Aquatic Mammals 2004, *30*(1), 159-174, DOI 10.1578/AM.30.1.2004.159

Ranging Patterns of Indo-Pacific Humpback Dolphins (*Sousa chinensis*) in the Pearl River Estuary, People's Republic of China

Samuel K. Hung[1] and Thomas A. Jefferson[2]

[1]*Hong Kong Cetacean Research Project, 12 Kak Tin Kung Miu Village, Tai Wai, New Territories, Hong Kong*
[2]*Southwest Fisheries Science Center, NOAA, NMFS, 8604 La Jolla Shores Drive, La Jolla, CA 92037, USA*

Abstract

Few studies have examined the home range characteristics of coastal dolphins or porpoises in detail. The location data of 40 Indo-Pacific humpback dolphins (*Sousa chinensis*) from Hong Kong waters and Lingding Bay, with a range of 10-67 sightings each, were analyzed. Range size of individuals varied greatly from 24 km^2 to 304 km^2, with an average of 99.5 km^2. Each estimated range encompassed only a small portion of the overall population's range. Age class, association with a fishing boat, distribution and availability of food resources, and human activities and disturbances all influenced ranging patterns of humpback dolphins in the Pearl River Estuary. Seasonal and annual variations in range use were observed among individual dolphins. While providing information previously unknown about these dolphins, this study also indicated that further investigations are needed to identify the exact ranging patterns and home range characteristics for this humpback dolphin population.

Key Words: Humpback dolphin, *Sousa chinensis*, ranging pattern, movements, home range, Pearl River Estuary, Hong Kong

Introduction

Indo-Pacific humpback dolphins (*Sousa chinensis*) are widely distributed in coastal and inshore waters of the Indian and western Pacific oceans (Jefferson & Karczmarski, 2001; Ross et al., 1994). Resident populations occur off Plettenberg Bay, South Africa (Saayman & Tayler, 1979), and Moreton Bay, Australia (Corkeron, 1990), and some individuals have been seen year-round off southern China and northern Queensland (Ross et al., 1994).

A population of humpback dolphins is found near the mouth of the Pearl River in the Hong Kong Special Administrative Region (SAR), Macau SAR, and Guangdong Province of the People's Republic of China (PRC) (Jefferson, 2000; Jefferson & Leatherwood, 1997; Zhou et al., 1995). Due to degradation of habitat, there is concern that the dolphins in Hong Kong waters may be adversely affected and, as a result, the Hong Kong SAR Government funded studies on the status and biology of these animals.

These studies suggested that humpback dolphins are residents in the Pearl River Estuary, with some individuals using Hong Kong waters seasonally and some throughout the year (Jefferson, 2000); however, home-range characteristics and ranging patterns of the humpback dolphins have not been studied in detail, and factors that may influence individual ranging patterns remain unclear. Moreover, it is uncertain to what extent these dolphins range beyond Hong Kong waters into the Pearl River Estuary in China.

Home range characteristics may be adaptive and, therefore, estimation of the home range area has been recommended for life-history studies (Morrissey & Gruber, 1993). It also is important to understand the factors that influence characteristics of home ranges. Moreover, spatial and temporal patterns of the home range also can have implications for energetics, social organization, and reproduction within a population (McNab, 1963; Morrissey & Gruber, 1993; Swihart & Slade, 1985).

Home range size can be influenced by body mass (Burt, 1943; Mace et al., 1983; McNab, 1963), sex (e.g., Lindstedt et al., 1986; Mace et al., 1983), age (Cederlund & Sand, 1994; Lindstedt et al., 1986), and reproductive status (e.g., Bertrand et al., 1996; Cederlund & Okarma, 1988; Ortega, 1990). Other determinants include the availability and distribution of resources such as food, mates, and shelter (Ford, 1983; Joshi et al., 1995; Mace et al., 1983). Seasonal variations in home range size (e.g., Cederlund & Okarma, 1988; Phillips et al., 1998) and human disturbances (e.g., Bowyer et al., 1995; Van Dyke & Klein, 1996), resulting in changes in home-range patterns also are well documented.

Although much is known about the home range of a wide variety of animals, studies on cetaceans are less common (even so, see Ballance, 1992; Bräger, 1998; Durham, 1994; Gruber, 1981; Karczmarski, 1996; Shane, 1987; Shane et al., 1986; Wilson, 1995). Obtaining sufficiently large samples of an adequate temporal scale to generate reliable estimates of home range of cetaceans is a substantial logistical and financial challenge. Würsig & Lynn (1996) noted many reports of residency, but few measurements of dolphin home range size appear in the literature. Detailed home range studies, such as those of populations of bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida (Scott et al., 1990; Wells et al., 1980) and along the California coast (Defran et al., 1999), are exceptional.

This paper reports the results of a seven-year study of Indo-Pacific humpback dolphins in Hong Kong and Lingding Bay, People's Republic of China, which provides an opportunity to assess individual ranging patterns of a coastal small cetacean species within a semi-enclosed estuarine habitat (the Pearl River Estuary). Using a Geographic Information System (GIS), we estimated the range size and examined the ranging patterns of individual dolphins and the factors that may affect them. This paper also updates the thesis work by Hung (2000) on a preliminary study of the ranging patterns of humpback dolphins in Hong Kong waters.

Materials and Methods

Study Area

The Pearl River Estuary is a large system with a complex mixing of freshwater and saltwater over a large area (Kot & Hu, 1997). The Pearl River drains a vast area of 442,440 km^2 of southern China (Dudgeon, 1995; Morton, 1996). The estuary has eight outlets, with its eastern four exits emptying into Lingding Bay. In this paper, we refer to Lingding Bay as the eastern section of the Pearl River Estuary, which extends to the west of Macau as well (there are four additional exits in the western section) (Figure 1). Lingding Bay also is located just west of the Hong Kong study areas (i.e., Northwest and Northeast Lantau, South

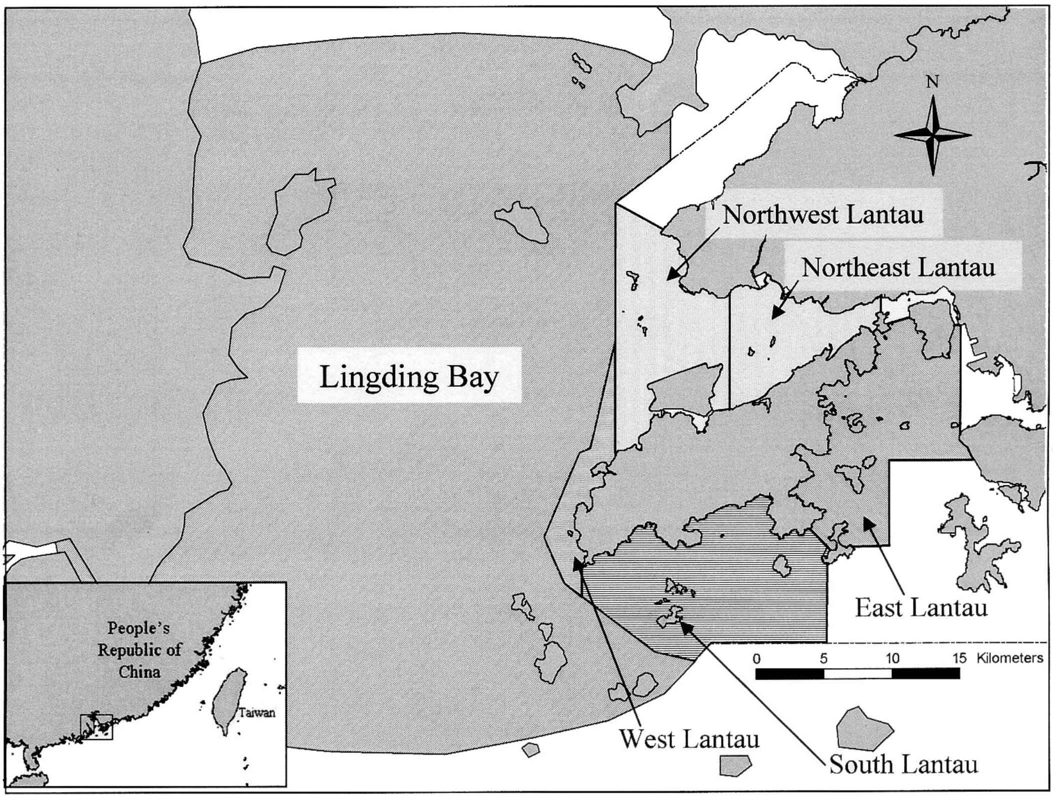

Figure 1. Pearl River Estuary study area on the southern coast of People's Republic of China, with survey areas within Hong Kong and Guangdong waters

Lantau, East Lantau). Hong Kong lies along the eastern border of the Pearl River Estuary and is situated on the southern coast of China (Figure 1). Its territorial waters consist of 1,827 km^2, including 235 islands (Morton, 1996). The coastline is deeply incised and is about 800 km long. The estuarine hydrography of the western waters of Hong Kong is complex, owing to outflow from the Pearl River. The salinity and visibility there are greatly reduced in the summer, and the variable effects of salinity and temperature can then result in significant vertical stratification in many areas (Broom & Ng, 1996; Morton, 1989). For survey purposes, the territorial waters of Hong Kong were divided into 11 areas: Northwest Lantau, Northeast Lantau, West Lantau, South Lantau, East Lantau, Deep Bay, Lamma, Po Toi, Ninepins, Sai Kung, and Mirs Bay (Figure 2).

Vessel Surveys

Vessel surveys for humpback dolphins were conducted two to three times a week from September 1995 through October 2002 by the Hong Kong Cetacean Research Project (HKCRP) and several other organizations. In addition to Hong Kong waters, photo-identification data were analyzed from a study of the distribution and abundance of humpback dolphins in Chinese waters of Lingding Bay from November 1997 to November 1998, and these data also were included in the present study.

Vessel survey coverage varied among surveys conducted by different organizations. Temporal coverage was relatively even in most survey areas, and the survey transect lines were drawn without respect to dolphin distribution (Jefferson, 2000). In other words, survey teams looked for dolphins throughout the entire area, not just in places where they may have been previously found. Therefore, sighting records should provide relatively unbiased data on the ranging patterns of these dolphins.

Photo-Identification

Whenever humpback dolphins were sighted, information on time, sighting position, group size, age classes, boat association, and environmental conditions were recorded. The survey

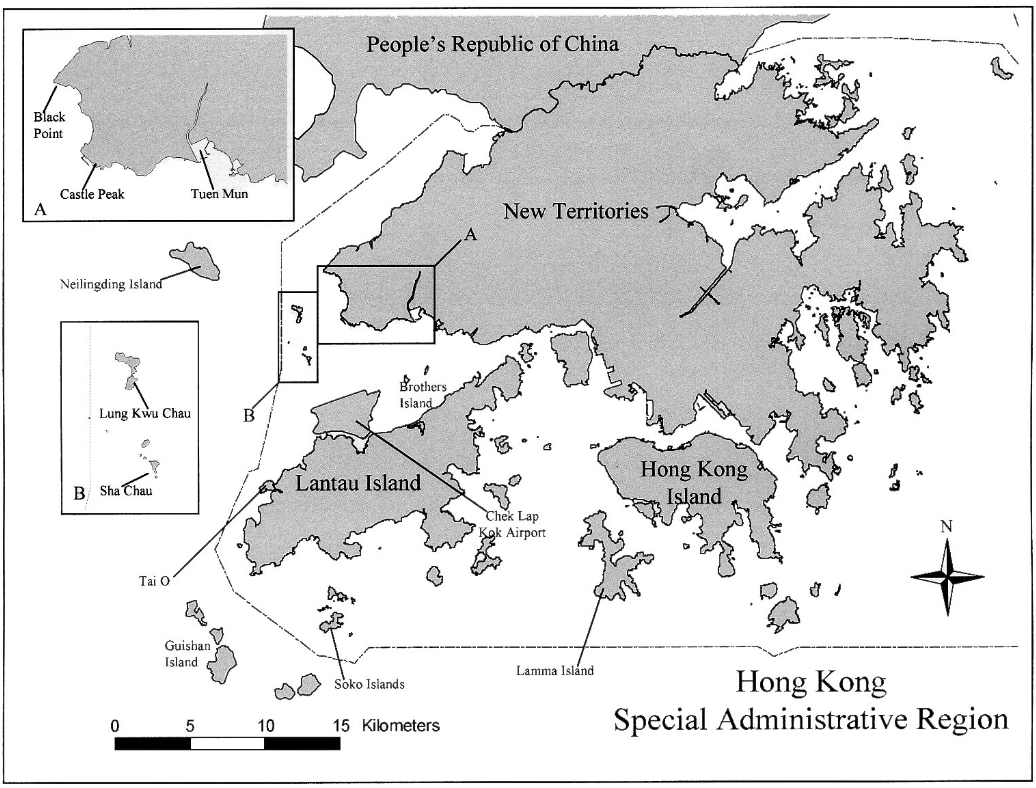

Figure 2. Map of Hong Kong Special Administration Region

vessel would then slowly approach the group of dolphins to take photographs (see Jefferson, 2000; Würsig & Jefferson, 1990). We carefully examined the slides and compared them to the existing HKCRP catalog of identified individual humpback dolphins. All photographs of each individual were compiled and arranged in chronological order, with data which included the date and location first identified (initial sighting), resightings, associated dolphins, distinctive features, and age classes entered into a computer database (*ENDNOTE*®) (see Jefferson, 2000).

Data Analysis

Location data from November 1995 to October 2002 were obtained from the HKCRP sighting database and photo-identification catalog. Only the individuals with ten or more sightings were included for analysis of individual ranging patterns.

We used a desktop GIS, *ArcView® 3.1*, with the Animal Movement extension, to determine size of individual ranges and to examine individual ranging patterns. Here, the term "range" is simply defined as the area where the individual was sighted during the study period, which is somewhat different from the definition of "home range." The size of each individual range was estimated by the Minimum Convex Polygon (MCP) method, which is commonly used to determine home range size (Anderson, 1982). Using the Animal Movement Extension for *ArcView*, a polygon joining the outermost sighting positions formed the area used by an individual dolphin during the study period, and range dimensions could then be calculated by GIS with land masses being excluded.

Although outliers might provide a false impression of the actual area covered by individual dolphins, they were not examined here since we only attempted to examine the "range size" instead of "home range size." Due to relatively small sample sizes and uneven sampling, sightings that appear to be clearly far away from the cluster of sighting concentration may not really represent outliers, especially for sightings made in Lingding Bay, where survey effort was less extensive.

Factors that might influence range size of humpback dolphins included age class and degree of boat association. Categories for age classes included mottled, speckled, spotted adult, and unspotted adult based on their color pattern. For the Pearl River Estuary population of humpback dolphins, mottled and speckled animals with heavy to moderate spotting were presumably older juveniles and subadults, while spotted and unspotted adults with pinkish white body color were presumably adults (Jefferson, 2000). The unspotted calves and unspotted juveniles were not included in the photo-identification study since most of them do not have distinct markings on their bodies to identify them effectively over time. These younger individuals presumably share the same home range of their closely associated mothers before they become independent.

Four different degrees of association with fishing boats were categorized, including seldom (0-24% of sightings with fishing boat association), often (25-49%), frequent (50-74%), and very frequent (75-100%). Sightings with boat association were defined as individual dolphins following and feeding around working fishing boats.

In addition, the sightings of each individual made in different seasons (wet season: June through November; dry season: December through May) and in different years (1995/1996, 1997, 1998, 1999, 2000, 2001, and 2002) were plotted separately to examine seasonal and annual range use.

Results

We identified a total of 264 individual dolphins during the study period: 175 first seen in Hong Kong waters and 89 first seen in Lingding Bay. At the end of the study period, 195 dolphins were seen four times, 29 were seen five to nine times, 21 were seen ten to 14 times, and 19 were seen 15 times. We included only those dolphins in the analyses which were seen ten times, as is commonly done in other home range studies. Thus, the following analyses were based on location data of the subsample of 40 dolphins.

Ranging Patterns

The estimated mean range size (± SD) of the 40 dolphins was 99.5 ± 61.04 km^2, varying from 23.76 km^2 to 303.84 km^2 (Table 1). Most individuals used ranges of 50 km^2 to 150 km^2 (Figure 3). We classified the ranging patterns into several categories for these 40 dolphins (see examples in Figure 4). Some dolphins used the North Lantau region exclusively (e.g., NL111, NL90). Others used North Lantau as their primary habitat, but also ranged into other areas, such as West Lantau (e.g., NL24, NL02), East Lantau (e.g., EL07, NL16), South Lantau (e.g., NL12, NL20), or Lingding Bay (e.g., NL11, NL89). Several individuals occurred only in Lingding Bay (e.g., CH24), and some (e.g., NL59) spent most of their time in Lingding Bay, but also used Hong Kong waters. Several dolphins (e.g., SL15, SL16) spent most of their time in South Lantau, although they were also seen in Lingding Bay (Figure 4). Among the 40 individuals, 47.5% of the ranges

Table 1. Range size of 40 individual humpback dolphins in the Pearl River estuary with ten or more sightings each

Individual ID	Age class	No. of sightings	Sex	Home range size (in km^2)
CH03	Mottled	12	?	83.90
CH06	Spotted Adult	11	?	113.30
CH24	Spotted Adult	13	?	250.61
CH50	Spotted Adult	13	?	108.81
EL01	Unspotted Adult	21	?	114.18
EL07	Mottled	37	?	139.04
NL02	Unspotted Adult	22	?	136.42
NL10	Spotted Adult	11	F	23.76
NL11	Spotted Adult	30	F	55.35
NL12	Spotted Adult	12	?	142.62
NL16	Mottled	20	?	77.56
NL17	Spotted Adult	10	?	95.14
NL18	Spotted Adult	14	F?	70.25
NL19	Spotted Adult	11	?	76.43
NL20	Unspotted Adult	15	F	237.37
NL22	Mottled	27	?	65.29
NL23	Unspotted Adult	22	F	53.37
NL24	Spotted Adult	67	?	115.38
NL32	Speckled	11	?	67.48
NL33	Speckled	14	?	30.60
NL35	Mottled	19	?	88.69
NL37	Mottled	27	?	69.32
NL40	Unspotted Adult	13	?	163.82
NL41	Mottled	19	?	77.96
NL49	Spotted Adult	10	?	69.38
NL57	Spotted Adult	26	F	77.32
NL58	Mottled	12	?	36.48
NL59	Spotted Adult	16	?	303.84
NL60	Unspotted Adult	11	?	203.16
NL89	Speckled	11	?	85.27
NL90	Spotted Adult	21	?	80.44
NL98	Speckled	25	?	83.93
NL104	Spotted Adult	12	?	29.78
NL111	Mottled	27	?	58.19
NL123	Speckled	12	?	117.76
NL139	Unspotted Adult	16	?	63.00
NL141	Spotted Adult	11	?	71.72
SL15	Speckled	12	?	127.49
SL16	Speckled	15	?	81.89
SL17	Unspotted Adult	13	F?	31.28

spanned the Hong Kong boundary with China's Guangdong Province (i.e., Lingding Bay).

Influencing Factor 1: Age Class

Humpback dolphins in the Pearl River Estuary were classified into one of six age classes. We excluded two classes (unspotted calf and unspotted juvenile) in the analysis, which were not represented among the 40 analyzed individuals. The average area used by the four age classes ranged from 77.4 km^2 for mottled to 125.3 km^2 for unspotted adults (Figure 5). There was no significant difference detected among the four classes (ANOVA, F=1.056, df=39, p=0.380). When pooled, the average range size (± SD) of mottled and speckled (80.7 ± 28.99 km^2, n=16) was smaller than the average range size of spotted and unspotted adults (112.0 ± 73.23 km^2, n=24);

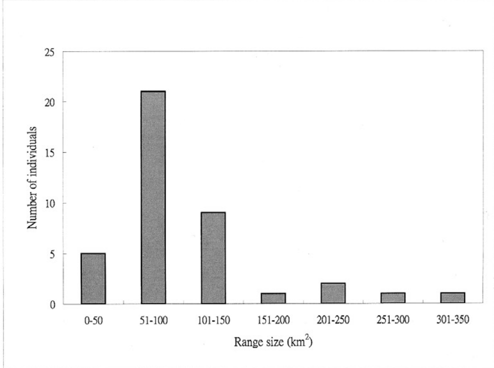

Figure 3. Size distribution of individual home ranges of individual humpback dolphins in the Pearl River Estuary

however, there was no significant difference detected among the two groups (*t*-test, p=0.069).

Influencing Factor 2: Fishing Boat Association
Range size averaged from 78.0 km^2 for those dolphins which seldom associated with fishing boats to 206.8 km^2 for those which frequently associated with fishing boats (Figure 6). Average range size varied significantly among individuals with four different degrees of boat association (ANOVA, F=4.549, df=39, p<0.05). Further analysis indicated that average range size (± SD) for those with seldom and often boat association (< 50%) (77.9 ± 29.72 km^2, n=27) were significantly smaller than those with frequent and very frequent boat association (> 50%) (134.5 ± 83.87 km^2, n=13) (*t*-test, p<0.05).

For most identified individuals, boat-associated sightings were made at the periphery of their range. For example, most of the sightings of NL24 associated with fishing boats occurred at the western section of its range, and the three sightings that were far away from the main range area were all boat-associated (Figure 7). For NL57 and NL20, the sightings far away from the main range area were boat-associated, while the rest of the sightings were located in the middle of the North Lantau study area (Figure 7). In contrast, the boat-associated sightings of NL23 were at the center of its range.

Influencing Factor 3: Seasonal Variation
Range use was roughly the same among different seasons for most individuals (i.e., there were no changes in range use throughout the year); however, for some individuals, range use among areas varied between the wet and dry seasons. For example, NL37 and NL139 mainly used Northwest Lantau and range more extensively in the dry season, while both of them used Northeast Lantau primarily and range less extensively in the wet season (Figure 8). In addition, CH24 used the northern part of Lingding Bay only in the dry season, while it used the southern part of Lingding Bay throughout the year, although more in the wet season than in the dry season.

Influencing Factor 4: Annual Variation
Range use of some individuals showed obvious variation among years. For example, before 1997, EL07 was only seen in East Lantau and Lamma, even though boat surveys were also conducted intensively in North Lantau (Figure 9). Since 1998, it has only been seen in North Lantau and has never been seen again in East Lantau (except once in 2001). Therefore, this animal might have shifted its range since 1998, now spending most of its time in North Lantau.

The apparent range use of some individuals (e.g., NL59, NL40) expanded significantly in 1998. All of these individuals were sighted in Lingding Bay in 1998, and these sightings were far away from their previous range use. The photo-identification work did not start in Lingding Bay until late 1997, and these individuals probably occurred there in 1996 or early 1997, but remained unobserved. Because of this possible sampling bias, these individuals were not included in the analysis of annual variation in range use.

Discussion

Ranging Patterns
Although the population size of humpback dolphins in the Pearl River Estuary was estimated to be over 1,000 animals (Jefferson, 2000), our interpretation of ranging patterns of these animals here is based only on a sample of 40 frequently sighted individuals, with most of them occurring primarily in North Lantau waters. Each estimated individual range size encompassed only a small portion of the overall population's geographic range in Lingding Bay and Hong Kong waters (>1,800 km^2). This is similar to bottlenose dolphins in Sarasota Bay, Florida, where the home ranges of individuals were subsets of the overall home range of the community (Wells, 1978; Wells et al., 1980).

Humpback dolphins in the Pearl River Estuary had overlapping ranges, suggesting that these dolphins probably do not have individual territories. Each dolphin used a preferred area within the population range, although the pattern varied substantially among individuals. Jefferson (2000) reported that humpback dolphins in the Pearl River Estuary lack stable associations. That pattern is similar to the one reported for humpback

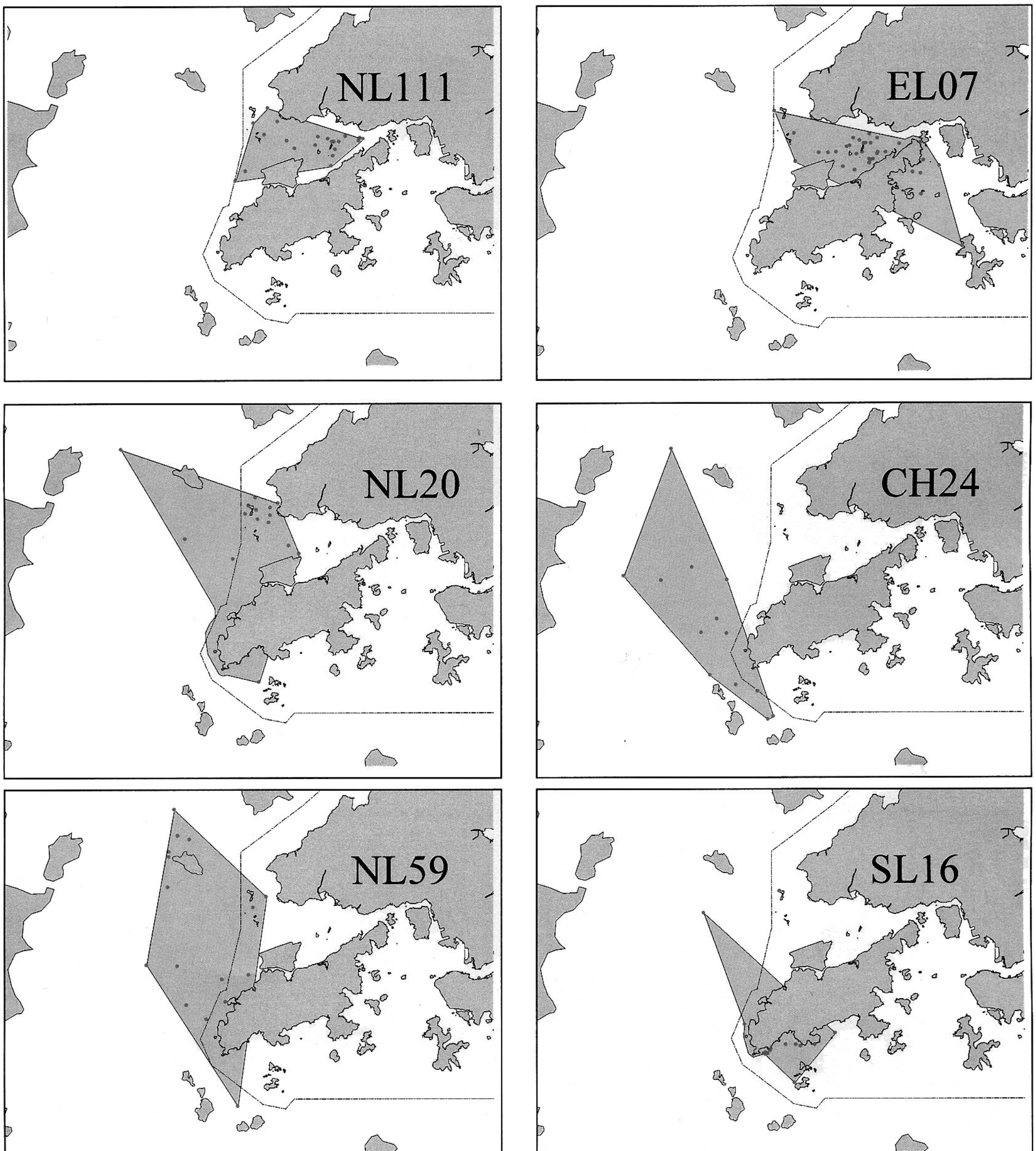

Figure 4. Ranging patterns of six identified individual humpback dolphins in the Pearl River Estuary

dolphins in South Africa (Karczmarski, 1996). The lack of stable associations among individuals might explain why individuals rarely used exactly the same area, and why there were such variations in ranging patterns. In addition, age, sex, reproductive status, and certain behaviors (e.g., preference for feeding behind fishing boats) also could explain some of the variation.

Nineteen of 40 dolphins had ranges extending from Hong Kong waters into Lingding Bay of Guangdong Province, PRC. This is not surprising, since there was no apparent geographic or environmental barrier to impede movements of these dolphins across this boundary. In contrast, this political boundary was a complete impediment to researchers conducting surveys. We have little doubt that the dolphins in Hong Kong waters and Lingding Bay comprise a single population because we have no evidence that the travel and mixing between these two areas may be limited.

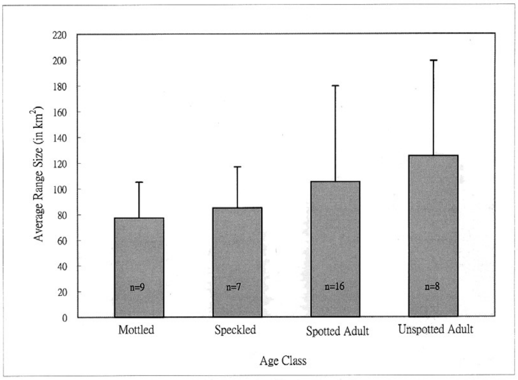

Figure 5. Average range sizes of different classes (SD shown by vertical lines above bars) of individual humpback dolphins in the Pearl River Estuary

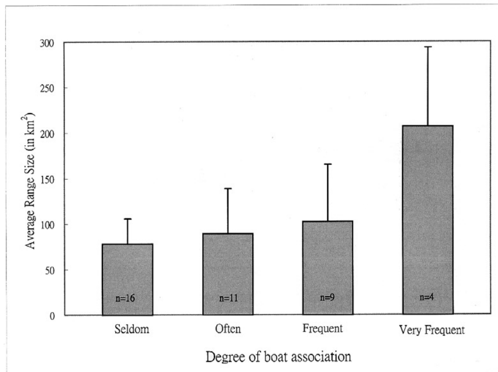

Figure 6. Average range sizes of individual humpback dolphins with different degrees of fishing boat associations (SD shown by vertical lines above bars)

Nonetheless, the degree to which they used PRC versus Hong Kong waters varied among individuals. Some individuals clearly showed preferences for Hong Kong waters or Lingding Bay, while other individuals used both areas.

In addition, some individuals used different survey areas around Lantau Island. A previous

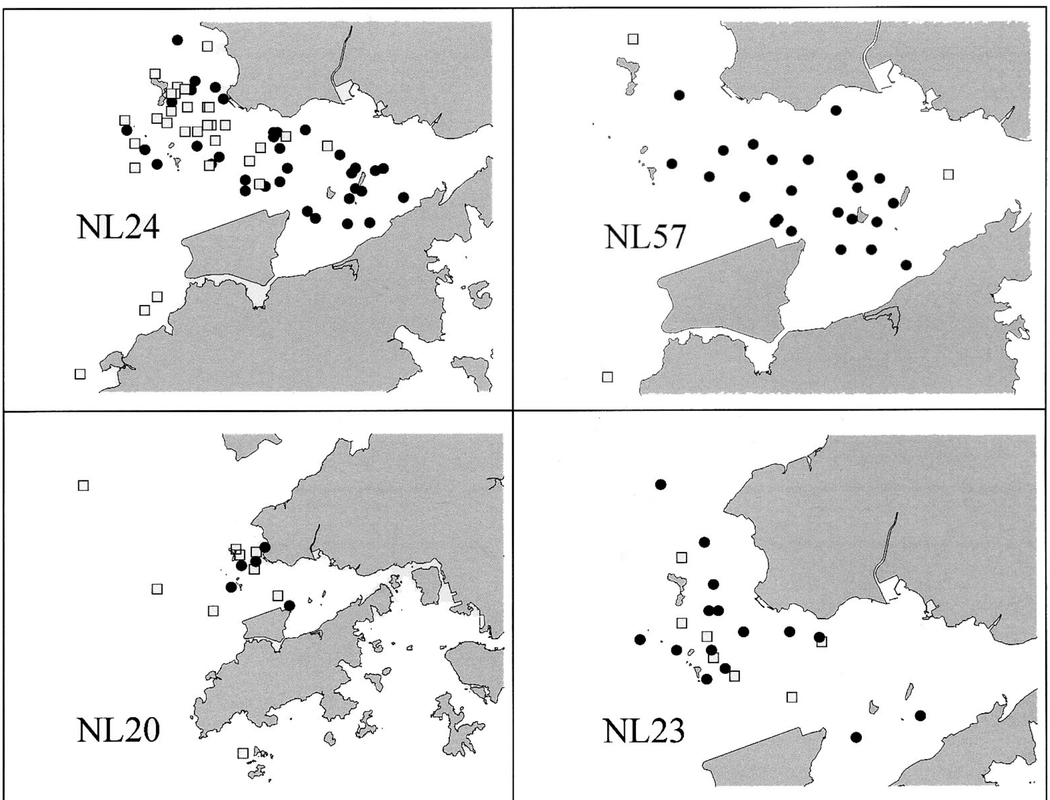

Figure 7. Sightings with (□) and within (●) boat associations for four individual humpback dolphins in the Pearl River Estuary

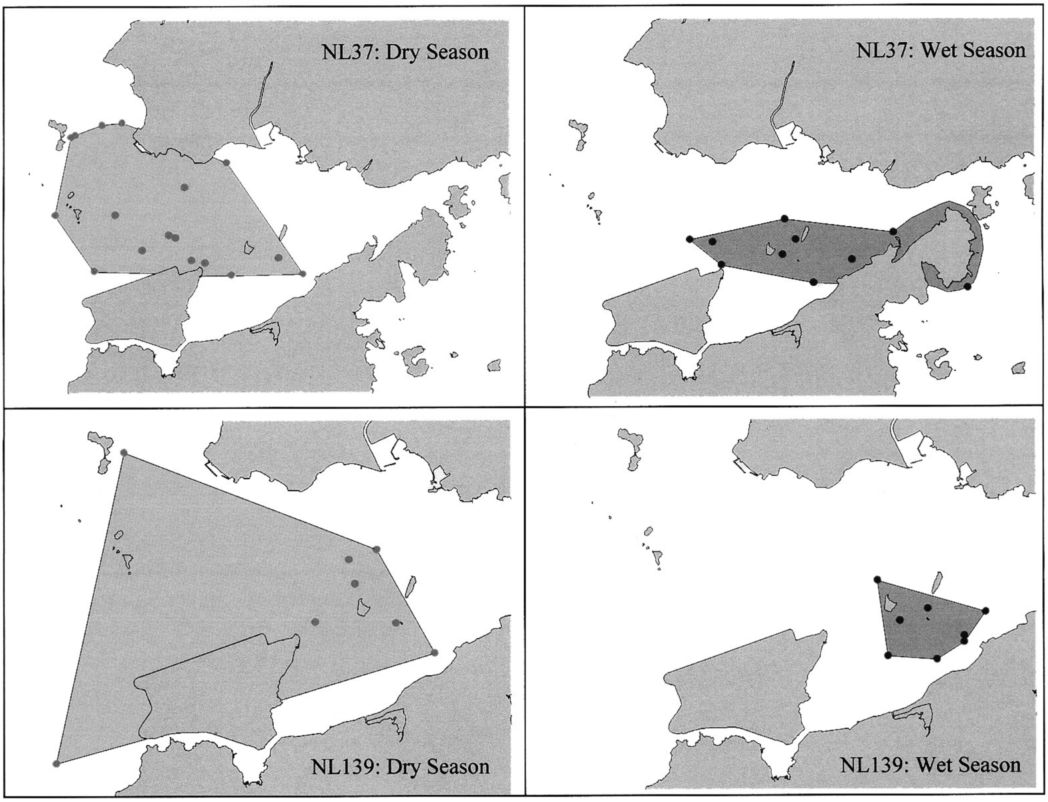

Figure 8. Range use of two humpback dolphins (NL37 and NL139) between dry and wet seasons

study by Porter (1998) on genetic analyses of microsatellite DNA from ten stranded carcasses was interpreted to suggest "a highly structured population with severely restricted gene flow between north and south Lantau Island." Photo-identification data from the same study also were interpreted to support those findings because no individuals photographed in South Lantau were sighted in North Lantau. These results differ from the present study, however. Both NL20 and NL12 used both North Lantau and South Lantau waters, and several other individuals (e.g., SL15, SL16) also were sighted in both North Lantau and South Lantau waters. In addition, although NL59 and NL40 concentrated most of their activities in Lingding Bay, they also used North Lantau and waters near South Lantau. Finally, genetic analyses reported in Jefferson (2000) did not support Porter's (1998) claim. Therefore, the claim of severely restricted gene flow between North and South Lantau Island may be inaccurate.

Influencing Factor 1: Age Class

The mottled and speckled animals used smaller areas and ranged less extensively than the spotted and unspotted adults. Although individual humpback dolphins were categorized into different "age classes," the "age class" does not necessarily accurately represent the age of an animal, except for an unspotted calf and an unspotted juvenile. Jefferson & Leatherwood (1997) first proposed that mottled and speckled animals with heavy to moderate spotting were older juveniles and subadults, while spotted and unspotted adults with pinkish white body color were adults. More recently, based on the suggestions that heavy spotting might relate to sexual dimorphism, Jefferson (2000) proposed that most of the mottled and speckled animals could possibly be males, and some of them could be adults, while spotted and unspotted adults could mostly be females and possibly old males.

If the mottled and speckled animals were juveniles and subadults, while spotted and unspotted adults were adults under the first scenario, younger animals would have used a smaller range area than older animals. Most studies of mammalian species have concluded that older animals (adults) have significantly larger home ranges. Adults have a greater energetic demand

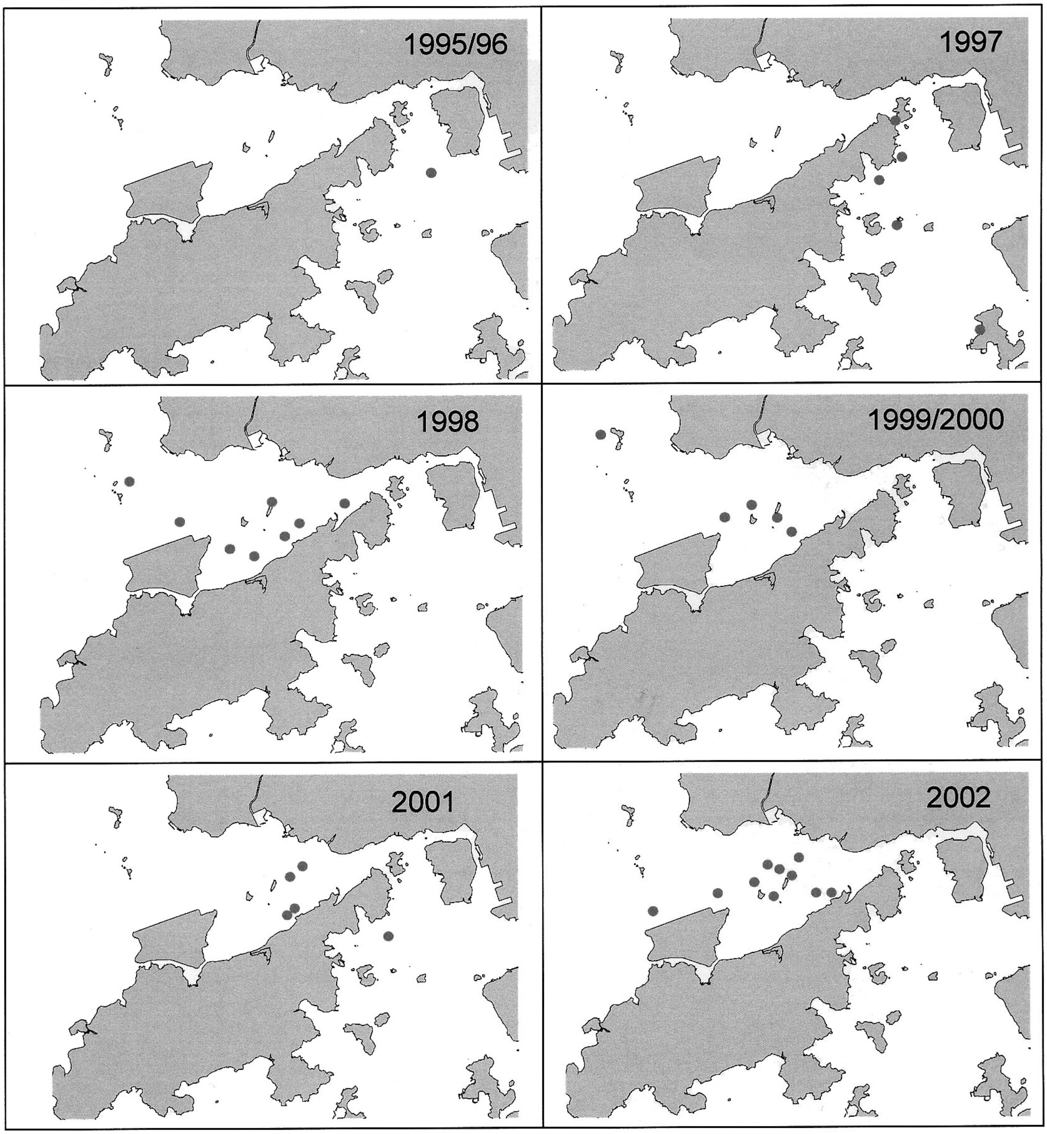

Figure 9. Annual variation of range use of an individual humpback dolphin (EL07) from 1996 to 2002

than juveniles and subadults in relation to their body size and weight, and they also use larger areas to ensure access to more mates for increasing reproductive success (Cederlund & Sand, 1994). Moreover, juveniles and subadults have yet to establish themselves socially, and they may have to travel in the peripheral area of the population range, living as "transients" (Lindstedt et al., 1986). The result presented here seemed to fit this general picture.

The interpretation would be very different if the mottled and speckled animals were males, with some of them being adults, while spotted and unspotted adults were mostly females. Under this scenario, most males (mottled and speckled animals) would range less extensively than females (spotted and unspotted adults), contrary to many studies on mammals in which males generally have larger home ranges than females (e.g., Phillips et al., 1998; Swihart & Slade, 1985). Males need to use a larger area, due to the influence of sexual selection for increased access to females (Mace et al., 1983); however, there are some exceptional species. Some female mammals have larger home ranges than males because they travel in large groups and need more food than males to meet their energetic needs (e.g., wood bison [*Bison bison athabascae*]) (Larter & Gates, 1990, 1994). Alternatively, females travel from male to male in search of mates, which would result in larger home ranges in females (e.g., California ground squirrels [*Spermophilus beecheyi*]) (Boellstroff & Owings, 1995).

Further studies are needed to investigate the mating strategy of these humpback dolphins and the underlying factors which influence the ranging patterns of females and males. Both social scenarios are tentative at this point, and the difference between mottled/speckled and spotted/unspotted adults cannot be fully explained. Therefore, it is very important to determine how the humpback dolphins in Pearl River Estuary with different color patterns should be categorized into age-sex classes.

Influencing Factor 2: Fishing Boat Association

The ranging patterns of individuals varied according to how often they interacted with fishing boats. Individuals with more boat-associated sightings used larger areas than those with fewer boat-associated sightings. Fishing boat association appears to present short-term benefits to the dolphins, which increased their feeding opportunities when the end of the trawl net concentrates prey into a small area and the net stirs up bottom fishes (Fertl & Leatherwood, 1997); however, the long-term negative effects, including the increased risks of net entanglement and increased exposure to sediments with toxic substances may outweigh the benefits.

Since individuals associating with boats ranged more extensively, this behavior might affect both the use and extent of individual ranges. Most of the boat-associated sightings were made on the periphery of the ranges, suggesting that following boats causes them to range to places they might seldom use (e.g., NL20). After following these fishing boats out of their normal ranges for a period of time, there were several possibilities for the dolphins, they could (1) return back to their normal ranges immediately, (2) begin to use these unfamiliar areas as an extension of their range, or (3) explore the area for a while eventually returning back to their familiar range. Because most of the boat-associated sightings were at the periphery of individual ranges, and given our short sampling period and small sample sizes for most individuals, we could not be certain that the locations of these boat-associated sightings were indeed part of their regular range. Therefore, it is too early to conclude that these boat-associated sightings should be considered outliers for ranging pattern analysis.

If the behavior of associating with fishing boats could indeed change the ranging pattern for some or most individuals, it will imply that human activities do affect the movements and change some aspects of the behavioral ecology of individual humpback dolphins. This should be taken into serious consideration in the conservation and management of the dolphins in the Pearl River Estuary.

Influencing Factor 3: Seasonal Variation

Some individuals showed distinct shifts of range use among different sectors during different seasons. This corresponds well with the seasonal variations in water temperature and salinity in the Pearl River Estuary, where rainfall, as well as freshwater input, increases and salinity decreases in summer (wet season) (Broom & Ng, 1996). Many studies of mammals reported that sizes and locations of home ranges varied seasonally relative to food availability (e.g., sloth bears [*Melursus ursinus*] [Joshi et al., 1995], raccoons [*Procyon lotor*] [Geihrt & Fritzell, 1997]). While the seasonal variations in range use of humpback dolphins at both the individual and the population level were indirectly affected by environmental parameters, we suggest that the distribution of prey were the direct cause of seasonal shifts in range use.

As suggested by Qiu & Chen (2001), the distribution of fishes in the Pearl River Estuary is strongly influenced by seasonal variations of environmental parameters such as water salinity and temperature. Many fish species (e.g., *Collichthys lucidus*, *Coilia mystus*) that are prey for humpback dolphins spawn in North Lantau in winter and spring; after May, the fish distribution shifts southward and eastward as the freshwater input from the Pearl River increases. As a result, it is speculated that movements of dolphins will correspond to the seasonal variation of the fish distribution. In addition, in a study east of Sha Chau, Ni (1997) found that there was an increase in fish species diversity and biomass (catch per unit effort) in wet months (especially in July and August). The seasonal variations in species diversity and biomass in North Lantau waters correlated with the seasonal variations in water temperature and salinity.

Influencing Factor 4: Annual Variation

Annual variations in range use were documented for some individuals. Some individuals that normally used one survey area as most of their range might shift to another area in other years. The cause of such shifts in different years was not clear, but it might relate to the health and social status of the individual, and this was likely to be the case with EL01. EL01 appeared to be heavily scarred and covered with diatoms or fungus when it was first seen in East Lantau, where it was mostly sighted before March 1997. Since then, however, it was frequently sighted in North Lantau, and was sighted only once near the periphery of East Lantau. At the same time, the scars disappeared and the individual appeared to be healthy again when it was sighted in North Lantau. Perhaps it was injured after a fight, and since then avoided the main area of dolphin distribution.

In addition, we suspect that some individuals might shift their range use in response to human disturbances (e.g., increased vessel traffic, major development project) like other mammalian species such as river otters (*Lutra canadensis*) (Bowyer et al., 1995) and white-tailed deer (*Odocoileus virginianus*) (Vercauteren & Hygnstrom, 1998). It should be stressed, however, that only a small proportion of dolphin individuals seemed to have dramatic shifts in range use. Also, as is the case for other species, the dolphins might return to their previous area after the disturbance was removed or lessened.

Comparisons with Other Studies

In the past, relatively little has been presented on the home range characteristics of coastal cetacean species, and the factors that influence ranging patterns or home ranges have rarely been discussed among different populations and species. Here, we compared the ranging patterns of humpback dolphins of two different populations (South Africa and Pearl River Estuary) to show the influences of habitat and resource availability. In addition, we also compared the ranging patterns between humpback dolphins and bottlenose dolphins to determine whether there are similarities or differences between these two coastal species (Table 2).

In South Africa, individual humpback dolphins have linear ranges of a few hundred kilometers, and they only occur within 150-350 m of the shore (Karczmarski, 1996). In contrast, the ranging patterns of humpback dolphins in the Pearl River Estuary are composed of irregularly shaped polygons, with linear distances of only tens of kilometers. We argue that the ranges of the two populations of humpback dolphins are not directly comparable because their ranging patterns are essentially different (linear vs. polygon). This difference is due to their habitats. The offshore distribution of South African dolphins may be limited, and the dolphins can only move up and down along the narrow strip of relatively straight coastline. In contrast, the Pearl River Estuary, which is situated on a broad continental shelf with shallow waters (< 20 m deep), is more two-dimensional, and the dolphins can range up to tens of kilometers from one coastline without actually moving offshore or into deeper water. The coastline of Hong Kong is convoluted, with many deep bays, incisions, and inshore islands, so as a dolphin moves away from the shore, it will not be too far away from land; this is not the case in South Africa. In addition, the patchiness of restricted inshore prey resources along the South African coastline may force the dolphins to range over great linear distances in search of food (Karczmarski, 1996), while the presumably more available prey resources in the Pearl River Estuary may allow dolphins to range less extensively.

The differences between linear and polygon-shaped home range patterns also were demonstrated in two populations of bottlenose dolphins (Table 2). Bottlenose dolphins in Sarasota Bay, Florida, occur in protected shallow bay ecosystems, and their ranging patterns are polygon-shaped with each individual using a small area (Wells et al., 1980). On the other hand, the bottlenose dolphins along the California coastline are highly mobile, ranging over extensive linear distances, and showing little site fidelity to any particular area (Defran et al., 1999). Distribution of dolphins in California was related to the fluctuating prey availability within the highly dynamic coastal ecosystem of the Southern California Bight. Defran et al. concluded that the dolphins in Sarasota Bay and Southern California might represent "two ends of a continuum" for a number of populations, with the variations being shaped by habitat differences.

Humpback dolphins in South Africa and the Pearl River Estuary, PRC, might also represent "two ends of a continuum," and their differences in ranging patterns also were shaped by habitat. Whether there is any population of humpback dolphins having ranging patterns between the "two ends" is unknown, since this species of dolphin has not been well-studied in other areas. As more information on other populations of humpback dolphins will be collected, comparisons of ranging patterns in different populations will clarify this issue.

Among different populations of bottlenose dolphins around the world, the range sizes of individuals from a population residing in Matagorda Bay, Texas (Würsig & Lynn, 1996), were similar to those of the humpback dolphins in the Pearl River Estuary, even though the methods used in the two studies were essentially different (radio-tracking versus photo-identification). This similarity in range size might be due to their similarity in habitat and resource availability; however,

Table 2. Comparisons of ranging patterns between different populations of coastal species of humpback dolphins; linear indicates the range was one-dimensional along the coast.

Species	Location	Range (average)	n	Research method	Source(s)
Sousa chinensis	Pearl River Estuary, Hong Kong and PRC	24-304 km^2 (99.5 km^2)	40	Photo-identification	Present study
Sousa chinensis	Algoa Bay, South Africa	Few hundred km (linear)	---	Photo-identification	Karczmarski, 1996
Tursiops truncatus	Sarasota Bay, Florida	14-41 km^2	---	Photo-identification & Radio-tracking	Wells, 1978; & Wells et al., 1980
Tursiops truncatus	Gulf of California, Mexico	>65 km^2	---	Photo-identification	Ballance, 1992
Tursiops truncatus	Sanibel Island, Florida	15-72 km^2	20	Photo-identification	Shane, 1987
Tursiops truncatus	Indian River System, Florida	1.8-80.6 km (linear) (32.8 km (linear))	60	Freeze-brand	Odell & Asper, 1990
Tursiops truncatus	Indian and Banana River System, Florida	14.8-90.8 km (linear) (>55.6 (linear)	21	Freeze-brand	Odell & Asper, 1990
Tursiops truncatus	Matagorda Bay, Texas	49-329 km^2 (140 km^2)	10	Radio-tracking	Würsig & Lynn, 1996
Tursiops truncatus	Southern California Bight	50-470 km (linear)	126	Photo-identification	Defran et al., 1999
Tursiops truncatus	Moreton Bay, Queensland	(53.6 km^2)	---	Photo-identification	Corkeron, 1997
Tursiops truncatus	Moray Firth, Scotland	51-594 km^2 (122.8 km^2)	21	Photo-identification	Wilson, 1995
Cephalorhynchus hectori	Banks Peninsula, New Zealand	10-60 km (linear)	---	Photo-identification	Bräger, 1998

both studies were limited by a short study period and restricted study areas, and the results should be interpreted with caution. On the other hand, individuals in Sarasota Bay, Florida (Wells et al., 1980); Sanibel Island, Florida (Shane, 1987); Gulf of California, Mexico (Ballance, 1992); and Moreton Bay of Queensland, Australia (Corkeron, 1997) have relatively smaller range sizes than the Pearl River Estuary humpback dolphins. We suspect that within these areas, resources might be more abundant and concentrated than in the Pearl River Estuary, and individual dolphins there may not need to search so extensively for food. In addition, the restriction of these study areas also may contribute to the smaller estimated range sizes for some individuals, since it has been shown that some individuals might use areas outside the limited study areas.

Home Range Implications

In the present study, the ranging patterns of individual dolphins were examined, and the factors that influenced them were discussed. The information on individual ranging patterns presented here should have some implications for individual home range sizes and patterns because the area in which the dolphins were sighted would be a portion of the home range of these animals. The "range" presented here is defined as the area where an individual was repeatedly sighted. It is distinct from the term "home range," which is defined as the temporally and spatially defined area over which an individual travels while engaged in its daily activities (Burt, 1943). Since the data we presented here are both temporally and spatially limited, it may not be useful to define "home" range area accurately. Only with details about their movements from larger samples and a longer study period can we provide information about their actual home range characteristics. The following discussion will identify the potential biases and limitations in determining home range characteristics at present.

The number of sightings needed to reach an asymptote in the observation curve varied among individuals, and it appeared that additional sightings of most individuals would be needed to define the actual home range area accurately. If a limited sample size of some individuals was used to determine the home range characteristics, the dimensions might not be stable over time, resulting in underestimating the home range size. The inadequate sample size for some or all individuals could be related to several factors, including the disproportionate survey effort between Hong Kong and Lingding Bay, the behavior of associating with fishing boats, and variations in range use over years.

Our data were dependent upon correctly identifying individuals from photographs collected during boat surveys. Since the surveys were conducted by several organizations for different projects and with different objectives, the study area and study period of each project varied somewhat. This might introduce biases in the location and time of the year when the photo-identification data were collected. The problem became even more apparent in the disproportionate survey effort between Lingding Bay and Hong Kong waters. Before the Tonggu Waterway study in 1997-1998, no information had been collected west of the Hong Kong Study area, and the movements of individuals outside of Hong Kong essentially were unknown. In fact, some individuals (e.g., NL20) previously sighted only in Hong Kong waters were found to use a much larger area in Lingding Bay after surveys began there. Despite the fact that the estimated abundance of humpback dolphins in Lingding Bay was much larger than for Hong Kong waters, survey effort was much higher in Hong Kong waters than in Lingding Bay (Jefferson, 2000). This could mean that the ranges of some or many individuals from the Pearl River Estuary might not be sufficiently described based on current photo-identification data. It would take considerable survey effort in Lingding Bay to correct that, and to provide an accurate estimate of individual home range size for the whole population.

In addition, as discussed above, sightings associated with fishing boats might expand an individual's apparent range at any time, which made those examined here somewhat unstable. Individual movements while following fishing boats were not examined in detail, and the influence of fishing boats on the daily activities of individual dolphins was unclear. With the small sample sizes of some individuals, it would be difficult to determine whether these boat-associated sightings were made inside their home ranges or were just excursions from the main home range area.

Nevertheless, these results provide a better understanding of individual ranging patterns, which could lead to a better understanding of individual home range characteristics. This study should provide a sound basis for a long-term home range study, and ranging patterns could be refined and monitored over time. In the future, when a larger, long-term sample is collected, the home range characteristics of humpback dolphins in the Pearl River Estuary can be examined in even greater detail.

Acknowledgments

The authors thank Drs. Hugh Ellis (University of San Diego) and Brent Stewart (Hubbs-Sea World Research Institute) for their contributions in every aspect of this project. The staff of Agriculture, Fisheries and Conservation Department of Hong Kong SAR Government, Dick Choi, Janice Lun and F. Y. Wong, are greatly appreciated in providing useful data and help for this study. We also are thankful to our colleagues and friends, Sammi Ng, Dickson Wong, Leo Yeung, Dr. Bernd Würsig, Kathy Maze, and Isabel Beasley. The research was conducted with funding from Agriculture, Fisheries and Conservation Department and Civil Engineering Department of Hong Kong SAR Government, Airport Authority, Ocean Park Conservation Foundation, and Aviation Fuel Supply Consortium.

Literature Cited

Anderson, D. J. (1982). The home range: A new nonparametric estimation technique. *Ecology*, *63*, 103-112.

Ballance, L. T. (1992). Habitat use patterns and ranges of the bottlenose dolphin in the Gulf of California, Mexico. *Marine Mammal Science*, *8*, 262-274.

Bertrand, M. R., DeNicola, A. J., Beissinger S. R., & Swihart, R. K. (1996). Effects of parturition on home ranges of social affiliations of female white-tailed deer. *Journal of Wildlife Management*, *60*, 899-909.

Boellstroff, D. E., & Owings, D. H. (1995). Home range, population structure, and spatial organization of California ground squirrels. *Journal of Mammalogy*, *76*, 551-561.

Bowyer, R. T., Testa, J. W., & Faro, J. B. (1995). Habitat selection and home ranges of river otters in a marine environment: Effects of the Exxon Valdez oil spill. *Journal of Mammalogy*, *76*, 1-11.

Bräger, S. (1998). *Behavioural ecology and population structure of Hector's dolphin* (Cephalorhynchus hectori). Ph.D. dissertation, University of Otago, Dunedin, New Zealand. 170 pp.

Broom, M. J., & Ng, A. K. M. (1996). Water quality in Hong Kong and the influence of the Pearl River. In Civil Engineering Department (Ed.), *Coastal infrastructure development in Hong Kong: A review* (pp. 193-213). Hong Kong SAR, PRC: Civil Engineering Department.

Burt, W. H. (1943). Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy*, *30*, 346-352.

Cederlund, G. N., & Okarma, H. (1988). Home range and habitat use of adult female moose. *Journal of Wildlife Management*, *52*, 336-343.

Cederlund, G., & Sand, H. (1994). Home-range size in relation to age and sex in moose. *Journal of Mammalogy*, *75*, 1005-1012.

Corkeron, P. J. (1990). Aspects of the behavioural ecology of inshore dolphins *Tursiops truncatus* and *Sousa chinensis* in Moreton Bay, Australia. In S. Leatherwood & R. R. Reeves (Eds.), *The bottlenose dolphin* (pp. 285-293). New York: Academic Press.

Corkeron, P. J. (1997). Bottlenose dolphins (*Tursiops truncates*) in south-east Queensland waters: Social structure and conservation biology. *Marine Mammal Research in the Southern Hemisphere*, *1*, 1-10.

Defran, R. H., Weller, D. W., Kelly, D. L., & Espinosa, M. A. (1999). Range characteristics of Pacific coast bottlenose dolphins (*Tursiops truncatus*) in the Southern California Bight. *Marine Mammal Science*, *15*, 381-393.

Dudgeon, D. (1995). River regulation in southern China: Ecological implications, conservation and environmental management. *Regulated Rivers: Research and Management*, *11*, 35-54.

Durham, B. (1994). *The distribution and abundance of the humpback dolphin* (Sousa chinensis) *along the Natal coast, South Africa*. Master's thesis, University of Natal, South Africa. 83 pp.

Fertl, D., & Leatherwood, S. (1997). Cetacean interactions with trawls: A preliminary review. *Journal of Northwest Atlantic Fishery Science*, *22*, 219-248.

Ford, R. G. (1983). Home range in a patchy environment: Optimal foraging predictions. *American Zoologist*, *23*, 315-326.

Geihrt, S. D., & Fritzell, E. K. (1997). Sexual differences in home ranges of raccoons. *Journal of Mammalogy*, *78*, 921-931.

Gruber, J. A. (1981). *Ecology of the Atlantic bottlenosed dolphin* (Tursiops truncatus) *in the Pass Cavallo area of Matagorda Bay, Texas.* Master's thesis, Texas A&M University, College Station. 138 pp.

Hung, S. K. (2000). *Ranging patterns of Indo-Pacific humpback dolphins* (Sousa chinensis) *in the Pearl River Estuary, People's Republic of China.* Master's thesis, University of San Diego. 178 pp.

Jefferson, T. A. (2000). Population biology of the Indo-Pacific hump-backed dolphin in Hong Kong Waters. *Wildlife Monographs*, *144*, 1-65.

Jefferson, T. A., & Karczmarski, L. (2001). *Sousa chinensis. Mammalian Species*, *655*, 1-9.

Jefferson, T. A., & Leatherwood, S. (1997). Distribution and abundance of Indo-Pacific hump-backed dolphins (*Sousa chinensis*, Osbeck, 1765) in Hong Kong waters. *Asian Marine Biology*, *14*, 93-110.

Joshi, A. P., Garshelis, D. L., & Smith, J. L. D. (1995). Home ranges of sloth bears in Nepal: Implications of conservation. *Journal of Wildlife Management*, *59*, 204-214.

Karczmarski, L. (1996). *Ecological studies of humpback dolphins* Sousa chinensis *in the Algoa Bay region, eastern Cape, South Africa.* Ph.D. dissertation, University of Port Elizabeth, Port Elizabeth, South Africa. 202 pp.

Kot, S. C., & Hu, S. L. (1997). Flows in the Pearl River Estuary. In *Proceedings of a Colloquium for Development of a Management Strategy for Chinese White Dolphins* (pp. 37-48). Hong Kong SAR, PRC: Hong Kong Agriculture and Fisheries Department.

Larter, N. C., & Gates, C. C. (1990). Home ranges of wood bison in an expanding population. *Journal of Mammalogy*, *71*, 604-607.

Larter, N. C., & Gates, C. C. (1994). Home-range size of wood bison: Effects of age, sex, and forage availability. *Journal of Mammalogy*, *75*, 142-149.

Lindstedt, S. L., Miller, B. J., & Buskirk, S. W. (1986). Home range, time and body size in mammals. *Ecology*, *67*, 413-418.

Mace, G. M., Harvey, P. H., & Clutton-Brock, T. H. (1983). Vertebrate home-range size and energetic requirements. In I. R. Swingland & P. J. Greenwood (Eds.), *The ecology of animal movement* (pp. 32-35). New York: Oxford University Press.

McNab, B. K. (1963). Bioenergetics and the determination of home range size. *The American Naturalist*, *97*, 133-139.

Morrissey, J. F., & Gruber, S. H. (1993). Home range of juvenile lemon sharks, *Negaprion brevirostris. Copeia*, *2*, 425-434.

Morton, B. (1989). Pollution of the coastal waters of Hong Kong. *Marine Pollution Bulletin*, *20*, 310-318.

Morton, B. (1996). Protecting Hong Kong's marine biodiversity: Present proposal, future challenges. *Environmental Conservation*, *23*, 55-65.

Ni, I-H. (1997). Seasonal variability of fisheries resources in the East of Sha Chau. In *Proceedings of a Colloquium for Development of a Management Strategy for Chinese White Dolphins* (pp. 69-84). Hong Kong SAR, PRC: Hong Kong Agriculture and Fisheries Department.

Odell, D. K., & Asper, E. D. (1990). Distribution and movements of freeze-branded bottlenose dolphins in the Indian and Banana Rivers, Florida. In S. Leatherwood & R. R. Reeves (Eds.), *The bottlenose dolphin* (pp. 515-540). New York: Academic Press.

Ortega, J. C. (1990). Home-range size of adult rock squirrels (*Spermophilus variegatus*) in southeastern Arizona. *Journal of Mammalogy*, *71*, 171-176.

Phillips, D. M., Harrison, D. J., & Payer, D. C. (1998). Seasonal changes in home-range area and fidelity of martens. *Journal of Mammalogy*, *79*, 180-190.

Porter, L. J. (1998). *The taxonomy, ecology and conservation of* Sousa chinensis *(Osbeck, 1765)* (Cetacea: Delphinidae) *in Hong Kong waters.* Ph.D. dissertation, University of Hong Kong, Pokfulam, Hong Kong. 202 pp.

Qiu, Y. S., & Chen, T. (2001). Report of Indo-Pacific hump-backed dolphin survey in the Pearl River Estuary. In Ministry of Agriculture, People's Republic of China

(Ed.), *Conference on Conservation of Cetaceans in China* (pp. 90-104). Shanghai: Government of People's Republic of China

Ross, G. J. B., Heinsohn, G. E., & Cockcroft, V. G. (1994). Humpback dolphins *Sousa chinensis* (Osbeck, 1765), *Sousa plumbea* (G. Cuvier, 1829) and *Sousa teuszii* (Kükenthal, 1892). In S. H. Ridgway & R. Harrison (Eds.), *Handbook of marine mammals. Volume 5: The first book of dolphins* (pp. 23-42). New York: Academic Press.

Saayman, G. S., & Tayler, C. K. (1979). The socioecology of humpback dolphins (*Sousa* sp.). In H. E. Winn & B. L. Olla (Eds.), *Behavior of marine animals. Volume 3: Cetaceans* (pp. 165-226). New York: Plenum Press.

Scott, M. D., Wells, R. S., & Irvine, A. B. (1990). A long-term study of bottlenose dolphins on the west coast of Florida. In S. Leatherwood & R. R. Reeves (Eds.), *The bottlenose dolphin* (pp. 235-244). New York: Academic Press.

Shane, S. H. (1987). *The behavioral ecology of the bottlenose dolphin.* Ph.D. dissertation, University of California, Santa Cruz. 147 pp.

Shane, S. H., Wells, R. S., & Würsig, B. (1986). Ecology, behavior and social organization of the bottlenose dolphin: A review. *Marine Mammal Science*, *2*, 34-63.

Swihart, R. K., & Slade, N. A. (1985). Influence of sampling interval on estimates of home-range size. *Journal of Wildlife Management*, *49*, 1019-1025.

Van Dyke, F., & Klein, W. C. (1996). Responses of elk to installation of oil wells. *Journal of Mammalogy*, *77*, 1028-1041.

Vercauteren, K. C., & Hygnstrom, S. E. (1998). Effects of agricultural activities and hunting on home ranges of female white-tailed deer. *Journal of Wildlife Management*, *62*, 280-285.

Wells, R. S. (1978). *Home range characteristics and group composition of Atlantic bottlenosed dolphins,* Tursiops truncatus, *on the west coast of Florida.* Master's thesis, University of Florida. 91 pp.

Wells, R. S., Irvine, A. B., & Scott, M. D. (1980). The social ecology of inshore odontocetes. In L. M. Herman, (Ed.), *Cetacean behavior: Mechanisms and functions* (pp. 263-318). New York: John Wiley & Sons.

Wilson, D. R. B. (1995). *The ecology of bottlenose dolphins in the Moray Firth, Scotland: A population at the northern extreme of the species' range.* Ph.D. dissertation, University of Aberdeen, Scotland. 201 pp.

Würsig, B., & Jefferson, T. A. (1990). Methods of photo-identification for small cetaceans. *Reports of the International Whaling Commission*, *12* (Special Issue), 43-52.

Würsig, B., & Lynn, S. K. (1996). *Movements, site fidelity, and respiration patterns of bottlenose dolphins on the central Texas coast* (NOAA Technical Memorandum NMSF-SEFSC-383). 111 pp.

Zhou, K., Leatherwood, S., & Jefferson, T. A. (1995). Records of small cetaceans in Chinese waters: A review. *Asian Marine Biology*, *12*, 119-139.