 5 m	<i>–0.012</i>	<i>–0.222</i>	<i>–0.240</i>	<i>0.105</i>	<i>0.171</i>	<i>0.143</i>	<i>0.131</i>	<i>0.074</i>	<i>0.061</i>	–	–	–	–	–	–
Dc 5 m	<i>0.157</i>	<i>–0.052</i>	<i>–0.070</i>	<i>0.275</i>	<i>0.341</i>	<i>0.312</i>	<i>0.301</i>	<i>0.244</i>	<i>0.230</i>	<i>0.170</i>	–	–	–	–	–
Dc 15 m	<i>0.179</i>	<i>–0.031</i>	<i>–0.049</i>	<i>0.296</i>	<i>0.362</i>	<i>0.334</i>	<i>0.322</i>	<i>0.265</i>	<i>0.252</i>	<i>0.191</i>	<i>0.021</i>	–	–	–	–
Cl	<i>0.224</i>	<i>0.015</i>	<i>–0.003</i>	<i>0.342</i>	<i>0.408</i>	<i>0.379</i>	<i>0.368</i>	<i>0.311</i>	<i>0.297</i>	<i>0.237</i>	<i>0.067</i>	<i>0.046</i>	–	–	–
Rm	<i>0.066</i>	<i>–0.143</i>	<i>–0.161</i>	<i>0.184</i>	<i>0.250</i>	<i>0.221</i>	<i>0.210</i>	<i>0.153</i>	<i>0.139</i>	<i>0.079</i>	<i>–0.091</i>	<i>–0.112</i>	<i>–0.158</i>	–	–

Table 5. Differences in mean distance to habitat types between snubfin and humpback dolphins. A negative difference indicates snubfin dolphins occurred closer to this habitat than humpback dolphins, a positive difference indicates humpback dolphins occurred closer to this habitat than snubfin dolphins. Significant differences ($P < 0.05$) in mean distances are indicated in bold italics. See Table 1 for description of habitat types and abbreviations

Habitat	Difference (m)	95%CI (m)	<i>P</i>
Depth 1 m	-331.5	-598.7, -95	0.017
Depth 2 m	-116.7	-324.4, 85.4	0.339
Depth 5 m	55.6	-215.36, 291.6	0.682
Depth			
10 m	350.6	-70.1, 784.5	0.120
Sg 1 m	-549	-854.5, -202.7	0.004
Sg 2 m	-412.3	-664.3, -115.3	0.015
Sg 5 m	-269.5	-540.8, 48.5	0.091
Dc 5 m	3865.2	2017, 5802	<0.0001
Dc 15 m	4297.3	2321, 6213	<0.0001
Cl	85.4	-154.52, 325.3	0.405
Rm	-771.5	-1282.8, -352.5	0.006

among habitats common to both species corroborated these differences. While snubfin dolphins occurred closer to waters 0–1 m deep, closer to waters 0–2 m deep with seagrass, and closer to river mouths than humpback dolphins, humpback dolphins occurred closer to the dredged channels than snubfin dolphins. Overall, these habitat preferences correspond well with the almost exclusive coastal and estuarine distribution of both species throughout their range (Stacey & Arnold 1999; Jefferson & Karczmarski 2001; Parra *et al.* 2002, 2004).

Despite the low survey effort along the eastern section of Cleveland Bay (section D, Fig. 1a) in comparison with other areas (due to weather and to sea conditions), I am confident that any biases introduced are minimal, for the following reasons. Aerial surveys covering the eastern section of Cleveland Bay have reported only a few sightings of humpback dolphins and none of snubfin dolphins (Preen 1999). Snubfin dolphins are known to occur close to river mouths in Australian waters (Parra *et al.* 2002). Humpback dolphins exhibit a similar pattern: most populations studied associate with areas receiving freshwater inputs (Jefferson & Karczmarski 2001). There are no river mouths in section D of the study area.

HABITAT SELECTION AS A PRINCIPAL MECHANISM OF RESOURCE PARTITIONING BETWEEN SYMPATRIC SNUBFIN AND HUMPBACK DOLPHINS

Differential use of space, difference in activity patterns and diet, and temporal segregation in space use have been proposed as strategies adopted by sympatric mammal species to promote coexistence (Palomares *et al.* 1996; Arlettaz, Perrin & Hausser 1997; Arlettaz 1999; Johnson *et al.* 2000; Abramsky, Rosenzweig & Subach 2001). Similar strategies have been proposed for sympatric delphinids (Bearzi 2005).

Snubfin and humpback dolphins in Cleveland Bay showed: (1) high degree of spatial overlap; (2) concordance in space use patterns; and (3) similarity in their behavioural activities according to space and time. Additionally, both species occur year round in the study area, and interspecific encounters were observed across the 4 years of study (Parra 2005). Thus segregation into exclusive ranges in space and time, and difference in behaviour patterns do not seem to be important factors promoting their coexistence.

One difference in the behavioural activities of both species that might, in part, promote the sharing of space while alleviating interspecific interactions was that of foraging behind trawlers. I did not see snubfin dolphins engaging in this behaviour, whereas humpback dolphins frequently foraged behind trawlers, especially within the core areas common to both species around the Port of Townsville. The frequent occurrence of this behaviour within this area for humpback dolphins can be explained as trawlers are limited by regulation to fishing only in the vicinity of the Port of Townsville.

Difference in habitat selection is considered one of the principal resource partitioning mechanisms promoting coexistence (Rosenzweig 1981; Morris 2003). The few studies on distribution patterns of sympatric dolphin species have suggested habitat partitioning as the mechanism mediating their coexistence (Gowans & Whitehead 1995; Acevedo & Burkhart 1998; Ferrero, Hobbs & VanBlaricom 2002). The results presented here suggest that the difference in fine-scale habitat selection between snubfin and humpback dolphins is one of the principal mechanisms promoting their coexistence. If species select different habitats within a common shared space they should have no difficulties coexisting. The considerable interspecific overlap in space use patterns between snubfin and humpback dolphins may be promoted by the mosaic of habitats (e.g. seagrass, dredged channels, river mouths, and coral reefs) found within the coastal waters of Cleveland Bay. This study supports the increasing acknowledgement that the key to coexistence relies on spatial heterogeneity (Chesson 1985, 2000).

WHAT UNDERLIES THE INTERSPECIFIC DIFFERENCES IN HABITAT SELECTION BETWEEN SNUBFIN AND HUMPBACK DOLPHINS?

Different factors (e.g. competition, predation, environmental conditions) with variable strengths and magnitudes may act simultaneously in the process of habitat selection (Rosenzweig 1981, 1991). Habitat selection in delphinids has been directly related to the distribution of their prey and predators (Heithaus & Dill 2002), and to physiographic and hydrographic features that may affect indirectly prey availability or reflect prey specializations by individual species (Gowans & Whitehead 1995; Smith & Whitehead 1999; Bräger, Harraway & Manly 2003). The considerable overlap and concordance in space use between snubfin and humpback

dolphins may be a result of convergence in areas where critical resources are abundant, or predation risks from shared predators are lowest, or both.

At least eight species of sharks of the families Carcharhinidae and Sphyrnidae including adult tiger sharks *Galeocerdo cuvier*, which are known predators of dolphins (Heithaus 2001) are present almost year round in Cleveland Bay (Simpfendorfer 1992; Simpfendorfer & Milward 1993). Both species' minor differences in habitat usage suggest similar vulnerability to shark predation, and shark marks on individuals of both species have been observed (GJP personal observations). Thus, it is likely that predation risk influences similarly habitat selection by both species. Future studies on the space use and patterns of habitat use of tiger sharks in Cleveland Bay, at a scale comparable with my work on dolphins, would help elucidate the influence of predation on the habitat preferences of snubfin and humpback dolphins.

Considering that the predominant behavioural state of snubfin and humpback dolphins in the coastal waters of Cleveland Bay is foraging, similarities and differences in their habitat preferences may be the result of their diet. Based on the available data, both species appear to be opportunistic-generalist feeders, eating a wide variety of coastal, estuarine and reef-associated fishes both on the bottom and within the water column (Heinsohn 1979; Barros, Jefferson & Parsons 2004).

The location of core areas of use for both species around river mouths (i.e. Bohle River and Ross River, Fig. 2) and near modified habitats such as dredged channels and breakwaters around Townsville's Port (Fig. 2) might reflect important aggregation areas for prey of both species. In effect, a comparison of their prey items in different areas shows dietary overlap with both species feeding on various prey belonging to the same family and even genus (Parra 2005). However, there also appears to be some dietary differences that may explain differences in habitat preferences.

All stomach contents of snubfin dolphins from Cleveland Bay contained cephalopods, whereas humpback dolphins contained only fish and crustaceans (Heinsohn 1979). Stomach contents from humpback dolphins in Hong Kong contained a very small proportion of cephalopods (Barros *et al.* 2004). Several species of cephalopods are abundant in shallow water (≤ 1 m deep) close to the coast, and along breakwaters of Cleveland Bay (Jackson 1991). If snubfin dolphins feed disproportionately on cephalopods found in shallow water, this may help explain their habitat preferences.

I suggest diet partitioning is likely, but it does not fully explain the differences in habitat selection between snubfin and humpback dolphins. First, similar fish families and genera are present in the stomach contents of both species indicating some dietary overlap. Second, despite the subtle differences in habitat selection that I have demonstrated, schools of both species use similar areas for foraging, and foraging schools of both species have occasionally been recorded within 100 m of each

other in Cleveland Bay. There may be other constraints contributing to interspecific differences in habitat selection.

Encounters between snubfin and humpback dolphins are predominantly of an aggressive/sexual nature (Parra 2005). During these encounters humpback dolphins were always dominant, initiating, chasing, and seeking physical contact with snubfin dolphins, while the latter tried to swim away or resist the interaction using their rostrum, head or side of body against humpback dolphins. These interactions appear to occur mainly between adult male humpback dolphins and snubfin dolphin females with calves. The nature of these interactions (e.g. interspecific competition, practising infanticide, interspecific mating) is unclear. Nonetheless, regardless of their function, aggressive interactions among sympatric species can lead to habitat segregation. For example, interspecific aggression among sympatric birds plays a key role in determining habitat selection and priority of access to productive habitats (Robinson & Terborgh 1995; Martin & Martin 2001). Among terrestrial mammals there are also several examples where interspecific aggression (including in some cases interspecific killing) has led to habitat displacement by dominant species (e.g. Johnson & Franklin 1994; Durant 1998; Linnell & Strand 2000; Loveridge & MacDonald 2002; Tannerfeldt, Elmhagen & Angerbjorn 2002).

I suggest that habitat partitioning between sympatric snubfin and humpback dolphins may be partly mediated by the aggressive exclusion of snubfin dolphins by humpback dolphins. As a result, shallow waters, close to river mouths and seagrass meadows may act as refuges for snubfin dolphins, places where encounters with dominant and aggressive humpback dolphins will be less likely.

If we are to provide effective measurements for the conservation of cetaceans occurring in direct sympatry, it is important that we understand their community dynamics. This study shows that fine-scale habitat selection may prove to be the principal mechanism of resource partitioning among coastal dolphins living in direct sympatry under similar ecological conditions. In the case of snubfin and humpback dolphins differences in habitat selection appear to be driven by diet and interspecific agonistic interactions. Studies of their feeding habits and prey distribution are needed to test diet divergence. If habitat selection by snubfin dolphins is mediated by aggressive interactions from humpback dolphins, concurrent tracking of individuals of both species and playback experiments should provide evidence of avoidance behaviour by snubfin dolphins and movements into shallower water habitats.

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