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台灣的中華白海豚社群結構及生殖參數

Social structure and reproductive parameters of Indo-Pacific humpback dolphins (*Sousa chinensis*) off the west coast of Taiwan

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謝　辭

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摘　要

台灣西岸的中華白海豚(*Sousa chienesis*)族群因數量不到 100 隻而被 IUCN (the International Union for Conservation of Nature)紅皮書列入”極危”。堅實的保育工作急需瞭解其族群的動態發展，社會結構與生殖動態是其中首要的基礎資訊。本論文以照片辨識追蹤的標記-再捕捉方法以瞭解牠們的行為與生殖動態。2007 到 2010 年中共執行 352 趟海上調查，藉由超過六萬張的照片辨識出 98 隻個體，包含 71 隻非嬰幼兒個體(其中有 22 隻哺乳中雌性)，以及透過母豚身份鑑定出 27 隻嬰幼兒。根據分層群聚分析(hierarchical cluster analysis)以及多因次等級分析(multidimensional scaling analysis)結果，台灣西岸中華白海豚族群含有兩個社群(community)，各自有不同年齡層及性別組成，形成不穩定的社交模式，社群之間尚未完全被隔離。同時棲地忠誠性模型指出動物在南北區間移動；雖然部分個體都會利用南北區，但不均質的移動模式指出動物各對北區或南區有所偏好，這個現象可能跟動物的生理狀態有關，間接反映出棲地的特性。兩社群的分隔也可能是人為開發、衝擊造成。動物的社交行為可能與尋覓交配有關。在生殖動態上，全年都有新生兒出生，春到夏季為生殖高峰(calving seasonality)。年自然出生率(crude birth rate)為 0.064 ± s.d. 0.037，幼豚生存率(calf survival rate)與存活率(calf survivorship, 至 1 歲)為 0.66 ± s.d. 0.20 及 0.78 ± s.d. 0.39，年族群補充率(recruitment rate)為 0.090 ± s.d. 0.030，生殖周期(calving interval)為 3.52 ± s.d. 0.28 年，幼豚約在 3-4 歲左右獨立(weaning age)、不再與母豚形成緊密連結。一系列的族群參數顯示台灣中華白海豚族群增長率低，屬於脆弱的族群、保育狀態極為敏感，牠們需要一個適切恰當的保育政策，以維持其族群延續：兩社群偏好不同的海域，維持與改善其棲地品質對社群的維持極為重要；此外，根據其生殖高峰，在南區實施季節性的禁漁期可確保母豚攝取足夠養分以補育幼豚。

關鍵字： *Sousa chienesis*、台灣、個體照片辨識、社群、群體動態、棲地忠誠性、繁殖參數。

Abstract

The Indo-Pacific humpback dolphin (*Sousa chinensis*) population that inhabits the western coastal waters of Taiwan was estimated to number less than 100 individuals and is listed under the IUCN criteria as "Critically Endangered". In this study, photo-identification mark-recapture techniques were applied to investigate their behavioral and reproductive dynamics. During a 4-year study period (2007-2010), 352 boat-based surveys were performed, resulting in over 60,000 photographs; 98 individuals were photo-catalogued, of which 22 were reproductively active females and 27 were calves. Hierarchical cluster analysis and multidimensional scaling revealed that the population consists of two communities, each with a moderately fluid pattern of geographic and social fidelity. Although the communities are not entirely discrete, their interactions are limited to *"casual acquaintances"* while modeled lagged identification rates suggest that *"emigration and reimmigration"* best describes their movement and ranging pattern. There seems to be further differences between individuals from both communities, including different percentages of coloration/age-stages and the number of mature females. Although some individuals can be seen in both communities, their heterogeneous movement pattern indicates that over a longer time scale they prefer a certain region which is their respective community range. The degree of separation between the two communities requires further investigation, but it seems to correspond with features of local habitat. It is also possible that the separation is a historically more recent event related to anthropogenic impacts, as there is an area of increased industrial activity located approximately in the middle between the two communities which might act as a human-caused barrier. The social behaviour might be performed as mate-searching behaviour, while parturition occurred throughout the year with a peak in spring and summer, resulting in a crude birth rate of 0.064 ± s.d. 0.037. The mean survivorship and survival rate to Age 1 were estimated at 0.66 ± s.d. 0.20 and 0.78 ± s.d. 0.39, respectively; the recruitment rate (at Age 1) was 0.090 ± s.d. 0.030 with a calving interval approximating 3.52 ± s.d. 0.28 years and the weaning age at around 3-4 years old. A suite of estimated population parameters indicating slow population growth rates further highlight the vulnerability and sensitive conservation status of Indo-Pacific humpback dolphins around Taiwan, indicating that an informed conservation management plan is urgently needed.

Keywords: Taiwan, *Sousa chinensis,* photo-identification, community structure, group dynamics, site fidelity, reproductive parameters.

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Chapter 1: Introduction

A good condition of top predators in the oceans, such as cetacean, helps maintain the balance of marine ecosystem (Estes *et al.* 1998, Williams *et al.* 2004), and cetaceans can serve as indicators for the health of marine ecosystem. The coastal species is even more important due to the coastal zone has been the major habitat for human, and usually under great stress of over development. The Indo-Pacific humpback dolphin (*Sousa chinensis* Osbeck, 1765) is one of the few species living in coastal waters, and very close to land with water depth usually < 15 m (Karczmarski *et al.* 2000). Unfortunately, our knowledge about them is still very limited. A population living in the west coast of Taiwan was formally reported by Wang *et al.* (2004). The west coast of Taiwan is highly developed, in order to help with conservation plan, the basic ecological information need to be collected urgently. The following review on the biology and ecology of Indo-Pacific humpback dolphins is mostly based on previous studies conducted in south Africa, Queensland, and Hong Kong waters, and anticipated to shed some light on Indo-Pacific humpback dolphin study in the west coast waters of Taiwan.

Taxonomy

The taxonomy of the genus *Sousa* remains unsettled; commonly cited taxonomic system is based on Rice (1998), which is accepted by IUCN Red List (Reeves *et al.* 2008), that there are three species of dolphins in the genus *Sousa* with distinct geographical distributions: the Atlantic humpback dolphin (*S. teuszii*) in coastal waters of West Africa, the Indian humpback dolphin (*S. plumbea*) off coasts from the southern South Africa to the eastern India, and the Indo-Pacific humpback dolphin (*S. chinensis*) in the eastern India and Pacific Ocean waters. Such distinctions are then supported by a taxonomic approach on skull morphology: Atlantic humpback dolphins possess the fewest teeth (27-32) on the upper jaw among the three species; Indian humpback dolphin possess longer and narrower skulls; and Indo-Pacific humpback dolphins possess a similar tooth count (31-38) to Indian humpback dolphins (33-39) but a skull shape resembling Atlantic humpback dolphins (Jefferson and Van Waerebeek 2004).

However, a recent phylogenetic approach from genetic perspective reveals that Indo-Pacific humpback dolphins in Australian waters should be considered as a divergent species (Frère *et al.* 2008). It is supported by a subsequent analysis on the population genetics of Indo-Pacific humpback dolphins (Lin *et al.* 2010); this study further shows that those Indo-Pacific humpback dolphins in Southeast Asia (South

China Sea, west part of Australia, and the west of Malacca Strait) were in a unique evolutionary clade.

Distribution and appearance

Indo-Pacific humpback dolphins are distributed throughout the shallow coast of Indian Ocean and western Pacific, from the south coast of Africa, surrounding waters of southeast Asia to the north coast of Australia (Jefferson and Karczmarski 2001).

This robust, medium-sized dolphin is characterized by having a long, projected rostrum and possessing a small dorsal fin on the top of a wide hump. The dolphins' body coloration and hump size vary from regions to regions: in general, for dolphins in the western Indian Ocean and off Queensland, the hump is obvious, and their body color remain grayish throughout their lives; in Southeast Asia and the western Pacific, on the other hand, dolphins always lack of an obvious hump and their body color turns to pink while entering into adulthood (Ross *et al.* 1994). The sequential change of body pigmentation is therefore considered to be applicable for estimating ages of humpback dolphins, at least for those in South China Sea (Jefferson and Leatherwood 1997). A recent study further revealed that this color-changing trait in Indo-Pacific humpback dolphins might be also sexually dimorphic, that is, the color of adult males does not turn to pink but of females it does (Jefferson *et al.* 2011).

Abundance of various populations

The abundances of Indo-Pacific humpback dolphin populations vary among regions (Table 1.1). The most abundant population is in the Pearl River Estuary and Hong Kong waters, there are 2555 individuals during the wet season and 2517 during the dry season (Chen *et al.* 2010); the smallest population is off Hepu, China (Chen *et al.* 2009), there are 39 dolphins (95% CI 17-92) living in a very limited habitat. Off the west coast of Taiwan, the population size is lower than the most Indo-Pacific humpback dolphin populations in the world— there are less than 100 individuals (Wang *et al.* 2007, Yu *et al*. 2010).

Conservation status

Indo-Pacific humpback dolphins suffer from serious anthropogenic disturbances due to their natural preference to coastal habitat. The major man-made threats to the dolphin are habitat loss, overfishing, incidental catches, ocean pollution, and intensive vessel traffic (Karczmarski 1996, Jefferson 2000, Parra *et al.* 2004). In particular, habitat loss and overfishing have been suggested to result prey reduction (Jefferson 2000); fishery incidental catches directly causes the injury and death of dolphins (Jefferson 2000, Keith *et al.* 2002); pollution discharged from factories may lead the dolphins to health problems (Jefferson 2000). Ill regulated vessel transportations may collide with dolphins (Parsons and Jefferson 2000), interfere with their acoustic communication (Van Parijs and Corkeron 2001), and force them to change social behavior (Karczmarski *et al.* 1997). Wildlife tourism (whale watching or swimming interactions) may also negatively impact on the dolphins once the guidelines are poorly obeyed (Parra *et al.* 2004). IUCN Red List has assigned this species in the category of “Near Threaten” (Reeves *et al.* 2008), urged immediate conservation actions.

Ecology of *Sousa chinensis*

Habitat preference

Indo-Pacific humpback dolphins prefer to live in reefs and rocky areas (Karczmarski *et al.* 2000), estuaries and bays (Atkins *et al.* 2004), or steep gradient rather than other benthic features areas (Hung 2008). The occurrence of Indo-Pacific humpback dolphins positively correlates with food resource and some hydrological parameters (*e.g.*, turbidity, oxygen and nitrogen concentration; Hung 2008). Water depth may be the most critical factor that limits the species’ distribution: in Algoa Bay, Indo-Pacific humpback dolphins were only observed in areas where water depth was shallower than 25 m (Karczmarski *et al.* 1998); in Mozambique waters, they were only observed in waters less than 10 m deep (Guissamulo 2008); and in Hong Kong, the sighting probability was significantly higher in shallow waters (depth < 30 m) than in deep waters (depth > 30 m; Hung 2008).

Group size

Indo-Pacific humpback dolphins tended to gather in small groups of less than six individuals (Table 1.2) with population variations. The Indo-Pacific humpback dolphins generally formed small group size in Cleveland Bay (3.5 ± s.e. 0.19, range 1-12; Parra 2005), Hong Kong waters (2.76 ± s.d. 2.29 from Parson 1998; or 3.8 ± s.d. 3.63, range 1-23 from Jefferson 2000), and the Algoa Bay population (6.0 ± s.d. 2.72, range 1-24; Karczmarski *et al.* 1999). However, the group sizes recorded in Arabian region (11.7 ± s.d. 14.6, range 1-20 with occasional up to 100; Baldwin *et al.* 2004), Madagascar (13 ± s.d. 7.61, range 5-25; Razafindrakoto *et al.* 2004), and Mozambique (14.9 ± s.d. 7.32, range 2-25; Guissamulo and Cockcroft 2004) were much larger than other regions.

The occurrence of prey and predator is a major factor influences the group size of dolphins (Heithaus and Dill 2002, Dunply-Daly *et al.* 2007, Pearson 2009). The mechanism of predator-prey could be applicable for the Indo-Pacific humpback dolphin as well; the larger group observed in summer and late winter in Algoa Bay might be correlated to the availability and seasonal migration of prey (Karczmarski *et* *al.* 1999).

The appearance of shark causes not only the anti-predator purpose but also competition with dolphins (Corkeron *et al.* 1987, Acevedo-Gutiérrez 2002, Heithaus 2001). However, the competitions between sharks and Indo-Pacific humpback dolphins have never been reported yet.

The behavior and the group function also play an important role in modifying the group size (Connor *et al.* 1992, Baird and Dill 1996, Mann *et al*. 2000, Connor *et al.* 2000). The different group size of the Indo-Pacific humpback dolphin related to the behavior was reported as well. In Cleveland Bay, Queensland, dolphin socialized with other five members or fed behind the trawlers with three dolphins, but foraging, milling, traveling happened within a group of three animals (Parra 2005). Bigger group size associating with trawlers was also observed in Hong Kong waters that up to 10 dolphins chasing the pair trawlers (Jefferson 2000).

Life history

The longevity of Indo-Pacific humpback dolphins is estimated as at least 38 years (Cockcroft 1989, Jefferson *et al.* 2011). Females reach their sexual maturity at 9-10 years old, which is 2-3 years earlier than the age of sexual maturity for males (Jefferson 2000, Jefferson *et al.* 2011). Parturition occurs throughout the year with seasonal peak (see Chapter 3, Saayman and Tayler 1979, Lal Mohan 1982, Cockcroft 1989, Karczmarski 1996, 1999, Jefferson 2000). The gestation period of Indo-Pacific humpback dolphins is estimated to be 11 months (Wang 1965, Wang and Sun 1982, Jefferson 2000). Litter size is always one per parturition, as other cetaceans (Ernest 2003). Neonate is born with an estimated body size of 101 cm; current record of the maximum body length is about 268 cm and the maximum weight is 240 kg (Jefferson *et al.* 2011).

Interactions with other species

Inter-species grouping is commonly observed between Indo-Pacific humpback dolphins and other marine mammal species, including bottlenose dolphins (*Tursiops* sp.) in Berbera, Queensland and South Africa (Saaywan and Tayler 1979, Corkeron 1990, Karczmarski *et al.* 1997, Schleyer and Baldwin 1999), Australian snubfin dolphins in Queensland (*Orcaella heinsohni*, Parra 2005), southern right whales (*Eubalaena australis*) and cape fur seals (*Arctocephalus pusillus*) in South Africa (Saaywan and Tayler 1979). Indo-Pacific humpback dolphins may interact with them either in a neutral or aggressive way, depending on the species or the stock involved. Stensland *et al.* (2003) raised several possibilities for reasoning mammalian mix-species grouping: it could be foraging advantages, predator avoidance, social or reproductive benefit to bring different species of mammals together. For example, between the humpback and bottlenose dolphins, both aggressive (Saaywan and Tayler 1979) and non-aggressive (Corkeron 1990, Schleyer and Baldwin 1999, Karczmarski *et al.* 1997) interactions were documented; such differences might be due to the level of habitat overlap were different. Indo-Pacific humpback dolphins' different reactions to the same species were also observed to Australian snubfin dolphins: mostly were the aggressive-sexual behavior, but affiliations and cooperative foraging had also been documented; the compositions of different age-stage and sex dolphins might be the reason leading Indo-Pacific humpback dolphins to perform different reactions to snubfin dolphins (Parra 2005).

Field study in Natal waters found that their Indo-Pacific humpback dolphins always bear attacked wounds, indicates the predation risk to Indo-Pacific humpback dolphins is most likely from the sharks (Cockcroft 1991). Indo-Pacific humpback dolphins had been observed to swim away from another potential predator, killer whales (*Orcinus orca*) in South Africa waters (Saaywan and Tayler 1979). However, Indo-Pacific humpback dolphins being directly attacked by killer whales had yet been reported.

Indo-Pacific humpback dolphins in Taiwanese waters

The existence of Indo-Pacific humpback dolphins off the west coast of Taiwan has been suspected for many years (Chou *et al.* 1995) and finally confirmed in 2004 (Wang *et al.* 2004). This population is categorized as “Critical Endangered” category in the IUCN Red List (Reeves *et al.* 2008), because of its small population size (Wang *et al.* 2007) and isolated circumstance (Wang *et al.* 2008). Our knowledge to this Taiwanese population is very limited; hence, this study is dedicated to approach their social behavior and reproductive dynamics, to accumulate scientific knowledge and to provide basis information for efficient conservation management.

Study area

This study was conducted along the coast of western Taiwan, where features with shallow waters (Figure 1.1a), from the Miaoli County (N 24°44’0” E 120°50’0”) to the Chiayi County (N 23°22’0” E 120°00’0”, Figure 1.1b). Assumed Indo-Pacific humpback dolphin habitat (water depth less than 15 m) was very close to the shore (2.5-10 km), and paralleled to the coastline. The basic components of seabed were sand and mud, lack of large-scale vegetation. The sea surface temperature was about 22-29℃ (Lee *et al.* 2010) and the salinity level was 33.4-33.6 ppt (Lee *et al.* 2011).

The concentration of chlorophyll A, which is positively correlated with primary production in a given area, was estimated to range between 0.32-5 mg/m^2 in the deeper areas off the west coast of Taiwan (Pan *et al.* 2010). It suggested the primary productivity in the west coast was low in a general view, although the primary productivity data of the study area is unknown because the water of study sites is too shallow for survey boat to access.

The dominant benthic fish species in the study area were from families Sciaenidae, Ariidae, Engraulidae, Soleidae, Trichiuridae, Synodontidae, Mullidae, and Polynemidae (Chen and Shao 2011). The first six families of fishes were frequently found in the stomach of stranded Indo-Pacific humpback dolphins in Hong Kong waters (Barros *et al.* 2004), therefore in this study, they were assumed as the major preys of Indo-Pacific humpback dolphins in Taiwanese waters. The dominated prey species in Taiwan varied with sections (Chen and Shao 2011), the prey abundance are unclear yet. In the north region, Sciaenidae, Ariidae families dominated the area with seasonal changing (Shao 2005, 2006). In the central region, the fish families of Ariidae, Engraulidae, Soleidae were found at 5-m isobaths, and Sciaenidae, Ariidae families were caught at 15-20 m (Chen and Shao 2011). Sciaenidae and Engraulidae families could be found in the south region (Luo *et al.* 2010).

Except Indo-Pacific humpback dolphins, there were six cetacean species reported to occur in the study site or adjacent areas (the Taoyuan, Tainan, and Penghu Counties): finless porpoises (*Neophocaena phocaenoides*), bottlenose dolphins, Risso’s dolphins (*Grampus griseus*), spotted dolphins (*Stenella attenuata*), false killer whales (*Pseudorca crassidens*), and killer whales (Chou 2007). However, among these species, only finless porpoises might coexist with Indo-Pacific humpback dolphins, because other four cetacean species usually inhabit in much deeper waters (depth > 30 m).

The predators of Indo-Pacific humpback dolphins in Taiwan Strait are not clear yet. The species of shark predators were reviewed by Gowans *et al.* (2007), and only tiger shark (*Galeocerdo cuvier*) might have overlap habitat with Indo-Pacific humpback dolphins off Taiwan. Another potential shark species might attack Indo-Pacific humpback dolphins is giant guitarfish (*Rhynchobatus djiddensis*) according to local fishermen. However, the abundance of both species might be low off Taiwan (S.-Z. Joung personal communication).

Objectives

Through photo-identification, I aim to understand the social behavior and reproductive dynamics of Indo-Pacific humpback dolphins off the west coast of Taiwan. The main theme of this thesis includes (Figure 1.2):

1. analyzing their social structure and behavioral dynamics, and examining the persistency of social bonds, and site fidelity (Chapter 2);
2. analyzing demography of calf cohorts, and estimating their reproductive parameters, the crude birth rate, calf survival rate, calf survivorship, the recruitment rate, calving seasonality, calving interval, and the weaning age (Chapter 3);
3. drawing conclusions about the behavioral and reproductive dynamics of Indo-Pacific humpback dolphins and urgent needs in conservation actions off the west coast of Taiwan (Chapter 4).

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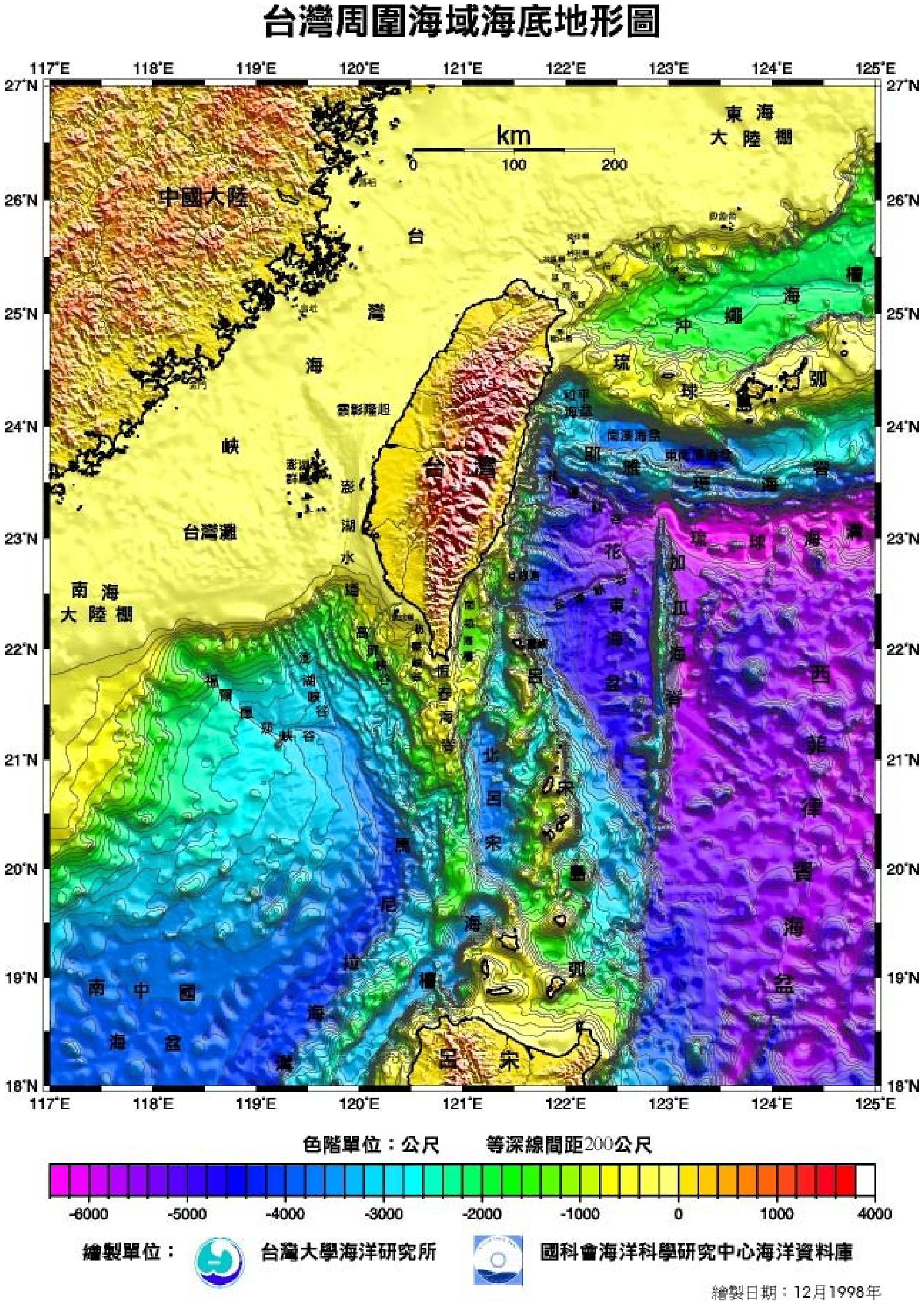
Table 1.1 A summary on population size of Indo-Pacific humpback dolphin populations in the world.

Stocks	Country	Abundance	Reference
Algoa Bay	South Africa	466	Karczmarski *et al.* 1999
KwaZulu-Natal	South Africa	160-165	Durham 1994
South coast of Zanzibar	Tanzania	63	Stensland *et al.* 2006
Maputo Bay	Mozambique	105	Guissamulo and Cockcroft 2004
Cleveland Bay	Australia	34-54	Parra *et al.* 2006
Moreton Bay	Australia	163	Corkeron *et al.* 1997
Moreton Bay	Australia	119	Corkeron *et al.* 1997
Great Sandy Strait	Australia	148	Cagnazzi *et al.* 2009
Goa Bay	India	842	Sutaria and Jefferson 2004
Gulf of Kachchh	India	174	Sutaria and Jefferson 2004
Khanom, Nakhon Si Thammarat	Thailand	49	Jaroensutasinee *et al.* 2010
Dafengjiang River	China	114	Chen *et al.* 2009
Hepu	China	39	Chen *et al.* 2009
Hong Kong and Pearl River Estuary	China	1028	Jefferson 2000
Pearl River Estuary	China	2555	Chen *et al.* 2010
Leizhou Bay	China	237	Zhou *et al.* 2007
Xiamen	China	76	Chen *et al.* 2009
Xiamen	China	87	Chen *et al.* 2008
West coast of Taiwan	Taiwan	75-80	Yu *et al.* 2010
West coast of Taiwan	Taiwan	99	Wang *et al.* 2007

Table 1.2 Group size of Indo-Pacific humpback dolphins in the world.

Stocks	Country	Mean group size	s.d.	s.e.	Range	Reference
Algoa Bay	South Africa	6.0	2.72	-	1-24	Karczmarski *et al.* 1999
Zanzibar	Tanzania	-	-	-	5-9	Stensland *et al.* 2006
Maputo Bay	Mozambique	14.9	7.32	-	2-25	Guissamulo and Cockcroft 2004
Madagascar	Madagascar	13	7.61	-	5-25	Razafindrakoto *et al.* 2004
Cleveland Bay	Australia	3.5	-	0.19	1-12	Parra 2005
Oman	Oman	11.7	14.6	-	1-20 (few up to 100)	Baldwin *et al.* 2004
Gulf of Kachchh	India	3.9	3.3	-	1-11	Sutaria *et al.* 2004
Goa	India	6.3	7.1	-	1-35	Sutaria *et al.* 2004
Khanom	Thailand	5.93	5.38	-	2-20	Jaroensutasinee *et al.* 2010
Hong Kong	China	2.76	2.29	-	-	Parson 1998
Hong Kong	China	3.8	3.63	-	1-23	Jefferson 2000

(a)


台灣周圍海域海底地形圖
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大陸棚
中國大陸
台灣海峽
雲彰隆起
澎湖群島
澎湖水道
台灣灘
南海
大陸棚
台灣
沖繩海槽
琉球島弧
和平海盆
南澳海盆
花東海盆
琉球海溝
加瓜海脊
西菲律賓海盆
福爾摩沙峽谷
澎湖峽谷
高屏峽谷
恆春海脊
北呂宋海槽
呂宋島弧
馬尼拉海溝
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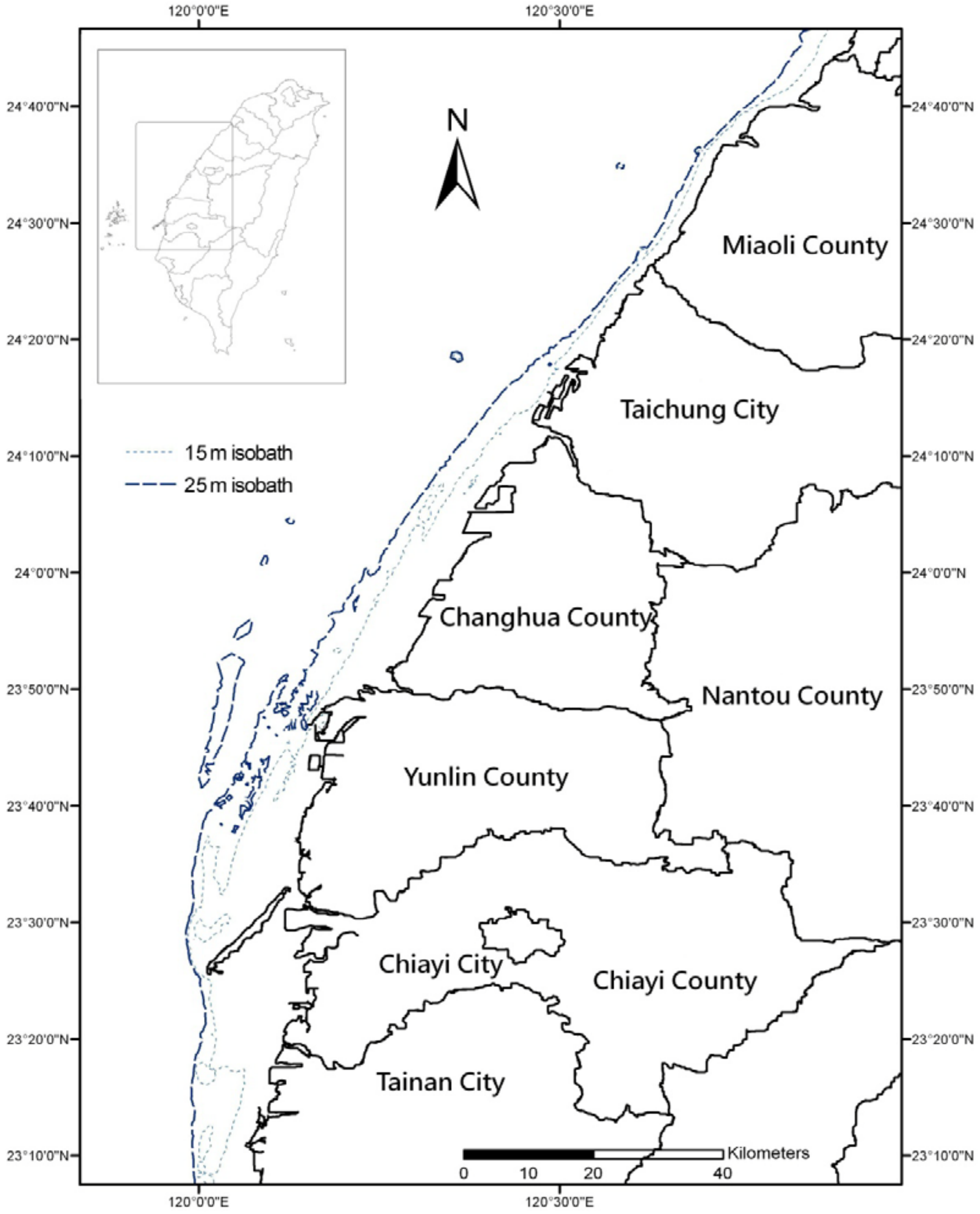

Figure 1.1 (a) Seabed topography of Taiwanese waters (courtesy of Institute of Oceanography, National Taiwan University and Oceanic Science Research Center, National Science Council); and (b) study area of the study, lines indicate 15-m (dot line) and 25-m (solid line) isobaths.

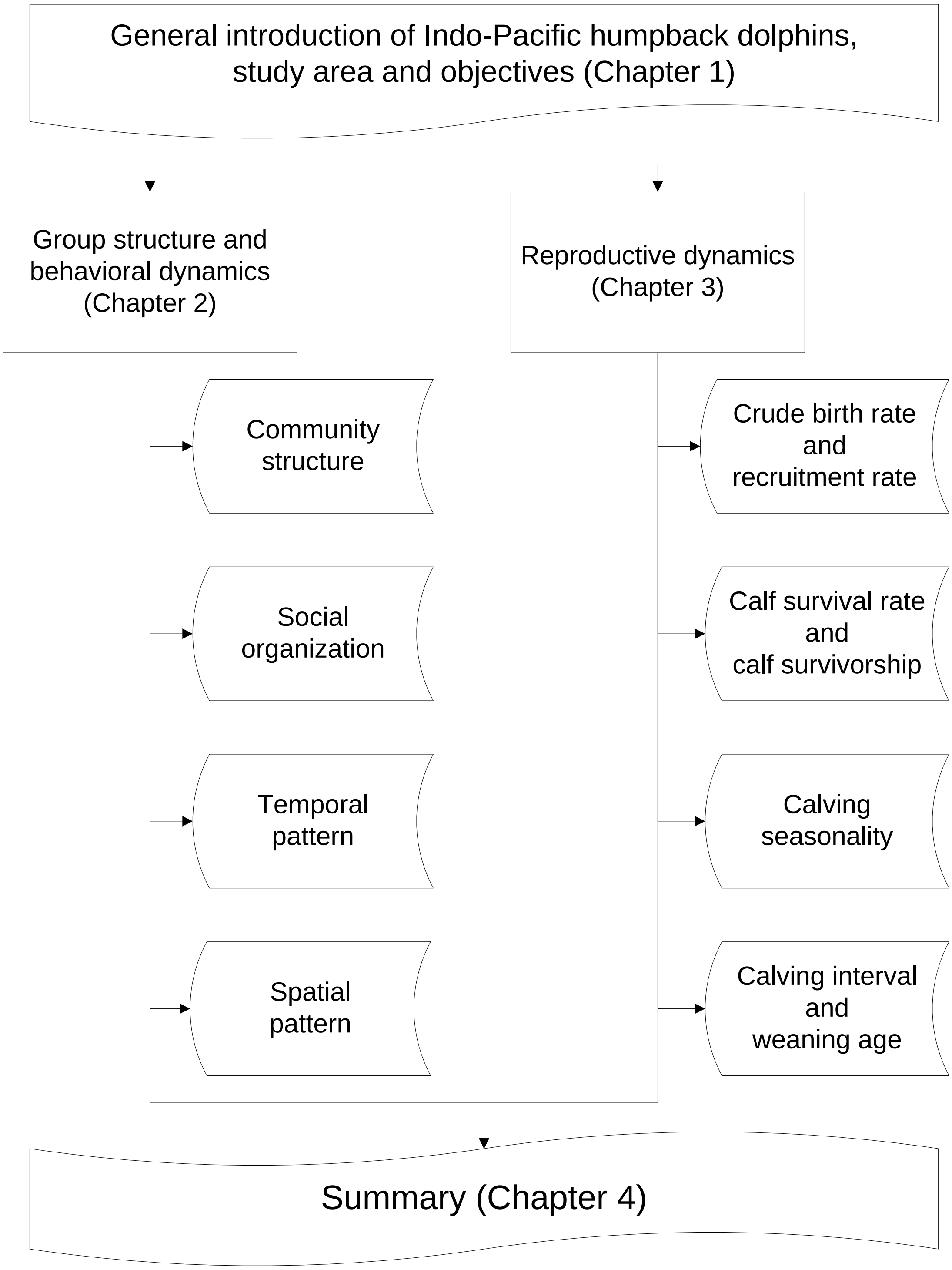

Figure 1.2 Framework of this study.

Chapter 2: Group structure and behavioral dynamics of Indo-Pacific humpback dolphins off the west coast of Taiwan

ABSTRACT

In Taiwan, Indo-Pacific humpback dolphins (*Sousa chinensis*) form a small population in the west coast and are endangered. To study their group structure and behavioral dynamics, this study analyzed the social affinities of all non-calf dolphins in this population. Seventy-one non-calf dolphins were identified from over 60,000 photographs taken in 352 field surveys during 2007-2010. Hierarchical cluster analysis and multidimensional scaling analysis revealed there were two communities and each community contained both stationary residents and traveling transients. The age-stage composition and number of mature females were seemly different between these two communities; since such differentiation corresponded to the differences on geographic features, such division could be due to different habitat preferences by different ages of dolphins, or perhaps, human disturbance in the recent decades. Their social dynamics could be best described as a causal association with short-term social bonding, and dolphins might leave their communities for a short term but return

frequently in long-term time scale. Further studies on the communications of Indo-Pacific humpback dolphins between these two communities and among populations in the eastern Asian waters are urgently needed, in order to elucidate the causes of this segregation, to alleviate possible anthropogenic impacts, and to reduce the risk of local extirpation of Indo-Pacific humpback dolphins.

INTRODUCTION

Social structure, the tempo-spatial interaction pattern among each conspecific individual in a given population (Hinde 1976), could affect a population's growth, gene flow, information dispersal and disease infection (Wilson 1975). In cetaceans, the male Gray's spinner dolphins (*Stenella longirostris longirostris*) were less socially bonded, had lower site fidelity and dispersed further than the females did; consequently the gene flow of male spinner dolphins was greater than the females in the French Polynesia Society Islands waters (Oremus *et al.* 2007). The prey abundance was uneven around the complex Doubtful Sound topography, therefore bottlenose dolphins (*Tursiops* spp.) had long-lasting associations for sharing food resource location information (Lusseau *et al.* 2003).

Environment influences on social patterns

Although it is believed that the social structure is inherited in each species, a recent review suggests that environmental factors (*e.g.*, habitat characteristics and ecological variables) can greatly influence the way dolphins interact with one another, result an intraspecific differentiation on social structures, and it can be substantial at times (Gowans *et al.* 2007). The divergence of social structures of spinner dolphins in Hawaiian waters could be a good example: since there are large and abundant resting habitats, dolphins living around the main island exhibit fission-fusion group dynamics as a consequence of diurnal activities – resting and socializing area of each dolphin varied from day to day, and feeding jointly in deep water at night (Würsig *et al.* 1994). On the other hand, those live around those isolated Hawaii far-western islands, there dolphins activate long-term stable groups and form more stable communities in particular lagoons (Karczmarski *et al.* 2005).

Socio-behavioral studies of Indo-Pacific humpback dolphins

Social behaviors, as the basis for social structure studies, have been studied for Indo-Pacific humpback dolphins at numerous sites -- Richards Bay (Keith *et al.* 2002) and Algoa Bay (*e.g.*, Karczmarski 1999), South Africa; Maputo Bay, Mozambique (Guissamulo and Cockcroft 2004, Guissamulo 2008); the Great Sandy Strait

(Cagnazzi *et al.* 2009) and Cleveland Bay (*e.g.*, Parra 2005), Australia; Hong Kong (*e.g.*, Parsons 1998, Jefferson 2000) and Xiamen (Zhai 2006), China. Although there seems to be a universal pattern of social dynamics for Indo-Pacific humpback dolphins, there might be some differences specific to individual research sites and populations.

The earliest study on social gregariousness of Indo-Pacific humpback dolphins was conducted off the Eastern Cape coast in South Africa; they found, at similar habitat, Indo-Pacific humpback dolphins tended to form into relatively small groups than other cetacean species (Saayman *et al.* 1972, Saayman and Tayler 1973). Their group size seems to be varied among study sites: less than seven in southeast South Africa (Karczmarski *et al.* 1999a), 10-15 in southern Mozambique (Guissamulo and Cockcroft 2004), and an occasional aggregation of up to 100 dolphins was recorded in Persian Gulf (Baldwin *et al.* 2004).

Association persistency patterns of Indo-Pacific humpback dolphins were first studied by Saayman *et al.* (1972). Humpback dolphin societies act with a fission-fusion social structure (Karczmarski 1999, Jefferson 2000, Keith *et al.* 2002), but perhaps there are some strong relationships between particular pairs in some areas (Parra 2005), for particular reasons.

The site fidelity and the movement pattern of Indo-Pacific humpback dolphins had been studied by multiple approaches. In Queensland waters, two populations feature two extremes: a strong site fidelity and long term residency population in the Great Sandy Strait (Cagnazzi *et al.* 2009); and a temporary residence pattern population in the Cleveland Bay (Parra *et al.* 2006), whereby the weak site fidelity was similar to those populations of Algoa Bay (Karczmarski *et al.* 1999b, Karczmarski *et al.* 2000b) and Maputo Bay (Guissamulo and Cockcroft 2004).

Socio-behavioral study of Taiwan Indo-Pacific humpback dolphin population

Indo-Pacific humpback dolphins in Taiwanese waters are believed to be a geographically isolated population (Wang *et al.* 2008). It is a small population (75-80; Yu *et al.* 2010) living in a restricted area that is highly disturbed by human activities (Ross *et al.* 2010). Their social behaviors, structures and dynamics are yet known and deserve a comprehensive study, since studying a population’s social structure can furnish valuable information for conservation (Sutherland 1998).

Objectives

The aim of this study was to investigate the socio-behavioral dynamics of the small, remote Indo-Pacific humpback dolphin population in the narrow, shallow coastal waters of Taiwan, by analyzing dolphins’ association patterns and social structure.

METHODS

Field survey

Photo-identification boat surveys were launched during the period of late spring to early autumn (between February and December, mostly from May to September), 2007-2010 (Table 2.1), when the weather was under a steady condition (Beaufort state ≤ 3). During the surveys, the boat travelled at a constant speed of 6-8 kt on two fixed survey lines, the near-shore and off-shore lines: the near-shore line was parallel to the coastline where water depth was about 2-10 m, and five off-shore lines were parallel to the near-shore line, where water depth was about 10-20 m (Figure 2.1). The near-shore line was divided into three regions including six sections, the effort devoted to each section varied among years (Table 2.1). Four survey platforms were also used at different sections: an 11-m vessel powered with a 180-HP outboard motor was used in Section A; an 18-m vessel powered with a 750-HP outboard engine was used for surveys at Sections B-C; an 11-m vessel powered with a 240-HP outboard motor was used for Section D; all surveys in Section E and F were conducted on an

11-m vessel powered with a 260-HP outboard motor. Each survey lasted about seven hours in average; the same section would not be surveyed on the same day.

Three to five observers were assigned on boat to search for dolphins by naked eyes, with either 8 X 30 or 7 X 50 zoom lens telescopes. Once an Indo-Pacific humpback dolphin group (definition, see below) was encountered, the boast speed would be reduced to 2-3 kt to approach the dolphins. Information including the date, global position system (GPS) location, and estimated group size were recorded. Dolphins were then photographed perpendicularly by two or three photographers with digital cameras (CANON, OLYMPUS, and PENTAX) equipped with variable lenses (70-300 mm) or a fixed focal 400 mm lens.

Photo identification

The photo quality (Q) was scored for all photos from Q1 to Q100 (derived from Friday *et al*. 2000 and Karczmarski *et al*. 2005). Each photo was rated based on the clarity of focus, contrast, angle, and the coverage of full dorsal fin. Only photos scored over Q80 were applicable to be used for photo-identification.

Each individual was cataloged by at least three unique characteristics, including (1) notches on its dorsal fin, and (2) spots on its body. However, identify of calves were unable to be confirmed because they possessed a few superficial traits (*i.e.*, scars or spots). The photo identification catalog was later re-checked by two experienced researchers, Hsin-Yi Yu and Paula Olson.

Definitions

The study area was divided into three regions according to the sighting frequency (Figure 2.1a) and the encounter rate (Chou *et al.* 2011): the north, central, and south regions. The north region was Section A-C, the central region was Section D, and the south region was Section E and F (Figure 2.1b).

The term “encounter” was defined as the event of encountering dolphins, regardless of photograph quality (equal to “sighting” in Karczmarski *et al.* 1999a).

The term “group” referred to the aggregation of dolphins (including solitary dolphin and mother-calf pairs) exhibiting the similar behavior within a range of 100 m (Karczmarski *et al.* 1999a).

The term “photo-ID group” referred to a group that contained at least one identifiable dolphin. The term “75% photo-ID group” referred to a group that at least 75% of its members were identifiable.

The term “community” was used to describe a school of dolphins sharing similar living range and interacting socially with each other, but it did not represent a closed reproductive unit (Wells *et al.* 1999, Karczmarski *et al.* 2005).

The dolphin’s body coloration pattern was classified into five coloration stages (derived from Jefferson 2000): calf, mottled-stage, speckled-stage, spotted-stage, and unspotted-stage. A calf could be easily distinguished by its dependency on a particular adult and its plain dark-grayish color pattern (equivalent to ‘calf’ and ‘juvenile’ in Jefferson, 2000). A mottled-stage dolphin was defined as a dolphin with gray and light spots. A speckled-stage dolphin was defined as a light pink dolphin with many dark spots on its body (more than 50% of its body area). A spotted-stage dolphin was those white dolphins with spots less than 50% of their body. An unspotted-stage dolphin was in pinkish color and had few or no spots.

Dolphins were classified into four age stages according to their visible appearance traits (derived from Karczmarski 1999a and X.-R. Xu personal communication) and relative size to a standard adult size (249 cm, derived from Jefferson *et al.* 2011). A calf, might it be a neonate, was defined as an unspotted dolphin accompanied with a particular adult and had a body length less than 3/4 of adult size (see Chapter 3). A juvenile was defined as a non-robust dolphin with 3/4 of adult size; sub-adult, a dolphin with a body length as 7/8 of adult size; and adult, was defined as (1) a full-sized dolphin, (2) having tooth worn down seriously, (3) having notable wrinkle behind earhole and loose skin, or (4) calving (see Chapter 3).

Association index

Association index between each dyad of individuals was calculated to evaluate the strength of social association. All these association indices were then used to construct a social web.

A half-weight index (HWI, Dice 1945) was applied to measure the strength of relationship between two individuals:

$$\mathrm{HWI} = \frac{x}{x + \frac{y_A + y_B}{2}} \qquad [1],$$

where x = the number of groups that contained both individuals A and B, y_A = the number of groups in which only A was identified, y_B = the number of groups in which only B was identified. The index would range from 0 (A and B were never seen being together) to 1 (A and B were always sighted in the same group).

Analysis was performed via SOCPROG 2.4 (Whitehead 2009) in Matlab 7.1 (MathWorks, Inc., 24 Prime Park Way, Natick, Massachusetts, USA). The strength of associations between/within sex and different historical identified regions were test by the mantel test. The null hypothesis of the mantel test was that associations between and within classes are similar (see Schnell *et al.* 1985).

Community structure

Average-linkage hierarchical cluster analysis (Milligan and Cooper 1987) and non-matrix multidimensional scaling analysis (Morgan *et al.* 1976) were applied to determine the community structure(s), based on individuals sighted more than 10 times from 75% photo-ID groups.

Average-linkage hierarchical cluster analysis was applied to construct a dendrogram model for clarifying the relationships between individuals (Morgan *et al.* 1976, Milligan and Cooper 1987). The cophenetic correlation coefficient was then calculated to examine dendrogram fitness (Bridge 1993), ranging from 0 (no relationship) to 1 (a perfect fit). An acceptable model should have a value higher than 0.8 (Bridge 1993). Two methods were used to generate a dendrogram: the gregariousness based on the identified association matrix, and the permutation test methods taken as many times as possible until the modularity value stable.

The modularity (q) is for evaluating the distinctness of associations between clusters (Newman 2004):

$$q = \frac{\sum_{A,\mathrm{B}} \alpha_{AB}\delta(c_A, c_B)}{\sum_{A,B} \alpha_{AB}} - \frac{\sum_{A,B} \hat{\alpha}_{AB}\delta(c_A, c_B)}{\sum_{A,B} \alpha_{AB}} \qquad [2],$$

where α_{AB} was the HWI between individuals A and B, and $\hat{\alpha}_{AB}$ was the expected value of α_{AB}. The value of $\delta(c_A, c_B)$ = 1 when A and B were in the same cluster, where $\delta(c_A, c_B)$ = 0 when A and B were in different clusters. The modularity q would range from 0 (random clusters) to 1 (no association exists between members from different clusters). The modularity *q* value of a well-divided dendrogram should be greater than 0.3 (Newman 2004).

The other approach to determine the community structure was the non-metric multidimensional scaling analysis, which transformed the monotonic *n*-dimensional relationship into a 2-dimentional plate (Morgan *et al*. 1976). The non-metric stress was the degree of failure in the non-metric multidimensional scaling representation (Manly 1994, Legendre and Legendre 1998), and a stress value under approximately 0.1 indicated a useful representation (Morgan *et al.* 1976).

Association strength between individuals within community

A sociogram was applied to display every possible social bond of dolphin dyads in a community clearly. Sociograms were drawn by NETDRAW program (Borgatti 2002).

Spatial-temporal relationship

The standardized lagged association rate was calculated to analyze the temporal pattern, and the lagged identification rate was for examining the spatial pattern of the social relationship on both population and community levels. All photo-ID groups dataset were used in both analyses.

The standardized lagged association rate

The standardized lagged association rate (*g'(τ)*) was the probability of a randomly-chosen pair associated after *τ* unit time lag (Whitehead 1995). This value was standardized because some associations may be missing to record.

$$g'(\tau) = \frac{\sum_{j,k|(t_k - t_j)=\tau} \sum_A \sum_{B \neq A} a_j(A,B) * a_k(A,B)}{\sum_{j,k|(t_k - t_j)=\tau} \sum_A (\sum_{B \neq A} a_j(A,B)) * (\sum_{B \neq A} a_k(A,B))} \quad [3],$$

where $a_j(A, B)$ = 1 if individuals *A* and *B* were associated in time period *j*; and $a_j(A, B)$ = 0 if they were not associated or not identified, during the sampling period.

The standardized lagged association rate ranges from 0 (*A* and *B* were never seen together) to 1 (*A* and *B* always being together and never separated). The null hypothesis of the standardized lagged association rate was that individuals associated with each other randomly in a constant value. Jackknifing was performed to estimate the standard error for each group of sampling periods.

The best models of standardized lagged association rate were selected (Whitehead 2007) according to the minimum Quasi Akaike Information Criterion value (QAIC):

$$\text{QAIC} = -(2 * L' / \hat{c}) + 2 * K \quad [4],$$

where $\hat{c}$ = the variance inflation factor for the most general of models being compared *K* = the number of parameters being estimated plus one, and *L'* = the sum of log-likelihoods. The calculated quantity of L' was:

$$L' = \sum_{\tau} \sum_{j,k|(t_j - t_k) = \tau} Log(L(g'(\tau) | \{a_j(A, B)\}, \{a_k(A, B)\})) \qquad [5],$$

where $L(g'(\tau))$ = the likelihood of the model $g'(\tau)$ is accurate, and $a_j(A, B)$ is as above.

The lagged identification rate

The lagged identification rate ($R(\tau)$) was the probability of resighting an individual in an area after τ unit time (Whitehead 2001) for demonstrating the residence time within a given region and the movement pattern between two or more regions. The lagged identification rate equaling to 1.0 would indicate an individual's permanent residency in a given area.

$$R(\tau) = \frac{\sum_{j,k|(t_k - t_j) = \tau} m_{jk}}{\sum_{j,k|(t_k - t_j) = \tau} n_j * n_k} \qquad [6],$$

where t_j = the time of sampling period j, n_j = the number of individuals identified in period j, m_{jk} = the number of individuals identified in both periods j and k.

The best models of lagged identification rate were selected (Whitehead 2007) according to the minimum Akaike Information Criterion value (AIC):

$$\text{AIC} = -2 * L' + 2 * K \qquad [7],$$

where K = the number of parameters being estimated plus one, and L' = the sum of log-likelihoods. The calculated quantity of L' was:

$$L' = \sum_{\tau} \sum_{j,k|(t_j - t_k)=\tau} Log(L(R(\tau) \mid m_{jk}, n_j, n_k) \qquad [8],$$

where: $L(R(\tau)|m_{jk}, n_j, n_k)$ = the likelihood of the model $R(\tau)$ is accurate, and m_{jk} and n_j are as above.

RESULTS

During 2007-2010, 352 survey trips were made and 335 groups of dolphins were encountered. Only six groups (1.79%) were sighted on off-shore lines, and nine groups (2.69%) were sighted in the central region. Of 222 photo-ID groups, 174 were qualified as 75% photo-ID groups. Out of 64,109 photographs, 20,172 of them were qualified for photo-identification analyses (Table 2.1).

Discovery curve, group size, sighting frequency and HWI frequency

A total of 71 individuals were photo-identified and catalogued (Table 2.2). The cumulative number of identified dolphins reached a plateau of 68 individuals at the 69th survey (in July 2008, Figure 2.2), implied that almost all non-calf dolphins had been identified. The slight increase of three individuals during 2009 and 2010 resulted from juvenile dolphin recruitment.

Out of 71 non-calf dolphins, there were two juveniles each was observed to continuously associate with a particular adult dolphin, therefore was referred to two mother-juvenile pairs. Because their dependency apparently disobeyed the assumption that each dolphin was randomly associated in a given population, these two juveniles were excluded from the following social structure analyses.

Estimated group size was general underestimated (Figure 2.3a). The median group size estimated from the photo-ID group was 5.66 ± s.d. 4.14 (range 1-22, calves excluded; Figure 2.3b). Median group size for those in north region was 6.28 ± s.d. 3.78 (range 1-15), and for those in south region was 6.88 ± s.d. 4.44 (range 1-22); no significant differences were found between them (Mann-Whitney *U* test, $W = 5495$, $p = 0.99$, Figure 2.3c). There were 113 encounters without any acceptable quality photograph, and the group size of these encounters were mainly estimated less than four (Figure 2.3d).

For photo-ID groups, each dolphin was sighted ranged from three to 38 times (Figure 2.4a). In 75% photo-ID groups, the sighting frequency of each dolphin ranged from three to 30; 53 dolphins (77.5%) were sighted more than 10 times, therefore the hierarchical cluster analysis, multidimensional scaling analysis, and the sociogram were conducted with these dolphins (Figure 2.4b).

The HWI frequency distribution of all dyads among dolphins sighted more than 10 times had a peak close to zero (range 0-0.84), which indicated the associations between dolphins were generally weak (Figure 2.5a). The average HWI of dyads for each individual was 0.14 ± s.d. 0.03 (range 0.09-0.19, Figure 2.5b). The maximum HWI for each dolphin ranged from 0.32 to 0.84 (mean = 0.56 ± s.d. 0.14, Figure 2.5b).

Community structure

Hierarchical cluster analysis

Two main clusters were identified by a high cophenetic correlation coefficient value (0.8991, Figure 2.6), indicating the dendrogram matched the association index matrix well. At the separated branch (HWI = 0.1722), identical results were generated by both gregarious and permutation methods with different modularity values ($q_{\text{gregariousness}} = 0.4519$ and $q_{\text{permutation}} = 0.0188$ after 4,000 times permutation). There was one cluster in the dendrogram engaged with 17 north dolphins and six transient dolphins, while the other cluster was composed by 10 south dolphins and 20 transient dolphins. Interestingly, there was a unit (HWI > 0.70) composed by two nursing females and one adult dolphin of unknown sex (Figure 2.6).

Multidimensional scaling analysis

The non-matrix multidimensional scaling analysis also revealed two major clusters, with a stress level (0.12447) that was slightly larger than the value of maximum useful indicator (Figure 2.7). The members in each cluster corresponded to the dendrogram constructed by the hierarchical cluster analysis. Moreover, from this non-matrix multidimensional scaling analysis, transient dolphins were found to have a closer relationship with the south than the north dolphins: most transient dolphins (*n* = 20) were mingled with all south dolphins well; only a few transients (*n* = 6) were with the north dolphins (Figure 2.8).

Community structure

Both analytical treatments (hierarchical cluster analysis and multidimensional scaling analysis) indicated that the Indo-Pacific humpback dolphin population off Taiwan was composed by two residential communities with different preferences to the regions: 23 dolphins in the north, and 30 dolphins in the south community. Six transient dolphins were constantly found in the north community (81.3 ± s.d. 13.5% sightings) in the north region; and 20 transient dolphins were frequently seen with the south community in the south region (88.6 ± s.d. 7.2%).

Coloration and age stage

Of the coloration-stage of 71 identifiable dolphins, the majority (77.5%) was mottled and speckled-stage. Notably, almost all spotted and unspotted-stage dolphins were found in the north region, while unspotted dolphins were never found in south dolphins, transient dolphins, and the south community. The coloration-stage compositions between the north and south communities were significantly different (χ^2-test, $p < 0.05$, Figure 2.8a).

Almost half (43.7%) of the identified dolphins were adults. More than half (59.1%) of the north dolphins were adults; however, of the south dolphins, it dropped to 22.2%. Almost 87.1% of transients were older than juvenile. The age-stage compositions between the north and south communities were significantly different (χ^2-test, $p = 0.002$, Figure 2.8b).

Social organization

The strength of individual relationships within the north community (HWI = 0.29 ± s.d. 0.07) was greater than in the south (HWI = 0.22 ± s.d. 0.05). Associations between the north and transient dolphins were weak in the north community (Figure 2.9a). On the other hand, the associations within the south community were more homogeneous than the north community (Figure 2.9b). There was no significant difference between sex and age-stages (Table 2.3).

Persistence of social relationship on temporal and spatial scales

The persistence of social association was analyzed in both temporal and spatial scales for 69 cataloged dolphins.

Temporal pattern

The standardized lagged association rates indicated this population of Indo-Pacific humpback dolphins possessed a non-random but fluid association pattern (Figure 2.10). The best fitting model at population level was "*two levels of casual acquaintances*" (Table 2.4), that is the Indo-Pacific humpback dolphin off the west coast of Taiwan shared casual, highly varied, and temporary associations, and supported the notion of two limited interacting communities (Figure 2.10a). Same model was suggested for the temporal pattern of the north community (Figure 2.10b, Table 2.4), revealing the relatively weak associations between the north dolphins and transient dolphins. The low persistence of relationships of the south community was best described as "*casual acquaintances*" (Figure 2.10c, Table 2.4), suggesting a fluid structure in the community.

Spatial pattern

Patterns of the lagged identification rates at both population and community levels declined before reached a stable state (Figure 2.11). For the whole population (Figure 2.11a) and the south community (Figure 2.11c), the patterns were best described by an "*emigration and reimmigration*" model (Table 2.5), indicating that dolphins had their own long-term, stationary range, but would move out this range temporarily. This result suggested inter- or intra-population migration was not rare for Indo-Pacific humpback dolphins off Taiwan. On the other hand, the lagged identification rates of the north community kept decline, which was best described by the "*emigration, reimmigration and mortality*" model (Figure 2.11b, Table 2.5). Other than the model showed above, this model also suggested some dolphins died.

Movement patterns between or within regions

The probabilities of dolphins moving between or within the north and south regions were different, suggesting heterogeneity on movement patterns in Taiwan Indo-Pacific humpback dolphin population (Figure 2.12). The best-fit model by the lagged identification rates for between the north and the south regions was "*fully mixed*" (Table 2.5), that there were many dolphins of infrequently traveled between regions.

DISCUSSION

This study investigated the group structure and behavioral dynamics, including community structure, group dynamics and site fidelity of Indo-Pacific humpback dolphins off the west coast of Taiwan. Generally speaking, these dolphins lived as a fission-fusion social structure, and each dolphin had its own stationary range, infrequently travelled between two recognized communities, and likely communicated with other adjacent populations.

The social structure of Taiwan Indo-Pacific humpback dolphin population

Population level

Temporal pattern

Highly fluid association patterns of Indo-Pacific humpback dolphins were reported that the group memberships were short-term associated, fluid and unstable (Saayman *et al.* 1972). Same pattern of social structure (‘fission-fusion’) was also observed in Hong Kong (Jefferson 2000) and Xiamen waters (Zhai 2006) populations. In Algoa Bay (Karczmarski 1999, Karczmarski and Cockcroft 1999), Richards Bay (Keith *et al.* 2002), tight social units with strong associations could be only observed between dyads and triads on occasion. Nevertheless, other than fission-fusion among Indo-Pacific humpback dolphin populations, strong and long-term bonds between dolphins were commonly observed for dolphins in Cleveland Bay (Parra 2005). In this study, Indo-Pacific humpback dolphins acted in casual and highly varied temporal association patterns especially the interactions between two communities, though particular dolphins exhibited some strong bonds, which seem Taiwan humpback dolphin population appeared to be in-between these two phenomenon.

This fluid society with strong bonds pattern might be driven by some habitat characteristics, suggested by Gowans *et al.* (2007). Off the west coast of Taiwan, Indo-Pacific humpback dolphins distributed along the open but restricted coast area similar to the Algoa Bay, where the isobaths were parallel to the coastline. On the other hand, Pearl River Estuary (including Hong Kong waters) and the Cleveland Bay were featured with much wider shallow waters. The patterns of dolphins ranged were influenced by the habitat shape; and different range patterns of dolphins leaded to different association patterns (Owen *et al.* 2002, Frère *et al.* 2010).

Food resource might be another important environmental factor impacted the association patterns (*e.g.*, Gowans *et al.* 2007). Indo-Pacific humpback dolphins mainly fed on fish (Jefferson 2000, Parra and Jedensjö 2009). The prey species of Indo-Pacific humpback dolphins off the west coast of Taiwan were remained unknown. By assuming the prey preference of Indo-Pacific humpback dolphins off Taiwan is similar to that reported from Hong Kong waters (Barros *et al.* 2004); those benthic prey families inhabited in the dolphin's habitat the west coast of Taiwan, and it is highly potential they also fed on those fishes since being as opportunists (Jefferson 2000, Parra and Jedensjö 2009). In South Africa and Queensland waters, both the benthic and the pelagic fish types were found in the stomach contents of Indo-Pacific humpback dolphins (Barros and Cockcroft 1991, Parra and Jedensjö 2009). Dolphins in these areas might apply different feeding strategies for fishes living in different level waters. For instance, it was common of Indo-Pacific humpback dolphins chasing and feeding behind the trawlers in Hong Kong waters (Parsons 1998, 2004, Jefferson 2000); however, this strategy was seldom recorded off Taiwan. Dolphins applying dissimilar foraging strategies might interact differently with others and have different social structure (Rossbach and Herzing 1999).

The strong bonds were found among few north-community female Indo-Pacific humpback dolphin individuals in this study; and they indeed represented the allomaternal caring behavior (Woodroffe and Vincent 1994). It was commonly observed that two calves sandwiched by their mothers, besides there was a case that an unknown sex dolphin in the strong-bonded unit of the north community cluster was observed to help a calf breath. The calf was known not belonging to the helper because this calf was companied by another female before by identifying its unobvious but identifiable features. Certain behaviors had also been observed from Indo-Pacific humpback dolphins in South Africa and Hong Kong waters (Saayman and Tayler 1979, Karczmarski *et al.* 1997, Parsons 1998). Kin-selection could be the reason of tight associated animals by altruism (Hamilton 1964, Emlen 1995); however, the consanguinity of those females was unknown and waited for the determination by the molecular study.

The strong bonds among the Indo-Pacific humpback dolphin were uncommon with only few cases being reported in the Cleveland Bay (Parra 2005) and Algoa Bay (Karczmarski 1999). However, rather than females formed tight associations in this study, strong bonds were contributed by males, which might be the alliances of male (Karczmarski 1999, Parra 2005) and the units of the courtship (Karczmarski *et al.* 1997). Although few strong bonds were associated by unknown sex dolphins that might be male, the similar courting behavior was never observed in this study, which indicated Indo-Pacific humpback dolphins might have different mating strategies in different regions. The intraspecies mating strategy might vary geographically (Perrin and Mesnick 2003).

Spatial pattern

The site fidelity of Indo-Pacific humpback dolphins had been studied by multiple approaches, although some contradictory interpretations might originate from the differences among the range of studying area and the distribution range of entire population. In the Great Sandy Strait, the population consists of two communities with a strong site fidelity and long term residency (Cagnazzi *et al.* 2009). In Cleveland Bay, however, dolphin emigration and reimmigration happen frequently, which resulting a temporary residence pattern (Parra *et al.* 2006). A weak site fidelity and immigration during summertime was also observed in those open populations of Algoa Bay (Karczmarski *et al.* 1999b, Karczmarski *et al.* 2000b) and Maputo Bay (Guissamulo and Cockcroft 2004), although the weak site fidelity is thought to result from sampling bias, *i.e.*, the surveyed area did not cover the full range of the whole population (Karczmarski *et al.* 1999b).

In this study, the site fidelity pattern, “immigration and reimmigration” model suggested by the lagged identification rate, indicated the study area was smaller than the utilized area of Indo-Pacific humpback dolphins off the western Taiwan. It might be due to the insufficient and uneven survey effort on both spatial and temporal concepts. The survey area in current study should have almost covered the population’s distribution range (Chou unpublished data); however, an encounter in a pre-survey in 2005 was recorded out of Jiangjun, where is located at south of the south region. Moreover, the survey efforts and the encounter rates at Section A and F were relatively low, which indicated that dolphins did use those areas with very low frequency. Meanwhile, the low lagged identification rate around 200 days might be due to the close of one year survey (mostly from late spring to early autumn).

Is this Taiwanese population an isolated population?

Taiwan Indo-Pacific humpback dolphin population is currently believed to be an isolated population (Wang *et al.* 2008). The discovery curve in this study reached a plateau, indicating no dolphin immigrated during the survey period. Wang *et al.* (2008) suggested it was a distinct population because the pigmentation pattern of this Taiwanese population is significantly different from nearby populations. Besides, these catalogued dolphins from Taiwan population were not found in any nearby areas (Xiamen waters, Hong Kong waters, Pearl River Estuary, and Leizhou Bay; Wang *et al.* 2008, Nanjing workshop 2010), and the survey area in current study should have almost covered the population's distribution range (Chou unpublished data), further supported its remoteness to other Indo-Pacific humpback dolphin populations in adjacent waters.

However, this population may not be exactly closed: the population's site fidelity examined by the lagged identification rate revealed that dolphin emigration and reimmigration from other populations were not rare. Pigmentation pattern descript for the Pearl River and Jiulong River Estuary (as per Wang *et al.* 2008) were in fact identified 10 individuals from Taiwanese waters (14.1%), indicating either using pigmentation as a population indicator is invalid, or these 10 dolphins were actually from the nearby populations. Furthermore, two of them had a tight association (HWI = 0.59) and less interacted with other dolphins; it might indicated that these two dolphins have stayed often at the un-surveyed area, or other populations' habitat range. In a word, the possibility of limited interactions between the dolphins off Taiwan and other populations cannot be completely excluded.

The role of transient dolphins

In this study, almost half of cataloged dolphins were sighted in both regions with low visiting rate (less than 20%). Although even a low level of interactions between communities might provide sufficient genetic flows to retain a population's genetic diversity (*e.g.*, Oremus *et al*. 2007), an obstruction that blocks the movement of transient dolphins might have negative implications and the impacts are more severe in the case of small isolated populations. Though the size of genetic minimum viable population (MVP_g, a threshold of population size that resists to stochastic process; Shaffer 1981, Lacava and Hughes 1984) has never been estimated for cetacean species, estimated size for terrestrial mammals was ranged from hundreds to thousands (Nunney and Campbell 1993, Harcourt 2002, Brito and Figueiredo 2003, Reed *et al.* 2003, Brito and da Fonseca 2006, Brito and Grelle 2006, Traill *et al*. 2007). Current estimates of the population size of the Taiwan population are much less than this threshold (Wang *et al.* 2007, Yu *et al.* 2010). If the movement of transient dolphins between the north and south communities was blocked, genetic impacts such as genetic drift, inbreeding depression and lethal alleles will likely be enhanced, and the process of losing genetic diversity might accelerate; meanwhile, the reproductive fitness might also negatively affected, and the size and fitness of the population would therefore suffer from a long-term decline decrease (Reed and Frankham 2003).

Community level

The Indo-Pacific humpback dolphin population off the west coast of Taiwan consisted of two communities with limited interactions, of them the spatiotemporal patterns and the region preference were different.

Spatiotemporal patterns

Since the sizes of both communities were small, their social pattern could be easy influenced by the behavior of particular schools of dolphins. For the north community, those different levels of casual acquaintances could be resulted from the combination of intimate relationship among nursing females and loose associations between transient and north dolphins. In the south community, on the other hand, the inclusion of a large proportion of transients might decrease its stability and result a fluid society. Although the number of nursing females was almost third times more than the north community, those nursing females in the south community did not form strong bonds.

In this study, most dolphins were found frequently emigrated in short term and then, in a longer temporal scale, re-immigrating back to their stationary sites. This movement pattern might relate to the mate-searching behavior (Karczmarski 1999), *i.e.*, the mating strategies of cetacean are promiscuous that they change mate partners every mating season. The lagged identification rate of the north community indicated some dolphins left the north region forever, there was a case that a dolphin (#16) dead stranded in September 2009. It might be also due to the limited and uneven survey effort among different sections (see above). For instance, one identified-four-time dolphin was encountered three times in Section A, however surveyed in 2009 only.

Habitat differentiation might have leaded the demography of community diverged

From this study, two fluid communities with different social structures and limited inter-community interactions have been identified for the Indo-Pacific humpback dolphin population off the west coast of Taiwan. Differences included the coloration and age-stage composition, the number of mature females (see Chapter 3), association patterns, and the spatiotemporal pattern of group dynamics. These differences might have revealed that their social behavior might be shaped by different habitat features.

Both examinations from age and coloration composition had revealed that dolphins in the south community were generally younger, consisting with calf, mottled, speckled, spotted-stage, but no unspotted-stage dolphin. The number of nursing females (see Chapter 3) in the south community occupied almost half of the community population size. Moreover, the sighting rate of nursing groups (the groups contained mother-calf pairs) increased progressively as the latitude decreased (see Chapter 3). These demographic cues suggest the south region might function of a nursery ground, which shall provide sufficient food resources and shelter to safeguard mother-calf pairs, as suggested in Scott *et al.* (1990).

The prey species details of Indo-Pacific humpback dolphins off the west coast of Taiwan remains unknown as discussed above. Their prey preference is similar to that reported from Hong Kong waters (Barros *et al.* 2004) by assuming, despite that the species was varied among surveyed sections (Chen and Shao 2011, see Chapter 1), and their actual abundance had yet been precisely estimated. Even though the prey richness in different regions is still open to questions, the surf zone of Waisanding Sand Bar located in the south region provided a refuge and suitable habitat for fishes (Robertson and Lenanton 1984, Lenanton and Caputi 1989), which could be a good energy resource for Indo-Pacific humpback dolphins.

Sheltering is another important characteristic to a good nursery ground. In many cetaceans, a shallow area would be a priority choice to keep the mothers and calves safe (*e.g.*, Scott *et al.* 1990, Elwen and Best 2004, Weir *et al.* 2008). This phenomenon was also observed for the Indo-Pacific humpback dolphin off the west coast of Taiwan: the average water depth of sighting nursing groups was significantly shallower than the groups without mother-calf pairs (Chang *et al.* 2010). Such preference might result from the same reasons as to other dolphin populations: mother-calf pairs of bottlenose dolphins (*Tursiops truncatus*) chose to stay in shallow areas with less predator (Scott *et al.* 1990) and wave disturbance (Barco *et al.* 1999), as well as for dusky dolphins (*Lagenorhynchus obscurus*) in Kaikoura waters (Weir *et al.* 2008). Off the western Taiwan, the major habitat for humpback dolphins in the north region (area less than 15 m depth) was very narrow (1-2 nautical mile, or ‘nm’, mostly 1 nm from shore, see Figure 1.1). In the south region, on the other hand, their major habitat had a distance of 1-3 nm (mostly more than 2 nm) and there was a wide space within 25-m isobaths that it provided a safer place for mother-calf pairs (see Figure 1.1).

The number of nursing females identified in the north region was relatively few, besides the coloration-stages of these nursing females were significantly different from those in the south region. By assuming that the coloration pattern coordinates with the aging process (Jefferson *et al.* 2011) and sexual maturity dolphins share a similar calving interval, calving females in the north region seems to be older than those in the south region, and one may infer that these mothers in the north region had more experiences on nursing offspring. Older or more experienced female dolphins might have higher reproductive success as reported in other mammal species, such as northern elephant seals (*Mirounga angustirostris*, Le Boeuf and Reiter 1988), mice (*Peromyscus polionotus*, Margulis *et al.* 2005), and hanuman langurs (*Presbytis entellus*, Borries *et al.* 1991).

Moreover, females in the north community might have the allomaternal calving behavior as discussed above. Despite that the habitat in the north region might be too narrow to be considered as an ideal nursing ground (see above), for older and experienced females employing cooperative calving strategy, their reproductive success should be still sustained.

Two communities with limited interactions I: Dolphins' physiological needs?

Two communities were also distinguishable from geographic perspective. Although more than 40% of all cataloged dolphins sighted in both regions (referred here as transients), they spent a majority of time (81-88%) in a particular region, either in the north or south. The dramatic difference in modularities of gregariousness and permutation methods with the identical dendrogram layouts indicates these dolphins had a strong tendency to form two clusters even if a possibility of dolphins associated in long-term was provided. Limited movement between communities is unlikely due to the distance, since the length of the overall study area (about 100 km) was far shorter than the documented traveling capability of humpback dolphins (120-160 km, Durham1994, Karczmarski *et al*. 1999a, Chen *et al.* 2010).

Dolphins' physiological needs might also influence the interaction pattern. More than half of transient dolphins were sub-adults and juveniles in this study; the range sizes across age stages also had a decreasing trend (Yeh 2011, master thesis). Younger animals might travel further to compensate their poor foraging skills to get demanded energy (Lindstedt *et al.* 1986). The reproductive status of animals could be another factor (Lindstedt *et al.* 1986, Karczmarski 1999). In this study, female transients tended to stay in a certain region once calving (see Chapter 3). Reproductive females' ranging behavior was usually limited by carrying calves (Karczmarski 1999) and mothers utilized the nutrient-rich regions for higher energetic requirements of lactation (Yasui and Gaskin 1986, Oftedal 1997, Lockyer 2007, Huang *et al.* 2009).

Two communities with limited interactions II: Natural or anthropogenic?

The separation found in this study is also likely resulting from both natural and anthropogenic causes, as reported for the Great Sandy Strait Indo-Pacific humpback dolphin population (Cagnazzi *et al.* 2009). These Indo-Pacific humpback dolphins off the west coast of Taiwan ranged in a continuous coast, open area, however, the topography of the central region might provide some insight for the reason that fewer dolphins were found in this region– the evenly flat bottom that is hard to utilize for dolphin effective foraging is seemly unflavored by dolphins (Yeh 2011, master thesis).

Recent anthropogenic activities, in particular the constructions along the middle part of the population's distribution range, may become a geographic barrier for the Indo-Pacific humpback dolphin in many ways. The commercial Mailiao Port, for instance, was artificially excavated to 24 m in depth, and could become a geographic barrier for those deep-water-phobic Indo-Pacific humpback dolphins (as suggested by Karczmarski *et al.* 2000a). Frequent boat trafficking, noises, and debits littering, all are foreseeable problems that would obscure the movements, behaviors, even lives of the dolphin (Janik and Thompson 1996, Van Parijs and Corkeron 2001).

Conservation actions are urged for Taiwan Indo-Pacific humpback dolphin population

Based on this study, Indo-Pacific humpback dolphins preferred a certain region, either the north or the south region, off the west coast of Taiwan. Moreover, the population size of this small population of Indo-Pacific humpback dolphins off the west Taiwan coast is likely decreasing (see Chapter 3) and possibly due to the fast growth of human population and economy in Taiwan the past decades. The carrying capacity influences the upper limit of the population size (Shaffer 1981, Reed *et al.* 2003). The reduction in the effective carrying capacity increases the risk of extinction due to demographic stochasticity, especially for the small population living in a confined area. This Taiwan Indo-Pacific humpback dolphin population was revised to the category of “Critically Endangered” in IUCN Red List (Reeves *et al.* 2008). Similar circumstance to the endangered Yangtze finless porpoise (*Neophocaena asiaeorientalis asiaeorientalis*) in Chinese waters (Zhang *et al.* 1993, Zhao *et al.* 2008). An effective management strategy on conservation with emphasis on uninterrupted gene flow between two communities and preservation or advanced the habitat quality, especially prevention of further habitat loss and fragmentation is urgently needed.

Questionable group size

This population of Indo-Pacific humpback dolphins off the west coast of Taiwan tended to gather in small groups, each group contained less than six dolphins. However, one should be aware that it might be problematic. Although in this study, the group size estimated by photo-ID was more accurate than the observation in the case of the big group (*i.e.*, size larger than 10), it could be still underestimated owing to normally incomplete shooting coverage. On the other hand, as photographing is limited by the dolphin behavior or wave disturbance; the smaller group was, the more difficult to be photographed well. About one third encounters had no Q80 photograph, and most of them composed of less than four members; that is, the photo-ID group size was likely biased upwards.

A more accurate estimation in the fieldwork can ameliorate this situation. A higher proper observer position height will enlarge observer’s eyesight, and the dolphin detectability will increase (Guenzel 1997). The consistency on the observer will increase the preciseness of estimation (L. Karczmarski personal communication). However, due to the limitation on the survey boat design and the manpower, it has difficulty to assign these two ameliorations in this study. Here a correction based on photo-ID data may help to supervise the observers revising the future group size less underestimated.

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Table 2.1 Effort of this study during 2007-2010 of the west cost of Taiwan Island (a) in year; and (b) in month. All groups with any photograph of quality ≧ 80 (Q80) are referred to as "photo-ID group". Groups that had at least 75% of the group members photographed with photographs of quality ≧ 80 (Q80) are referred to as "75% photo-ID group".

(a)	2007	2008	2009	2010	Sum
Survey region (number of surveys)	20	114	154	64	352
North region (number of surveys)	Jul-Oct (12)	Apr-Oct (44)	Jun-Sep (41)	May-Sep (15)	(112)
Central region (number of surveys)	-	May-Jun (10)	Mar-Dec (65)	Feb-Apr (5)	(80)
South region (number of surveys)	Jul-Oct (8)	Apr- Sep (60)	Jun-Dec (48)	May-Nov (44)	(160)
Total number of photographs	790	16,941	20,267	26,111	64,109
Number of photographs ≧ Q80	428	6,706	7,381	8,227	22,742
Number of encounters	24	125	105	81	335
Number of photo-ID groups, total/75%	8/7	80/69	74/49	60/49	222/174

(b)	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar
Number of surveys	17	33	42	101	87	38	11	6	2	0	2	3

Table 2.2 Regional sighted history of 71 cataloged Indo-Pacific humpback dolphins off the west coast of Taiwan.

Region sighted history	Number of dolphin (♀/unknown sex; north/south community/unanalyzed)	Percentage (%)	Assignment
Only in the north region	22 (6/16; 17/0/5)	31.0	North dolphin, “N”
Only in the south region	18 (3/15; 0/10/8)	25.4	South dolphin, “S”
In north and south regions	31 (13/18; 6/20/5)	43.6	Transient dolphin, “T”
Total	71 (22/49, 23/30/18)	100.0	

Table 2.3 The average and maximum half-weight indices between and within sex and different age stages of (a) the north community; and (b) the south community.

	(a)		(b)	
	Average	Maximum	Average	Maximum
All individuals	0.29 (0.07)	0.58 (0.13)	0.23 (0.05)	0.50 (0.11)
Female-female	0.30 (0.08)	0.60 (0.18)	0.24 (0.04)	0.40 (0.06)
Unknown-unknown	0.29 (0.06)	0.58 (0.11)	0.22 (0.04)	0.49 (0.12)
Female-unknown	0.28 (0.08)	0.55 (0.16)	0.23 (0.06)	0.45 (0.13)
Within class	0.30 (0.07)	0.57 (0.13)	0.23 (0.04)	0.45 (0.10)
Between class	0.28 (0.07)	0.51 (0.14)	0.23 (0.06)	0.44 (0.13)
Mantel test	$r > 0$, $p = 0.78$		$r < 0$, $p = 0.40$	
Juvenile- Juvenile	NaN (NaN)	NaN (NaN)	0.24 (0.03)	0.33 (0.02)
Subadult-subadult	0.27 (0.09)	0.49 (0.15)	0.22 (0.03)	0.48 (0.09)
Adult-adult	0.29 (0.06)	0.55 (0.12)	0.25 (0.05)	0.41 (0.07)
Juvenile- subadult	0.33 (0.00)	0.50 (0.00)	0.22 (0.04)	0.42 (0.15)
Juvenile- adult	0.25 (0.00)	0.43 (0.00)	0.23 (0.07)	0.47 (0.18)
Subadult-adult	0.30 (0.08)	0.56 (0.15)	0.23 (0.07)	0.41 (0.12)
Within class	0.28 (0.07)	0.53 (0.13)	0.24 (0.04)	0.42 (0.09)
Between class	0.29 (0.07)	0.56 (0.14)	0.23 (0.06)	0.45 (0.14)
Mantel test	$r < 0$, $p = 0.44$		$r > 0$, $p = 0.81$	

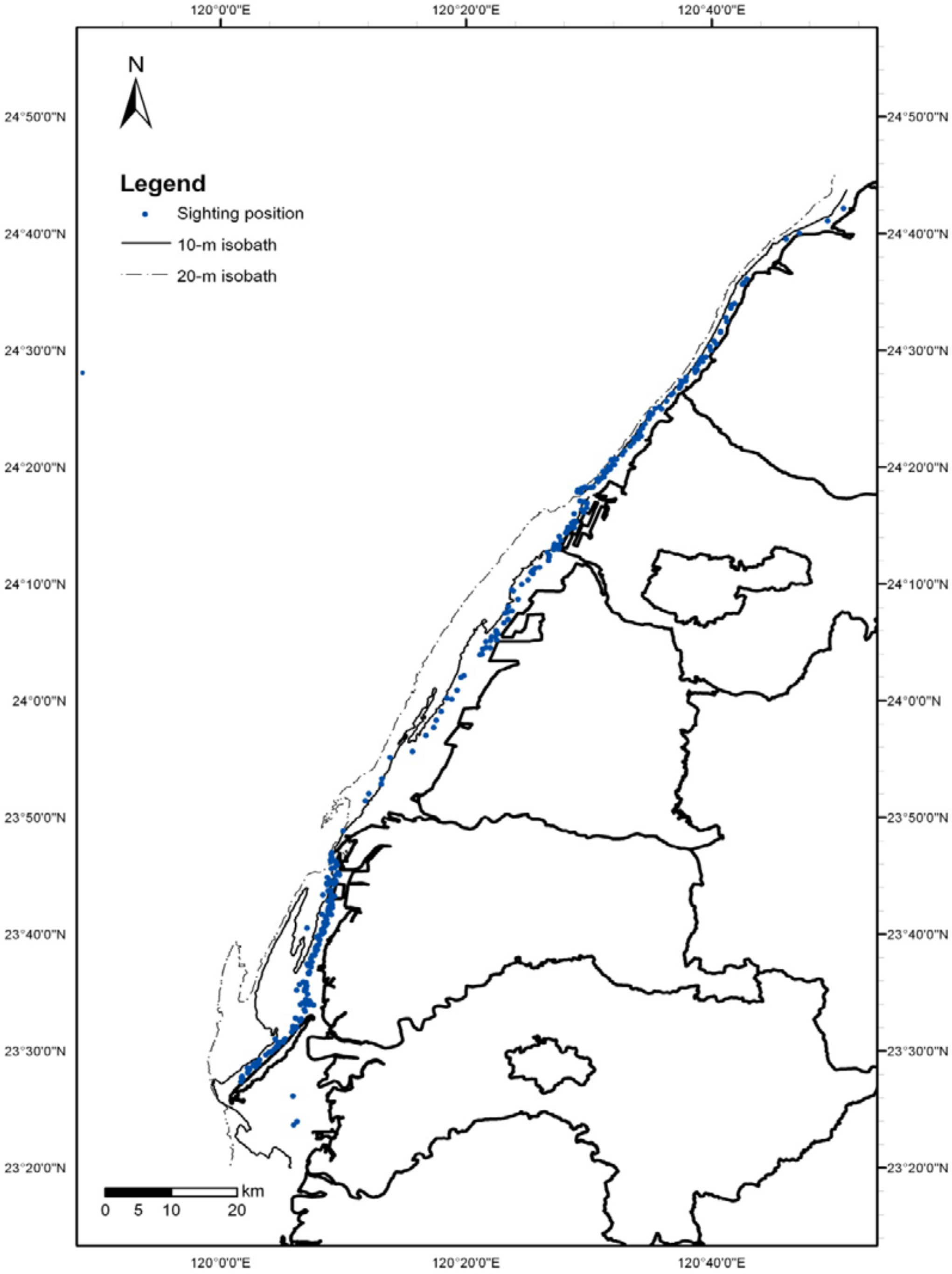
Table 2.4 The QAIC values of the lagged association rates. The best fitted model is shown in bold.

Regions	Model	QAIC	△QAIC
Taiwan population	Casual acquaintances	57728.8	9.7
	Constant companies + casual acquaintances	57742.2	23.1
	Two levels of casual acquaintances	**57719.1**	**0**
North community	Casual acquaintances	29235.7	2.1
	Constant companies + casual acquaintances	29238.6	5.0
	Two levels of casual acquaintances	**29233.6**	**0**
South community	**Casual acquaintances**	**46430.7**	**0**
	Constant companies + casual acquaintances	46431.5	0.8
	Two levels of casual acquaintances	46435.5	4.8

Table 2.5 The AIC values of the lagged identification rates. The best fitted model is shown in bold.

Regions	Model	AIC	△AIC
Taiwan population	Emigration/mortality	100138.1	61.3
	Emigration + reimmigration	**100076.8**	**0**
	Emigration + reimmigration + mortality	100107.7	30.9
North community	Emigration/mortality	25050.0	0.8
	Emigration + reimmigration	25050.0	0.8
	Emigration + reimmigration + mortality	**25049.2**	**0**
South community	Emigration/mortality	57900.6	5.2
	Emigration + reimmigration	**57894.8**	**0**
	Emigration + reimmigration + mortality	57897.0	2.2
Movements between the north and south regions	**Fully mixed**	**2743.3**	**0**
	Migration-full interchange	2744.8	1.5

(a)


120°0'0"E
120°20'0"E
120°40'0"E
24°50'0"N
24°40'0"N
24°30'0"N
24°20'0"N
24°10'0"N
24°0'0"N
23°50'0"N
23°40'0"N
23°30'0"N
23°20'0"N
N
Legend
Sighting position
10-m isobath
20-m isobath
km
0 5 10 20

(b)

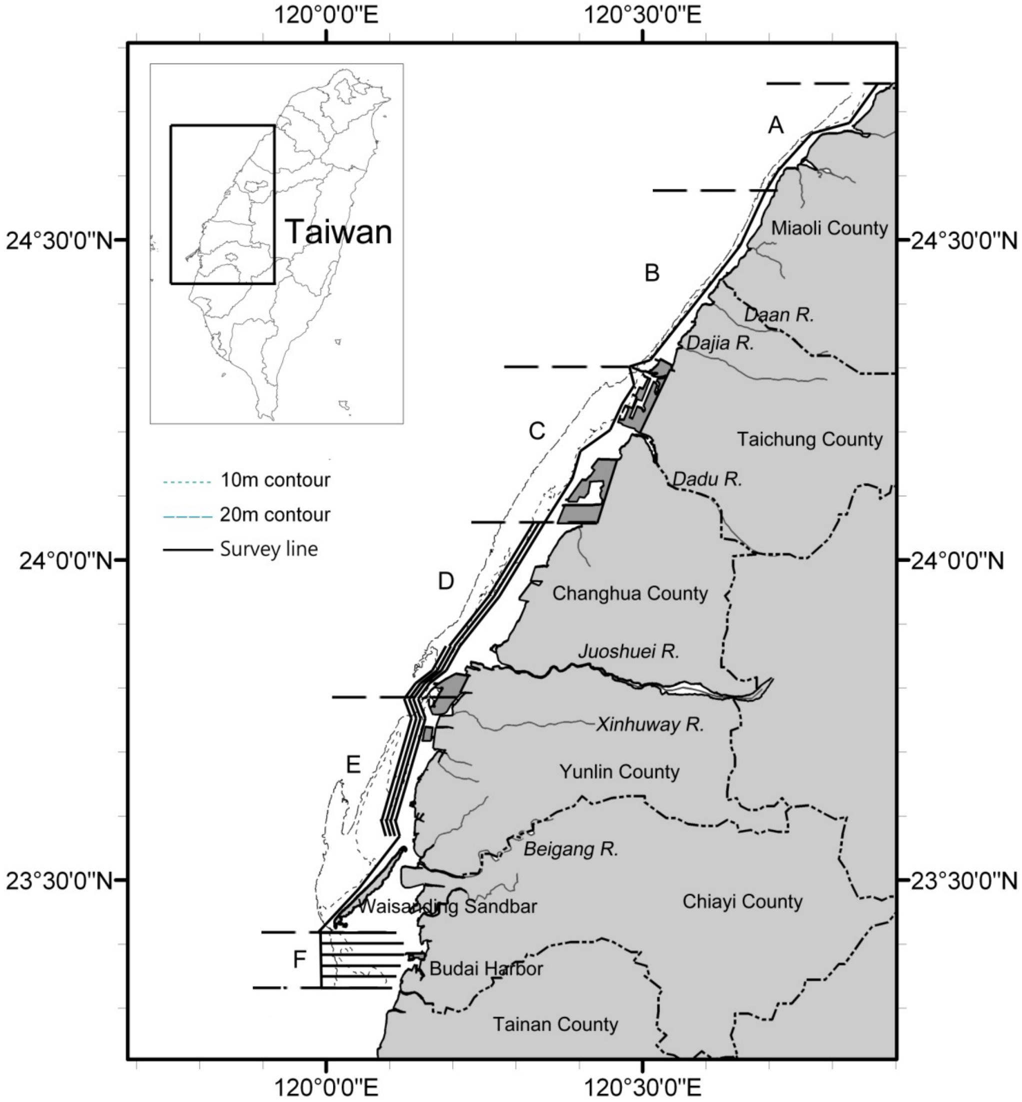


Figure 2.1 Survey area with (a) sighting position (n = 335) distribution of Indo-Pacific humpback dolphins off the west coast of Taiwan during July 2007 to November 2010; and (b) survey lines of this study. The north region contained Section A-C, the central region was Section D, and the south region included Section E and F. In 2007-2008, Section C, E, and F, were surveyed; in 2009, surveys were conducted throughout all sections; and in 2010, surveys were focused on dolphin-rich area, that is, Sections B and E.

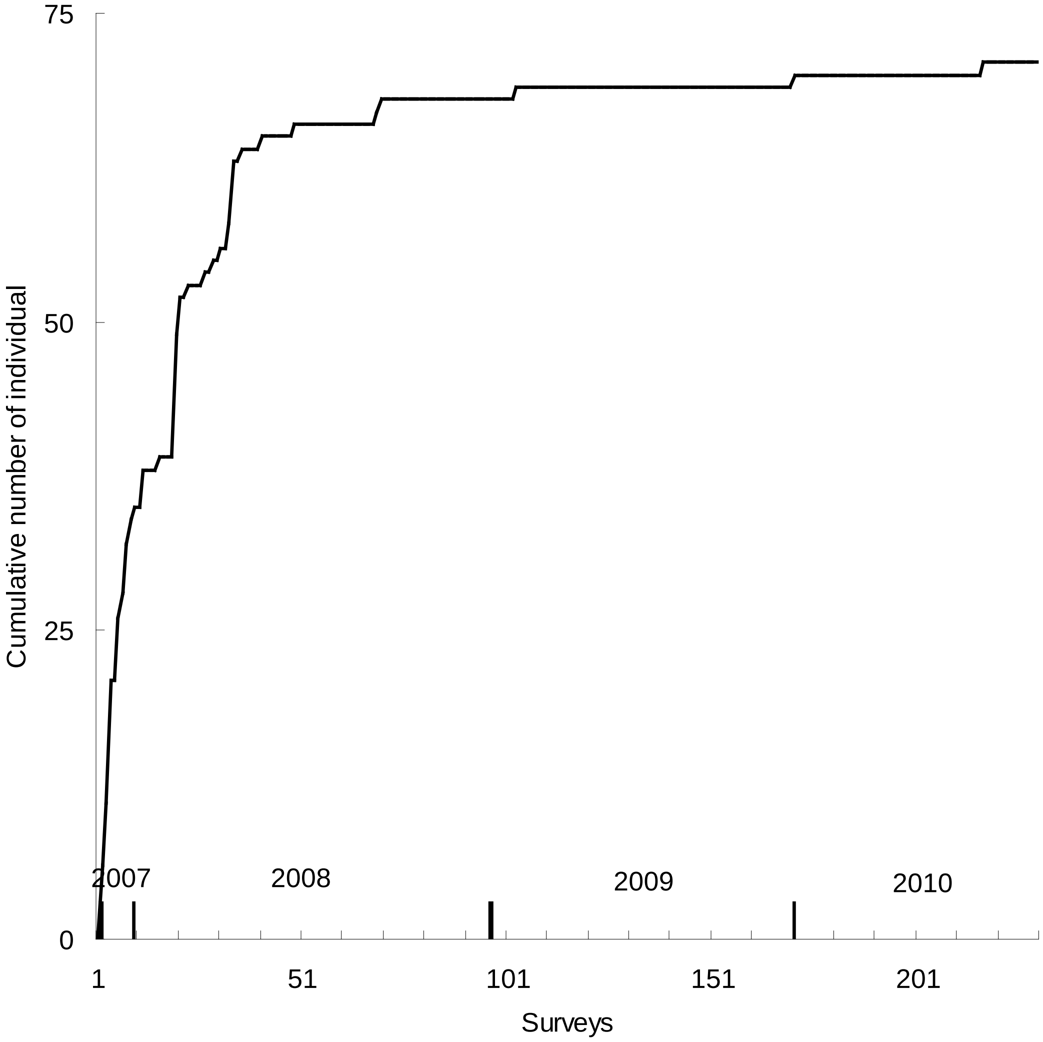


Figure 2.2 Cumulative number curve of Indo-Pacific humpback dolphins identified off the west coast of Taiwan waters from July 2007 to September 2010. The curve reached a plateau at 68 dolphins at the 69th survey in July 2008.

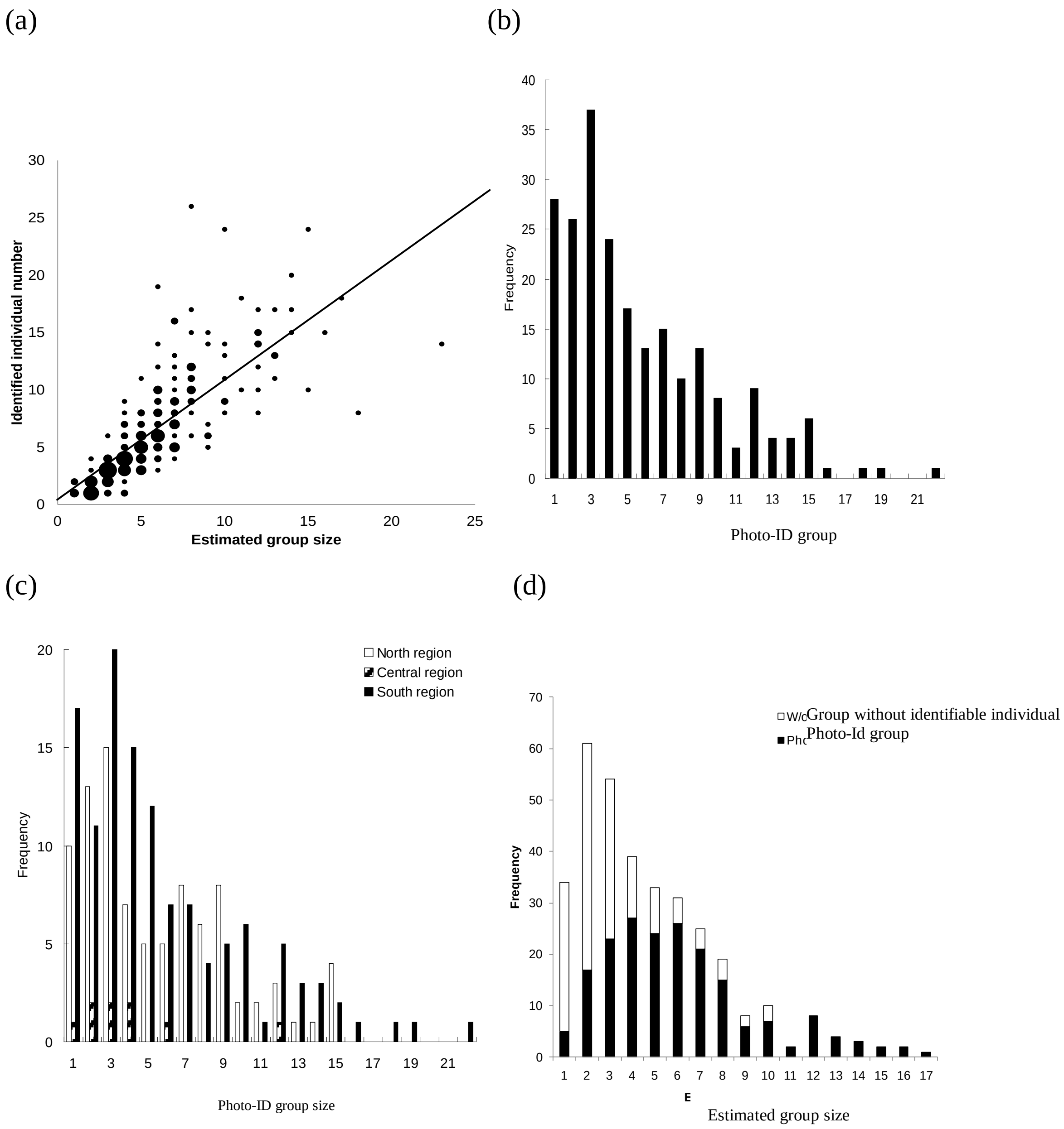
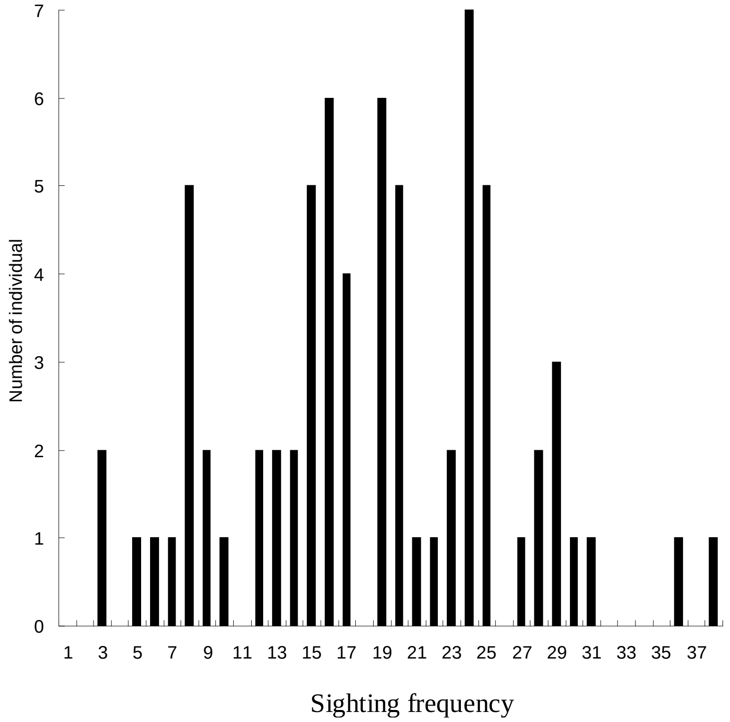


Figure 2.3 Group size. (a) The relationship between estimated group sizes by observations and identified individual numbers. The circle size represented the sample size (minimum, 1; maximum, 12). The diagonal line represented an ideal condition that the observation and photo-identification were the same. (b) Frequency distribution of group size (calves excluded) in the survey area. (c) Frequency distribution of group size (calves excluded) in three regions. (d) Frequency distribution of groups with (Photo-ID group) or without any identifiable individual.

(a)



(b)

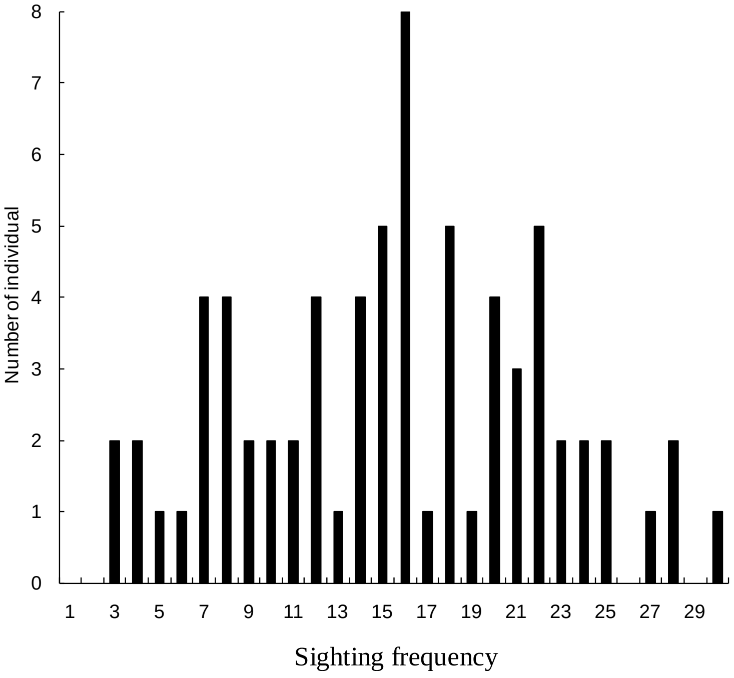


Figure 2.4 Distribution of individuals sighting frequency from (a) all photo-ID groups and (b) 75% photo-ID groups. There were 55 (77.5%) of cataloged dolphins sighted more than 10 times in 75% photo-ID groups.

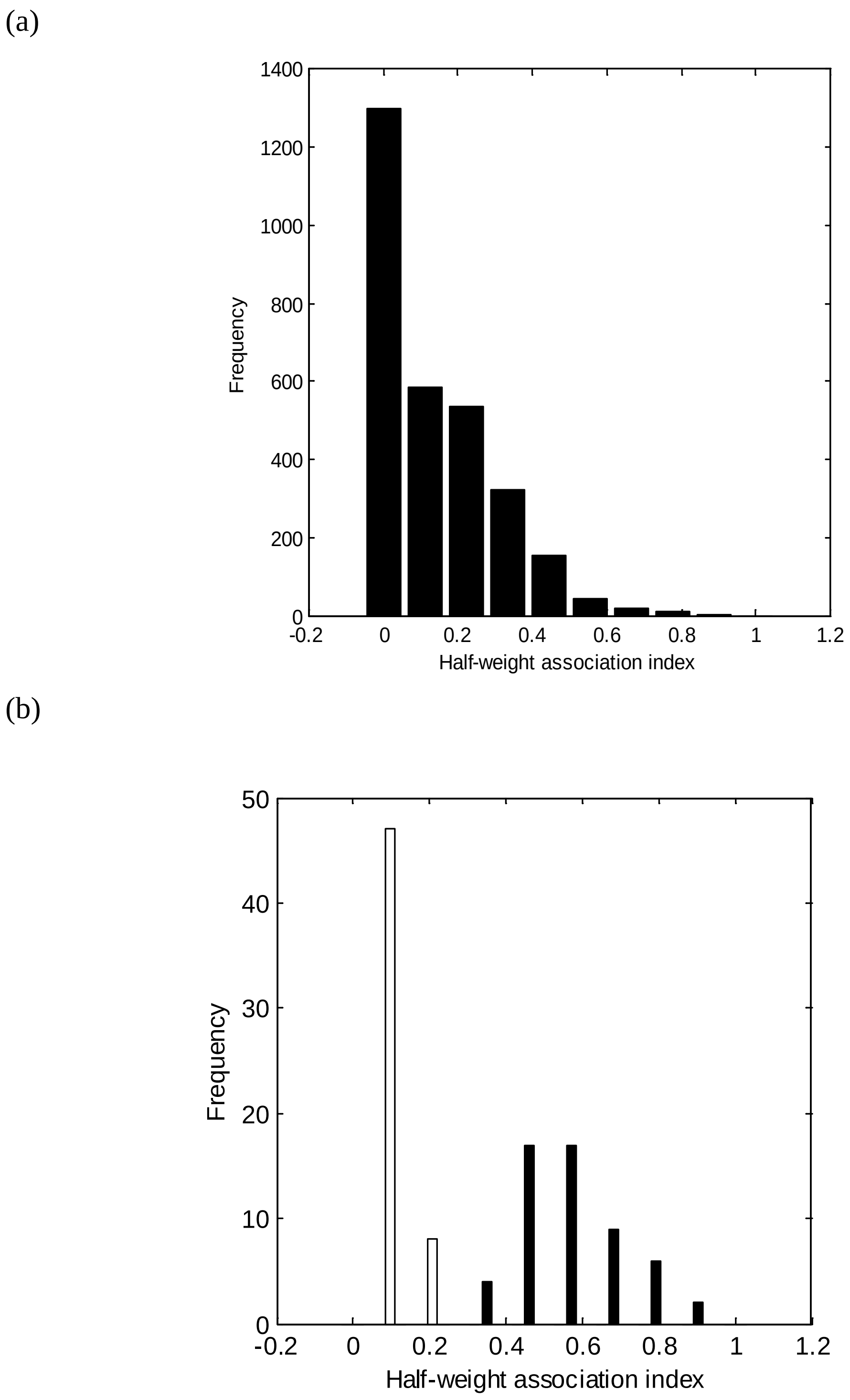


Figure 2.5 Frequency distribution of half-weight association index (HWI) for Indo-Pacific humpback dolphins in the western coast of Taiwan by (a) HWIs of all association bonds (mean = 0.14, SD = 0.03); and (b) mean (□) and maximum (■) HWIs by each individual. Note this HWI was only calculated for individuals sighted more than 10 times in 75% photo-ID groups (77.5% of all photographically catalogued individuals).

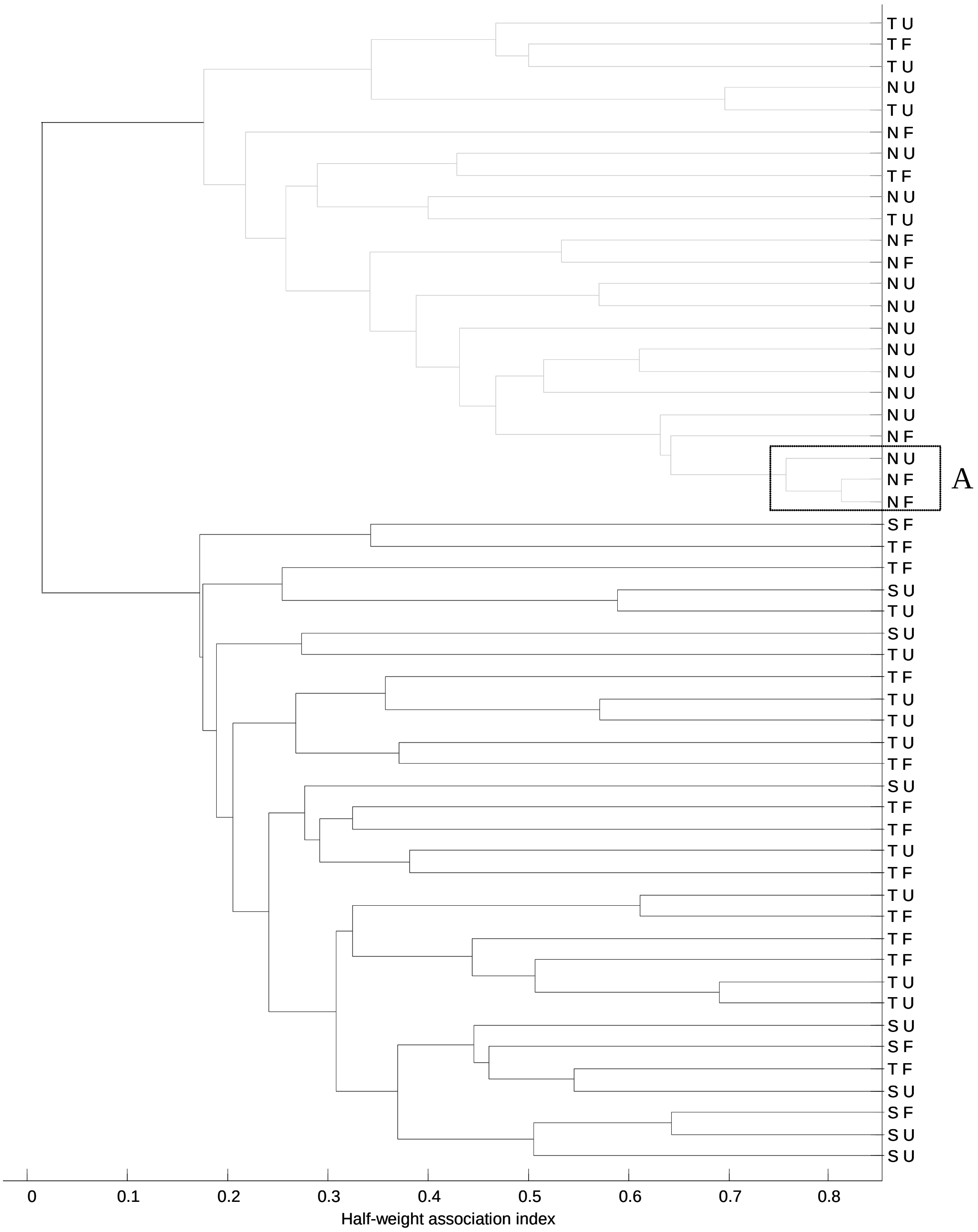


Figure 2.6 Dendrogram for the individual affinity of Indo-Pacific humpback dolphins in the west coast of Taiwan by hierarchical cluster analysis. Two major clusters were separated at HWI = 0.1722. The branches of highly-associated clusters are drawn at the end of the dendrogram. The sighting location ('N' for the north dolphin, 'S' for the south dolphin, 'T' for the transient dolphin) and sex ('F' for nursing females or 'U' for unknown sex dolphins) of each individual are represented. Unit A contained two females and an unknown sex adult dolphin. Only individuals sighted more than 10 times in 75% photo-ID groups were included (77.5% of all photographically catalogued individuals). The cophenitic correlation coefficient was 0.8991.

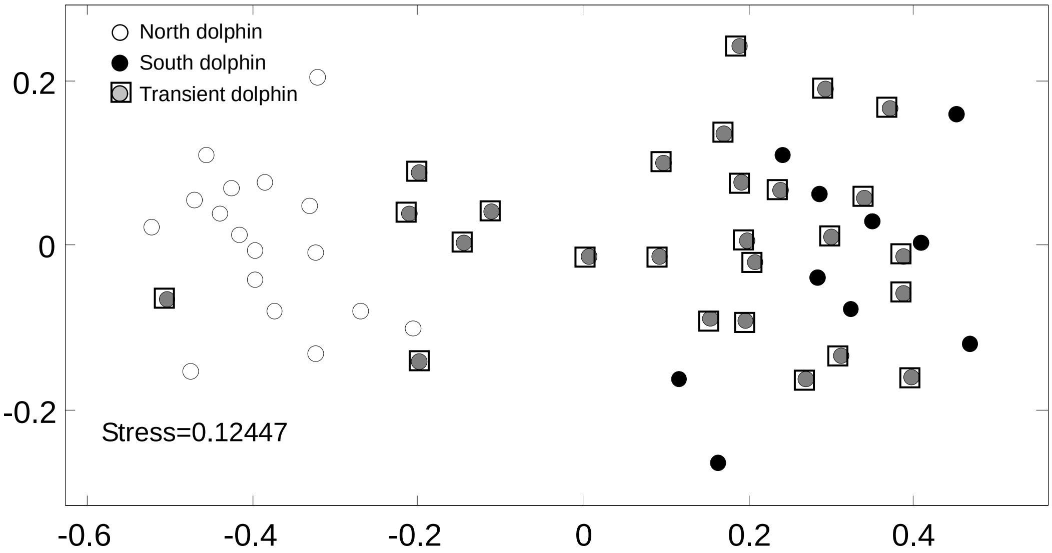
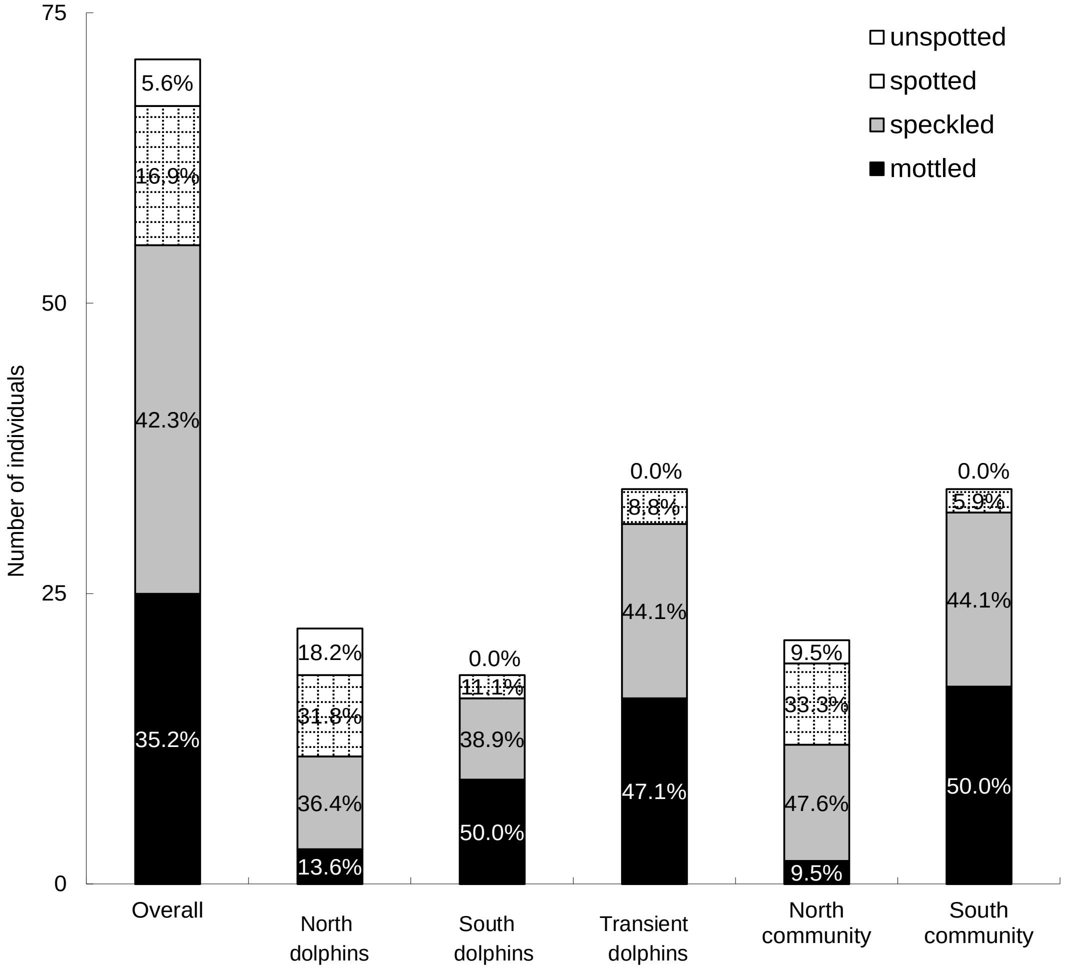


Figure 2.7 Nonmetric multidimensional scaling analysis showed that there were two clusters in this Indo-Pacific humpback dolphin population; two clusters positioned at the left and right sides in the figure. The distance between individual points reflected the closeness of their relationship; the greater the association index value a dyad had, the closer the dyad points in a non-metric multidimensional scaling figure were. Only individuals sighted more than 10 times in 75% photo-ID groups were included (77.5% of all photographically catalogued individuals).

(a)


75
50
25
0
Number of individuals
unspotted
spotted
speckled
mottled
Overall
5.6%
16.9%
42.3%
35.2%
North dolphins
18.2%
31.8%
36.4%
13.6%
South dolphins
0.0%
11.1%
38.9%
50.0%
Transient dolphins
0.0%
8.8%
44.1%
47.1%
North community
9.5%
33.3%
47.6%
9.5%
South community
0.0%
5.9%
44.1%
50.0%

(b)

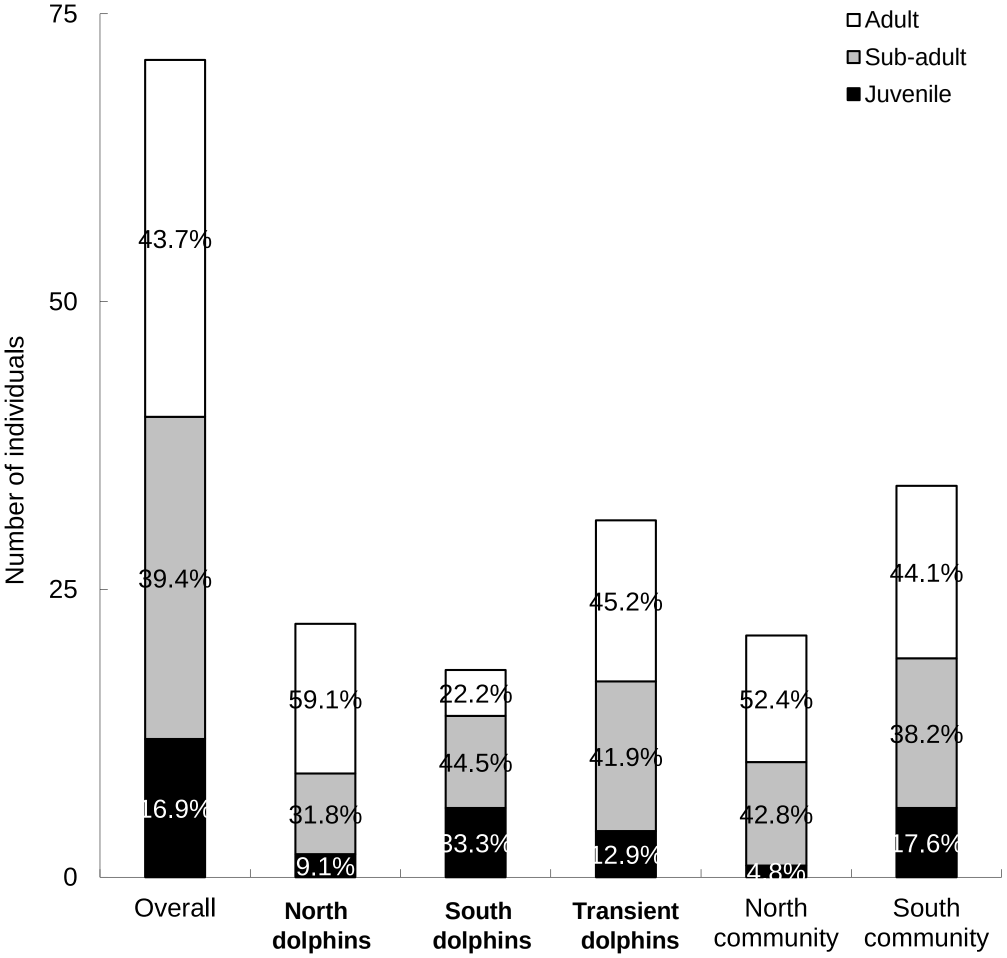


Figure 2.8 Dolphin compositions by (a) coloration stage; and (b) age stage compositions in different regions or communities. “Overall”, all cataloged individuals (n = 71); “north dolphins”, all dolphins sighted only in the north region (n = 22); “south dolphins”, all dolphins sighted only in the south region (n = 18); “transient dolphins”, all dolphins sighted in both regions (n = 31); and “north community” or “south community”, dolphins belonged to the north or south community conducted by hierarchical cluster and multidimensional scaling analysis (n = 23, 30). Percentages of each coloration/age stage were noted in columns.

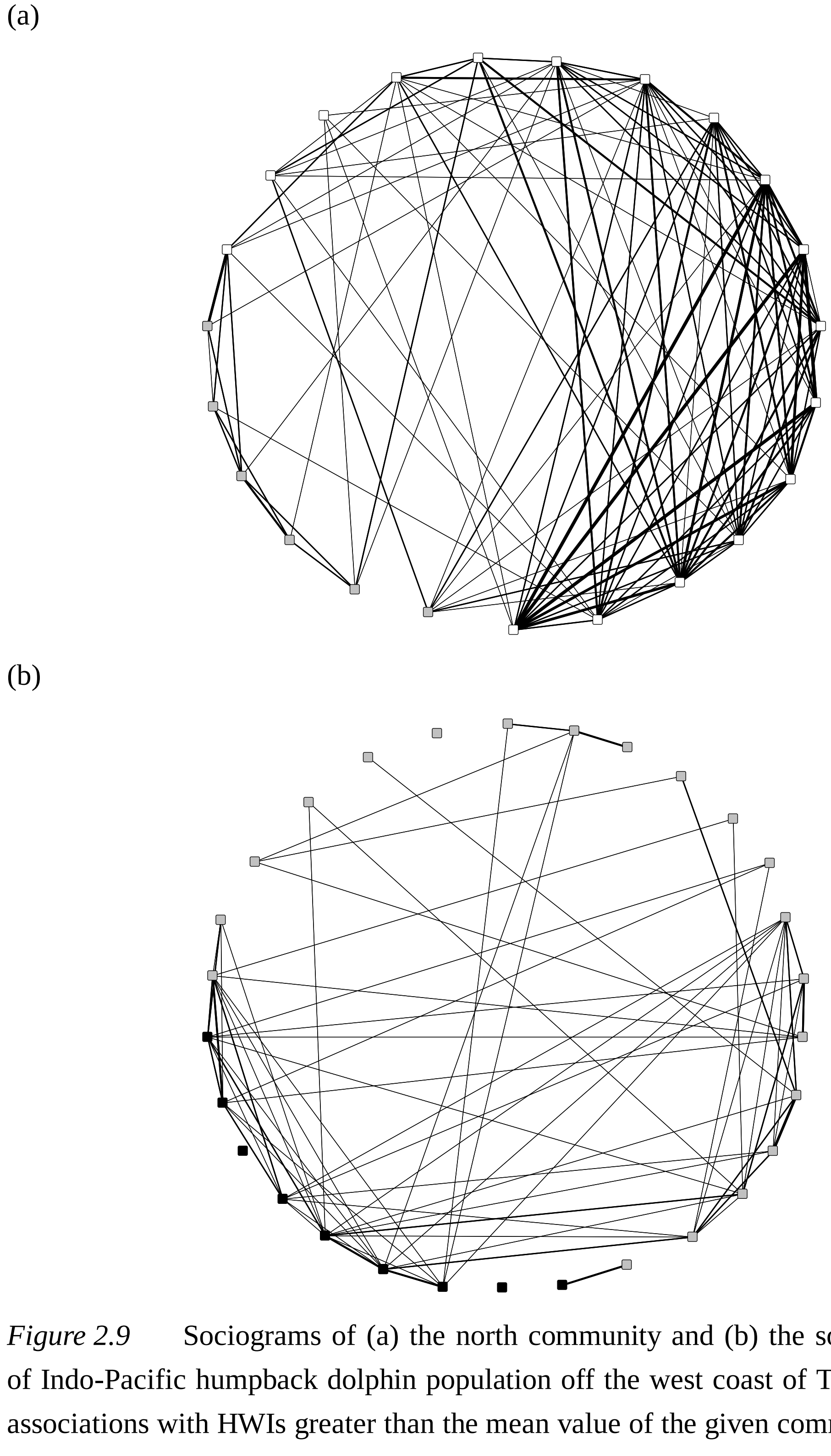


Figure 2.9 Sociograms of (a) the north community and (b) the south community of Indo-Pacific humpback dolphin population off the west coast of Taiwan. Only the associations with HWIs greater than the mean value of the given community (0.29 for the north community and 0.22 for the south community) were represented. The strength of relationship between individuals was demonstrated by the thickness of each connecting line. White squares, north dolphins; gray squares, transient dolphins; and black squares, south dolphins.

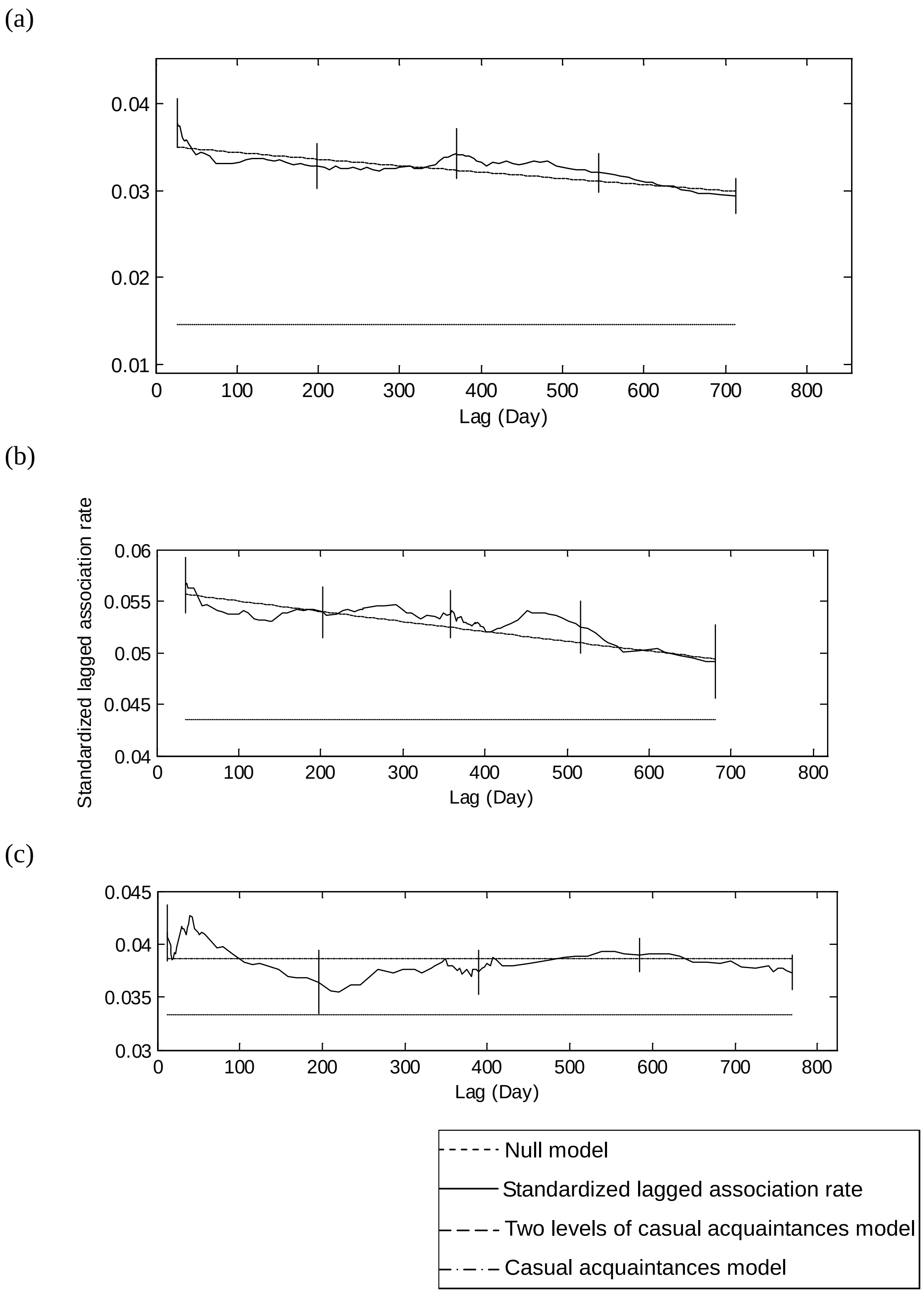


Figure 2.10 Standardized lagged association rates of (a) Indo-Pacific humpback dolphin population; (b) the north community; and (c) the south community. The jackknife error bars (vertical bars) were generally short, indicating those estimates were reliable. The non-random associations decayed with time that fitted the best with one or two levels of casual acquaintance(s) model.

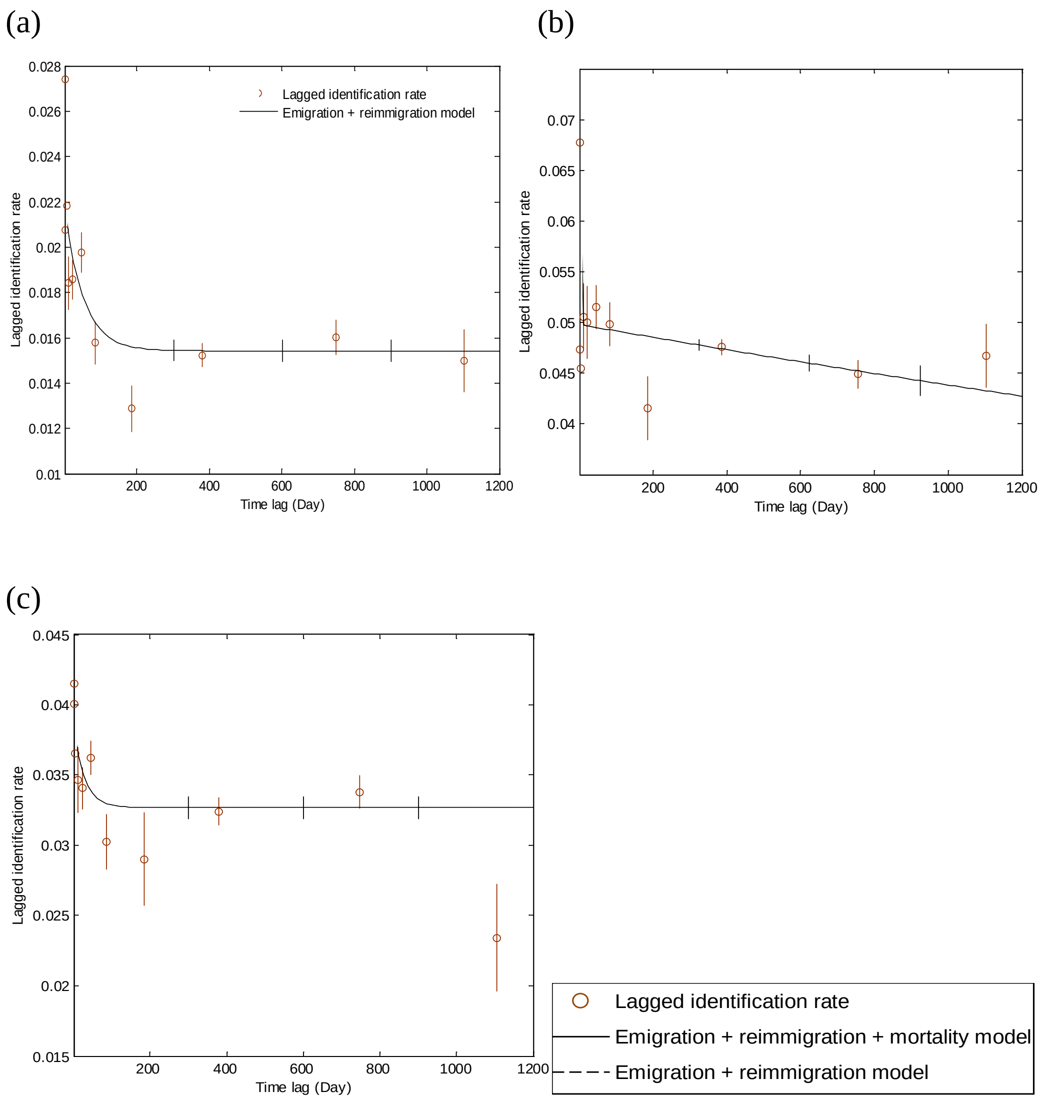


Figure 2.11 Lagged identification rate of (a) Indo-Pacific humpback dolphin population; (b) the north community; and (c) the south community. The vertical bars represented the bootstrap error bars. Those patterns were similar that indicated dolphins moved in and out frequently while some dolphins in the north community had low resighting frequency.

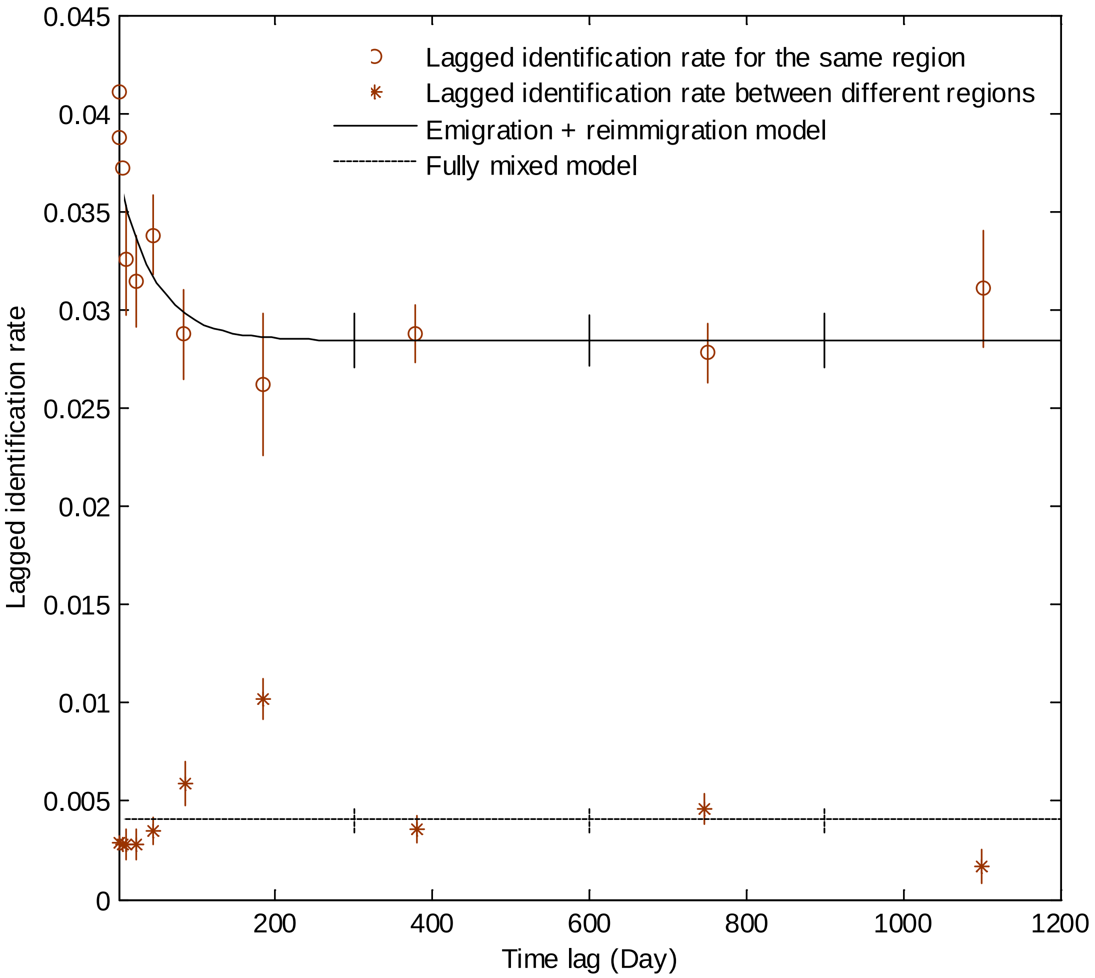


Figure 2.12 Lagged identification rate for between (asterisk) or inside (open circle) the north and south regions. The vertical bars represented the bootstrap error bars. The heterogeneous movement patterns were indicated by distinct model curves that dolphins preferred staying in a certain region. A raising peak indicated that the dolphins exhibited a variable movement pattern.

Chapter 3: Reproductive parameters of Indo-Pacific humpback dolphins off the west coast of Taiwan

ABSTRACT

Reproduction and mortality play an essential role in the trend of population dynamics and this information is important for wildlife conservation management. The aim of this study is to assess the reproductive dynamics of a critical endangered population of the Indo-Pacific humpback dolphin (*Sousa chinensis*) off the west coast of Taiwan. Based on 984 mother-calf pair photographs taken from 352 field surveys during 2007-2010, 22 reproductively active females and 27 calves were identified, resulting in a crude birth rate of 0.064 ± s.d. 0.037. Parturition occurs throughout the year, with a significant increase during spring and summer. To Age 1, the survivorship was 0.66 ± s.d. 0.20, the survival rate was 0.78 ± s.d. 0.39 and the recruitment rate was 0.090 ± s.d. 0.030, comparable to those reported for other populations in South Africa and Hong Kong waters, while the calving interval of 3.52 ± s.d. 0.28 years was longer than anticipated. Anthropogenic stressors affecting calf survival also require attention, as does a properly orchestrated management effort that a seasonal closure is recommended.

INTRODUCTION

The parameters of life history can furnish a basic understanding of the ecology of a species and are vital in considering management strategies (Crouse *et al.* 1987, Stolen and Barlow 2003). The reproductive parameters serve as a key part of this information, such as gestation period, calving interval, and weaning age, which can determine the species' life strategies and patterns of population growth (Huang *et al.* 2009, 2011). Understanding the pattern of population growth in particular is essential for predicting the fate of a vulnerable population, including the unique population of Indo-Pacific humpback dolphins (*Sousa chinensis*) inhabiting the western coastal waters of Taiwan. This population is listed by the IUCN under the category of Critically Endangered status (Reeves *et al.* 2008) since its population size has been estimated to be 75-80 (Yu *et al.* 2011). Unfortunately, in addition to long-term overfishing, this population also has to face the increased anthropogenic threats of numerous industrial programs either planned or proposed for the coastal area critical to their population persistence. Before a population dynamic trend can be simulated and predicted, information on life history parameters should be continuously collected and monitored. Estimation of reproductive parameters can serve as the first step towards a better understanding of this vulnerable species.

Cetaceans' reproductive parameters are usually accessed via stranded or by-caught specimens, on the anatomical characteristics of their reproductive organs (*e.g.*, the size of testes, the numbers of corpora lutea or corpora albicans in ovaries; Perrin and Reilly 1984). For captive cetaceans, reproduction status can be checked directly by diagnostic tools such as ultrasonography or haematological examinations (Brook *et al.* 2004). However, samples of carcasses are often not enough in some study area, and some cetacean species are not suitable to be captive, non-invasive methodology, *i.e.*, long-term observation on wild populations based on photographic identification, was becoming a popular and effective tool for studying the reproductive dynamic of cetaceans in recent years (Hammond 1990).

Many studies had attempted to access the reproductive parameters of Indo-Pacific humpback dolphins, either by examining stranded individuals (*e.g.*, Jefferson 2000, Jefferson *et al.* 2011) or interpreting from photo-identification data collected during field surveys (*e.g.*, Karczmarski 1999, Guissamulo and Cockcroft 2004, Chang *et al.* 2010). Based on the examination of 120 stranded specimens from Hong Kong waters, Jefferson *et al.* (2011) reported the seasonal calving peaks estimated by fetal and neonatal specimens, and indicated the relationship between coloration and age-stage by age-determination based on the teeth growth layer groups (GLG).

Alternatively, for those populations of Indo-Pacific humpback dolphin, where dolphin carcasses are rarely salvaged from the coast, photo-identification becomes an effective alternative approach to study their reproductive dynamics. For example, derived from field observation in Xiamen waters, Wang (1999) suggested a mating season from April to June and the gestation period estimated to be 10-12 months. Comparable information was also reported for the population off KwaZulu-Natal, South Africa (Cockcroft 1989). Photo-identification was later used to determine a calving seasonality in Algoa Bay (Karczmarski 1999), Maputo Bay (Guissamulo and Cockcroft 2004), and Hong Kong waters (Jefferson 2000, Jefferson *et al.* 2011). Field surveys with photo-identification revealed that the calving interval of Indo-Pacific humpback dolphins can range between 3-5 years (Karczmarski 1999, Jefferson *et al.* 2011), and calf might accompany its mother for 3-4 years or more (Karczmarski 1999). Also, other reproductive parameters such as birth rate, recruitment rate, and calf mortality could be estimated by photo-identification (Guissamulo and Cockcroft 2004).

Our knowledge on the reproductive parameters of Indo-Pacific humpback dolphins in Taiwanese waters remains very limited. As this population was newly published (Wang *et al.* 2004) and only a few badly rotten specimens salvaged from the coasts were available, there were not enough data for a meaningful assessment of their reproductive parameters. Therefore, this study aims to investigate the reproductive dynamics of Indo-Pacific humpback dolphins off the west coast of Taiwan by profiling the demographic status of nursing females and analyzing the reproductive parameters based on datasets produced from photo-identification analysis.

METHODS

Study area

This study was conducted along the coast of western Taiwan from the Miaoli County in the north (N 24°44’0” E 120°50’0”) to the Chiayi County in the south (N 23°22’0” E 120°00’0”, Figure 3.1). The study area covers what is understood as the Indo-Pacific humpback dolphins’ preferred habitat that lies within close proximity to the shore (2.5-10 km) in waters less than 15 m deep.

Survey procedures

Systematic boat surveys during daytime hours (7 am-4 pm) under steady weather conditions (Beaufort scale < 3) were conducted along the west coast from the Miaoli

County to Chiayi County (Figure 3.1) between February and December (mostly from May to September) in 2007 through 2010 (see Table 2.1).

The survey boat traveled at a constant speed of 6-8 kt following planned survey lines (Figure 3.1). Three to five observers (of them two to three were also photographers) were on board to observe dolphins with either binoculars (8 X 30, 7 X 50) or unaided eyes. Date and location (via global position system, GPS) of sighting were then recorded during surveys. Perpendicular photographs were taken by digital cameras (CANON, OLYMPUS, and PENTAX) with vari-focal lenses (70-300 mm) or a fixed focal 400mm length lens.

Quality (Q) of dolphin images was scored on a range from Q1-100 (derived from Friday *et al.* 2000 and Karczmarski *et al.* 2005), based on clarity of focus, color contrast, shot angle, and the coverage of full dorsal fin. Photographs with a Q score over Q50 were used for further analysis.

Dolphin identification, age, and coloration

Non-calf dolphins were identified individually according to at least three distinctive characteristics, such as notches on the dorsal fin or spots on the body. It was difficult to apply the same criteria to the identification of calves because they seldom carried enough identifiable physical characteristics (*i.e.*, scars or spots). The tight maternal connection and fast somatic growth during the lactation period of a mammalian life history, however, could provide an alternative method to identify individual calve indirectly. In this study, individual calves were identified by (1) its consistent association with a particular and identifiable adult (thus forming a mother-calf pair) and (2) a noticeable body size increase in subsequent sightings.

A mother-calf pair in a photo is defined as two dolphins that swam in an “echelon” position (*e.g.*, Gubbins *et al.* 1999); and when either of the following two scenarios were seen: (1) the larger dolphin (“mother”) is a spotted or unspotted adult, and the body of the smaller dolphin (“calf”) is of a gray to dark gray color, with a body length less than 3/4 of adult size; or (2) a mottled/speckled-stage mother is seen accompanied by a calf in more than two consecutive encounters.

The photographs of the mother-calf pairs were also used to inform the month of birth and age of the calf by evaluating its body color, presence of neonatal characteristics (clear or weak fetal-fold marks, a flaccid or taut dorsal fin, or the body shape posterior to the blowhole), and its relative size to adult dolphin(s) present in the same photograph (examples see Figure 3.2). The estimated birth month and the age of each calf were confirmed with Dr. Leszek Karczmarski of the University of Hong Kong.

The color pattern of non-calf dolphins also informs the status of sexual maturation in Indo-Pacific humpback dolphin (Jefferson 2000, Jefferson *et al.* 2011). Beside calf class, four other coloration stages are distinguished by modifying those used by Jefferson (2000): mottled-stage, speckled-stage, spotted-stage, and unspotted-stage. A mottled-stage dolphin is defined as a gray dolphin with light spots. A speckled-stage dolphin is defined as a light pink dolphin with many dark spots on its body (50% or more of their body area). A spotted-stage dolphin has spots on 50% or less of its body. An unspotted-stage dolphin is pinkish color and has few or no spots. The dolphins in spotted and unspotted stages were defined as adults (Jefferson 2000, Jefferson *et al.* 2011), while the dolphin in mottled and speckled stages were as defined as the sexually mature ones of the mother-calf pairs.

Reproductive parameter estimation

Calving interval and calving seasonality

Calving interval and calving seasonality were evaluated from the sighting dates of each mother-calf pairs during the four-year survey period. The calving interval is defined as the time period (in years) between the estimated birth months of the first successive calf to the next calf (Clapham and Mayo 1990).

To determine the seasonality of neonate occurrences, a year was divided into four seasons based on the mean sea surface temperatures (SST, as in Karczmarski *et al*. 1999). Summer was defined as the four continuous months with the highest mean SST (from June to September, 28.6-29.8 ℃); winter was defined as the four continuous months with the lowest mean SST (from December to March, 18.1-20.9 ℃). Spring was defined as the months when the mean SST increased rapidly between winter and summer (April and May, 24.5-26.9 ℃); and the autumn was defined as the months when mean SST decreased rapidly between summer and winter (October and November, 23.8-26.0 ℃). SST records were obtained from the meteorological station in Hsinzhu, Taiwan (Taiwan Central Weather Bureau, 1997-2009). The calving seasonality was defined as dolphins giving more births in a particular season (Caughley 1977b).

Crude birth rate

A yearly crude birth rate (*CBR*) was defined as the proportion of neonates in the population of a given year (Clapham and Mayo 1990), and was calculated as the ratio of the total number of neonates (n) to the sum of calves (equal to the number of mother-calf pairs, mc) and the total of individuals (i) observed in a given year x, x =

2007, 2008, 2009, 2010:

$$CBR_x = \frac{n_x}{mc_x + i_x}$$ (Clapham and Mayo 1990) [1].

Calf survival rate and calf survivorship

A calf's survival period was estimated as the time interval between the inferred month of birth to the month of last sighting of a calf (Krebs 1999). The calf survival rate ($l_{x,y}$) in a given year x to the age y was defined by:

$$l_{x,y} = \frac{s_y}{n_x}$$ [2],

where s_y = the number of calves surviving to the specific age y, y = 0.5, 1, 2, 3 and n_x = the number of calves born in the year x. The value of $l_{x,0}$ was defined as 1 (Stolen and Barlow 2003). The age-specific calf survivorship ($p_{x,y}$) was estimated by:

$$p_{x,y} = \frac{l_{x,y+1}}{l_{x,y}}$$ (Moore and Read 2008) [3].

Recruitment rate

The recruitment rate, *RR*, was also estimated; although recruitment is technically affected by (1) numbers of yearling calves (Age 1) in the population (s_1) and (2) immigrates from other populations. However, because no matched individual was found, it was assumed that no individuals moved from the neighboring populations

(Kinmen, Xiamen, Hong Kong waters and Pearl River Estuary) into the Taiwanese population, as also suggested by Reeves *et al.* (2008) and Wang *et al.* (2008). Therefore, the recruitment rate in the year x (RR_x) was calculated as:

$$RR_x = \frac{s_1}{EF_x} \qquad [4],$$

where EF_x = number of non-calf females in a given year (Caughley 1977a, Taylor *et al.* 1987). Assuming an equal sex ratio, EF_x is one half of all photo-identified dolphins.

Weaning age

Weaning is a period when calves decrease the intake of milk and increase the amount of solid food (Martin 1984), which is also a transitional period leading to calf independence. In this study, weaning is defined as when the consistently strong near-neighbor associations between a nursing female and her calf decreases to a value that corresponds to the mean value of association in the community. The "near-neighbor association" is defined as two individuals captured on the same photographic frame as they move in the same parallel direction, where the dorsal fins of the animals are less than one body-width apart (when next to each other), and less than one body-length apart (when behind the other).

The strength of the mother-calf association in each age category was measured with the half-weight index (HWI, Dice 1945) and with the use of SOCPROG 2.4 (Whitehead 2009) in Matlab 7.1 (The MathWorks, Inc., 24 Prime Park Way, Natick, Massachusetts, USA):

$$\text{HWI} = \frac{x}{x + \frac{y_M + y_c}{2}} \qquad [5],$$

where x = number of groups containing both mother and its calf, y_M = number of groups in which only mother was identified, y_C = number of groups in which only calf was identified. Only the calves sighted more than 15 times in total and not sighted less than 10 times in any given two years were used to estimate the weaning age.

RESULTS

From 2007 to 2010, a total of 64,109 photographs were taken from 352 boat surveys. Out of all photographs, 1,330 framed mother-calf pair(s) while 984 were of a quality level (Q score > Q50) acceptable for use to identify parental relationships.

A total of 22 mothers and 27 calves were cumulatively identified during the survey period (Table 3.1). Among the 22 identified mothers, more than half (54.5%) of them were in speckled stage (Figure 3.3a). Among the reproductive individuals of varied coloration stages, the highest proportion of breeding individuals was observed in the unspotted-stage (50%, Figure 3.3b).

Among 22 mothers, 10 of them were sighted only in the north or south regions (n = 6, 4), remaining 12 mothers were transient dolphins (see Chapter 2); however, they stayed in only one region with three cases sighted in another region (Table 3.1).

Of the 27 calves, estimates of the month of birth and age were made for 17 calves (Table 3.1), while estimates were not obtainable for the other 10 calves for a lack of either distinguishable neonatal features (seven calves) or photograph images of an acceptable quality (three calves). A total of 13 calves (76.5%) were sighted more than once and 14 calves (82.4%) were first sighted when they were neonates (Age 0.5, Table 3.1).

Calf survival rate and calf survivorship

Calf survival rates ($l_{x,y}$) and survivorships ($p_{x,y}$) for four different age groups are listed in Table 3.2. The majority of calves survived the first 6-months of their neonatal life; four neonates, calves of mother #19 and #21, and two calves of #15 in 2007 and 2009 disappeared within a few months following their birth, although their mothers were re-sighted. These four neonates appeared to die before reaching 6-months of age (Table 3.1). In general, calf survival rates ($l_{x,y}$) decreased with age; the highest survival rate was at Age 0.5 (0.77 ± s.d. 0.25, range = 0.50-1.00) and the lowest (0.47 ± s.d. 0.19, range = 0.33-0.60) at Age 3 (Table 3.2a). A similar trend was observed for the calf survivorships, with the highest survivorships ($p_{x,y}$) in Age Group 0.5-1 ($p_{x,0.5-1}$ = 0.89 ± s.d. 0.19, range = 0.50-1.00) and the lowest one in Age Group 2-3 ($p_{x,2-3}$ = 0.62 ± s.d. 0.18, range = 0.50-0.75, Table 3.2b). Calves born in spring and summer had significantly higher survival rate at Age 0.5 and 1 than those born in autumn and winter (*t*-test, *p*-value < 0.5, Table 3.2c). The calf survivorship showed a similar pattern of higher survivorship for calves born in spring and summer than in autumn and winter (Table 3.2d). These results indicated that the newborn calves were the most vulnerable during their first year of life, and the calves born in autumn and winter were more vulnerable than those born in spring and summer.

Crude birth rate (CBR)

For 2007 through 2010, the *CBR* estimates was 0.064 with wide variation (s.d. = 0.037, range = 0.036-0.114, Table 3.3). However, the *CBR* estimate for 2007 was particularly high (0.114), which could result from a low survey effort and a low total number of identified individuals (see Chapter 2). Excluding the data of 2007, the mean *CBR* estimate would be 0.048 ± s.d. 0.020 (range = 0.036-0.071).

Calving interval and calving seasonality

Five mothers (22.7%) were seen with their second calf during the study period

(Table 3.1); however, one of them (1.42 years) was excluded from the estimation of calving interval because her first calf disappeared before reaching the general weaning age (3-4 year-old, see Karczmarski 1999 and this study below). The average of calving interval estimated from the four mothers was 3.52 ± s.d. 0.28 years (range between 3.25-3.92 years).

Birth months of the 27 calves showed that the breeding events of Indo-Pacific humpback dolphins off the west coast of Taiwan occurred year round (Figure 3.4). However, the number of calves born in spring or summer was significantly higher (64.7%, $n = 17$, χ^2-test, $p < 0.05$) than in autumn and winter (Table 3.4, Figure 3.4), indicating a significant calving seasonality.

Recruitment rate

On average, there were 2.5 ± s.d. 1.29 calves surviving to Age 1 every year (ranging from 2 to 4, Table 3.2). The range of recruitment rates was between 0.062 and 0.121 (0.090 ± s.d. 0.030, Table 3.3).

Weaning age

Weaning age was estimated only from data pertaining two mother-calf pairs. The near-neighbor half-weight indices of two mother-calf pairs decreased with the age of the calves (Figure 3.5) and reached numeric values similar to those of the mean community values (HWI = 0.29 ± s.d. 0.07 and HWI = 0.22 ± s.d. 0.05 for the north and south communities, respectively, see Chapter 2) at Age 3 for the calf of mother #10 (HWI = 0.20) and at Age 4 for the calf of mother #1 (HWI = 0.33). Therefore, weaning of the Indo-Pacific humpback dolphin calves in the waters off western Taiwan can be estimated to take place when they are 3-4 years old.

DISCUSSION

Reliability of parameter estimation

Directly investigating the mother-calf dynamics of marine mammals in the field is often less efficient and informative because of some uncontrollable difficulties. The ability to detect the dolphins, especially the mother-calf pairs, is highly restricted by the weather condition during field investigation. It is almost impossible to conduct boat surveys during the winter season off coastal Taiwan due to common extremely hazardous weather conditions (Beaufort state usually > 5), resulting in skewed and uneven survey effort and increased uncertainty over the trend in mother-calf dynamics during the winter months (*within-community sampling error*, Cairns and Schwager 1987). Furthermore, photographing and observing mother-calf pairs is more difficult than other adult dolphins, as the mother-calf pairs tended to avoid vessels (*e.g.*, Nowacek *et al.* 2011, Tseng *et al.* 2011), and mothers often displayed a calf-protecting behavior that tended to keep their calves aside away from the vessel (Karczmarski *et al.* 1997). The surfacing time of the calf also seemed less predictable than adult dolphins (personal observation). All of these behavioral factors reduce the chance to produce qualitative photographs of the mother-calf pairs for further analysis (*within-group sampling error*, Cairns and Schwager 1987). While these factors are beyond control and can hardly be eliminated by the investigation design, they could increase uncertainty in estimation of important reproductive parameters.

Among those reproductive parameters, the number of neonates and the length of calf survival time are most crucial to the present study since the estimation of most of other parameters were based on these two values. The number of neonates might be underestimated if some calves, especially those born during winter, died prior to being sighted. An inaccurate count of the neonates could then lead to an underestimate of the crude birth rate. If such case occurred often, the calving seasonality of Indo-Pacific humpback dolphins off the west coast of Taiwan could be less significant than presented. Occasionally, some mother-calf pairs were not photographed in some group sightings due to uncontrollable difficulties mentioned above, which might result in an underestimation of calves at certain ages. This uncertainty will also lead to underestimate of recruitment rate of calves and overestimates of the calf survival rate and the calf survivorship. On the other hand, the calving interval and weaning age were free from the influences of the uncertainty since those two estimates were based on the presence-only identified history.

Although some uncertainty could be involved, the presented crude birth rate of 0.06 ± s.d. 0.037 (or 0.048 ± s.d. 0.020 if 2007 data were excluded) relatively robust compared to the estimate for the same species in Maputo Bay based on data of a two-year study (0.11 ± s.d. 0.04, Guissamulo and Cockcroft 2004). Considering the published estimates of bottlenose dolphins (*Tursiops aduncus*) around Mikura Island (0.07 ± s.d. 0.02, Kogi *et al.* 2004) or at Port River Estuary (0.064 ± s.d. 0.05, Steiner and Bossley 2008) for their phylogenetic, morphological and ecological similarity, the presented crude birth rate of Taiwanese Indo-Pacific humpback dolphin population indicates a comparable result. Other parameters, including calf survivorship and the recruitment rate, obtained from this study are also within a comparable range of other reports, *e.g.*, $l_{x,0.5}$ of 0.53-0.61 for Indo-Pacific humpback dolphins (Guissamulo and Cockcroft 2004[1], Jefferson *et al.* 2011) and $l_{x,1\text{-}3}$ of 0.63-0.80 for bottlenose dolphins

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[1] Minimum calf mortality rate (q, $\frac{death_{0.5}}{birth\ number}$) = 0.47; maximum calf survivorship = 1 - q

(Wells and Scott 1990[2], Mann *et al.* 2000[3], Stolen and Barlow 2003); the *RR* of 0.03 for Indo-Pacific humpback dolphins (Guissamulo and Cockcroft 2004) and 0.096 for bottlenose dolphins (Wells and Scott 1990[4]). In contrast to the parameters described above that are sensitive to neonate estimates, the estimated calving interval (3.52 ± s.d. 0.28 years in this study) is based on presence-only data and thus free from uncertainties over the compared values. Our estimate is within the range of estimates for the Algoa Bay population (3-4 years, Karczmarski 1999) and is comparable to the estimate for the Hong Kong population (5.22 ± s.d. 3.98 years, Jefferson *et al.* 2011). This consistence indicates that, despite of some uncontrollable difficulties, the presented estimated parameters are still highly representative and are useful for policy-making decisions and conservation management of the Indo-Pacific humpback dolphin population off the west coast of Taiwan.

Recommendations for conservation measures

Evaluation of population sustainability as well as the effectiveness of conservation measures relies considerably on the estimates of population trends

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[2] Annual survival rate = $\dfrac{1-\dfrac{\sum death}{\sum survey\ number}}{365.26}$ (DeMaster and Drevenak 1988).

[3] Minimum calf mortality rate (q, $\dfrac{death_1}{birth\ number}$) = 0.29; maximum calf survivorship = 1 - q

[4] Recruitment rate = $\dfrac{Number\ of\ calf\ surviving\ to\ Age\,1}{identified\ individual\ number + neonate\ number}$

(IUCN 2001). These estimates provide information of changes in population size (*e.g.*, Chaloupka *et al.* 1999) and then reliable forecast for the outcomes of a given population (Taylor *et al.* 2007). However, the standard methods to estimate population trends, either by analyzing changes in historical abundance (*e.g.*, Chaloupka *et al.* 1999) or via standard life-table analysis (*e.g.*, Dans *et al.* 2003), often require long years of investigation or extensive specimen collection to reach enough conclusive power (Gerrodette 1987, Thompson *et al.* 2000, Taylor *et al.* 2007). These methods are not suitable for studying the Taiwan Indo-Pacific humpback dolphin population due to the short period of time of its identification and few carcasses from stranding or by-catch. The photo-ID analysis, requiring relatively fewer years of investigation, is an alternative approach to population trend estimates by studying the survival as well as breeding and calving of a species (Stevick *et al.* 2003, Currey *et al.* 2009, Verborgh *et al.* 2009). Applying the general life history parameters of Indo-Pacific humpback dolphins (Karczmarski 1999, Jefferson *et al.* 2011), the estimated population growth rate could be -0.0017 ± s.d 0.0022, assuming that the adult survival rate was 0.95 or the adult survival rate, to exceed 0.960 (S.-L. Huang personal communication). After this study on the calf survival rate of the Taiwan Indo-Pacific humpback dolphin population, the next important study is to estimate the survival rates of adults, which further informs population trends.

Before the survival rates of adult and hence the population trend estimate are available, however, precautionary conservation should be implemented for this vulnerable population of Indo-Pacific humpback dolphins off the west coast of Taiwan. As indicated by this study, the calf survivorship during the first year of life according to the equation [4] is crucial for the recruitment rate. A reduction in calf survivorship will reduce the population's recruitment rate, which, in turn, will decrease population growth rate. Effective management that leads to increase calf survivorship or reduce calf mortality will be the first step towards sound conservation measures for this Indo-Pacific humpback dolphin population.

In this study, the annual counts and survivorships of new-born calves show significant seasonality that more calves were born and survived during the warmer spring-summer season than the colder autumn-winter season. This seasonality trend may correspond to the seasonal variance of some factors, for example, dolphin's prey abundance. An ecological activity that is highly synchronized to the calving seasonality of Indo-Pacific humpback dolphin comes from the annual migrations of Indo-Pacific humpback dolphins' preys, migrating into (Chen and Shao 2011) and reproducing (see in Chen and Shao 2011) at inshore waters during the warmer spring-summer season. The influx of prey resources can be especially essential for the lactating mothers who need to meet the extraordinarily high energetic requirements of lactation (Yasui and Gaskin 1986, Oftedal 1997, Lockyer 2007, Huang *et al.* 2009).

The resource competition between Indo-Pacific humpback dolphins and coastal fisheries can be high as they both aim to similar target preys (Ko 2011, master thesis). Furthermore, recent study on the movement of Indo-Pacific humpback dolphins shows that a calf-carrying female dolphin tends to utilize within a confined area. The potential resource competition between coastal fishery and humpback dolphins can therefore be stressful to nursing females. It may take mothers longer time to forage for food yet without success to meet the high energetic needs of lactation.

As a result, a season-specific closure of coastal fisheries, including trawler and gillnet fisheries, will effectively protect the prey resources of the Indo-Pacific humpback dolphins and maintain local productivity. More essentially, a seasonal closure during spring and summer should be enforced immediately. It will not only ensure enough amounts of prey available to the dolphins during the calving season but also strategic closure of coastal fisheries can contribute to the conservation and sustainability of the coastal ecosystem (Mora *et al.* 2009) with positive spillover effect (Stobart *et al.* 2009, Goñi *et al.* 2010, Russ and Alcala 2011). The enclosure will protect the fish larval resources which will in turn help reviving the declined fishery sources in the western coastal waters of Taiwan, while a portion of the conservation goals for Indo-Pacific humpback dolphins in Taiwan can be met.

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Table 3.1 Mother-calf pairs list with coloration class of mother, the time of first and last sighting of calf, estimated birth time and age of first sighting in month, and calving interval in month and year, if any. The coloration stages (Col. stage) are labeled as MT (mottled-stage), SK (speckled-stage), SA (spotted-stage), and UA (unspotted-stage) of each mother. The historical regions of sighting mother-calf pairs are labeled as N (the north region), S (the south region).

			Calf 1				Calf 2				Calving interval	
Mo.	Col. stage	Nurs. region	Time first sighted	Age of first sighting (mn)	Esti. birth time	Time last sighted	Time first sighted	Age of first sighting (mn)	Esti. birth time	Time last sighted	(mo)	(yr)
1*	SK	NS†	4/2008	24-30	12/2005-5/2006?	8/2010						
2*	MT	S	5/2008	18-24	5-11/2006?	8/2008	6/2009	4	2/2009	9/2010	47	3.92
3*	SK	S†	5/2008	18-24	5-11/2006?	8/2008	8/2009	0.25	8/2009	9/2010	39	3.25
4*	SA	N†&	9/2007	12	9/2006?	9/2010						
5*	SK	S†&	5/2008	18	12/2006?	8/2009	7/2010	2-2.5	5/2010	9/2010	41	3.42
6*	SK	S†	8/2008	12-18	2-8/2007?	6/2010	7/2010	0.25	7/2010	8/2010	42	3.50
7	SK	S	6/2008	10-13	5-8/2007	9/2010						
8*	SA	S	5/2008	10-18	12/2006-7/2007?	9/2010						
9*	UA	N	4/2008	6-12	4-9/2007?	4/2008						
10*	SK	S	6/2008	12	6/2007?	7/2010						
11	SK	N	9/2007	2-3	6-7/2007	7/2010						
12	SK	S†&	6/2008	10-12	6-8/2007	9/2010						
13*	UA	N	9/2007	1-2	7-8/2007?	9/2007						
14	SK	N	9/2007	1	8/2007	8/2009						
15	SK	S†	5/2008	6	12/2007	5/2008	6/2009	2-3	3-4/2009	7/2009	#	#

Table 3.1 (continued)

16	SK	N	7/2008	3-4	3-4/2008	9/2010
17	MT	S[†]	5/2009	6-7	11-12/2008	8/2010
18	SA	N	8/2009	6-10	11/2008-2/2009	8/2009
19	SK	S[†]	6/2009	3-4	2-3/2009	6/2009
20	MT	S[†]	6/2009	1	5/2009	8/2010
21	SA	S[†]	2/2010	4-5	9-10/2009	2/2010
22	MT	S[†]	7/2010	0.25-0.5	7/2010	8/2010

[†]: Mother who was transient during the entire survey period.

[&]: Mother who was sighted mainly in only one region with once sighted in another one region while calving.

*: The calf 1 was not included in the analysis.

[#]: The calf 1 disappeared before general weaning age.

?: The estimated birth times for those calves not-included in the analysis.

Table 3.2 Calf survival rate ($l_{x,y}$) and calf age-specific survivorship ($p_{x,y}$) of Indo-Pacific humpback dolphins in Taiwanese waters in year x at age y: (a) estimated calf survival rate; (b) estimated calf survivorship; (c) estimated calf survival rate of calves born during spring/summer (*s/s*) and autumn/winter (*a/w*); and (d) estimated survivorship of calves born during spring/summer (*s/s*) and autumn/winter (*a/w*).

(a)

	Age 0.5	Age 1	Age 2	Age 3
$l_{2007,y}$ (n=5)	0.80	0.80	0.80	0.60
$l_{2008,y}$ (n=3)	1.00	0.67	0.67	0.33*
$l_{2009,y}$ (n=6)	0.50	0.50	0.17*	-
Mean (s.d.)	0.77 (0.25)	0.66 (0.15)	0.54 (0.33)	0.47 (0.19)

(b)

	Age 0-0.5	Age 0.5-1	Age 1-2	Age 2-3
$p_{2007,y}$ (n=5)	0.80	1.00	1.00	0.75
$p_{2008,y}$ (n=3)	1.00	0.67	1.00	0.50*
$p_{2009,y}$ (n=6)	0.50	1.00	0.33*	-
Mean (s.d.)	0.77 (0.25)	0.89 (0.19)	0.78 (0.39)	0.62 (0.18)

(c)

	Age 0.5		Age 1		Age 2		Age 3	
	s/s	*a/w*	*s/s*	*a/w*	*s/s*	*a/w*	*s/s*	*a/w*
$l_{2007,y}$ (n=4,1)	1	0	1	0	1	0	0.75	0*
$l_{2008,y}$ (n=2,1)	1	0.5	1	0	1	0	0.5	-[†]
$l_{2009,y}$ (n=3,3)	0.67	0.33	0.67	0.33	0*	-[†]	-[†]	-[†]
$l_{2007\text{-}2009,y}$ (n=9,5)	0.89	0.40	0.89	0.20	0.67*	0	0.44	0
t-test, *p*-value	<0.05		<0.05		0.18		-[†]	

(d)

	Age 0-0.5		Age 0.5-1		Age 1-2		Age 2-3	
	s/s	*a/w*	*s/s*	*a/w*	*s/s*	*a/w*	*s/s*	*a/w*
$p_{2007,y}$ (n=4,1)	1	0	1	-[#]	1	-[#]	0.75	-[#]
$p_{2008,y}$ (n=2,1)	1	0.5	1	0	1	-[#]	0.75	-[#]
$p_{2009,y}$ (n=3,3)	0.67	0.33	0.67	1	0	-[†]	-[†]	-[†]
$p_{2007\text{-}2009,y}$ (n=9,5)	0.89	0.28	0.89	0.5	0.67	-	0.63	-
t-test, *p*-value	< 0.05		0.05		-		-	

[†]: The entire survey period starting from summer in 2007 up to the end of the study was less than three years; $l_{x,3}$ and $s_{x,2}$ could not be achieved for autumn/winter of 2010 as a result.

*: The last year of the study had to be discontinued at the end of September; hence the 2010 data are based on only a 9-month survey period.

[#]: No more survived calf could be estimated for survivorship.

Table 3.3 Annual reproductive parameters of Indo-Pacific humpback dolphins off the west coast of Taiwan during 2007-2010. The crude birth rate (*CBR*) represents the ratio of the number of neonates (n) to the sum of the number of identified individuals (i) and the number of female-calf pairs (mc) in a given year. The number of identified individuals represents the total number of photographically identified individuals in a given year; none of the calves in mother-calf pairs was individually identifiable. By the end of the study period 22 reproductively active females were identified, which represents 31.0% of all photographically identified individuals. The recruitment rate represents the ratio of the number of calves of Age-1 (s_1) to the estimated total number of females (*EF*, assuming that females consisted of one half of the photographically identified individuals).

Year	2007	2008	2009	2010
Number of identified individuals (i)	30	66	65	68
Estimated total number of females (*EF*)	15	33	32.5	34
Number of female-calf pairs (mc)	14	17	19	15
Number of neonates (n)	5	3	6	3
Crude birth rate ($CBR = n / (mc + i)$)	0.114	0.036	0.071	0.036
Cumulative number of identified females	14	18	21	22
Number of calves at Age 1(s_1)	-	4	2	3
Recruitment rate ($=s_1/EF$)	-	0.121	0.062	0.088

Table 3.4 The number of neonates of Indo-Pacific humpback dolphins off the west coast of Taiwan. The parturitions in warmer seasons (spring and summer) were more than in colder seasons (autumn and winter, χ^2-test, $p < 0.05$).

Seasons	2007	2008	2009	2010	Sum
Spring and summer	4	2	3	3	12
Autumn and winter	1	1	3	0	5

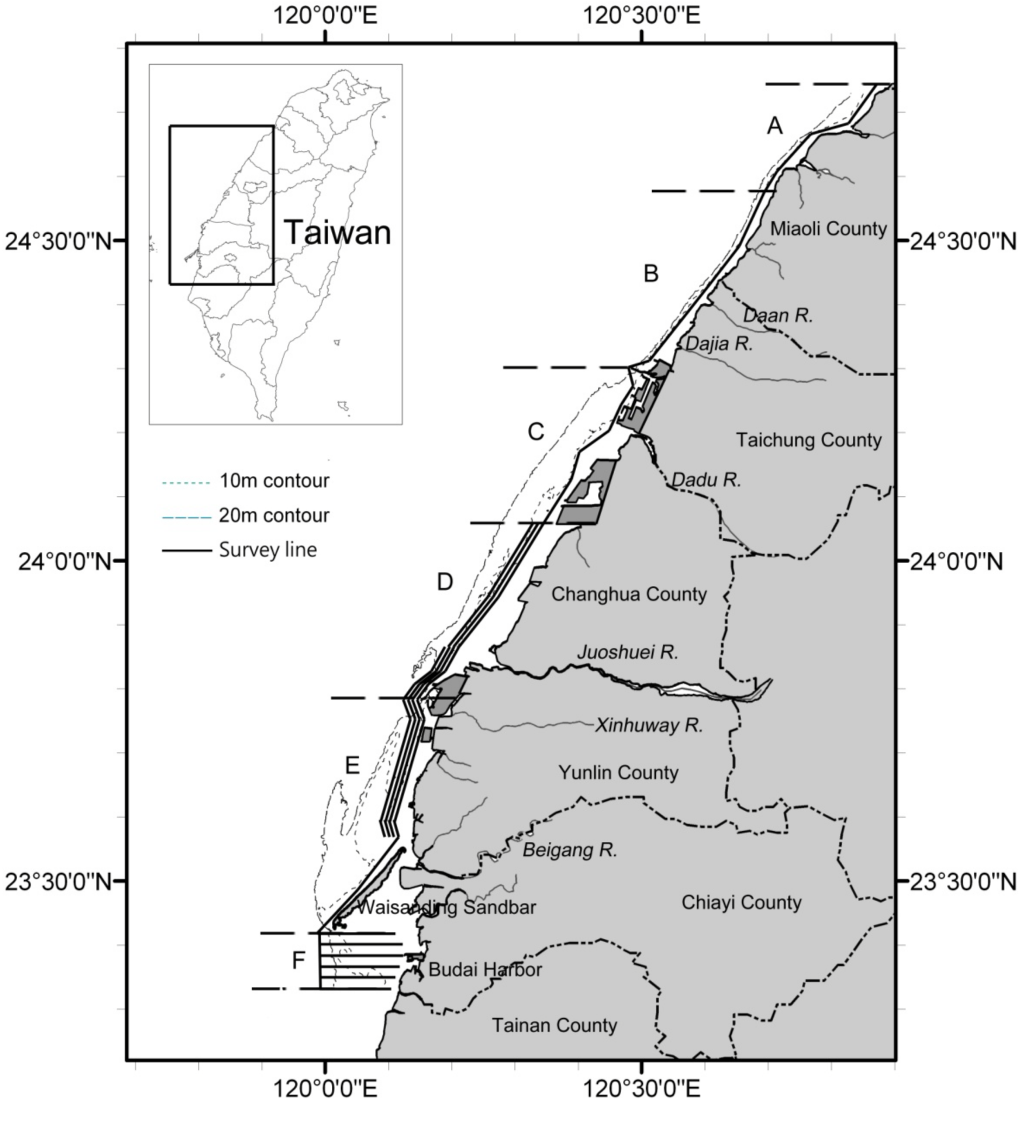

Figure 3.1 Survey areas. The survey sections in 2007-2008 were C, E, and F, the survey sections in 2009 were from A to F, and the survey sections in 2010 were B and E.

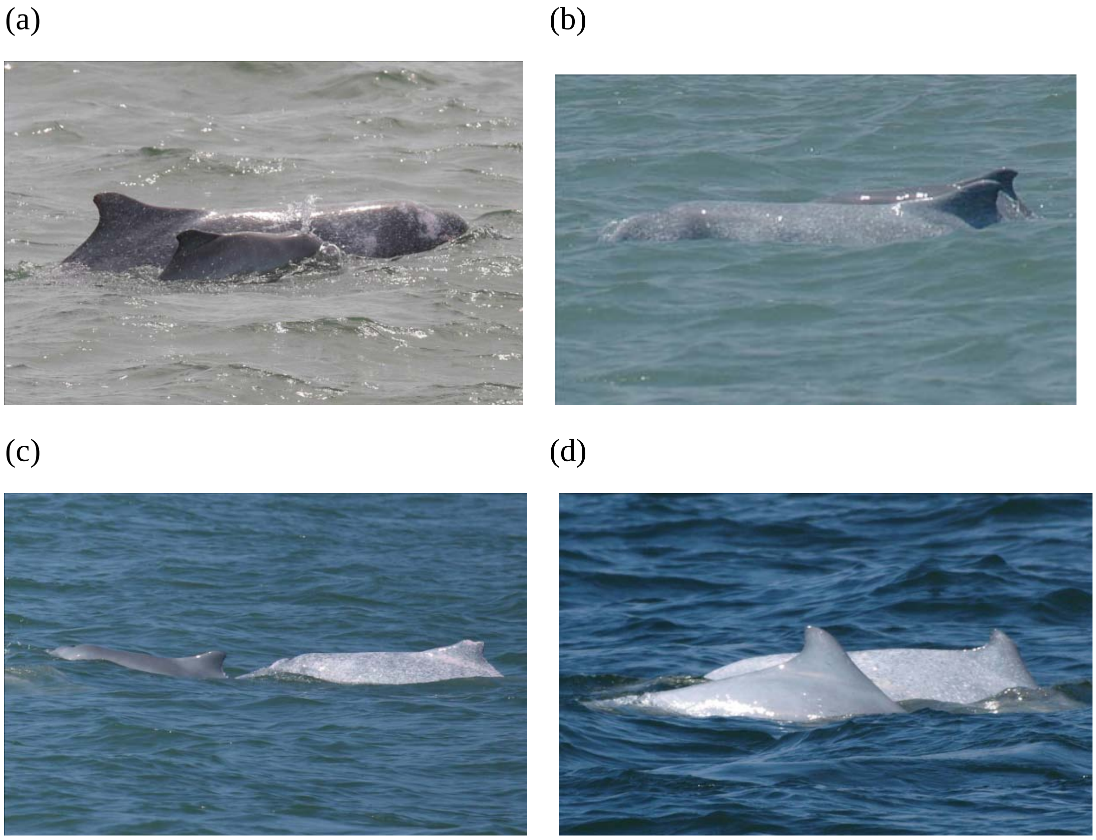

Figure 3.2 Photograph samples of calves in four age groups: (a) neonate, 0.25-0.5 months old; (b) 6 months old calf (the individual in the foreground is the mother); (c) 10-13 months old calf; and (d) 18-24 months old calf.

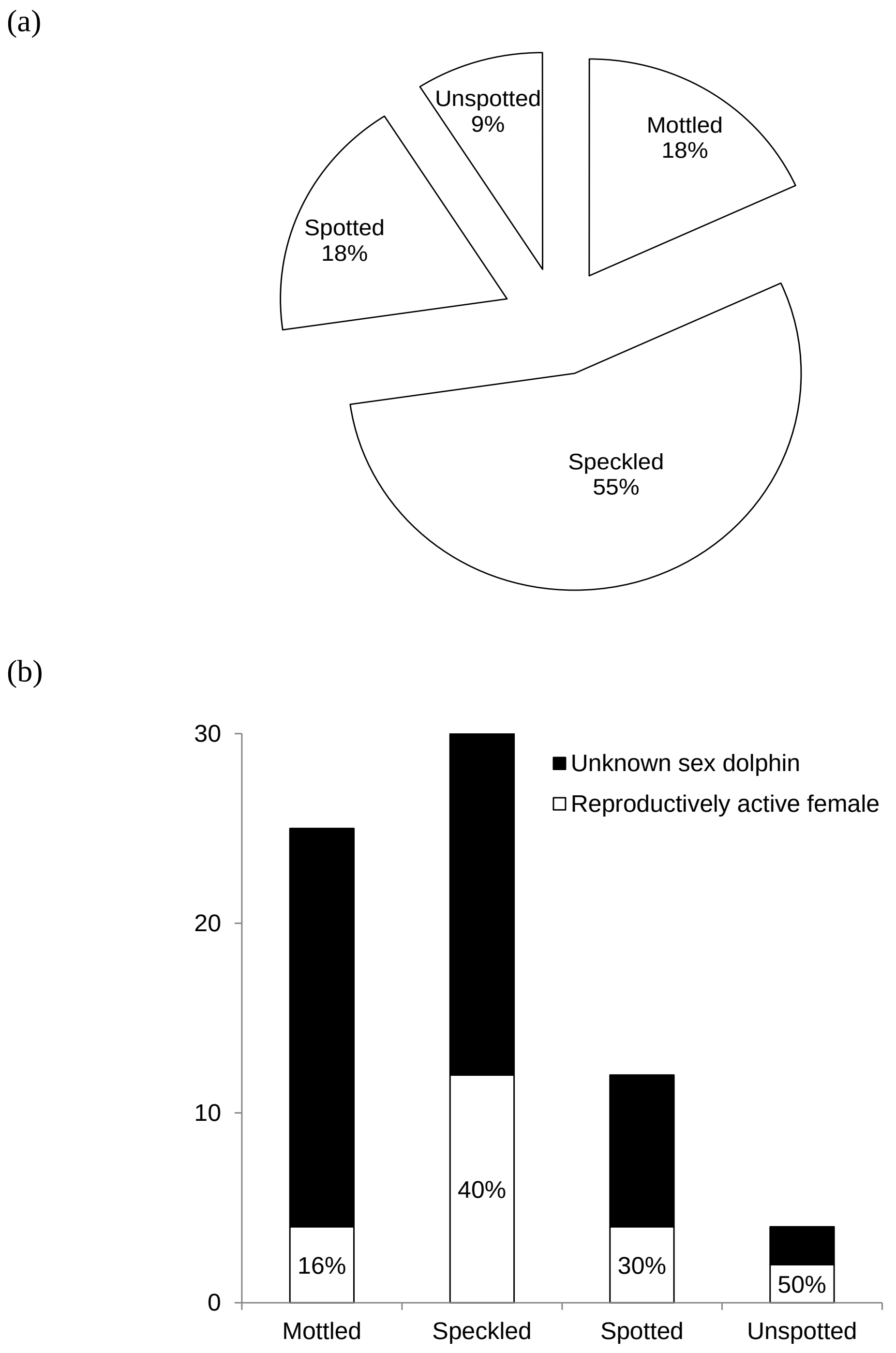

Figure 3.3 (a) Coloration-stages of 22 reproductively active female Indo-Pacific humpback dolphins off west Taiwan during 2007-2010 and (b) percentages of reproductively active females at four different coloration stages. Reproductively active females were identified by its carrying calves. A reproductively active female was defined by its carrying a calf. Dolphins never accompanied a calf was defined as unknown sex.

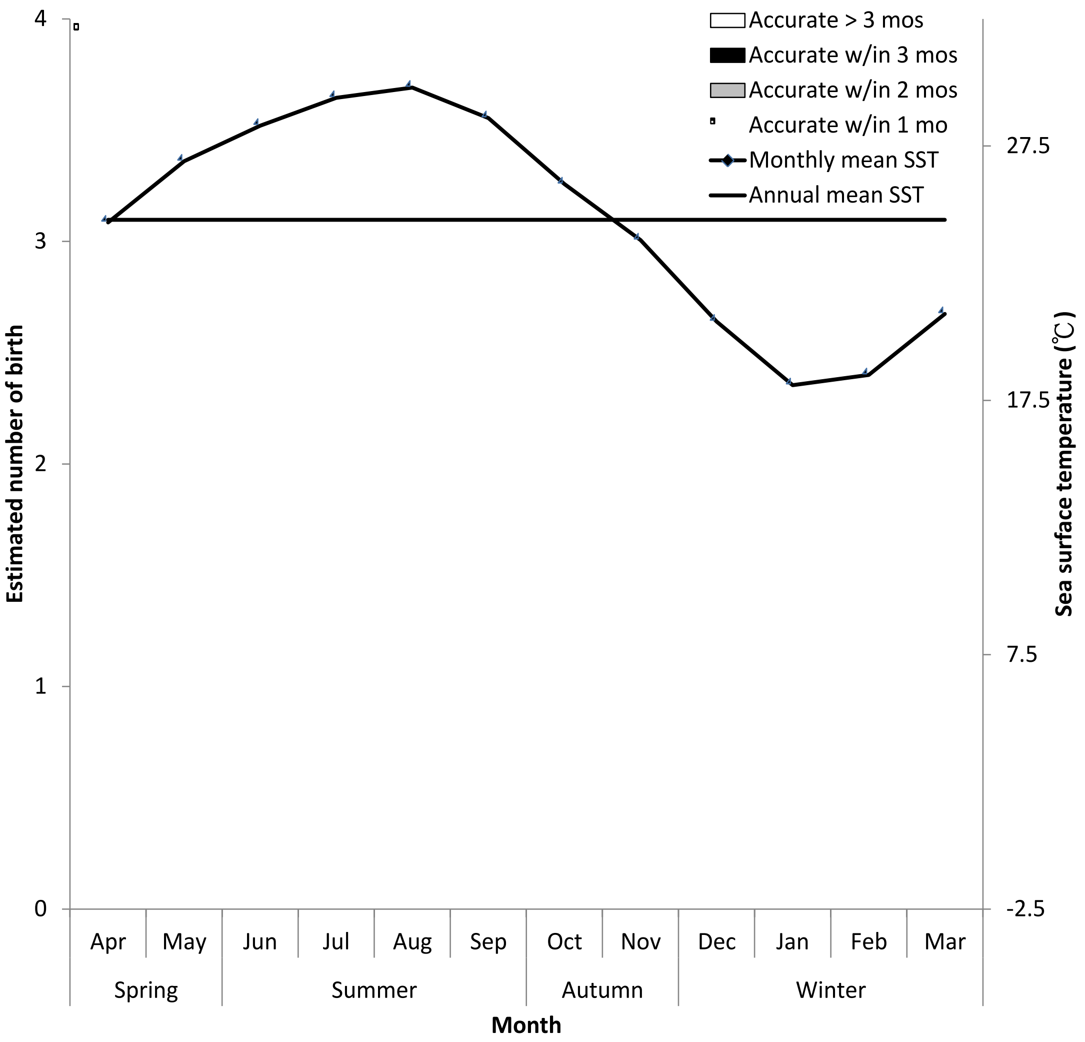

Figure 3.4 Distribution of estimated months of birth of 17 calves estimated off the west coastal waters of Taiwan between 2007 and 2010 (solid columns). The birth month of each calf was estimated by the neonatal characteristics (fetal-fold marks, a flaccid or taut dorsal fin, the body shape posterior to the blowhole) and its relative size to adult. Mean monthly sea surface temperature (SST) (—◆—) and annual mean SST (——) are also shown (courtesy of Taiwan Central Weather Bureau).

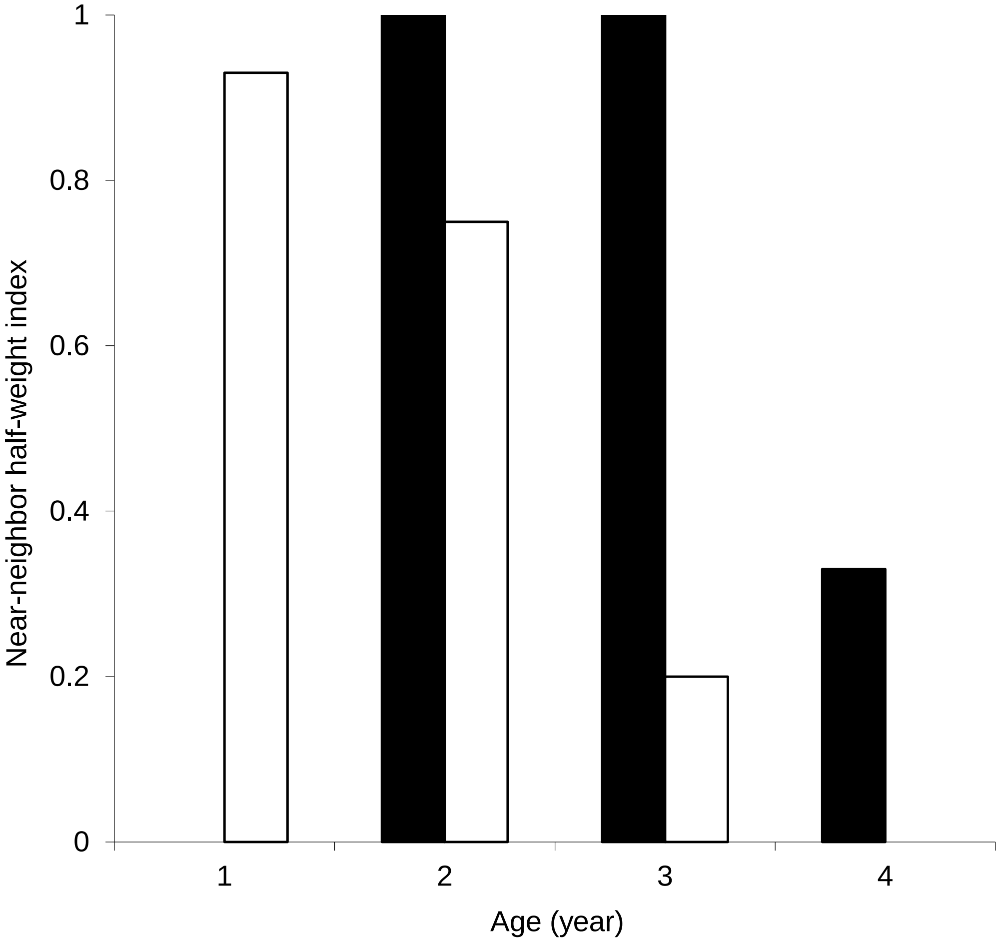

Figure 3.5 Decreasing near-neighbor half-weight index value with calf ages of two mother-calf pairs, mother #1-calf (■, no data for Age 1) and mother #10-calf (□, no data for Age 4), which showed the weaning age happened around 3-4 years old.

Chapter 4: Summary

1. The Taiwan *Sousa chinensis* population was spatiotemporally separated into two communities, one in the north, the other in the south; individuals of both communities frequently emigrated on a short temporal scale, with frequent re-occurrence on a longer temporal scale. This pattern also indicates dolphin preferences for certain regions.
2. The two communities exhibit moderately different compositions in age and sex, which might be related to the habitat functions. The south community has more young animals and females; they may use the south region, which features a wider, shallow and fecund area, as a nursery ground.
3. The social pattern of Indo-Pacific humpback dolphins in Taiwan is one of small dynamic groups with a fluid social structure; they exist as a fission-fusion society with occasional stronger bonds within, perhaps related to the age-class, sex, or even the reproductive status of an individual.
4. The subdivision into communities might be caused by the regular topography. It could also be a recent event related to manmade geographic barriers in the middle of the population range such as the deep water zone around commercial ports. Gene flow between the two communities, which is critical

for the population's survivorship, may be limited.

5. A relatively weak site fidelity indicated by the emigration and reimmigration pattern and the presence of a pigmentation that is similar to that of nearby populations might indicate limited interactions between Taiwanese and other populations.
6. The estimated reproductive parameters (calving interval, calving seasonality, crude birth rate, calf survivorship, calf survival rate, recruitment rate, and weaning age) were comparable to other populations, but they imply a slow population growth trend.
7. The calving seasonality in warmer seasons and vulnerable calf during the first year of life requires a seasonal fishery closure, which can preserve enough food resources for nursing females to increase the reproductive success.
8. For a small population of long-lived and slow reproducing mammals, the current environmental concerns off the Taiwan western coast call for concern and a precautionary approach in coastal development plans with a proper management strategy. Long-term monitoring on the population trend based on photo-identification techniques is much needed.