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The behaviour of Hong Kong's resident cetaceans: the Indo-Pacific hump-backed dolphin and the finless porpoise

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Abstract

A series of behavioural surveys were conducted in Hong Kong upon resident populations of Indo-Pacific hump-backed dolphins (*Sousa chinensis*) and finless porpoises (*Neophocaena phocaenoides*). The surveys were carried out from land-based vantage points in areas of known cetacean abundance. Hump-backed dolphins were present year-round in the waters to the north of Lantau Island and to the south during the summer monsoon season. Seasonal changes in abundance were significantly correlated with water temperature (positively) and salinity (negatively). Changes in the outflow of the Pearl River influence hump-backed dolphin distribution in the western waters of Hong Kong.

Finless porpoises were only sighted south of Lantau Island and were more frequently observed during the winter. Their abundance was correlated with water temperature (negatively) and salinity (positively) and also with the number of reported neonatal porpoise strandings. Seasonal distribution appears to be linked with reproductive cycles and hydrography. Diurnal patterns and tidal state affect the abundance of both species.

Introduction

Hong Kong is situated adjacent to the Pearl River delta on the south coast of the Chinese province of Guangdong (22°20′N; 114°10′E). Sixteen species of cetacean have to date been reported from Hong Kong's territorial waters (Parsons *et al.*, 1995; Parsons, 1997). Of these species, two are resident year-round in Hong Kong: the Indo-Pacific hump-backed dolphin (*Sousa chinensis*) and the finless porpoise (*Neophocaena phocaenoides*). The remainder of the species recorded from Hong Kong were probably from transient South China Sea populations.

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The first record of cetaceans in Hong Kong dates from 1637, when Peter Mundy reported white and 'ruddy' porpoises from the waters of the Pearl River Delta (Carnac-Temple, 1919). These cetaceans were officially recognised as a species new to science a hundred years later by Per Osbeck (1765). These 'Chinese white dolphins' were what is now known to be the resident Hong Kong population of Indo-Pacific hump-backed dolphin. However, since then, and until only relatively recently, little had been done to increase local knowledge of the species.

In order to gather baseline information on the behaviour of Hong Kong's resident cetaceans, a series of land-based surveys were carried out at selected vantage points around Hong Kong in known areas of high dolphin abundance. As there could possibly be seasonal changes in behaviour, these initial surveys extended for one calendar year. The main aims of this study were to determine whether there were any seasonal differences in cetacean abundance and whether abundance was correlated with various physical, oceanographic, environmental and anthropogenic factors.

Materials and Methods

Survey sites

Three vantage points were selected for the land based surveys (Fig. 1): Castle Peak, Kau Ling Chung and Shek Pik. The former site allowed observation of waters to the north of Lantau Island, including the islands of Sha Chau and Lung Kwu Chau. The two latter sites overlooked waters to the south of Lantau. These three sites were chosen as they had a local reputation for being frequented by cetaceans. The area overlooked by the Shek Pik vantage point was of particular interest, as it had been put forward as a potential marine reserve by the Hong Kong Marine Conservation Society in 1993.

The Castle Peak survey site was at Castle Peak local power station, on top of a coal ash storage tower, standing 30.9 m above chart datum. A strut of the Castle Peak service jetty was used to gauge

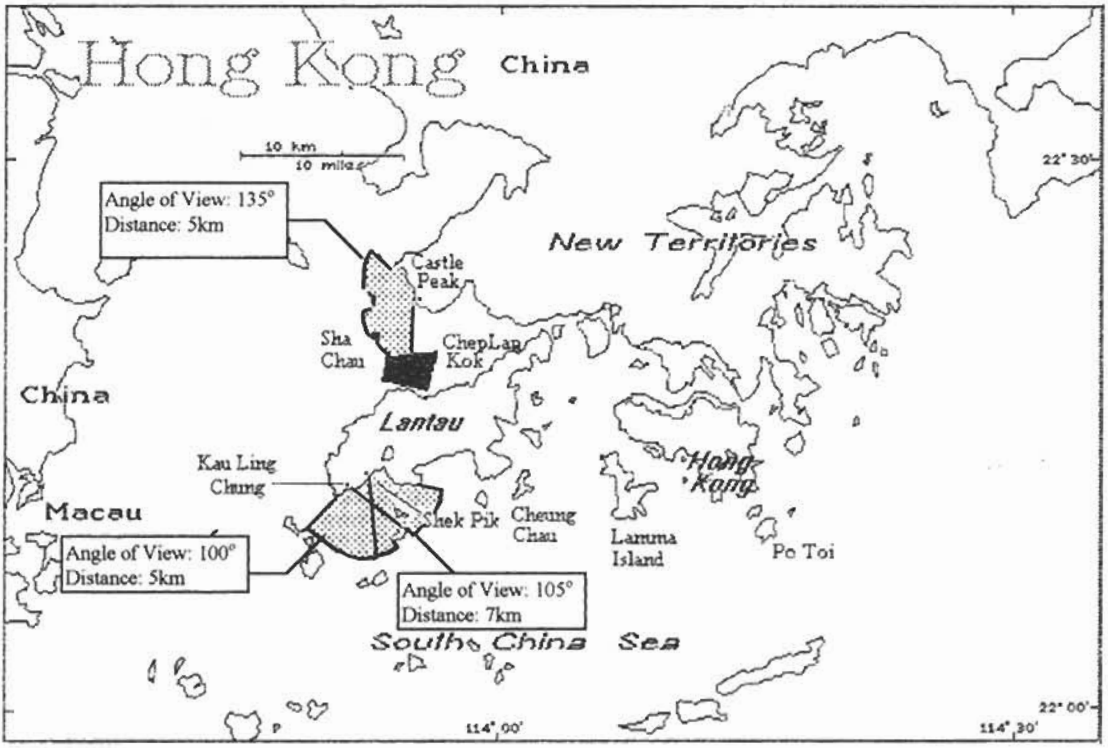

Figure 1. Map showing the positions of the three survey sites and demonstrating the fields of view.

tidal height. Surveys at Kau Ling Chung were from a tourist viewpoint 94.2 m above chart datum. This site allowed observations to a distance of 5 km. Beyond this point, visibility was too poor to observe dolphins due to haze and sea state. A nearby, flat-sided rock was used to gauge tidal height. The surveys at Shek Pik were carried out upon a disused helicopter landing pad which was situated on the end of a headland east of Kau Ling Chung. The edge of a pier at Shek Pik prison was used to gauge tidal heights.

Survey protocol

The surveys were undertaken weekly with a crew of one researcher and up to four volunteer observers. A total of 7 h of observation effort was made for each Castle Peak survey and between 8–10 h for each South Lantau survey. Hourly measurements were taken on a variety of environmental conditions and other factors, i.e., sea state (beaufort scale), visibility and tidal height. Visibility was scored on a subjective scale of 1–5, with 5 denoting the worst conditions due to swell, sea state, haze and glare. On a day with a visibility score of 1, observations of cetaceans were possible to a distance of 5 km, with a range of <1 km on a day with a visibility score of 5. Whenever feasible, observers were split into two shifts. Observations would be made for 2 h before switching to the second shift of observers. This ensured volunteers did not become fatigued. Within each shift, one person would observe using binoculars whilst the other would use the naked eye. This compensated for disadvantages inherent in the two observation techniques. An experienced observer was present on each shift. The binoculars used for initial observations were Tasco 10 × 63 mm binoculars, equipped with an extra 4 × zoom.

Definitions

The term 'group' used in this paper refers to each separate sighting of dolphins, whether it be an aggregation of individuals of all ages and sexes or a solitary animal. Animals within a group were, generally, within 10 m of the nearest group member, moved as a cohesive unit and exhibited the same category of behaviour.

'Summer' refers to the period of the south-westerly monsoon winds, which are prevalent from May to August/September. 'Winter' refers to the north-easterly monsoon, which typically lasts from October until March of the following year.

The categories used in this chapter to distinguish between stereotypical behavioural patterns are

Table 1. A summary of hump-backed dolphins sighted at the three main land survey sites. Percentages of the total number of sightings are in brackets

	Kau Ling Chung	Shek Pik	Castle Peak
No. of dolphin groups	37 (29.4)	3 (2.4)	86 (68.2)
Mean no. of individuals sighted	97.5 (29.7)	4 (1.2)	226.5 (69.1)
Groups/hour effort	0.154	0.019	0.444
Individuals/hour effort	0.501	0.025	1.171

'milling', 'socialising', 'travelling', 'feeding' and 'boat-chasing'. All but the last are analogous to the categories used by Shane (1990). The latter was the active pursuit of a fishing vessel by dolphins, with the animals, presumably, catching fish either directly through the net or escaping from it, or catching fish forced out of the trawl net by the bow wave created by its leading edge. The behaviour of observed cetaceans was usually fluid and groups often engaged in several behaviour types during an observation period. A behaviour category was assigned if the majority of the group exhibited the particular behaviour class during a period of observation. Hence, a particular group could be allocated for more than one behaviour category. In the Results section, percentages are allocated for the number of groups which displayed the particular behaviour category for at least 25% of the total observation period.

Results

Hump-backed dolphins

In the first year of surveying (March 1994–February 1995), a total of 112 surveys were carried out with a total of 609 h spent in observation. Over this period, 126 groups of hump-backed dolphins were sighted, a mean total of between 328 individuals sighted. Of these, 69.1% were sighted from the Castle Peak survey site, 29.7% from Kau Ling Chung and 1.2% from Shek Pik (Table 1). Dolphin abundance is, therefore, greatest at Castle Peak, with a frequency of individuals and groups sighted that was 2.34 and 2.88 times greater, respectively, than the frequencies observed at Kau Ling Chung (Table 1). Hump-backed dolphins were hardly sighted at Shek Pik and the area is, therefore, not considered to be part of their normal range.

The number of dolphin sightings was significantly correlated with visibility (Pearson's rank correlation: $r = -0.992$; $P<0.001$) and sea state (Pearson's rank correlation: $r = -0.934$; $P<0.001$) but not with the total number of shipping vessels present within the field of view, i.e., within a 5 km radius of the survey platform. The proportion of survey hours subjected to different visibility scores and sea states were, fortunately, distributed relatively evenly throughout the year. June was the only month when poor visibility might be a significant factor in observation rates and has been considered subsequently.

Seasonality

There were noticeable and significant (Fig. 2) changes in dolphin abundance throughout the year. The frequency of sightings from the South Lantau survey sites was significantly greater during the summer ($\chi^2=21.78$; 1 d.f.; $P<0.01$), but there was no statistical difference in abundance between seasons at the Castle Peak survey site. The Hong Kong summer is a period of the year associated with south-westerly winds, heavy rainfall, low sea salinity and a tenfold increase in outflow from the Pearl River (Shen, 1983). The abundance of South Lantau dolphin sightings was significantly correlated with water temperature (Spearman: $r=0.9429$; $P<0.05$) and salinity (Spearman: $r=-0.9429$; $P<0.05$) in North Lantau waters. Seasonal changes in dolphin abundance near Castle Peak were correlated with neither salinity nor water temperature.

Time and tide

Tidal cycle affected dolphin abundance, with 75% of sightings from Castle Peak and 70% of the South Lantau sightings occurring during the ebb tide. Dolphin sighting frequency was significantly greater during the ebb tide (Castle Peak: $\chi^2=17.01$; 1 d.f.; $P<0.01$ and South Lantau: $\chi^2=5.121$; 1 d.f.; $P<0.05$). There were also diurnal rhythms in dolphin abundance. At Castle Peak, dolphin sightings were greatest in the morning ($\chi^2=34.17$; 7 d.f.; $P<0.01$; Fig. 3a), whereas in southern Lantau waters dolphin abundance was greatest in the afternoon ($\chi^2=45.25$; 10 d.f.; $P<0.01$; Fig. 3b).

Group size and behaviour

The mean size of the hump-backed dolphin groups was 2.76 individuals/group ($\pm$ 2.29 SD). The mean group size recorded at Castle Peak (range: 1–13; mean: 2.63 ± 2.55 SD) was significantly different from the group sizes recorded from South Lantau

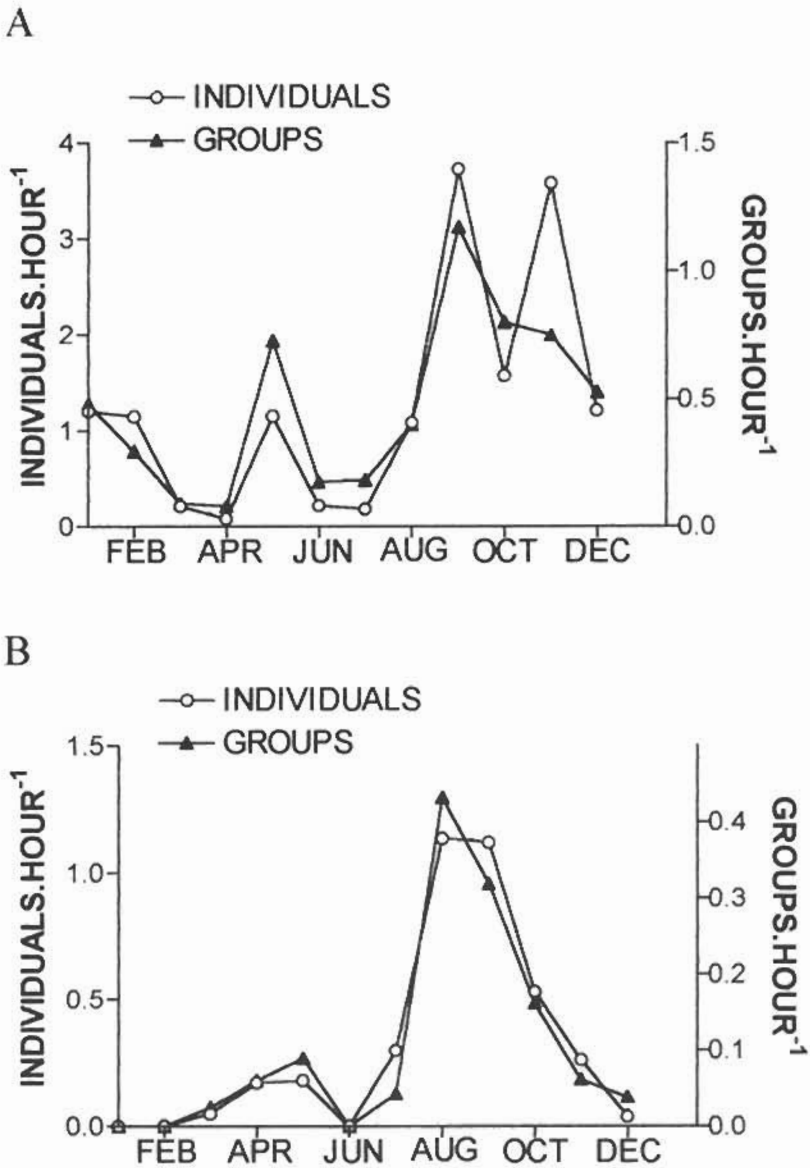

Figure 2. Monthly changes in hump-backed dolphin sightings made from the Castle Peak (A) and South Lantau (B) survey sites.

(range: 1–7; mean: 3.07 ± 1.46 SD) (Welch's t-test: $t=2.797$; $P<0.01$). The modal group size for both Castle Peak and South Lantau was two (Fig. 4). There were no significant changes in group size for either location throughout the year and there was no discernible influence of salinity or temperature on group size.

Feeding was the most commonly observed behaviour from the Castle Peak survey site, with 55% of encounters showing some aspect of this. Milling was observed in 29% of encounters, travelling in 23%, socialising in 18% and 16% of encountered groups were pursuing fishing trawlers (Table 2). Most (41.2%) foraging dolphin groups at Castle Peak were seen either at, or adjacent to, the seawater/freshwater mixing zone, which was clearly visible to the naked eye.

At Castle Peak there were significant differences in group size for dolphins observed engaging in different behaviours (ANOVA on log+1 trans-

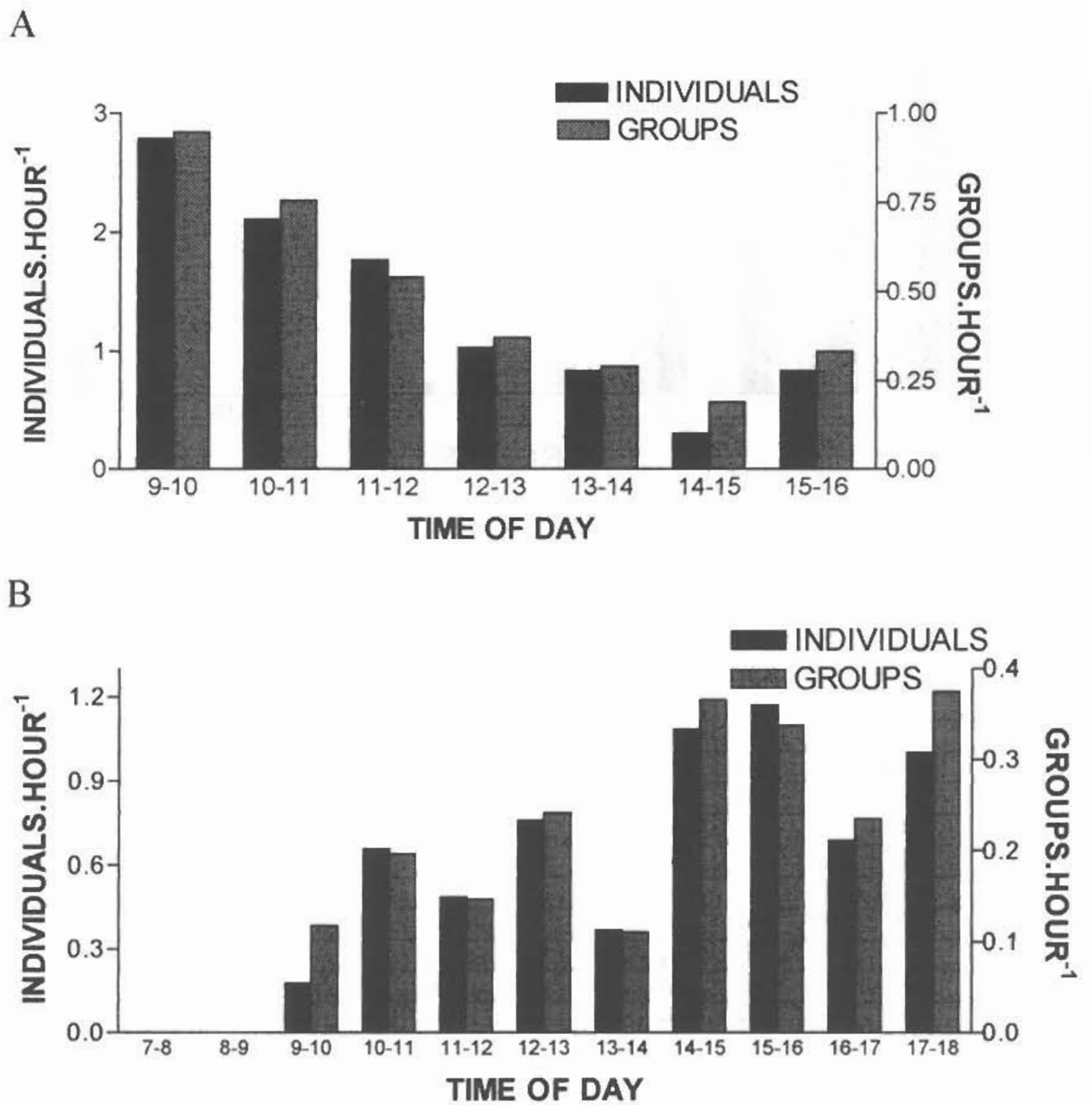

Figure 3. Diurnal pattern of hump-backed dolphin sightings made from the Castle Peak (A) and South Lantau (B) survey sites.

formed data: $F=5.27$; $P<0.001$; Table 2). Groups chasing fishing trawlers were significantly larger than those seen milling, travelling and foraging (Tukey–Kramer multiple comparison test on log+1 transformed data: milling vs boat-chasing: $q=5.976$; $P<0.001$, travelling vs boat-chasing: $q=5.549$; $P<0.01$ and feeding vs boat-chasing: $q=5.241$; $P<0.01$).

Travelling was the most frequently observed category of behaviour from the South Lantau survey sites (travelling was exhibited in 41% of all encounters). Milling (26%), feeding (23%), boat-chasing (23%) and socialising (23%) were also observed. There was no significant difference between the sizes of groups engaged in different types of behaviour (Table 2). There was, however, a significant difference in the size of milling groups observed in North and South Lantau waters (Welch's t-test on log transformed data: $t=2.098$; $P<0.05$).

There appeared to be a seasonal variation in the number of social interactions observed, with social behaviour occurring predominantly between

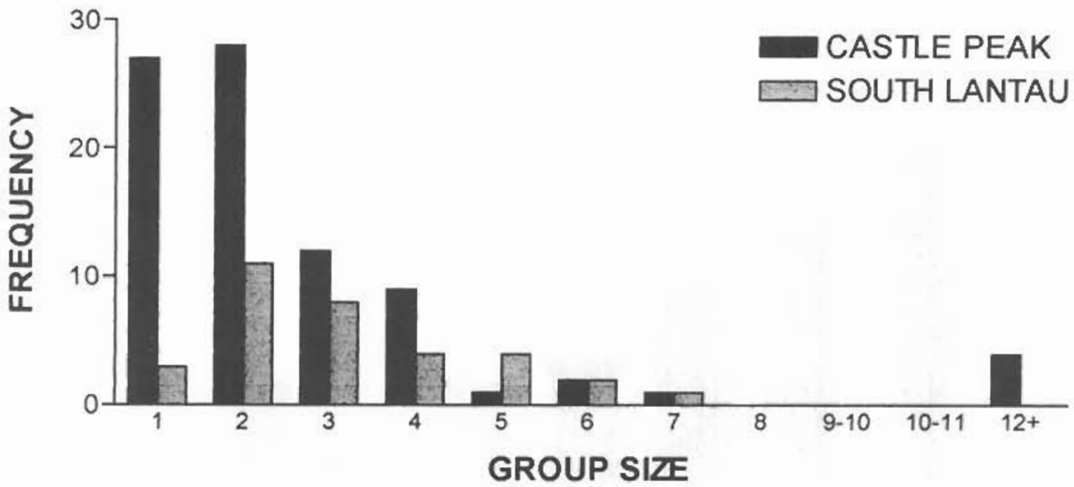

Figure 4. The relative frequency of hump-backed dolphin group sizes recorded from the Castle Peak and South Lantau survey sites.

Table 2. Hump-backed dolphin behaviour types observed from the Castle Peak and South Lantau survey sites. The percentage values denote the proportion of recorded groups that displayed this category of behaviour at some time during the sighting period

	Milling	Travelling	Feeding	Boat-chasing	Socialising
Castle Peak					
Percentage	29	23	55	16	18
Minimum group size	1	1	1	2	1
Maximum group size	6	6	7	13	6
Mean	2.08	2.14	2.59	6.65	2.77
Std. Dev.	1.29	1.37	1.55	5.20	1.39
South Lantau					
Percentage	26	41	23	23	23
Minimum group size	1	1	1	1	2
Maximum group size	4	3	6	6	6
Mean	2.80	2.28	3.17	3.67	3.44
Std. Dev.	0.89	0.58	1.46	1.50	1.31

August and November (Fig. 5). This peak in social behaviour was not correlated with either season or changes in salinity and temperature. It was, however, positively correlated with the number of sightings off South Lantau (Rank–Spearman: $r=0.6084$; $P<0.05$), and Castle Peak (Rank–Spearman: $r=0.6270$; $P<0.05$) and with the total number of dolphin sightings (Rank–Spearman: $r=0.6202$; $P<0.05$).

An inventory of the various types of behaviour displayed by Hong Kong's *Sousa chinensis* population was also collated, for the benefit of future behavioural studies. The behaviours were categorised into: (i), feeding; (ii), inquisitive; (iii), aggressive and (iv), social/mating. This ethogram is summarised as an appendix to this paper.

Succourant behaviour

Succourant behaviour is a sub-category of epimeletic, or care-giving behaviour, wherein care and attention is directed towards animals in distress (Caldwell & Caldwell, 1966). There is one anecdotal report of this type of behaviour in Hong Kong: a male Indo-Pacific hump-backed dolphin was attended by several other dolphins in a shallow bay near the village of Tai O. The dolphins accompanied the distressed animal, according to local villagers, for a whole morning until the animal died and stranded (11 February 1995).

Two other cases of epimeletic behaviour have occurred during this study. In both occasions 'nurturant' (Caldwell & Caldwell, 1966) behaviour was exhibited towards dead calves. Fertl and Schiro

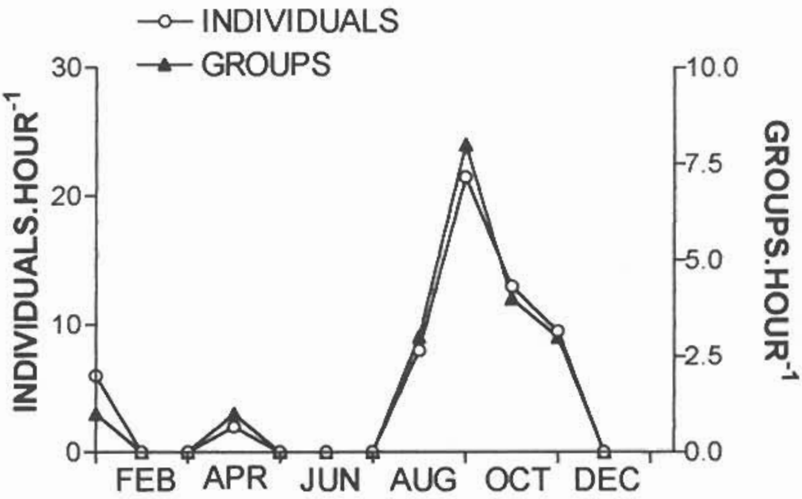

Figure 5. The seasonal variation in observed hump-backed dolphin social interactions showing a considerable increase in social behaviour in the months of September. This is related to an increase in the number of dolphin sightings recorded at all of the survey sites in Hong Kong.

(1994) comment on the carrying of dead calves by several cetacean species, including common dolphins, rough-toothed dolphins, striped dolphins and bottlenose dolphins (Moore, 1955; Brown *et al.*, 1966; Lodi, 1992). An adult Indo-Pacific hump-backed dolphin was observed on 16 June and again on 22 June 1994 (J. Wong, pers. comm.), attending the corpse of a dead calf. On both occasions the adult carried the calf on its rostrum, even as it attempted to dive. The second case occurred in early June 1996, when a local operator of dolphin-watching tours (W. Leverett, pers. comm.) observed a dead calf being supported by a group of adult dolphins.

Finless porpoises

In addition to the hump-backed dolphins sighted, 19 groups of finless porpoise (*Neophocaena phocaenoides*) comprising a total of between 71 and 86 individuals, were observed from the South Lantau survey sites.

Seasonality

There were distinct seasonal changes in finless porpoise abundance. Finless porpoises were present off the south coast of Lantau Island from the start of the surveys in February 1994 until May 1994 (Fig. 6). They were absent from the area from June 1994 until November 1994. During this latter period, finless porpoises were observed to the south of Hong Kong Island near the islands of Po Toi and Waglan. Animals were sighted again off the south of Lantau from November 1994 until the cessation of surveying in January 1994. Research has since confirmed this pattern of seasonal pattern of local migration between different areas of Hong Kong's waters (Jefferson & Braulik, in press).

There were significantly more finless porpoises present in South Lantau waters during the winter ($\chi^2=18.22$; 1 d.f.; $P<0.01$). Finless porpoise abundance was, moreover, shown to be significantly correlated with water temperature (Spearman: $r=0.8804$; $P<0.05$) and salinity off South Lantau (Spearman: $r=0.8804$; $P<0.05$). Sighting frequency was also positively correlated with the number of neonate finless porpoises stranded each month along the Hong Kong coastline (Spearman rank correlation, neonate strandings vs individuals/hour^{-1}: $r=0.663$; $P<0.05$ and neonate strandings vs groups/hour: $r=0.7534$; $P<0.005$; Fig. 7). There was, interestingly, a significant relationship between the presence of hump-backed dolphins and the absence of finless porpoises (Spearman: $r=-0.5769$; $P<0.05$). There was, however, no discernible effect of tidal cycle on porpoise abundance, but there were diurnal differences in sighting frequency ($\chi^2=19.4$; 7 d.f.; $P<0.01$; Fig. 8), with more individuals seen per unit effort in the early morning.

Group size and behaviour

Finless porpoise group sizes ranged from 1 to 10 individuals, with a mean value of 3.90 (± 2.98 SD).There was no significant difference between the group sizes recorded from the two South Lantau survey sites. Mean group size was negatively

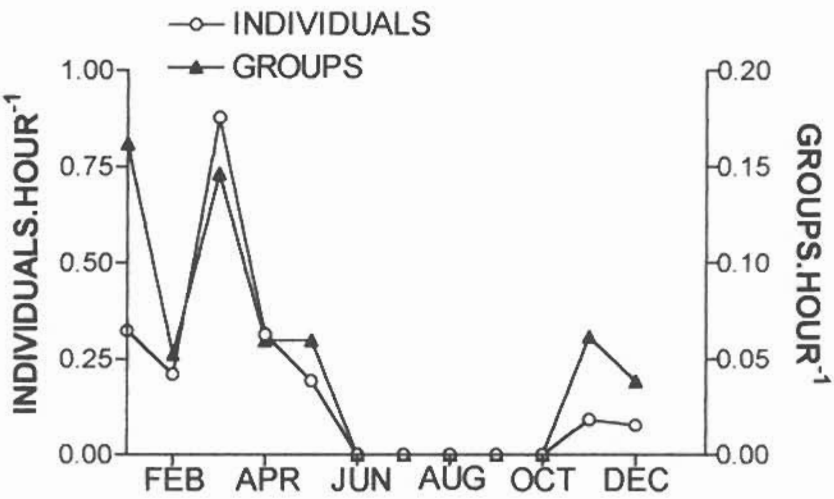

Figure 6. Monthly changes in finless porpoise sightings made from the South Lantau survey sites.

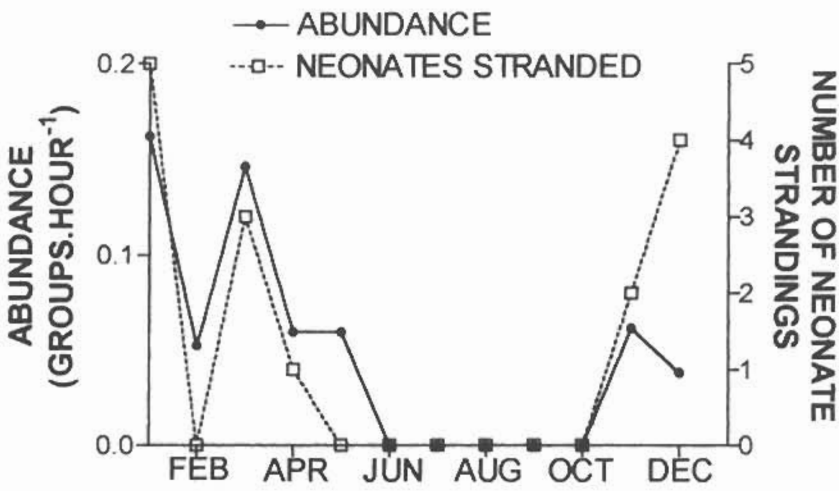

Figure 7. The relationship between the number of neonate finless porpoise strandings reported in Hong Kong each month (using strandings data collated from 1973), and the sighting frequency of finless porpoises off the South Lantau survey sites.

correlated with water temperature (Spearman: $r=-0.8804$; $P<0.05$) and salinity (Spearman: 0.8804; $P<0.05$), but was more strongly correlated with changes in abundance (Spearman, individuals/hour: $r=0.9228$; $P<0.0001$ and groups/hour: $r=0.8038$; $P<0.005$) and the correlations with temperature and salinity are likely to be a by-product of this. Mean group size tended to be higher in months with more stranded neonates, although this was not statistically significant (Spearman: $r=0.5144$; $P=0.087$).

Feeding was the behaviour most frequently displayed by finless porpoises. This was recorded in 48% of the groups observed. Travelling (38%) and milling (29%) porpoises were also observed (Table 3). There were significant differences in the mean group size recorded for porpoises displaying these different types of behaviour (ANOVA on log transformed data: $F=17.731$; $P<0.0001$). Travelling groups were significantly smaller than both feeding (Tukey–Kramer multiple comparison test: $q=7.534$; $P<0.001$) and milling groups (Tukey–Kramer: $q=6.961$; $P<0.001$; Table 3).

The behavioural repertoire of Hong Kong's finless porpoises was limited, and the only inventoried behaviours observed were 'shuttling', 'feeding

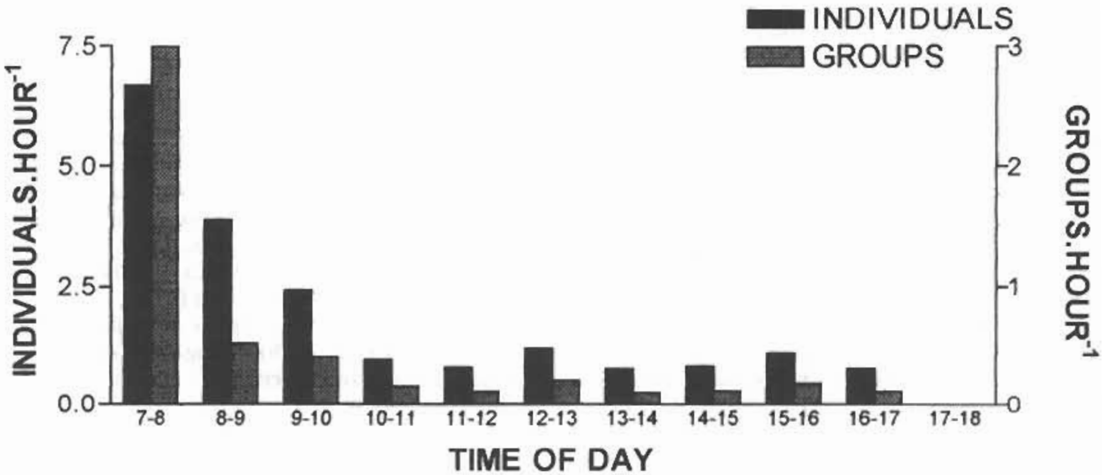

Figure 8. Diurnal changes in finless porpoise sighting frequencies from the South Lantau survey sites.

circles' and 'leaping' (see Appendix). However, one unusual aspect of the behaviour of this species was that gouts of water issued from their mouths when feeding at the surface. This 'spitting' behaviour is, as far as is known, unique to this population of finless porpoises and the significance or reason behind this is, as yet, unknown.

Discussion

Hump-backed dolphins

Studies which have been conducted thus far to an understanding of the behaviour of *Sousa chinensis* have mainly been concerned with animals occurring off the coast of South Africa and Australia. In these areas, hump-backed dolphins typically occur within 1 km of the shore (although Lear & Bryden (1980) noted a group of Australian hump-backed dolphins 5 km from the coastline) and in waters less than 20 m deep (Saayman *et al.*, 1972; Saayman & Taylor, 1979; Corkeron, 1990; Durham, 1995; Corkeron & Marsh, 1995; Karczmarski, 1996). This near-shore predominance makes the species an ideal candidate for land-based observations. With most encounters occurring within 2 km, the results of this survey record the near-shore behaviour of Hong Kong's hump-backed dolphins. It is important to note that behavioural observations from survey boats (the presence of which may affect behavioural patterns) which occur further from land and in deeper waters may obtain different results when compared to the near-shore behaviours reported in this study. One example of this difference is seen in Jefferson (1997) wherein more 'boat-chasing' groups are observed, a result of surveys being carried out in predominantly mid-channel areas of denser boat traffic.

Table 3. Finless porpoise behaviour types observed from the South Lantau survey sites. The percentage values denote the proportion of recorded groups that displayed this category of behaviour at some time during the sighting period

	Milling	Travelling	Feeding
Percentage	29	38	48
Minimum group size	2.5	1	2.5
Maximum group size	9.5	2	9.5
Mean	6.42	1.63	6.25
Std. Dev.	2.67	0.52	2.98

The seasonal increases in abundance noted in this study reflect an influx of dolphins into South Lantau waters. This influx could be due to either the immigration of individuals from regions outside Hong Kong or to a shift in the distribution of the animals normally inhabiting North Lantau waters. Subsequent photo-identification studies within Hong Kong suggest that the former is true (Jefferson, 1997).

Hong Kong's close proximity to the Pearl River, the largest in southern China, has a dramatic effect on the hydrography of the region, notably with regard to turbidity, salinity, pH, tides, currents and temperature of Hong Kong's waters (Shen, 1983; Ridley-Thomas & Osorio, 1992). The influence of salinity and water temperature on cetacean distribution has been noted in several studies (Sergeant & Fisher, 1957; Gaskin, 1968; Perrin *et al.*, 1983; Au & Perryman, 1985; Polacheck, 1987; Ross & Cockcroft, 1990; Wells *et al.*, 1990; Findlay *et al.*, 1992). Water temperature and salinity are unlikely to have much effect on the cetaceans themselves, but rather determine the distribution of prey species (Wells *et al.*, 1990). The seasonal distribution and availability of prey species has been related to the abundance and distribution of many cetaceans (Sergeant, 1962; Evans, 1971; Gaskin, 1977; Gaskin & Watson, 1985; Shane & Schmidly, 1978; Shane, 1980; Wells *et al.*, 1980; Würsig & Würsig, 1980; Irvine *et al.*, 1981).

Little is known about the distribution and abundance of fish species in Hong Kong. Published information on fish distribution in areas of high dolphin abundance is limited to one study by Richards & Wu (1985) in North Lantau waters. These authors noted considerable spatial variation in fish distribution, but no clear seasonal variation. They did, however, record peaks in the abundance of *Leiognathus brevirostris* (April–May) and sciaenids (*Wak sina* and *Argyrosomus macrocephalus*) in August and September. These are prey species of the Hong Kong hump-backed dolphin population (Parsons, 1997; Barros *et al.*, in prep.) and, therefore, the slight peaks in North Lantau dolphin abundance during these periods may reflect an increase in such prey items.

The high proportion of dolphins feeding in the freshwater/saltwater mixing zone may be indicative of prey abundance affecting distribution. The freshwater/saltwater interface can cause an up-welling of nutrients with bands of fish feeding upon these nutrients. It is feasible that Hong Kong's hump-backed dolphins follow this interface and its associated band of fish.

Diurnal and tidal changes in group size, occurrence and behaviour are also likely to reflect changes in food resources (Wells *et al.*, 1980; Shane *et al.*, 1986). Diurnal variations in behaviour and distribution have been observed in several cetacean species (Layne, 1958; Saayman *et al.*, 1973; Wells *et al.*, 1980; Würsig and Würsig, 1980; Scott *et al.*, 1990; Hanson & DeFran, 1993; Sekiguchi, 1995; Stone *et al.*, 1995). Saayman & Tayler (1979) noticed an increase in hump-backed dolphin feeding during the flood tide, a period associated with a greater abundance of prey. The movement of dolphins with tides has also been suggested by many researchers (True, 1885; Gunter, 1942; McBride & Hebb, 1948; Irvine & Wells, 1972; Caldwell & Caldwell, 1972; Würsig & Würsig, 1979; Shane, 1980). The energetic benefits may be gained by travelling with a tidal current, as the flow of water can propel a dolphin with a minimal effort on the part of the individual. Benefits may also be gained by moving against the tidal flow, as the dolphin would be swimming into schools of oncoming fish. Dolphins which congregate to feed in either near-shore areas or reefs during low tide also have a foraging advantage in that there is a smaller volume of water into which prey may escape; this effectively concentrates their food supply.

A high proportion of hump-back dolphin encounters in South Africa are with solitary animals (20%: Durham, 1995; 15.4%: Karczmarski, 1996), more so than many other cetacean species (Wells *et al.*, 1980, 1987; Dos Santos & Lacerda, 1987; Shane, 1990). Other studies on hump-backed dolphins have shown small group sizes (Zbinden *et al.*, 1977; Saayman & Tayler, 1979; Corkeron, 1990). In West and South Africa and the northern Indian Ocean, group size ranged from 1–25 animals (Pilleri & Gihr, 1974; Pilleri & Pilleri, 1979; Saayman & Tayler, 1979). Wang (1995) reported a modal group size of between 3–5 individuals for China and Corkeron (1990) reported upon groups of between 1–9 animals in Moreton Bay, Australia (mean: 2.4; $n=9$). The size of Hong Kong's hump-backed dolphin groups are, thus, similar to values for other regions. The mean group size observed in Hong Kong is comparable to those reported upon by Saayman & Tayler (1973; mean group size: 6.6 ± 1.4 SE and 1979; mean group size: 6.5 ± 0.38 SE), Karczmarski (1996; mean group size: 6 ± 12.72 SD) and Findlay *et al.* (1992; 6.83 ± 1.94 SD and 4.83 ± 3.04 SD).

In general, cetacean group size varies according to habitat, behaviour and the abundance of food sources (Shane *et al.*, 1986). The fact that hump-backed dolphin group size is similar to that of bottlenose dolphins (Irvine *et al.*, 1981; 4.8 ± 0.16 SE) in an estuarine environment emphasises this. Moreover, the largest groups sighted in Hong Kong were animals seen following fishing trawlers ('boat-chasing'), a potentially large source of resources. Seasonal increases in group size may also reflect seasonal increases in abundance.

Saayman & Tayler (1979) showed that most hump-backed dolphin pairs were adults, juveniles typically occurring as members of larger groups. In Hong Kong, most observed pairs comprised one adult accompanied by either a calf or a juvenile. In dolphins, the larger sizes of groups containing calves reflect the need to protect young animals from predators (Wells *et al.*, 1987) which, in the case of hump-backed dolphins, are predominantly the great white shark (*Carcharodon carcharias*), the bull (or Zambezi) shark (*Carcharinus leucas*) and the tiger shark (*Galeocerdo cuveri*). Tiger sharks are a potential predator of hump-backed dolphins in Morton Bay, Australia (Corkeron, 1990) and bull sharks are a likely candidate for the source of many shark attacks on hump-backed dolphins in South Africa. Both tiger and bull sharks have been recorded from Hong Kong (D. Cook and H. Kvam, pers. comm., respectively). Although great white sharks have not, as yet, been recorded from Hong Kong they are probably present in the region.

Predatory sharks appear to migrate seasonally into eastern Hong Kong waters, notably around Sai Kung, during the summer months, where they have been deemed to be responsible for several attacks on human swimmers (Morton, 1994). Tiger sharks are, however, intolerant of low salinity conditions which may have a narcotic and, in the extreme, fatal effect on this species due to the osmotic absorption of water (Bannister, 1992). It is unlikely, therefore, that any would occur in the low salinity waters of North Lantau. Bull sharks are, however, capable of inhabiting brackish and even freshwater bodies and have, moreover, been recorded from near Tuen Mun, an area of high hump-backed dolphin abundance (H. Kvam, pers. comm.). Other large carcharinids (D. Cook, pers. comm.) and false killer whales (*Pseudorca crassidens*), both of which are potential predators of small cetaceans, have also been recorded from North Lantau waters (Parsons *et al.*, 1995; Parsons, 1997). One would expect that if predation is a serious threat to Hong Kong's hump-backed dolphins, group sizes, in particular groups containing calves, would be large. This does not appear to be the case. In South African estuaries bull shark abundance increases between December and March (Bannister, 1992) and this may, in part, explain larger group sizes noted by Karczmarski (1996) during this period. Seasonal changes in the mean group size of Hong Kong's hump-backed dolphins could, possibly, reflect seasonal changes in predator abundance.

Other researchers have observed hump-backed dolphins displaying an adverse reaction to boat traffic (Pilleri & Gihr, 1974; Roberts *et al.*, 1983; Ross *et al.*, 1994; Karczmarski *et al.*, 1997). The large volume of boat traffic in Hong Kong probably has an effect on dolphin behaviour and animals often vanished as boats passed through groups, staying underwater for sizeable periods of time and, in several cases, disappearing. The most noticeable change in behaviour occurred over a period of two weeks, in December 1994. During this period, animals observed from Castle Peak engaged in longer dives and changed direction frequently underwater. This period coincided with sea-bed drilling next to Sha Chau, an area of high dolphin abundance. Based on the information given in a recent study by Beasley (1996), it is highly probable that this drilling was the cause of the observed change in behaviour.

From this study, it appears that Indo-Pacific hump-backed dolphins spend a considerable amount of their time engaged in feeding activities (55% for North Lantau), relatively more so than South African animals (Saayman & Tayler, 1979: 27% feeding). In addition, individuals were never observed 'resting' (Saayman & Tayler, 1979: 8% resting). Admittedly, there would probably be an observational bias for foraging groups seen off Castle Peak, as the area is undoubtedly a prime feeding ground, with the warm water outflow from the power station making the immediate area particularly verdant (Lam, 1987). The high proportion of the day spent foraging may, however, be linked to the fact that Hong Kong's waters are intensely fished. The local fishery is in decline due, in part, to over-exploitation (Morton, 1989; Leung, 1997; Parsons, 1997). Finding an adequate supply of food may, thus, be a more onerous task for Hong Kong's animals than for other hump-backed dolphin populations. However, the mean group size of hump-backed dolphins in Hong Kong is, as mentioned previously, similar to group sizes observed elsewhere in the world. Group size may, thus, reflect the optimal size for a particular method of foraging, rather than resource abundance.

In summary, the behaviour and occurrence of Indo-Pacific dolphins observed in Hong Kong are shaped largely by the distribution and the abundance of resources. Seasonal changes in hydrography, due mainly to the dynamics of the Pearl River outflow, appear to influence these resources and, hence, the occurrence of hump-backed dolphins in the waters south of Lantau Island. Dolphins are observed throughout the year in the waters north of Lantau Island, suggesting that this area possesses characteristics which are integral to *Sousa chinensis*. These characteristics may include an abundance of appropriate prey species (Parsons, 1997), rock and boulder reefs (c.f. Saayman & Tayler, 1979) and the Pearl River/oceanic water interface.

It should be noted, however, that these observations apply only to the portion of the hump-backed dolphin population inhabiting near-shore Hong Kong waters. Individuals swimming more off-shore and utilising other regions of the Pearl River Delta, outside of Hong Kong's territorial boundaries, may differ both ethologically and ecologically from the individuals observed in this study.

Finless porpoises

The seasonal migration of finless porpoises has been documented from other regions they inhabit. Kasuya and Kureha (1979) noted seasonal changes in abundance in the Inland Sea of Japan with the lowest density (40% of the peak season value) of porpoises occurring in early winter and with a peak in April. Shirakihara *et al.* (1994) also noted seasonal variations in Japanese porpoise sighting frequencies, this time in the coastal waters of Western Kyushu, with an increase in the central waters of Ariake Sound in winter and an increased number of sightings in the mouth of Araike Sound and Tachibana Bay in summer. Mizue *et al.* (1965) also recorded seasonal changes in the number of by-caught porpoises in this region, with a peak in the autumn and winter months. Both Kasuya & Kureha (1979) and Shirakihara *et al.* (1994) ascribed increases in porpoise density to breeding seasonality, as such an increase was accompanied by an increase in the number of mother and calf pairs sighted and the number of stranded and by-caught neonates (Shirakihara *et al.*, 1993).

Wang (1984) notes seasonal changes in the numbers of the finless porpoise population dwelling in the Bohai Sea (North-East China), with the greatest values being recorded in the summer and autumn, with the lowest in winter. Yellow Sea individuals move from shallow to deeper water in the winter. As finless porpoises in the region calve in the spring (Wang, 1984), this migration may be linked to changing food resources rather than reproduction.

In the Indus Delta, finless porpoise numbers are highest between October and April, with individuals departing for deeper waters for the rest of the year, allegedly following seasonal migrations of prawns (Pilleri & Gihr, 1972; Pilleri & Pilleri, 1979). As parturition also occurs in October (Adsel, 1965), this seasonal migration may also be linked to the porpoise's breeding cycle.

The reasons behind the seasonal changes in occurrence recorded in Hong Kong's finless porpoises appear to be complex and involve several factors. As the porpoise sighting frequency recorded from South Lantau is correlated with both salinity and water temperature, there may be a change in the amount of resources available, as suggested above for *Sousa chinensis*.

The reciprocal correlation between dolphin and porpoise numbers is interesting as it suggests there is competitive exclusion between the two species. Certainly, in other regions of the world, dolphins and porpoises come into conflict, most notably in the Moray Firth where bottlenose dolphins are known to attack harbour porpoises (Taylor, 1995). The larger size of *Sousa chinensis* would suggest, intuitively, that this species would be the aggressor if one were involved in the exclusion. There have, as yet, been no observed instances of aggression between the two species and no mortalities have shown signs of inter-specific conflict. Liu *et al.* (1986) report *Lipotes vexillifer* co-existing with finless porpoises in the Yangtze River. Until evidence is presented to the contrary, therefore, mere avoidance behaviour appears to be the norm for either one or both of the species.

The correlation between abundance and neonate mortality suggests strongly that the seasonal appearance of finless porpoises around South Lantau is linked to their reproductive cycle.

During the summer months, predatory sharks have been observed in the eastern waters of Hong Kong and, as noted previously, have been held responsible for several human mortalities. Both bull and tiger sharks have, moreover, been recorded from areas of high finless porpoise abundance (H. Kvam and D. Cook, pers. comm., respectively). It is possible, therefore, that the presence of predators may influence finless porpoise distribution and group size.

During the winter, therefore, finless porpoises are more numerous in the waters off South Lantau, when parturition occurs. During the summer, a change in the distribution of hump-backed dolphins, prey species and possibly predators may cause finless porpoises to move from the inshore bays of South Lantau to the waters off the Soko Islands and Hong Kong Island. Unfortunately, information on porpoise abundance in the latter areas is scant and reliant upon stranding information and anecdotal sightings of animals. A dedicated study of the numbers and seasonal changes in Hong Kong's finless porpoise distribution is required to fill the present gaps in our knowledge.

Although the behaviour of finless porpoises has been observed in captivity, notably in the Toba Aquarium (Kataoka, 1977), there is little information on porpoise behaviour in the wild. Of the behaviour categories listed in this paper (Appendix), only 'spyhopping' (Chen *et al.*, 1979; Liu *et al.*, 1986), 'leaps' (Chen *et al.*, 1979) and 'bodyslamming' (Zhou *et al.*, 1993) have been recorded for finless porpoises in the Yangtze River. Pilleri *et al.* (1976) note that Yangtze River animals are more active than those in Pakistan, the latter being elusive and evasive in the presence of boats (Pilleri & Gihr, 1974). This boat-shy behaviour is also apparent in Hong Kong and adds to the difficulty of researching this species.

The unusual practice of finless porpoise calves clinging to and being carried on the backs of adults which has been described for the Yangtze River individuals (Chen *et al.*, 1979; Pilleri & Chen, 1979; Zhou *et al.*, 1980; Liu, 1981) has not been observed in either Japan (Kasuya & Kureha, 1979) or Hong Kong.

In most regions, finless porpoise groups are usually small. In the Yangtze River, group size ranges from solitary individuals to eight (typically 5–6) although groups can be as large as 20, especially in areas where tributaries join the main body of the river, areas which are typically abundant in fish (Chen *et al.*, 1979; Zhou *et al.*, 1980). In the Indus Delta, either solitary individuals or pairs were most frequently observed, with no group being larger than four animals (Pilleri & Gihr, 1974).

Shirakihara *et al.* (1994) report groups of 1–10 animals, with a mean group size of 1.7 ($\pm$ 0.05 SE), from Western Kyushu. Group size was larger from April to September, but this was not related to the porpoise's reproductive cycle as parturition occurs from autumn to spring in Western Kyushu

(Shirakihara *et al.*, 1993). In the Inland Sea of Japan, group size ranged between 1–13 with a mean size of 1.97. Larger groups were observed during the same period as group size increased off Western Kyushu. Unlike the Kyushu population, however, the mating season of the Inland Sea population also coincided with larger group size (Kasuya & Kureha,1979).

The mean group size for Japanese finless porpoises is significantly smaller than the mean group size observed in Hong Kong (Welch's *t*-test on data in Shirakihara *et al.*, 1994: $t=3.209$; $P<0.005$). This may reflect the fact that, as noted above, groups observed from South Lantau may be breeding.

In summary, the seasonal changes in the occurrence and behaviour of local finless porpoises appear to be due to the interaction between and seasonal changes in several factors: reproductive state, competition with *Sousa chinensis* and resource availability. There may also be an influence of predators on finless porpoise behaviour. Due to the inconspicuous, undemonstrative and boat-shy nature of local finless porpoises, our knowledge of the behaviour and distribution of this species is limited for other regions of Hong Kong. This study serves as a model upon which other studies of finless porpoise behaviour could be based.

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Appendix. A summary and brief description of specific types of behaviour exhibited by hump-backed dolphins in Hong Kong

Feeding behaviour

Bodyslamming (Plate 1): the 'bodyslam' is a behavioural pattern also known as 'breaching' or a 'log' jump (Bel'kovich *et al.*, 1991). The animal rises out of the water at an angle of between 90° to 45° to the sea surface. While exiting the water the dolphin's flippers, its abdomen or peduncle may clear the surface. It then falls back into the water either dorsally or laterally. There are many theories as to the significance of this behaviour and it may have several functions depending on circumstances. Postulated theories include: announcing the presence of a dolphin to other pod members; as an 'exclamation mark' to acoustic behaviour; to allow observation of activities above the surface; an aggressive display; a courtship display; a foraging related activity, with the pressure wave caused by the slam aiding the schooling of fish; or, possibly, to loosen ectoparasites from the dolphin's dermis.

Carousels: a behaviour described by Bel'kovich *et al.* (1991) wherein a group of dolphins in a circle formation herd and encircle a shoal of fish. In this study only carousels in the horizontal plane were observed.

Feeding circles: individual dolphins rapidly swimming just beneath the surface in tight circles 'like a cat chasing its tail' (Shane, 1990).

Feeding flower: several animals converging on fish either by diving into and converging on the school or coming up from the centre of the school and radiating outwards, a formation which, when viewed from above, looks like the rosette of a flower (Bel'kovich *et al.*, 1991).

Feeding rush: a sudden acceleration of a dolphin directly towards its prey (Shane, 1990).

Fish toss: fish are thrown into the air by either a flick of the dolphin's head or rostrum (Shane, 1990).

Fish-whacking: sometimes called fish-kicking; the dolphin uses its tail flukes near the water's surface to slap a fish into the air (Wells *et al.*, 1987; Shane, 1990).

Fluking dives (Plate 2): a variation of diving in which the dolphin dives steeply downwards, with the flukes coming clear of the surface, often becoming vertical and perpendicular to the water surface. This type of behaviour has been observed frequently in dolphins swimming near the two islands known as 'the Brothers' adjacent to the Chek Lap Kok airport platform. This type of dive was assumed to be associated with forays to the seabed in search of bottom-dwelling fish.

Line-outs: so called because the feeding formation resembles a rugby line-out, with two single files of animals, parallel to one another, sandwiching a school of fish between them. This behaviour was also referred to as a 'wall' formation by Bel'kovich *et al.* (1991).

Porpoising (Plate 3): fast, shallow, arching leaps with the dolphin coming either partially or entirely out of the water. This type of behaviour was only observed when the dolphins were 'boat-chasing' and undoubtedly allows the animals to combine shallow dives for fish with a fast rate of travel. Porpoising adults demonstrated noticeable colour changes, turning from white to a deep pink. This is probably due to vascular dilation in the blubber layer and is, possibly, a flush response to prevent overheating.

Scrum-downs: a behaviour also described as a 'wall' formation by Bel'kovich *et al.* (1991) and observed only once during this study. A group of dolphins align themselves in an extended line, parallel to one another and drive a school of fish towards the shore.

Shuttling: the rapid zig-zagging backwards and forwards of an individual dolphin as it chases a specific fish (Bel'kovich *et al.*, 1991).

Inquisitive behaviour

Peeping (Plate 4): the head of the dolphin is raised out of the water so that the eyes break the surface. The dolphin's head is often inclined towards a boat or some other disturbance.

Spyhop: this consists of a dolphin coming out of the water vertically and returning vertically. The dolphin usually comes out of the water to a level either just in front of or just behind the flippers. Spyhopping is assumed to be an example of dolphins visually investigating the surroundings above water (Shane, 1990). It typically occurs when boats, especially dolphin watching and research vessels, are in close proximity. It does, however, also occur in the absence of boat traffic and other visual ambiguities and may, therefore, have other functions.

Appendix. Continued.

Aggressive behaviour
Bite: the rapid biting of one dolphin by another.
Body-slamming: as above.
Headbanging: during this type of behaviour, an individual would raise its head out of the water to the level of its flippers. The animal would then forcibly slam its head, lower jaw first, onto the surface of the water. This type of behaviour has, in other species, been associated with either aggression or disturbance (Herman & Gordon, 1974).
Headbutt: one dolphin swims into another, ramming it with its rostrum.
Head toss: an abrupt jerk of the rostrum, either laterally or vertically.
Flipper/fluke strike: a sharp blow to another dolphin with either the flipper or flukes.
Tail slap: the flukes of the dolphin are raised above the surface and brought downwards swiftly to slap against the water's surface. This display was frequently observed when boats were in close proximity to dolphins, particularly adult/calf pairs.
Social/sexual behaviour
Body-slamming: as above.
Slam dancing (Plate 5): the dolphin swims with its ventrum breaking the surface whilst simultaneously nodding (as below) and tail slapping (as above).
Fencing: a pre-mating behavioural display. The heads of paired dolphins break the surface of the water and the animals touch their partner's beak perpendicularly with their own. The way the beaks cross is reminiscent of a pair of swordsmen fencing.
Flipper waving: a pectoral flipper waving in the air.
Harassing: two dolphins sandwich a third between them. Both outside animals (presumably males) mounted and rubbed their ventrums against the middle animal (presumably female). The centre animal displayed aggressive behaviour including 'strikes' (see above) and 'tail slaps' (see above). This encounter was assumed to be two males attempting to mate an unwilling female.
Leap: an individual dolphin leaps clear of the water and re-enters head first. The animal can re-enter the water with the dorsum (backward leap), ventrum (forward leap) or side (side leap) facing down (Shane, 1990).
Mating: on occasions when this has been observed, animals swam slowly, ventrum to ventrum, either on their sides or one individual uppermost.
Nodding: vertical, rapid, multiple movements of the head up and down.
Push-up: one or more dolphins pushing up an individual from below with their rostrums. As this occurred during the 'harassing' incident mentioned above, the action was taken to be two males trying to manipulate an unwilling female into a better position for mating.
Rolling: the rolling behaviour pattern is undoubtedly an indication of mating/courtship. Two dolphins in close proximity either twist laterally next to each other or twist around and roll over each other. Fins and flukes often break the surface of the water. A similar pattern of behaviour was described by Karczmarski *et al.* (1997) for South African hump-backed dolphins.

Plate 1. A hump-backed dolphin body-slamming in North Lantau waters (credit: T. A. Jefferson).

Plate 2. A hump-backed dolphin executing a 'fluking dive' (credit: T. A. Jefferson).

Plate 3. A porpoising hump-backed dolphin chasing the net of a pair trawler (credit T. A. Jefferson).

Plate 4. A hump-backed dolphin 'peeping' (credit W. Leverett).

Plate 5. A young hump-backed dolphin 'slam dancing' (credit W. Leverett).