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Population differences in the pigmentation of Indo-Pacific humpback dolphins, *Sousa chinensis*, in Chinese waters

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Abstract

Spotting pigmentation was compared amongst three putative populations of *Sousa chinensis*: eastern Taiwan Strait (ETS; n=31), Pearl River Estuary (PRE; n=188) and Jiulong River Estuary (JRE; n=10). Spotting intensity on dorsal fins and bodies of each dolphin was scored from 1 (least spotted) to 4 (most spotted) by nine independent subjects and the means of their scores were analysed using analysis of variances (with post-hoc comparisons) and multiple t-tests. Dorsal fins of ETS dolphins were more spotted when compared to those of the PRE ($p<0.0001$) and JRE ($p<0.0001$), but those of PRE vs. JRE dolphins were not significantly different. Body spotting comparisons for all regions were not significantly different. The most noticeable character was the relative differences in spotting intensity between dorsal fins and bodies; dorsal fins were generally as, or more, spotted than bodies of ETS dolphins, while dorsal fins were generally less spotted than bodies of PRE and JRE dolphins. ETS dolphins also maintained spotting on their dorsal fins throughout all spotting phases of the body, whereas dorsal fins of PRE and JRE dolphins became unspotted well before their bodies. These results show that the ETS dolphins are distinct and apparently diagnosable from the PRE and JRE populations.

Keywords: Chinese waters; eastern Taiwan Strait; Indo-Pacific humpback dolphin; Jiulong River Estuary; Pearl River Estuary; pigmentation; *Sousa chinensis*.

Introduction

The Indo-Pacific humpback dolphin (henceforth "humpback dolphin"), *Sousa chinensis* (Osbeck 1765), is a poorly-known species. Although its distribution overlaps considerably with areas of dense human populations, even the most basic knowledge of its biology, including population structure, is lacking throughout most of its range (Jefferson and Karczmarski 2001, Jefferson and Hung 2004).

Humpback dolphins, residing in the coastal waters of western Taiwan (=eastern Taiwan Strait or ETS), were discovered in 2002 during an exploratory cetacean survey of the region (Wang et al. 2004a). Although this was an interesting and important discovery for cetacean science, there were concerns about the continued existence of these dolphins because the waters in which they live are in a dire state, with a myriad of human activities that are harmful to the dolphins and their environment (e.g., development projects in coastal areas and waters, some of which may include considerable land reclamation; discharge of industrial, agricultural and residential pollution; entanglement in fishing nets diversion of freshwater away from river estuaries) (Wang et al. 2004b). Subsequent studies have shown this population likely numbers less than 100 individuals and its main distribution is a small area (approximately 515 km^2) of coastal waters in central western Taiwan (Wang et al. 2007). The small population size, restricted distribution and numerous existing threats confirm the initial concerns that the ETS population is seriously threatened.

Based on reliable records, the existence of approximately eight provisional populations of humpback dolphins in Chinese waters have been hypothesised (Jefferson 2000, Jefferson and Hung 2004). The nearest provisional population, geographically, to the ETS humpback dolphins is that of the Jiulong River Estuary (JRE; also known as the Xiamen/Chinmen population) and the next nearest known sizable and studied provisional population is that of the Pearl River Estuary (PRE; Hong Kong waters). The JRE and PRE provisional populations have been estimated at 86 (Chen et al. 2008) and 1400 dolphins (Jefferson 2007), respectively. Knowing if the ETS humpback dolphins comprise a distinct and isolated population from those in adjacent waters is fundamental for understanding their biology and conservation status and will influence priorities for future research. This knowledge will also affect decisions of managers and how the general public perceives the urgency of the con-

servation situation. The dolphins of the ETS were assumed to comprise a population that was distinct from others in neighbouring waters based on direct observations of pigmentation differences (Wang et al. 2004b,c) and present knowledge of the species in Chinese waters (preference for coastal, estuarine habitats; e.g., see Jefferson 2000). However, the actual distinctiveness of the ETS dolphins remained unresolved. Colouration patterns are considered a useful phenotypic character for understanding cetacean taxonomy (e.g., Heyning and Perrin 1994, Rosenbaum et al. 1995, Perrin 2002). In this paper, we present a quantitative comparison of the pigmentation patterns of humpback dolphins in Chinese waters to determine if the provisional ETS population is distinct from the adjacent JRE and PRE provisional populations.

Materials and methods

Dataset

Photographs of 229 individually-recognisable dolphins that were obtained from the ETS (n=31), JRE (n=10) and PRE (n=188) were analysed in this study (Figure 1). The ETS, PRE and JRE photographs represented all individuals for which photographs of sufficient quality for this study were available. However, photographs of two PRE individuals whose dorsal fins appeared light grey (but could not be determined if they were fine spots) were omitted from the analyses, so the PRE sample size in the analysis was 186. Completely grey individuals with little to no spotting (i.e., representing young calves and juveniles) were not considered in the present analysis.

The intensity of spotting on the dorsal surface of the body below the dorsal fin and on the dorsal fin of each dolphin was scored independently by nine individuals (the authors and four other scorers) on a scale from 1 to 4 (1 being least spotted and 4 being most intensely spotted). Four of the scorers (the authors) had some familiarity with the dolphins of the catalogues from at least one of the provisional populations. Five scorers had little to no experience with the individuals of these catalogues or the species. All subjects were provided with the same scoring instructions and reference examples of the score categories for the bodies and dorsal fins (see Appendix A for examples of each category) and had no information on location.

Data analyses

To test the null hypothesis that these populations were not different from each other, the mean of the scores (by the nine subjects) of the bodies, dorsal fins and the differences between the body and dorsal fin (that were obtained by subtracting the means of the scores by the nine subjects) were compared separately amongst the three provisional populations (one of the main differences observed between the ETS and the other provisional populations was that the ETS dolphins did not have a contrastingly unspotted dorsal fin relative to the spotting intensity on the body, so it was important to examine this character). Analyses were conducted using multiple pairwise t-tests and one-way analysis of variances (ANOVAs) with a 0.05 level of significance. For t-tests, the critical threshold values for significance were adjusted for multiple comparisons. The sequential Bonferroni correction was used, because it is more powerful than the standard Bonferroni correction (see Rice 1989). Post-hoc comparisons to investigate differences between provisional populations (for ANOVAs that resulted in significance) included Scheffe's, least significant difference, Duncan's multiple range, Tukey's honestly significant difference and the Newman-Keuls methods. All analyses were per-

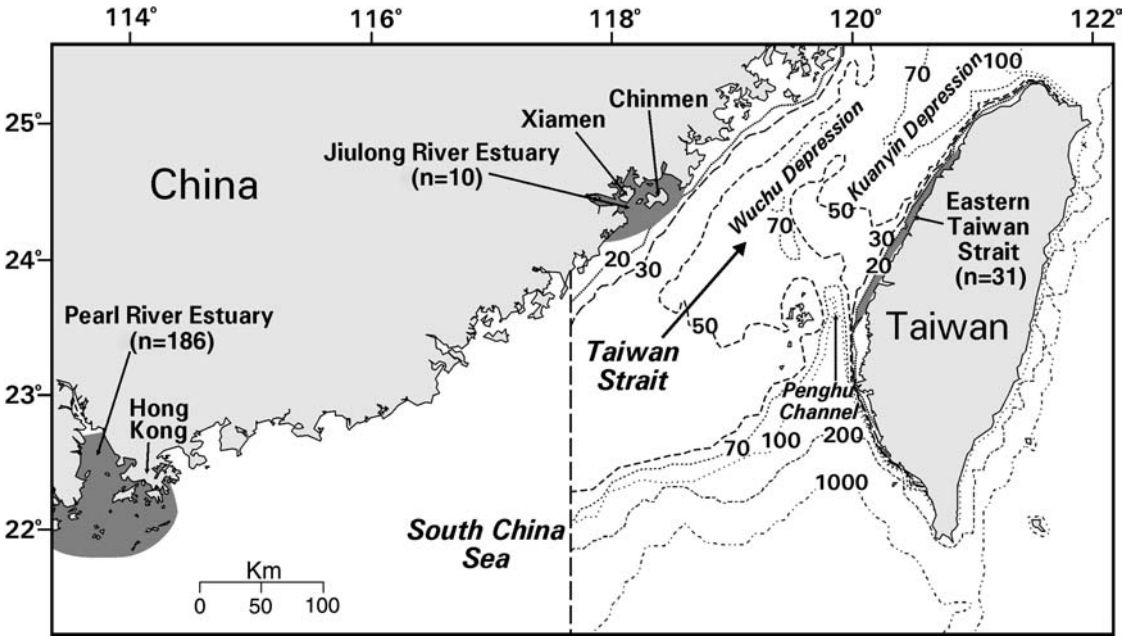

Figure 1 Map showing the three provisional Indo-Pacific humpback dolphin, *Sousa chinensis*, populations examined in this study and the bathymetry of the Taiwan Strait. Sample sizes are shown in parentheses.

formed using STATISTICA 5.1 (StatSoft Inc, 1995, Tulsa, Oklahoma, USA).

Results

The means of the spotting intensities of the bodies and dorsal fins of dolphins from the ETS population were greater than those of the other provisional populations, whereas the mean difference between the spotting intensities of the bodies and dorsal fins was much less (actually negative) (see Table 1). Regardless of the statistical analyses conducted (i.e., multiple pair-wise t-tests with sequential Bonferroni correction or ANOVAs with planned post-hoc comparisons), the general results were the same. The intensity of spotting on the bodies of dolphins from the PRE, JRE and ETS did not differ from one another (but the ETS dolphins tended to be slightly more spotted than those of the other provisional populations). In contrast, when the spotting intensity on the dorsal fins, or the difference between the body and dorsal fin spotting were compared, the ETS dolphins differed significantly in both these characters from those of the PRE and JRE (see Tables 2 and 3). Furthermore, the differences in spotting pigmentation were not due to a specific developmental stage. The overall greater intensity of spotting on the dorsal fins of ETS dolphins appeared to be consistent for all categories of body spotting.

In contrast, when the PRE and JRE populations were compared, there were no significant differences between these populations in the spotting intensity of the body, dorsal fin or the difference between the body and dorsal fin.

Table 2 Results of ANOVAs conducted on the body, dorsal fin and the difference between body and dorsal fin for dolphins from the eastern Taiwan Strait (ETS), Jiulong River Estuary (JRE) and Pearl River Estuary (PRE) provisional populations.

	F	p-value
Body	1.153	0.318, n.s.
Dorsal fin	120.96	<0.0001*
Difference (body–dorsal fin)	76.12	<0.0001*

ETS (n=31), JRE (n=10) and PRE (n=186). F-statistic and p-values are shown. Note: for all ETS vs. JRE and ETS vs. PRE comparisons for dorsal fin scores and the differences between body and dorsal fin scores, multiple pair-wise comparisons (using least significant difference, Scheffe's, Duncan's multiple range, Newman-Keuls and Tukey's honestly significant difference tests) resulted in significant differences ($p<0.001$). However, all comparisons between PRE and JRE populations did not reveal significant differences.

Discussion

ETS population is distinct

In general, humpback dolphins of Chinese waters are medium-to-dark grey at birth with the ventral surface being slightly paler. A dramatic colour transformation occurs with age. The darker grey pigmentation appears as an overlay that is lost in small specks to gradually reveal the white base layer (somewhat resembling molting). The dolphins transform from being mainly dark with light-coloured spots to mostly white with dark spots, and the amount of dark spots decreases with age to the point that some dolphins appear completely unspotted. The white colour often appears with a "bubblegum" pink tinge (Jefferson and Leatherwood 1997). And because both the youngest and oldest individuals are the least spotted, the spotting on humpback dolphins does not appear to function as camouflage against detection by predator or prey (see Perrin 2002). Instead, the intensity of spotting may function as an indicator of relative maturity to conspecifics.

Pigmentation patterns and development exhibited by the ETS population of humpback dolphins were reliably and diagnosably different from those of populations found in adjacent coastal waters of China. Regardless of the general age class (assumed to be reflected in spotting intensity; see Jefferson 2005) of the dolphins, the colour transformation of the ETS dolphins was different from the dolphins of the PRE and JRE. The ETS dolphins are generally more spotted overall (and thus far, no white, unspotted dolphins have been observed). The most distinguishing feature of the dolphins of this population is the difference in the spotting intensity of the dorsal fin relative to the body and the developmental transformation. The dorsal fins of ETS dolphins are as, or more, intensely spotted than their bodies throughout the colour transformation (Figure 2). The rate of reduction of spots on the dorsal fin appears to be equal to, or slower than, the loss of spots on the body. Even dolphins with minimal spotting on the body will still have spotting on the dorsal fin.

In contrast, the dorsal fins of JRE and PRE dolphins are strikingly devoid of spots compared to their bodies throughout most of the colour transformation, with the exception of two stages, when: 1) the animals are young and almost completely grey; and 2) the transformation is at or near completion and the animals are more or less spotless. The loss of spots on the dorsal fin occurs well

Table 1 Means (and standard errors) of spotting intensity of the body, dorsal fin and difference between the body and dorsal fin for the eastern Taiwan Strait (ETS), Jiulong River Estuary (JRE) and Pearl River Estuary (PRE) provisional populations.

Population	n	Body score (Mean±SE)	Dorsal fin score (Mean± SE)	Difference of body – dorsal fin scores (Mean±SE)
ETS	31	2.92±0.13	3.30±0.13	-0.38±0.08
JRE	10	2.60±0.37	1.53±0.14	1.07±0.24
PRE	186	2.66±0.07	1.43±0.04	1.23±0.05

The sample size from each population is also shown.

Table 3 Matrix of the results of multiple pair-wise t-test comparisons of the spotting intensities of the body, dorsal fin and difference between body and dorsal fin of dolphins from three provisional populations of humpback dolphins (ETS, eastern Taiwan Strait; JRE, Jiulong River Estuary; PRE, Pearl River Estuary).

		Provisional populations		
		ETS	JRE	PRE
ETS	Body		1.06, n.s.	1.54, n.s.
	Dorsal fin		7.07*	15.50*
	Difference		7.70*	12.38*
JRE	Body	0.297		0.21, n.s.
	Dorsal fin	$\ll$0.0001		0.55, n.s.
	Difference	$\ll$0.0001		0.73, n.s.
PRE	Body	0.126	0.838	
	Dorsal fin	<0.001	0.583	
	Difference	$\ll$0.0001	0.468	

Data above and below the diagonals are the t-statistics and associated p-values, respectively. Note: the 0.05 level of significance was adjusted for the multiple comparisons using the sequential Bonferroni correction.

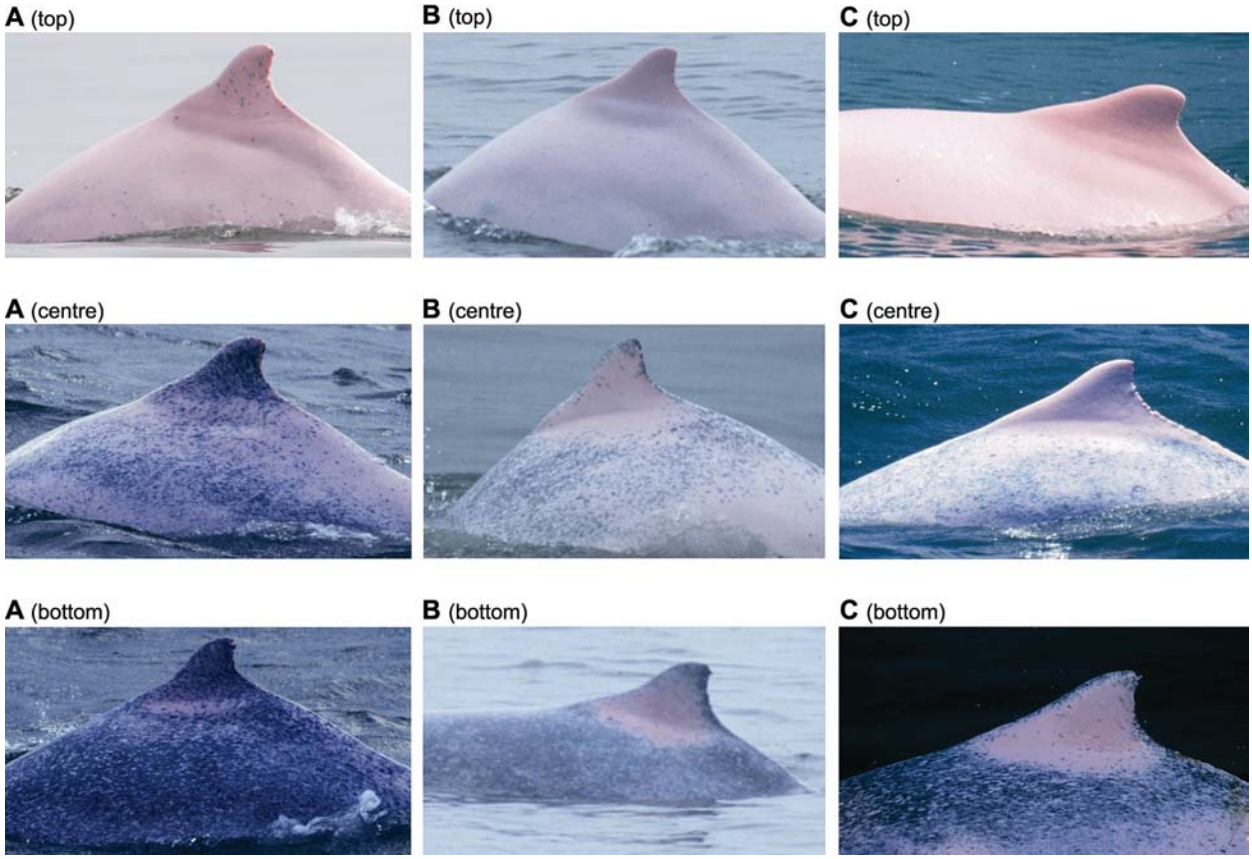

Figure 2 Examples of Indo-Pacific humpback dolphins, *Sousa chinensis*, from: (A) the eastern Taiwan Strait (western Taiwan), (B) the Jiulong River Estuary (Xiamen, China), and (C) the Pearl River Estuary (Hong Kong). The least spotted dolphins (top row) are presumed to be the oldest individuals from each of the populations. The centre dolphins are likely mature individuals and the bottom dolphins may be sub-adult or recently sexually matured. Photographs are courtesy of S.C. Yang – A (top, centre, bottom) and Hong Kong Cetacean Research Project – B (top, centre, bottom) and C (top, centre, bottom).

before the same transformation on the body and appears to spread, upwards and outwards, from the centre of the fin base, so the last remnants of spotting are often found along the edges of the fin. Even a mostly grey dolphin can possess a mostly unspotted and highly contrasting dorsal fin. The rate of reduction of spots on the dorsal fins of the JRE and PRE dolphins is clearly faster than for their bodies.

Even though there is great individual variation in the spotting patterns of humpback dolphins, the maintenance of consistent differences in colouration by the dolphins of the ETS suggests they are reproductively isolated from those in adjacent waters. Furthermore, even though the geographical distance between the PRE and JRE is greater than that between the ETS and JRE regions, the lack of difference in pigmentation between

the JRE and PRE provisional populations suggests that the Taiwan Strait may be a more effective barrier to dolphin dispersal than geographical distance (see below for a description of the Taiwan Strait).

This study provides the first quantitative evidence for the existence of an isolated and phenotypically distinct population of *Sousa chinensis*. However, differences in pigmentation (and possibly external morphology – e.g., relative size of the dorsal fin and dorsal "hump") may also be useful for understanding population structure of humpback dolphins elsewhere and should be examined. Analyses of photographs of these characters may help to overcome the major obstacle of a lack of specimens for morphological studies to better understand the taxonomy of dolphins. For example, dolphins from the waters of Thailand and Australia also appear to possess pigmentation (and maybe external morphology) that is different from those of Chinese waters (unpublished data).

Other evidence for a distinct ETS population

A detailed comparison of more than 450 individually-recognisable dolphins in the catalogues for the three provisional populations revealed no matches. Thus, there is no evidence of movement and exchange of individuals amongst these regions. This is further evidence that the ETS dolphins comprise an isolated population. This is also suggestive that the PRE and JRE provisional populations, although appearing similar to each other with regards to pigmentation patterns and developmental transformation, may also represent distinct entities (also see Jefferson 2000).

All humpback dolphins appear to be restricted to waters less than approximately 25 m in depth (Saayman and Tayler 1979, Ross et al. 1994, Karczmarski et al. 2000, Ross 2002) and in Chinese waters, the species also seems to be tied to, and resident in, estuarine waters with minimal linear distance movement (on the order of tens of kilometres) (Hung 2000, Jefferson 2000, Hung and Jefferson 2004). Compared to the mainland of China, western Taiwan's river systems are small and the strip of coastal waters that is less than 25 m deep is narrow, so the offshore extent of habitat available to the ETS population is limited (see Figure 1). This view is supported by the lack of sightings of the species beyond 2 km from shore, even though waters out to approximately 6 km (and deeper than 40 m) were surveyed (Wang et al. 2007). Most of the sightings of the ETS dolphins were made in and around river estuaries and in waters less than 10 m deep, with only two sightings in water between 20 and 25 m deep (note, however, that the latter sightings were made in the waters around the Formosa Plastics Group's Mailiao industrial area, where there is continual dredging of the sea floor for shipping, so should not be considered a natural phenomenon). The depth of most of the middle of the Taiwan Strait is much greater than that preferred by humpback dolphins, with a considerable part of the central to northern Taiwan Strait being deeper than 70 m (Wuchu and Kuanyin Depressions) and deeper than 100 m (the Penghu Channel) in the southeastern portion (for an overview, see Liao and Yu 2005). It is also often influenced by intrusions of high salinity, warm and clear oceanic waters of the Kuroshio Current (e.g., Chuang 1986, Wang and Chern 1988, Jan et al. 2006). Even though the Taiwan Strait is only approximately 140–200 km wide between Taiwan and mainland China, its bathymetry and possibly salinity appear to represent an effective barrier to movements of humpback dolphins between the ETS to JRE regions (especially given the species' resident tendencies and preference for estuarine and shallow waters).

Future research

Although the present study provides evidence of distinctness, much still needs to be understood about the level of differentiation amongst these populations. DNA analyses would be the most direct method for quantifying the level of genetic differences, gene flow, separation and divergence amongst populations and determining the closest relatives of the ETS population. However, tissue samples from the ETS population are highly limited, due to the small population size and the few stranded carcasses. Furthermore, the precarious state of the population's future existence, the small risk of injuries or potentially even death (see Bearzi 2000) caused by biopsy sampling of free-ranging dolphins may be too great to justify biopsy sampling for this population (see Wang et al. 2004b). Given the results of the present study, the need for intrusive sampling for population genetic analyses are reduced greatly. Genetic analyses to address some of above questions in the future will be challenging and dependent upon opportunities to obtain additional samples without risk to the dolphins.

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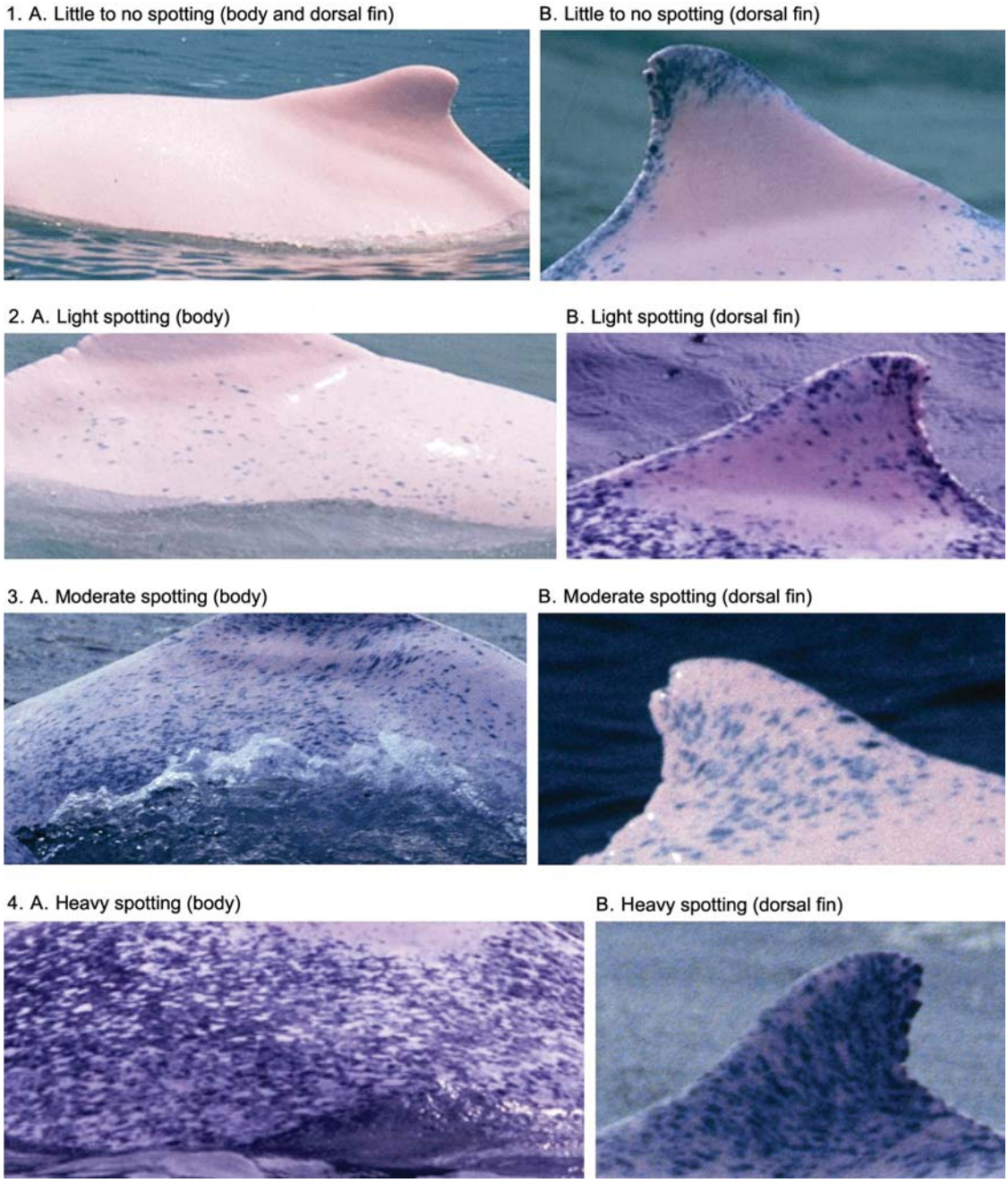
Appendix A

Examples of the intensity of spotting on the bodies (left series) and dorsal fins (right series) of Indo-Pacific humpback dolphins, *Sousa chinensis*, for scorers to reference. Scoring categories vary from 1 (least spotting) to 4 (heavy spotting). Photographs are courtesy of Hong Kong Cetacean Research Project (scoring area photograph, 1A and B, 2A and B, and 4A), S.C. Yang (3A and 4B) and J.Y. Wang (3B).



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