

**POPULATION ECOLOGY OF SPINNER DOLPHINS  
(*STENELLA LONGIROSTRIS*) IN AN OFFSHORE  
RESTING HABITAT IN THE RED SEA**

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**POPULATION ECOLOGY OF SPINNER DOLPHINS (*STENELLA LONGIROSTRIS*) IN AN OFFSHORE RESTING HABITAT IN THE RED SEA**

Submitted by

**Amina Cesario**

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Populations of coastal and semi-pelagic dolphins that frequently use well-defined sites and habitats provide a great opportunity to investigate their population ecology, which is considerably more challenging in wide-ranging offshore species. However, their inshore occurrence also exposes them to anthropogenic impacts such as dolphin-watch tourism, which pose conservation challenges. In the Egyptian Red Sea, spinner dolphins (*Stenella longirostris*) frequently visit a small offshore reef, Samadai reef, to rest during the day. The site is a popular swim-with-dolphins destination, regulated by a management plan since 2004. To investigate the population ecology of spinner dolphins at Samadai reef and assess the effectiveness of the current management measures, a 4-year study was undertaken between 2011 and 2014.

Capture-recapture techniques applied to photo-identification data indicated a stable population of ~200 non-calf spinner dolphins, composed of long-term year-round residents of both sexes and transient individuals, with a high adult

survival rate (0.99; SE=0.02). The probability of temporary emigration was low (0.15; SE=0.004), with females seemingly more philopatric than males. Photographic cross-matching with spinner dolphins seen in other resting areas indicates low-level interchange with neighbour reef-associated communities.

Female spinner dolphins appear to reach sexual maturity at 8-10 years, typically having a 2-year calving interval. The presence of tooth rake marks on females suggests coercive male sexual behaviour. There is one well-pronounced annual calving peak between June and August, which coincides with warmer water temperatures. Calf survival to 1-year of age was generally high (0.79; 95%CI 0.73-0.87), but was significantly lower for calves born to younger females than older females (0.61, 95%CI 0.43-0.87 and 0.80, 95%CI 0.71-0.90, respectively). The crude birth rate (0.10; SD=0.016), the annual recruitment rate (0.08; SD=0.007) and the fecundity rate (0.20; SD=0.018) indicate a healthy population.

The Red Sea spinner dolphins showed pigmentation features apparently unique to the region. Adults were found to be sexually dimorphic. Underwater photogrammetry showed that female and male individual growth began to diverge at the length of ~151 cm, and that physical maturity was attained at the length of ~165 cm for females and ~180 cm for males, at approximately 7 and 10 years of age, respectively.

The findings of this study confirmed the importance of Samadai reef as resting habitat for resident and transient spinner dolphins and indicated that the animals are not subject to obvious natural or anthropogenic stressors. The currently implemented management measures appear to be adequate and effective, although some modifications to the management practice are suggested. However, as long-term effects of human activities may take some time to emerge, further long-term monitoring and research is strongly recommended to ensure that expansion of tourism will not menace the viability of spinner dolphins at Samadai reef and more broadly in the Egyptian Red Sea. Resolution of apparent taxonomic uncertainties of the Red Sea

spinner dolphins is recommended, as it is important in addressing conservation issues and informing management decisions at an appropriate geographic scale.

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**Amina Cesario**

M.Sc. in Biological Science, University of Milan

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Perfect reflection. Red Sea Dolphin Project 2012. (Photo: Watter Al Bahry)

To Luca.

## **Eppure soffia**

Pierangelo Bertoli

(1977)

E l'acqua si riempie di schiuma il cielo di fumi  
la chimica lebbra distrugge la vita nei fiumi  
uccelli che volano a stento malati di morte  
il freddo interesse alla vita ha sbarrato le porte  
un'isola intera ha trovato nel mare una tomba  
il falso progresso ha voluto provare una bomba  
poi pioggia che toglie la sete alla terra che è vita  
invece le porta la morte perché è radioattiva

Eppure il vento soffia ancora  
spruzza l'acqua alle navi sulla prora  
e sussurra canzoni tra le foglie  
bacia i fiori li bacia e non li coglie

Un giorno il denaro ha scoperto la guerra mondiale  
ha dato il suo putrido segno all'istinto bestiale  
ha ucciso, bruciato, distrutto in un triste rosario  
e tutta la terra si è avvolta di un nero sudario  
e presto la chiave nascosta di nuovi segreti  
così copriranno di fango persino i pianeti  
vorranno inquinare le stelle la guerra tra i soli  
i crimini contro la vita li chiamano errori

Eppure il vento soffia ancora  
spruzza l'acqua alle navi sulla prora  
e sussurra canzoni tra le foglie  
bacia i fiori li bacia e non li coglie  
eppure sfiora le campagne  
accarezza sui fianchi le montagne  
e scompiglia le donne fra i capelli  
corre a gara in volo con gli uccelli

Eppure il vento soffia ancora!!!

## Declaration

I declare that this thesis represents my own work, except where due acknowledgment is made, and it has not been previously included in a thesis, dissertation or report submitted to this University or to any other institution for a degree, diploma or other qualifications.

Signed

A handwritten signature in blue ink, appearing to read 'Amina Cesario'.

Amina Cesario

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## Chapter 1. General Introduction

### 1.1 Species description

The spinner dolphin, *Stenella longirostris* (Gray, 1828), is distributed worldwide in tropical waters (Jefferson et al., 2008). Four subspecies are currently recognized (Perrin et al., 2009; Committee on Taxonomy, 2014): the eastern spinner dolphin (*S. longirostris orientalis*; Perrin, 1990), Central American spinner dolphin (*S. longirostris centroamericana*; Perrin, 1990), dwarf spinner dolphin (*S. longirostris roseiventris*; Wagner, 1846) and the nominate subspecies the Gray's spinner dolphin (*S. longirostris longirostris*; Gray, 1828). In the offshore Eastern Tropical Pacific (ETP), an apparent hybrid form between *S.l. orientalis* and *S. l. longirostris* has been described and named the whitebelly spinner dolphin (see Chapter 3, Figure 3.1).

In the ETP, the eastern and whitebelly spinner dolphins have a pelagic distribution. In contrast, the other subspecies are primarily found in the vicinity of coasts and islands, atolls and reefs (summarized in Andrews et al., 2013). This dichotomy in habitat use exposes them to different environments and different ecological trade-offs between the benefits of group living and environmental constraints, which may affect their socio-behavioural dynamics, demographic parameters and vital rates.

The ETP spinner dolphins experienced high level of mortality in the offshore tuna purse-seine fishery during the 1960s and 1970s and although their populations have now ceased to decline, they still do not show signs of recovery (Gerrodette and Forcada, 2005). The inshore subspecies are instead more likely to be by-caught in gillnet fisheries or, in smaller numbers, through direct killing in harpoon or drive fisheries (Perrin and Gilpatrick Jr, 1994; Oremus et al., 2015). Moreover, nature-based tourism activities are emerging as a new threat for Gray's spinner dolphins (Bearzi et al., 2012) that typically frequent inshore habitats for daily resting

and socialising (Norris et al., 1994; Karczmarski et al., 2005; see also further).

The International Union for the Conservation of Nature (IUCN) lists spinner dolphins as Data Deficient (Bearzi et al., 2012), although the eastern spinner dolphin meets the IUCN's Red List category of Vulnerable, under criteria A2d (Hammond et al., 2012), with by-catch in the tuna purse-seine fishery being the main pervasive threat (Wade et al., 2007). As pointed out by Bearzi and colleagues (2012), there is a need to assess the conservation status of each subspecies and regional population(s) as the available estimates of abundance and removals suggest that some of them may fall into a Threatened category.

Gray's spinner dolphins (hereafter spinner dolphins) are among the commonest small cetaceans in tropical oceans (Perrin, 2009) and are also very common in the Red Sea (Costa, 2015). In several tropical locations, spinner dolphins are known to use sheltered shallow sandy bays and reef lagoons during daytime for resting, and move offshore to deeper oceanic waters during night time to forage on the mesopelagic boundary micronekton community (Perrin, 1998; Benoit-Bird and Au, 2003). Various aspects of ecology of spinner dolphins associated with islands, atolls or reefs have been studied in several locations: off the Main Hawaiian Archipelago (Norris and Dohl, 1980; Norris et al., 1994; Marten and Psarakos, 1999; Lammers, 2004; Danil et al., 2005; Tyne et al., 2014; Tyne et al., 2015), in the Northwestern Hawaiian Islands (Karczmarski et al., 2005; Andrews et al., 2010), in French Polynesia (Poole, 1995; Gannier and Petiau, 2006; Oremus et al., 2007; Gannier, 2009), off American Samoa Island (Johnston et al., 2008), in Fiji Islands (Cribb et al., 2012), Fernando de Noronha Archipelago (SW Atlantic) (Silva et al., 2005; Silva and Silva, 2009), Mayotte Islands (somewhat atypical in reef use, see Kiszka et al. (2010)), Maldives (Anderson, 2005), Mauritius (Webster et al., 2015) and in the study site described in this thesis, Samadai reef in the Egyptian Red Sea (Notarbartolo di Sciara et al., 2009). Their occurrence and the temporal use of these resting areas may vary between

different locations. For example, Gannier and Petiau (2006) found that dolphin presence and residence time in a bay of Tahiti is negatively affected by surface water turbidity and lagoon current strength. Benoit-Bird et al. (2009) demonstrated that off the Main Hawaiian Islands the relative abundance of spinner dolphins increased with increasing lunar illumination and suggested that lunar phase is likely to affect the behaviour of delphinid species that, as spinner dolphins, forage on vertically migrating prey.

Demographic and social dynamics of spinner dolphins, studied in some detail in the Hawaiian Archipelago and Society Islands (French Polynesia), revealed a great intraspecific variability. Off the Main Hawaiian Islands, spinner dolphins have generally a fission-fusion social structure (Norris and Dohl, 1980; Norris et al., 1994; but see more recent work of Tyne et al. 2014) in which most animals associate with a number of other animals at different times, but associations form and break over a wide range of time scales. Group sizes are relatively small and comparable to those reported in the Society Archipelago. In the south Pacific, genetic data suggest that discrete island-associated communities, such as those in the Society Archipelago, are connected through male and female gene flow, which leads to a larger scale metapopulation structure (Oremus et al., 2007). Another scenario is reported from far-western Hawaii, Midway and Kure atolls, where spinner dolphins form much larger groups compared to those off the Main Hawaii and Society Islands, with long-term social and geographic fidelity. They are socio-behaviourally discrete, with philopatry of both sexes, and parallel dispersal by mixed-sex groups that occasionally switch between otherwise stable dolphin communities (Karczmarski et al., 2005).

## **1.2 The Red Sea Environment**

The Red Sea is one of the most important repositories of marine biodiversity on a global scale, it has many sites of unique beauty that

support populations of globally important species or contain ecologically critical habitats (Edwards and Head, 1987; Sheppard et al., 1992; DiBattista et al., 2015). Fortunately, the Red Sea is one of the least disturbed seas compared to other enclosed marine habitats and it remains mostly unexplored.

The Red Sea is a narrow oceanic semi-enclosed basin separating the African and the Asian continental shelves and extending for 2250 km from north (30°N) to south (12°30'N). A deep trench in the central part of the basin stretches from north to south, reaching maximum depth of about 2850m. At its northern end, the Red Sea extends into the Gulf of Aqaba and the Gulf of Suez and connects with the Mediterranean Sea through the artificial Suez Canal. The southern region connects with the Indian Ocean through the Gulf of Aden via the strait of Bab-el-Mandeb (Morcos, 1970).

The Red Sea has the highest salinity of any major oceanic basin (up to 40-41‰) and is considered an oligotrophic domain (Acker et al., 2008). Based upon the spatiotemporal distribution and abundance of surface Chlorophyll-a, the Red Sea can be divided into four distinct domains, that are, starting from North to South, the Northern-Red Sea (NRS), the North-Central Red Sea (NCRS), the South-Central Red Sea (SCRS), and the Southern Red Sea (SRS) (Raitsos et al., 2013).

Samadai reef is located within the most oligotrophic area, the North-Central Red Sea (NCRS) (Raitsos et al., 2013). The climate in this domain is characterized by a bimodal pattern, with a cold season (winter) from mid-October to mid-April and a warm season (summer) during the remaining six months of the year (Edwards and Head, 1987). The NCRS is characterized by north-westerly winds year-round (Raitsos et al., 2013). Sea surface temperature in this part of the Red Sea is not markedly influenced by the wind direction induced by the monsoon regime that instead characterizes the southern Red Sea (SCRS and SRS), and it ranges approximately between 22°C and 28°C (mean 24°C) during winter

and between 25°C and 31°C (mean 28°C) during summer (Acker and Leptoukh, 2007). Permanent rivers are missing in the region and precipitation is scarce: sporadic winter rains are the only source of freshwater in the area (Sheppard et al., 1992).

### 1.3 The Red Sea spinner dolphin

The current knowledge of the ecology and behaviour of spinner dolphins in the Egyptian Red Sea is based primarily on the data collected at Samadai reef during a 2-year monitoring project carried out in 2004-2005 (Notarbartolo di Sciara et al., 2009), a 1-year research project in 2005-2006 (Shawky and Afifi, 2008; Costa et al., 2012; Costa et al., *in preparation*) and 15-months study in 2012-2013 (Shawky et al., 2015). Between 2010 and 2015, three further research projects were carried out in the Southern Egyptian Red Sea (Costa, 2015; Fumagalli, 2016), including the study at Samadai reef presented in this thesis.

Red Sea spinner dolphins daily rhythms resemble that of Gray's spinner dolphins (Notarbartolo di Sciara et al., 2009): during daylight hours they frequently associate with sheltered and shallow waters of sandy-bottom lagoons for resting, after having foraged cooperatively at night in the open sea over the mesopelagic boundary community.

In the Southern Egyptian Red Sea, four sites are known to be important resting habitats for spinner dolphins (Notarbartolo di Sciara et al., 2009; Costa, 2015): Samadai reef (24°59'N; 34°59'E), 1.4 km long and 1 km wide, located 7 km off Marsa Alam (Chapter 2); Satayah reef (24°9'N; 35°40'E), 2 km long and 4.4 km wide, located approximately 13 km from shore and intensively visited by tourist operators that offer swim-with-dolphins activities; Abu Fandira (22°54'N; 36°16'E), 1 km long and 7 km wide, ~25 km offshore; and Ghubbat 'Isa (or Abu Tess) (22°9'N; 36°50'E) located ~4 km off the shore and stretching for 1.5 km in length and 1.5 km in width (Figure 1.1). These reefs display the physical features of suitable

resting areas (*i.e.* shallow, calm, sheltered, sandy lagoon that provide easy access to deep water foraging areas, Figure 1.1) and are considered “primary resting areas” for spinner dolphins (*sensu*, Thorne et al., 2012; Tyne et al., 2015). Spinner dolphins visit also other lagoons and bays in the region, for resting or as anti-predatory strategy (Norris and Dohl, 1980) that are suitable but not optimal (“secondary resting areas”), *i.e.* they may not exhibit all the features mentioned above. Known “secondary resting areas” are Marsa Alam reef (25°04’N; 34°56’E) and the sheltered side of the Wadi el Gemal Islands (25°40’N; 34°09’E), both approximately 3.5 km offshore. Occasional sightings of spinner dolphins are also reported in apparently non-suitable areas (Costa, 2015; pers. obs.). In overall, the spinner dolphin resting habitats in the Egyptian Red Sea represent a mosaic of primary, secondary and occasional resting areas located in relative proximity to each other and to both the shore and the foot of the continental slope (Figure 1.1).

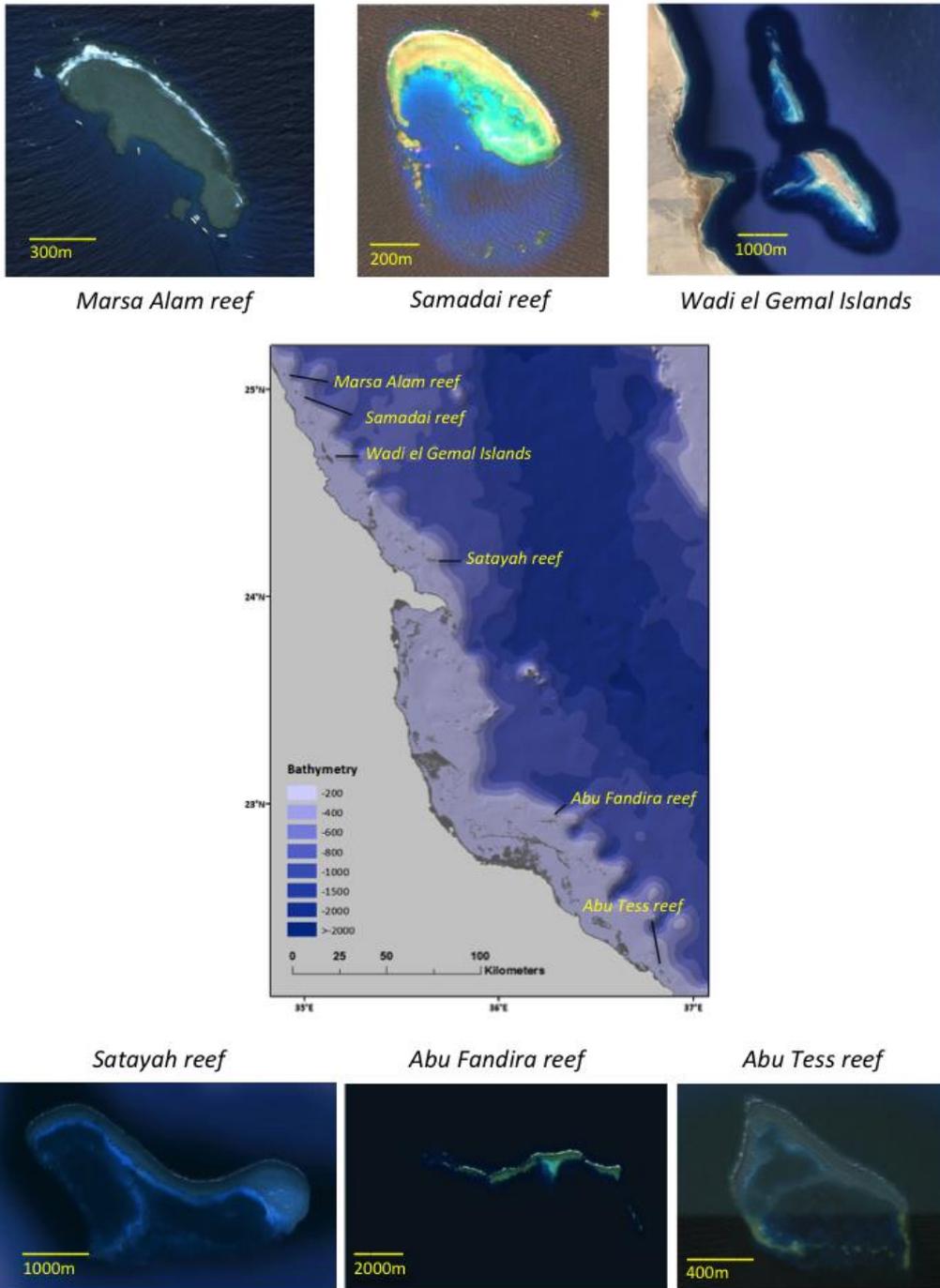


Figure 1.1. Bathymetric map for the southern Egyptian Red Sea (generated with ArcGIS 10.3.1; courtesy of Marina Costa). Resting areas in the region are indicated on the map and individual satellite images (Google Earth V 7.1.5.1557).

Line transect surveys conducted across approximately 400 km of the southern Egyptian Red Sea (Figure 1.2) generated an abundance estimate of ~7000 spinner dolphins (Costa, 2015), and it was exclusive of the reef-associated spinner dolphins, as navigation on transect occurred in open-waters (Costa, 2015). A 4-year study in Satayah reef and 1-year project in Samadai reef estimated community sizes of 300-400 individuals in each of the reefs (Fumagalli, 2016; Costa et al., *in preparation*). Spinner dolphins made extensive use of the primary resting areas, with groups encountered ~75% of the time when these areas were surveyed, with mean group sizes inside the lagoons ( $63 \pm 34.6SD$ ) generally larger than those encountered offshore ( $43 \pm 36.1SD$ ) (Costa, 2015).

Some of these resting areas are included within the boundaries of protected areas: the Wadi El Gemal- Hamata National Park and the Gebel Elba Conservation Area (Figure 1.2). This, however, does not ensure protection or implementation of a conservation strategy, as resources, and therefore enforcement, are generally low in the region (Fumagalli, 2016). In this sense, Samadai reef represents an exception (Notarbartolo di Sciara et al., 2009) (see also further).

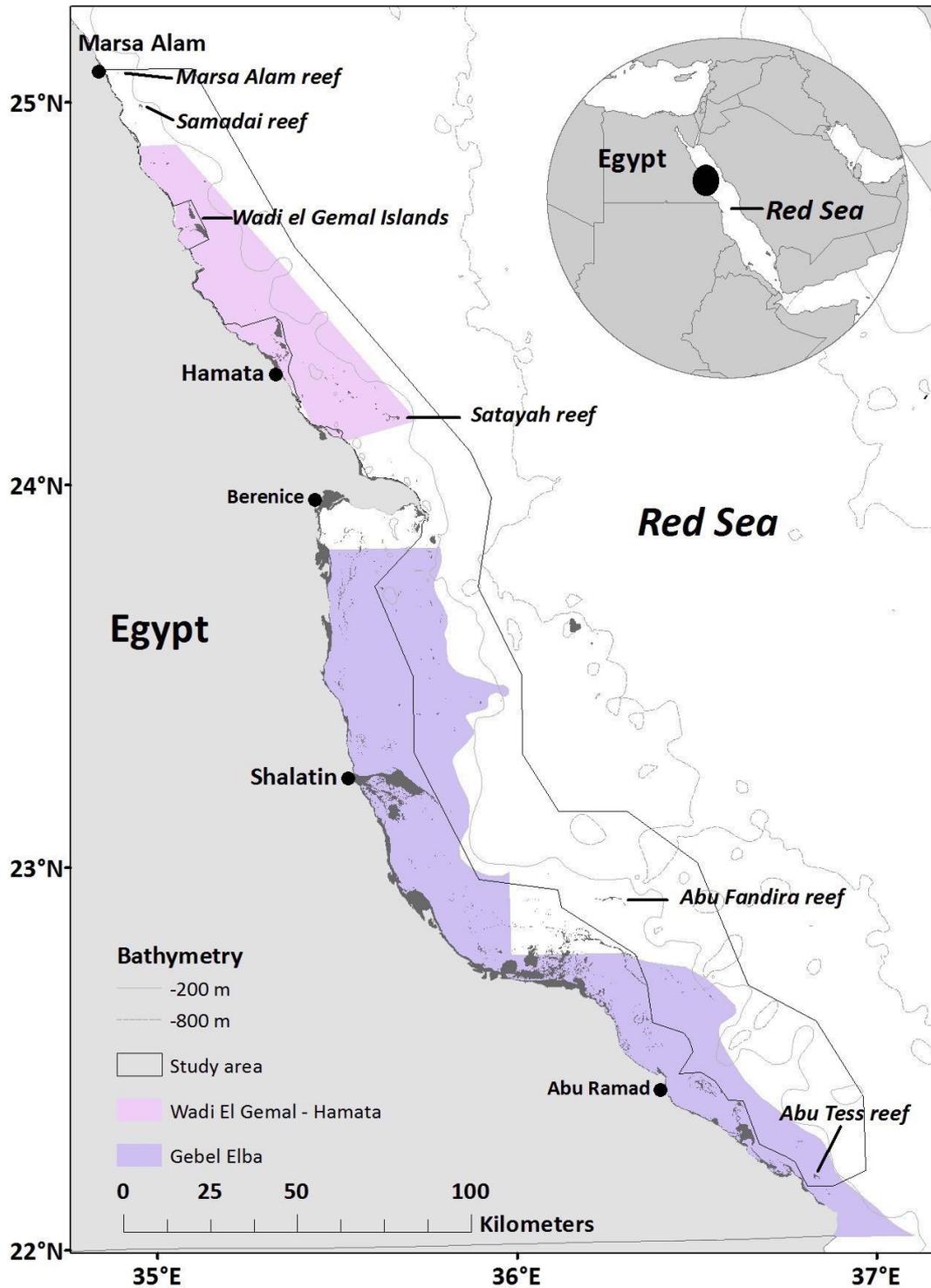


Figure 1.2. Map of the study area (black line) that encloses the area where line transects were conducted in the southern Egyptian Red Sea. The coloured areas indicate the marine portion of Wadi El Gemal - Hamata National Park (pink) and Gebel-Elba Conservation Area (purple). The known resting areas of spinner dolphins are also indicated. Map generated with ArcGIS 10.3.1 (courtesy of Marina Costa).

## 1.4 Project background

Until approximately 2000, Samadai reef was solely a destination for scuba-divers, who would enjoy diving in the outer side of the reef and would consider the dolphins resting in the lagoon a pleasant brief distraction between dives. In the early 2000s, following a generalized tourism development in the Egyptian Red Sea that commenced in the 1990s (Shaalán, 2005), swim-with-dolphins activities grew rapidly in Samadai reef, peaking in 2003 with hundreds of tourists converging daily to swim with the resting dolphins (Notarbartolo di Sciara et al., 2009). Excessive numbers of swimmers paired with a complete lack of code of conduct was said to be causing noticeable distress to the dolphins and concerns grew that the dolphins would abandon the reef as result of the disturbance. Community mobilisation led to the suspension of all access in December 2003 and, in January 2004, to the implementation of a provisional management plan (Chapter 2) based on the scant knowledge available at the time and on a precautionary principle (Notarbartolo di Sciara, 2003).

Since the declaration of Samadai reef as a special managed area, two research projects were conducted (in 2004-2005 and 2005-2006, as indicated above) to monitor the population of spinner dolphins. The work presented in this thesis is a follow-up of the previous studies and it is part of a large project entitled “Sustainable Development in the Southern Egyptian Red Sea” conceived by Dr. Notarbartolo di Sciara, developed by the Italian Cooperation in Egypt and the Egyptian Hurghada Environmental Protection and Conservation Association (HEPCA). The project involved a set of interconnected activities to support the social and economic development of Egypt’s southern coastal and marine zone and the promotion of sustainable use involving local communities, while ensuring that its biodiversity remained intact. One of the objectives was to provide a description of the local cetacean fauna, estimating abundance and describing distribution patterns of cetacean species and their exposure to potential anthropogenic threats (Costa, 2015; Fumagalli,

2016), including the investigation of the population ecology of spinner dolphins in Samadai reef (this study).

## 1.5 Thesis goal and objectives

As a consequence of the commercial whale/dolphin-watching expansion and the increasing evidence of its detrimental impacts (e.g. Senigaglia et al., 2016), it is becoming an imperative to develop and implement effective management strategies that ensure tourism activities do not menace the viability of cetacean populations (Higham et al., 2014). However, cetaceans are long-lived animals with low fecundity and any impact, and its potentially long-term consequences such as cetacean-based tourism (Lusseau and Bejder, 2007), requires long-term monitoring and research in order to detect non stochastic variations in population and reproductive parameters.

The goal of the study described in this thesis was to advance the knowledge on the population ecology of the Red Sea spinner dolphins, assess the effectiveness of the management plan that is in force at Samadai reef since January 2004, and provide a scientific basis for further enhancement of the conservation measures. This thesis addresses the following:

**Chapter 1** provides a general introduction of the spinner dolphin, the Red Sea environment and the background of the project.

**Chapter 2** describes the study area (Samadai reef) and the general methodologies employed in this study.

**Chapter 3** investigates the phenotype, morphology and morphometrics of the Red Sea spinner dolphins through the use of underwater observation and parallel-laser photogrammetry techniques. The degree of sexual

dimorphism is assessed and a comparison with conspecifics elsewhere is provided in order to evaluate intra-specific variability.

**Chapter 4** describes the growth pattern of the Red Sea spinner dolphins and sex-specific differences.

**Chapter 5** quantifies the reproductive parameters for this species in the Red sea: calving interval and seasonality, crude birth rate, recruitment and fecundity rate, calf survivorship, weaning age and reproductive success.

In **Chapter 6** dolphins' occurrence, population size, survival, and geographic fidelity are presented. Despite the research site being limited to Samadai reef, a collective effort was put into other well-known resting areas (Fumagalli, 2016; Costa, 2015), which allowed me to explore the connectivity (*i.e.* individual interchange among neighbour reefs) in the southern Egyptian Red Sea.

**Chapter 7** contains the conclusive remarks and conservation management implications.

## Chapter 2. General methodologies

### 2.1 Study area

The study was conducted at Samadai reef (Sha'ab Samadai in Arabic; 24°59'N 34°59'E), a shallow, submerged, horseshoe-shaped reef located approximately 7 km off the Egyptian Red Sea coast (Figure 2.1). The reef's inner lagoon is ca. 350 m in diameter, 2-20 m deep, with sandy bottom and south-facing opening, surrounded by deep waters that ~1500 m outside the reef reach the depth of ~260 m. The reef's morphological configuration protects the inner lagoon from the prevailing northerly winds (Edwards and Head, 1987; Raitzos et al., 2013). In this part of the Red Sea the continental shelf extends approximately 18km offshore, at which point the slope descends steeply eastwards and ~4 km North-East from Samadai reef reaches depths of 500-600 m, which represents the foot of the continental slope.

The circadian rhythms of Red Sea spinner dolphins (Chapter 1) make their presence in sites like Samadai reef highly predictable, while the easy accessibility of Samadai reef have rendered the site a popular touristic destination and the dolphin population tolerant to human presence in the water (Notarbartolo di Sciara et al., 2009).

A management plan in force since January 2004 regulates tourist visits and activities (Notarbartolo di Sciara et al., 2009). The lagoon waters are subdivided into three zones: Zone A, the northernmost portion of the lagoon is a dolphin only zone with no entry for tourists; Zone B, is designed for swimmers and snorkelers only and transit of any boats is prohibited; and Zone C, the remainder of the lagoon, where large boats can moor at designated buoys, small inflatables are allowed to navigate and snorkelling and diving activities may occur freely. Lines of buoys mark the separation between the zones (Figure 2.1). Limitations on time and

number of visitors as well as the payment of an entrance fee are also in place (Notarbartolo di Sciara et al., 2009).

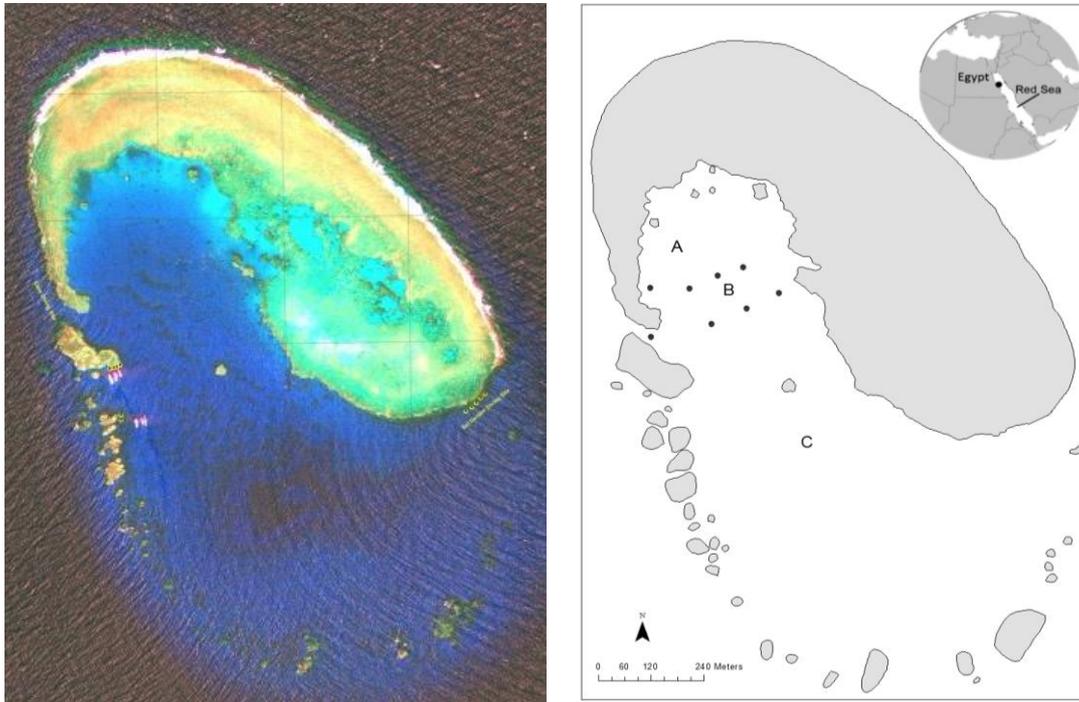


Figure 2.1. Satellite image of Samadai reef ( $24^{\circ}59'$  N,  $34^{\circ}59'$  E) (left) situated in the southern Egyptian Red Sea; map of Samadai reef (right) generated with ArcGIS 10.1 (ESRI, 2011). The buoys (grey dots) demarcate the management zones: A (dolphins only), B (snorkelers only) and C (any activity).

## 2.2 Data collection

### 2.2.1 Field effort and field protocol

Underwater photographic-identification (photo-ID) surveys were conducted in Samadai Reef from May 2011 to August 2014. From May 2011 to November 2012, a team of three researchers visited the study site monthly for five consecutive days each month, weather permitting. In 2013 and 2014, the field effort concentrated on three summer months (June, July, August) and two researchers collected the underwater photo-ID data, but the monthly field effort was intensified (Table 2.1).

The research site was reached using a small rigid-hull inflatable boat (RIB) or a commercial tour boat. Searching for dolphins was carried out by

naked eyes and with the aid of binoculars Steiner Navigator 7x50. Researchers searched for dolphins by standing on the observation platform with an eye-height level of 1.5-1.7 meters above the sea surface (when using RIB) or *ca.* 3 m above the sea surface when using tourist vessels, while moored to one of the buoys in zone C (Figure 2.1). If dolphins were present, data collection began immediately; otherwise, the observers searched for dolphins every 10 minutes for 5 minutes until a sighting occurred or the survey day ended. The research team usually arrived at Samadai Reef at 8:30 and left at 15:30 (n=271).

This study followed up an earlier pilot study conducted by the same research team from October 2005 to September 2006 (Costa et al., *in preparation*) and in April 2010.

Table 2.1. Research effort carried out in Samadai reef. Occasionally, it was not possible to approach the animals (e.g. dolphins left the site before the team could reach them) and photo-identification data were not collected. Dolphin occurrence is calculated as the number of times the dolphins were found in Samadai over the number of times the team visited the site (Sightings/Survey days); survey success is calculated as the time photo-identification data were collected over the number of times the team visited the site (Photo-ID/Survey days); both are reported in percentage. Subtotals per year are reported in italics.

| Year         | Month | Survey days (n) | Sighting (n) | Photo-ID (n) | Survey success (%) | Dolphin occurrence (%) |
|--------------|-------|-----------------|--------------|--------------|--------------------|------------------------|
| <b>2005</b>  |       | <b>28</b>       | <b>23</b>    | <b>21</b>    | <b>75</b>          | <b>82</b>              |
|              | Oct   | 9               | 6            | 5            | 56                 | 67                     |
|              | Nov   | 13              | 12           | 12           | 92                 | 92                     |
|              | Dec   | 6               | 5            | 4            | 67                 | 83                     |
| <b>2006</b>  |       | <b>80</b>       | <b>60</b>    | <b>57</b>    | <b>71</b>          | <b>75</b>              |
|              | Jan   | 9               | 8            | 6            | 67                 | 89                     |
|              | Feb   | 12              | 7            | 5            | 42                 | 58                     |
|              | Mar   | 7               | 3            | 5            | 71                 | 43                     |
|              | Apr   | 5               | 4            | 4            | 80                 | 80                     |
|              | May   | 10              | 8            | 8            | 80                 | 80                     |
|              | Jun   | 8               | 7            | 6            | 75                 | 88                     |
|              | Jul   | 11              | 9            | 9            | 82                 | 82                     |
|              | Aug   | 7               | 6            | 6            | 86                 | 86                     |
|              | Sep   | 11              | 8            | 8            | 73                 | 73                     |
| <b>2010</b>  |       | <b>4</b>        | <b>4</b>     | <b>4</b>     | <b>100</b>         | <b>100</b>             |
|              | Apr   | 4               | 4            | 4            | 100                | 100                    |
| <b>2011</b>  |       | <b>30</b>       | <b>22</b>    | <b>23</b>    | <b>77</b>          | <b>73</b>              |
|              | May   | 5               | 5            | 5            | 100                | 100                    |
|              | Jul   | 5               | 3            | 3            | 60                 | 60                     |
|              | Aug   | 5               | 3            | 3            | 60                 | 60                     |
|              | Sep   | 5               | 3            | 4            | 80                 | 60                     |
|              | Oct   | 5               | 4            | 4            | 80                 | 80                     |
|              | Dec   | 5               | 4            | 4            | 80                 | 80                     |
| <b>2012</b>  |       | <b>49</b>       | <b>34</b>    | <b>34</b>    | <b>69</b>          | <b>69</b>              |
|              | Jan   | 8               | 5            | 4            | 50                 | 63                     |
|              | Feb   | 3               | 3            | 3            | 100                | 100                    |
|              | Mar   | 4               | 4            | 4            | 100                | 100                    |
|              | Apr   | 4               | 3            | 3            | 75                 | 75                     |
|              | May   | 6               | 4            | 5            | 83                 | 67                     |
|              | Jul   | 7               | 4            | 4            | 57                 | 57                     |
|              | Aug   | 3               | 3            | 3            | 100                | 100                    |
|              | Sep   | 4               | 2            | 2            | 50                 | 50                     |
|              | Oct   | 5               | 2            | 2            | 40                 | 40                     |
|              | Nov   | 5               | 4            | 4            | 80                 | 80                     |
| <b>2013</b>  |       | <b>43</b>       | <b>36</b>    | <b>33</b>    | <b>77</b>          | <b>84</b>              |
|              | Jun   | 14              | 12           | 11           | 79                 | 86                     |
|              | Jul   | 13              | 12           | 10           | 77                 | 92                     |
|              | Aug   | 16              | 12           | 12           | 75                 | 75                     |
| <b>2014</b>  |       | <b>37</b>       | <b>29</b>    | <b>26</b>    | <b>70</b>          | <b>78</b>              |
|              | Jun   | 9               | 9            | 8            | 89                 | 100                    |
|              | Jul   | 17              | 13           | 11           | 65                 | 76                     |
|              | Aug   | 11              | 7            | 7            | 64                 | 64                     |
| <b>Total</b> |       | <b>271</b>      | <b>208</b>   | <b>198</b>   | <b>75*</b>         | <b>77*</b>             |

\* Mean values

"Sighting" is defined as the time when a dolphin group was kept under focal observation, and it began when dolphins were sighted in the proximity of the reef, entering in the lagoon, or if dolphins were already in the lagoon at the time the research team arrived. The sighting ended either when the dolphins left, sufficient data were collected, or when the team had to terminate the observation due to deteriorating sea conditions (n=4) or the hosting tourist boat had to leave as per management plan regulations (Notarbartolo di Sciara et al., 2009). A mean duration of a sighting was 5h19min  $\pm$  2h35min SD (n=208).

Group size and composition were estimated from both above the surface and underwater. A group was defined as an aggregation of individuals within the waters of the lagoon, usually engaging in the same behaviour (Norris and Dohl, 1980; Karczmarski et al., 2005). Each researcher carried out estimations independently and, subsequently, the data were compared between researchers after the data collection session ended. Surface estimates were done only at the beginning of the sighting. Underwater estimates were performed several times during the underwater data collection. Underwater visibility was excellent (rarely below 30 m) allowing the researchers to see the entire dolphin group at one time. Underwater sessions lasted 1-2 hours, depending on dolphin group size, and two researchers were in the water at the same time, both collecting photo-ID data and group size/composition estimates. Evident changes in dolphin number and/or composition were recorded as different sets of the same sighting and estimates were kept separately. The final group size and composition estimates were obtained by combining the maximum number of individuals counted for each age class. An estimation of quality was also given as: best (exact number of individuals), good ( $\pm$ 5 individuals), rough ( $\pm$  >5 individuals). As the underwater group size and composition estimates were considered more accurate, only these data were used for further analyses. In 2014, paired laser underwater photogrammetric data were collected; for details see Chapter 3.

In order to reduce harassment, a code of conduct was applied including careful approach of the group, slow swim in proximity of dolphins and always parallel to their course. Free diving was minimised to avert any possible avoidance reaction by the dolphins.

### **2.2.2 Age and sex composition**

Four age classes were recognised in the field: newborn, first year calf, second/third year calf, and non-calf individual (*sensu* Perrin and Henderson, 1984). Newborn animals were identified by the presence of features such as: visible foetal folds along the body, size less than half the length of a larger animal presumed to be the mother with whom they were strictly associated, behaviour (mainly clumsy at swimming and head-slapping when breathing). Dolphins were considered calves when their size was estimated at less than 3/4 of the average adult length and swam in close association with an adult. According to the size, calves were subdivided into first year calf (half the size of the associated adult) and second or third year calf (2/3 to 3/4 of an adult size). All the other larger individuals were classified as non-calves, including adults and animals that were visibly younger (lighter in colouration and less robust; see also “Age estimation” below).

The sex of the individuals was determined by direct observations of the genital area (the presence of mammary slits for females and extruded penis or evident post-anal hump for adult males), association with a newborn/calf that regularly swam in echelon position or evident pregnancy status.

### **2.3 Photographic-identification**

Natural markings have long been used for individual identification in cetaceans. For most species, features appearing above the surface of the water during respiration exhibit markings and/or pigmentation patterns unique to each individual. For most delphinid species, photographs of dorsal fins are primarily used to identify individuals (Hammond et al.,

1990). In this study, photo-identification data were collected underwater while snorkelling. As natural marks on the whole body of an individual could be used, underwater photo-identification facilitated a greater use of a matrix of features (e.g. Karczmarski and Cockcroft, 1998) compared to the traditional above-water photo-ID protocol. For a distinctive feature to be considered suitable for individual identification it had to be visible from both sides of the animal, e.g. notches, nicks and scars on the edges of dorsal fin or the body profile. Secondary markings, such as tooth rakes, scrapes, scars, peculiar pigmentation patterns and marks on the edges of pectoral fin, that were visible only from one side, were at times used to confirm individual matches (Würsig and Jefferson, 1990) and to assess the accuracy of photographic coverage (see also further).

During each underwater session, a large number of photographs were taken of as many individuals as possible, irrespective of distinctive marks. Photo-identification data collection was terminated if researchers considered that all dolphins were photographed, the dolphins left the site, weather condition deteriorated, or other factors forced the team to return to the boat (e.g. late hour). Attempts were made to attain an even coverage of the group and to collect at least one high quality image of the entire body for each individual.

Throughout the study, photographs and videos were taken using a Canon G10, Panasonic Lumix tz7, Canon PowerShot S110, Canon PowerShot D10, and Go Pro cameras, all equipped with 10 bar underwater housings. Pictures and videos were taken at the distance of 2-10m from the dolphins.

### **2.3.1 Photographic processing**

Photographs were edited using the software *Adobe Photoshop CS6* (ver. 13.0.6, Adobe Systems Inc., Delaware, USA) and its *Camera Raw 9.1* plug-in (see Appendix I), processed and archived using the default file

manager available on Macintosh operating systems (*Finder*) and the software *DISCOVERY* (Gailey and Karczmarski, 2012).

The quality of the pictures containing at least one dorsal fin was first assessed based on four characteristics: focus/clarity, contrast, angle and dorsal fin visibility. Each characteristic was scored separately and the overall photographic quality was given by the sum of the characteristics' scores resulting in "Excellent" (Q1), "Very Good" (Q2), "Good" (Q3), "Fair" (Q4) and "Poor" quality pictures (Q5) (see Appendix I for details).

Individual animals were considered "highly marked" (D1 and D2), "marked" (D3) or "non-distinctive" (D4 and D5) according to the number and size of notches, nicks and/or deformation observed on their dorsal fins or body profiles. The categories were assigned adopting existing photo-ID protocols developed for small cetaceans (see Appendix I for details). Very distinct fins or body profiles, with large notches or deformations, were assigned to the category D1; fins with one nick and/or a matrix of smaller nicks were ascribed to the D2 category; category D3 included all those fins with only 1 nick or with 1 or more small marks on the body profile; fins with 1 or 2 small nicks were ascribed to category D4 whereas clean fins were assigned to D5 category (for details and definition of notch, nick and small nick see Appendix I).

Individuals in categories D1 to D4 were included in the ID-catalogue and different subsets of the catalogue were used for different type of analysis. Each individual was compared with all other individuals in the catalogue before being assigned with a unique identification code and included in the catalogue, which was further verified by two other experienced researchers.

Individuals assigned to D5 category, with no distinctive fins or body profiles, that displayed secondary markings on either side of their body (e.g. tooth rakes, scrapes, scars) were considered distinctive enough for individual identification within the sighting and were assigned a temporary

identification code, and were included in the Photo-ID group size. By comparing field estimates performed underwater with those from photographic processing, the accuracy of group coverage was assessed (Appendix V).

## **2.4 Pregnancy and age estimation**

Underwater photo-identification allowed the estimation of female reproductive status as follows: females were classified as in (1) early visually detectable stage of pregnancy (referred hereafter as “early pregnancy”), (2) late pregnancy or (3) postpartum status (Figure 2.2). All other females were classified as not pregnant.

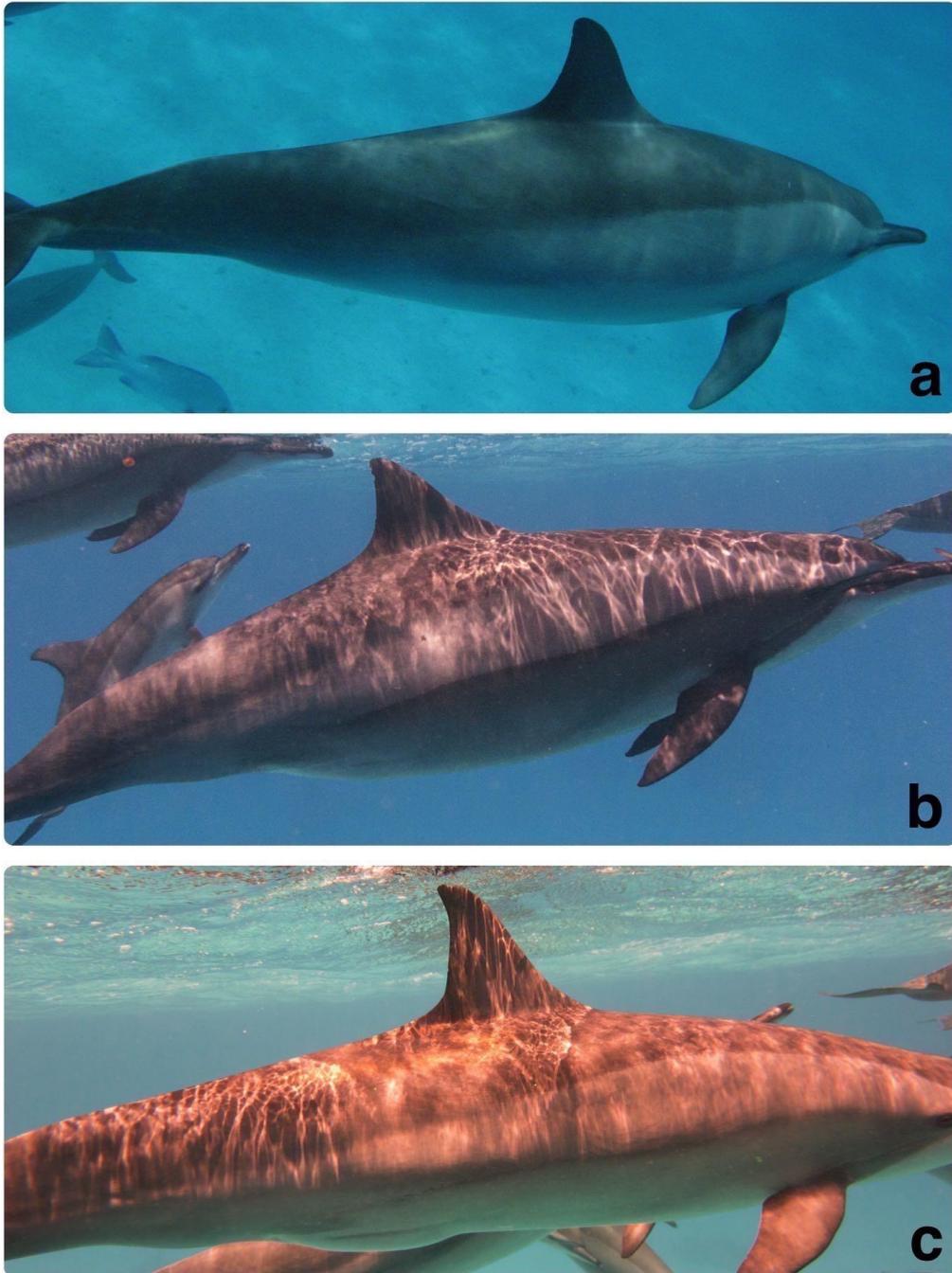


Figure 2.2. Reproductive stages of females: (a) early pregnancy (*i.e.* slightly swollen; approximately midterm pregnancy.); (b) late pregnancy (*i.e.* visibly swollen; starting from *ca.* eighth month); (c) postpartum (*i.e.* distended mammarys; for ~2-4 weeks after delivery, recognizable regardless of the association with a neonate).

Considering that spinner dolphin gestation period last approximately 10.7 months (Whitehead and Mann, 2000), for newborns and first year calves, the dates of birth (DOB) were estimated based on last sighting of the mother seen pregnant and the first sighting of the mother-calf pair. DOB

accuracy was classified as follow: “Exact”:  $\pm 3$  days; “Best”:  $\pm 1$  week; “Good”:  $\pm 2$  weeks; “Fair”:  $\pm 1.5$  month; “Year”:  $\pm 3-6$  months. For all other individuals, a tentative DOB year (labelled as “Tentative year”) was assigned based on the age class recorded on the first encounter and the reported average age for such class in the literature (Perrin et al., 2009b). Because it was not possible to distinguish visually between second and third year calves, both were assigned a minimum age of 2 years. Individuals that were light in colour, less robust and independent from other visibly larger individuals, were considered juveniles and were given a minimum age of 4 years (post-weaning; Chapter 5). Physically mature females and males (hereafter referred to as adult individuals) were assigned a minimum age of 6.5 (Whitehead and Mann, 2000; Mann et al., 2000b) and 8.5 years (Perrin, 1998), respectively, although they could have been not yet sexually mature (Chapter 5). Mature individuals of unknown sex were also assigned an age of 6.5 years.

## **Chapter 3. Morphological and morphometric characteristics of the Red Sea spinner dolphins**

### **3.1 Introduction**

Geographic variation is found in nearly every group of organisms and represents the intrinsic evolutionary potential within a species (Wright, 1943). When populations differ from each other on average (modally) rather than absolutely, they are recognized as geographic forms or ecotypes (Perrin, 2009a). Cetaceans may geographically vary in size, shape, colouration, osteology, genetic features, behaviour, sounds produced, breeding systems, life history traits (such as growth, reproduction, survival) and other characters (Perrin, 2009a). Traits that diversify geographically to the greatest extent are usually those that are most variable within a population. Whenever sufficient samples of cetacean specimens from different regions have been collected and examined, geographic variation has been found (Perrin, 2009a). Recognizing intraspecific taxonomic groups is key to conservation efforts because it provides a foundation for protecting these unique biological entities by: (1) including them in national and international lists that have important legal and financial ramifications, (2) appropriately managing resource allocation (e.g. research funding, conservation initiatives), and (3) increasing the sense of ownership and conservation responsibility of locals towards wildlife (Haig et al., 2006).

Among cetaceans, the spinner dolphin (*Stenella longirostris*, Gray, 1828) is one of the species that best exemplifies geographic variability (Perrin, 1972; Perrin et al., 1991; Douglas et al., 1992; Perrin et al., 2007). It has a pantropical distribution, encompassing tropical and subtropical waters in both hemispheres (Jefferson et al., 2008) and although its taxonomic status at the level of subspecies and geographic forms has been modified

multiple times (Perrin, 1975; Perrin et al., 1977; Perrin et al., 1989; Perryman and Westlake, 1998; Perrin et al., 1999), it is likely far from settled (Robineau and Rose, 1983; Van Waerebeek et al., 1999; Andrews et al., 2010). Currently, four subspecies have been described based on morphological characters (Perrin et al., 2009a; Committee on Taxonomy, 2014): *S.l. orientalis* or eastern spinner dolphin (Perrin, 1990), mostly found in the offshore eastern tropical Pacific waters, *S.l. centroamericana* or Central American spinner dolphin (Perrin, 1990) found only along the coasts of Central America, *S.l. roseiventris* or dwarf spinner dolphin (Wagner, 1846) found in waters of Southeast Asia and northern Australia, and the nominate subspecies *S.l. longirostris* or Gray's spinner dolphin (Gray, 1828), pantropically distributed in all other waters. Two more ecotypes are recognized based on phenotypic differences (summarized in Andrews et al., 2013) (Figure 3.1). The so called “whitebelly spinner dolphin”, an apparent hybrid form between *S.l. orientalis* and *S.l. longirostris*, is found in the offshore eastern tropical Pacific; the “Tres Marias” ecotype, identified off the northern coast of Mexico, is ascribed to the eastern subspecies (Figure 3.1). Other potentially divergent ecotypes have been described in Oman (Van Waerebeek et al., 1999) and in the Gulf of Aden (Robineau and Rose, 1983); however, adequate samples of specimens are needed to confirm these geographic variations.

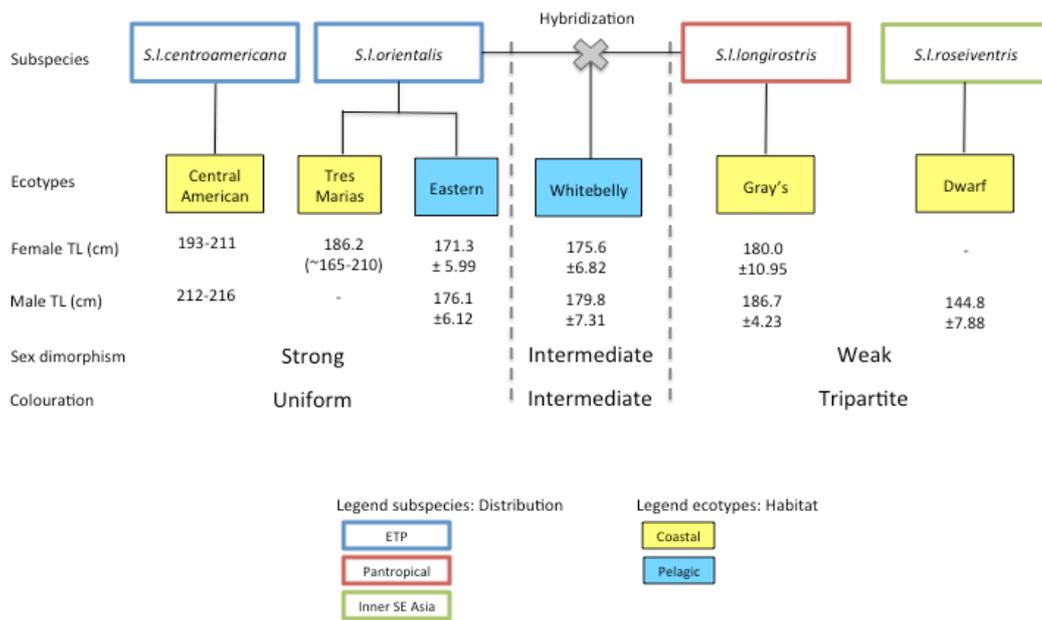


Figure 3.1. Phenotypic differences between spinner dolphin ecotypes (grouped in four recognized subspecies as shown); after Andrews et al. (2013), modified. TL stands for Total Length; ETP stands for Eastern Tropical Pacific.

In contrast to the pelagic distribution of the eastern and whitebelly spinner dolphin, the other ecotypes are primarily coastal (Figure 3.1). The Gray's spinner dolphin is primarily inshore in habitat preference (Perrin and Gilpatrick Jr, 1994) and usually feed at night on mesopelagic squid and fish following the rising of the deep scattering layer toward the ocean surface (Benoit-Bird and Au, 2003). During the day, these dolphins use inshore habitats (lagoons, reefs or islands) to rest and socialize, probably to reduce the chances of deep-water shark predation (Norris and Dohl, 1980). The Red Sea spinner dolphins display similar diurnal resting behaviour and are currently ascribed to the Gray's subspecies (Notarbartolo di Sciara et al., 2009).

Despite being one of the most studied species globally, the spinner dolphin is relatively poorly known in the Red Sea and until late 1980s it was thought to be absent in this region (Frazier et al., 1987). Recent data, collected during 2010-2013 in the Southern Egyptian Red Sea, indicate

that spinner dolphins are in fact one of the most abundant species in the region (Costa et al., 2016). The present knowledge of the ecology and behaviour of the Red Sea spinner dolphins is mostly based on data collected in Samadai reef during a 2-year monitoring project carried out in 2004-2005 (Notarbartolo di Sciara et al., 2009), followed by a 1-year study in 2005-2006 (Shawky and Afifi, 2008; Costa et al., 2012; Shawky et al., 2015).

Reeves (2004) recommended that in order to formally recognize an intraspecific taxon, referring specifically to a subspecies level, there has to be at least either appropriate morphological or genetic evidence. For most cetaceans, however, it is challenging to collect a sufficient number of samples to properly provide such evidence (Wang, 2009). On the other hand, analyses of external phenotypical characters (*e.g.* size, shape, colouration) have been successfully carried out on several species of free-ranging cetaceans, including spinner dolphins (Perrin et al., 1991; Perryman and Westlake, 1998) and proved to be informative for population description, sometime differentiation (*e.g.*, Evans et al., 1982; Koopman and Gaskin, 1994; Wang et al., 2008), leading to reviews of the taxonomic status of several species and management recommendations (*e.g.*, Heyning and Perrin, 1994; Perryman and Lynn, 1993; Jefferson and Rosenbaum, 2014; Wang et al., 2015; Brown et al., 2015).

A combination of photo-identification and photogrammetric techniques is particularly useful in exploring morphological and phenotypical features as it does not require any capture of the animals; with photogrammetry proven to be effective in obtaining measurements of free-ranging cetaceans (Durban and Parsons, 2006). Three main approaches to photogrammetry have been used in both terrestrial and marine environments: (1) stereo-photogrammetry, where stereo photographs are taken simultaneously from a pair of aligned cameras (*e.g.* elephants, Hall-Martin and Ruther, 1979; sharks, Klimley and Brown, 1983; whales, Cabbage and Calambokidis, 1987; dolphins, Bräger and Chong, 1999; bluefin tuna, Harvey et al., 2003; pinnipeds, Waite et al., 2007), (2) the use

of a single camera, along with an instrument to determine the distance between the camera and the target (e.g. range finder for elephants, Shrader et al., 2006; and gorillas, Breuer et al., 2007; or altimeter for aerial photogrammetry of whales, Best and R  ther, 1992; and dolphins, Perryman and Lynn, 1993; Perryman and Westlake, 1998) and (3) the use of a single image which includes something of known size at the same distance of the target to provide scale (e.g. whale shark, Bradshaw et al., 2008).

Although stereo-photogrammetric techniques are powerful and accurate, they can be expensive to implement (e.g. aerial surveys, although the increasing use of unmanned drones proved to be more cost effective; Durban et al., 2015) and cumbersome to use in the field and during processing and analysis (Harvey et al., 2003). Moreover, stereo photographs are not suitable for intrinsically flexible animals such as cetaceans (Dawson et al., 1995). However, a paired-laser photogrammetric technique has now been used for over a decade and proved to be simple, efficient, cost-effective, and portable (Durban and Parsons, 2006; Webster et al., 2010). Paired-laser photogrammetry uses two parallel laser pointers mounted onto a single camera. The known distance between the two dots projected on the target works as a scale from which the size of the target can be inferred, provided that the target is perpendicular to the axis of the lasers. This technique has been successfully employed in measuring horn size in ibex (Bergeron, 2007), monkeys' tail length (Rothman et al., 2008) and cetacean dorsal fins (Durban and Parsons, 2006; Rowe and Dawson, 2008; Webster et al., 2010). More recently, it has also been successfully applied underwater to measure the length of large cartilaginous fish, (e.g. manta rays, Deakos, 2010; Best and R  ther, 1992; whale sharks, Rohner et al., 2011). As an additional benefit, the same images used for photogrammetric analyses can be simultaneously used to detect pigmentation patterns and morphological variability.

The initial objective of my photogrammetric investigations was to examine, qualitatively and quantitatively, the external phenotypical characteristics (morphometrics, sexual dimorphism and ontogenic development of pigmentation patterns and dorsal fin shape) of the Red Sea spinner dolphin to develop a morphometric-ontogenetic classification system to accurately estimate age classes. Subsequently, the phenotypic characteristics of the Red Sea spinner dolphins were compared to other geographic forms, leading to the suggestion of a new ecotype, the Red Sea form of the spinner dolphin, which is presented in this chapter.

## **3.2 Materials and methods**

### **3.2.1 Photogrammetry**

#### *Equipment, data collection and photo processing*

Photogrammetric data were collected during 12 underwater photo-identification surveys at Samadai reef, between June and August 2014.

As seawater absorbs green light to a lesser extent than red light, green lasers can be viewed over a greater distance. In this study, two underwater green-beam laser pointers (model: Amphibian Green Laser) with output power < 5 mW (class IIIa, in compliance with safety regulations in case of inadvertent exposure of cetaceans retina to laser beam; Zorn et al., 2000) and wavelength of 532nm (Sea Turtle Scuba Inc., <http://www.seaturtlescuba.us/>) were used. The lasers were mounted in parallel, 200 mm apart, onto a stainless steel plate. The plate was mounted to the bottom of a Canon WP-DC47 Waterproof Case for a PowerShot S110 Digital Camera. Each laser was held in place by a custom-made hard PVC drilled cube with a threaded mechanism which allowed a fine-scale adjustments of each laser pointer to ensure the projected beams were in parallel (Figure 3.2).



Figure 3.2. Underwater green-beam laser pointers mounted in parallel onto underwater camera housing.

Before each underwater photogrammetric data collection, the laser alignment was verified on land at 1, 3 and 7 metres by photographing a graph paper. Adjustments were made until the distance between the projected dots was constant at 200mm ( $\pm 1$ mm). To ensure the lasers remained parallel, alignment was also checked at sea before entering the water by photographing an identical measured grid on the boat at a range of approximately 1 and 3 metres.

Once the dolphins were approached underwater, the camera was positioned so that the plane of the dolphin body was perpendicular to the direction of the laser projections, with the two laser dots projected as much as possible onto the centre of the dolphin flank, at a distance that allowed the full length of the dolphin to be captured on the image within the calibration range. However, images representing only the dorsal fin were also retained for further analysis. Webster et al. (2010) showed that there is no evidence for bias introduced by whether the laser dots are projected on the body or the dorsal fin. To prevent any accidental exposure to the dolphins' eyes, the laser were switched on only when directed at the dolphins' body and switched off immediately after the photograph was

taken. No avoidance reaction was ever noticed during the collection of photogrammetric data.

Photographs were selected, edited and processed as described in Chapter 2 and Appendix I. High quality (Q1 and Q2) photographs (in focus, un-obscured, with the dorsal fin perpendicular to the plane of the photographer) of any distinctiveness category (D1 to D5) were used for subsequent analyses.

#### *Morphometric measurements*

Total body Length (TL), dorsal fin height (DFH), dorsal fin base width (DFW) were measured from the digital images using the freely available software ImageJ64 (<http://rsbweb.nih.gov/ij/>) (Figure 3.3). The known distance between the projected lasers (200 mm) was used to calibrate the photographs. TL is defined here as the standard total length (Norris, 1961), *i.e.* the length from the tip of the rostrum to the fluke notch; dorsal fin measurements were obtained by drawing reference lines as described in Olesiuk et al. (1990) and shown in Figure 3.3.

The dorsal fin Canting Index (CI) (Jefferson, 1990) was used to test quantitatively for variation in dorsal fin shape, and it was estimated as  $a/DFH$ , where  $a$  is the length from posterior insertion of dorsal fin to a perpendicular from tip (Figure 3.3). The higher the CI the larger the degree of forward canting. Jefferson's CI was preferred over Amano and Miyazaki's (1993) as it best accounted for variation in spinner dolphin dorsal fin shape.

Following Yezerinac et al. (1992), to minimize type II error, at least 3 independent measurements (" $b$ " in the formula below) on either side of the dolphin body were attempted (this, however, proved challenging; see Appendix III). Consequently, the values of TL, DFH, DFW and  $a$  represent the mean values for each individual. On every image, as many morphometric measurements as possible were done. At times, however, not all measurements were possible for a given image and therefore the

sample size for analyses of the various morphometric characteristics differ. Precision of the paired-laser system was assessed by calculating the percentage coefficient of variation (CV) from several measurements of the same individual during the same survey and across different surveys.

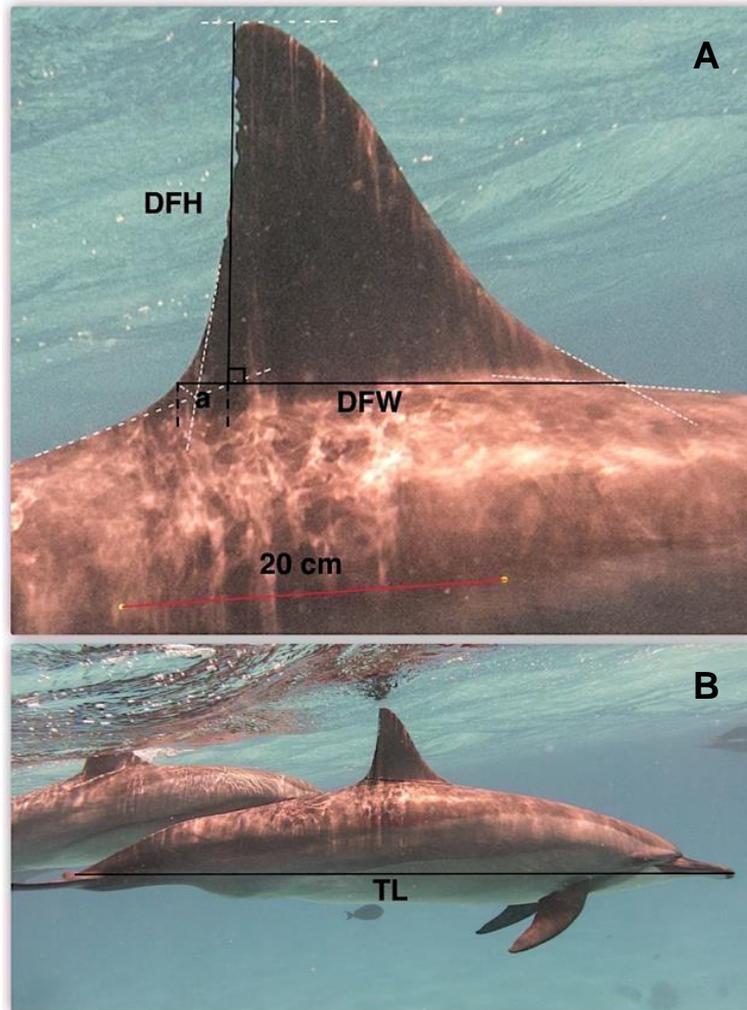


Figure 3.3. Digital underwater photograph of a male spinner dolphin dorsal fin (A) and whole body (B) with projected laser dots and a schematic representation of the measurements performed. DFW: Dorsal Fin Width, DFH: Dorsal Fin Height, TL: Total Length, *a*: length from posterior insertion of dorsal fin to a perpendicular from tip which was used to calculate dorsal fin Canting Index (see text for details).

#### *Sources of error, quantification and mitigations*

Potential sources of measurement error include: (1) non-parallel alignment of the lasers; (2) parallax error (3) definition error (4) inherent flexibility of the animals (5) image distortion caused by light refraction (above water vs. underwater measurements).

(1) Non-parallel alignment of the laser pointers affects the distance between the laser projections on the target, which changes depending on the distance from the target and whether the lasers diverge or converge. Calibrating the lasers daily before use at different ranges minimized this potential error.

(2) Parallax error, along both the vertical and horizontal axes, occurs when the laser projections are not perpendicular to the plane of the target. The greater the deviation of the individual from perpendicular to the focal plane of the camera/laser, the greater the error (Durban and Parsons, 2006). A previous study on Hector's dolphins (Webster et al., 2010) showed that if photographs were taken at an angle not greater than  $20^\circ$  from perpendicular, the dorsal fin measurements remained within 2% of the actual fin height or base length. In my study, a conservative approach was adopted and all images with an apparent angle of the dolphin relative to the focal plane of the image greater than  $10^\circ$  were discarded. Furthermore, to assess whether the measurements were replicable and the laser system reliable, the coefficients of variation (CV%) were calculated for each metric for each individual photographed multiple times and the mean CVs per each metric were then compared to that from other studies employing similar photogrammetric techniques.

(3) Definition error may result from subjective determination of the placement of the anterior and posterior insertions of the dorsal fin and/or by the precise localization of the fluke notch (Durban and Parsons, 2006). To ensure consistency in data processing, all procedures, from taking the underwater photographs to image processing were performed by the same researcher. Furthermore, to minimize human error, reference lines were drawn along the main axes of the dolphins' back and dorsal fin and the intersection of these lines was used to define the fin's insertion (Figure 3.3; see also further).

(4) Dolphins are inherently flexible along the dorsal plane, condition that adds variability to the measurements of dorsal fin and body total length (Dawson et al., 1995). Therefore, all photographs where the dolphins' bodies were not completely extended were not considered suitable and discarded. Also, photographs where the fluke notch was not visible (*i.e.* the flukes were obscuring the notch, hampering its localization) were excluded.

To quantify this variability, randomly chosen photographs of individuals photographed multiple times were repeatedly measured.

A model II nested analysis of variance (ANOVA) was used to investigate within- and among-photograph measurement errors by partitioning the total variance of total length, dorsal fin width and dorsal fin height measurements into “within” and “among” components (see Rowe and Dawson, 2008). “Within” component represents the precision of the method to repeatedly identify the anterior and posterior insertion points of the dorsal fin or the fluke notch on the same photograph. This error was assessed using 5 non-consecutive repeated measurements ( $n$ ), taken without the knowledge of previous measurements (the “Subgroup” in the formula) of all morphometrics for each individual. “Among” component represents the variance in measurements taken from different pictures ( $b=3$ ; as indicated above) of the same individual (the “Group”).

The within- and among-photographs percentage measurement errors (%ME) were calculated for each metric (TL, DFW, DFH; following Rowe and Dawson, 2008; Blackwell et al., 2006):

$$\%ME_{within} = 100 \left( \frac{S^2_{withinSubgr}}{S^2_{withinSubgr} + S^2_{amongSubgr} + S^2_{amongGr}} \right)$$

$$\%ME_{among} = 100 \left( \frac{S^2_{amongSubgr}}{S^2_{withinSubgr} + S^2_{amongSubgr} + S^2_{amongGr}} \right)$$

Where:

$$s^2_{withinSubgr} = MS_{withinSubgr} ,$$

$$s^2_{amongSubgr} = \frac{MS_{amongSubgr} - MS_{withinSubgr}}{n}$$

and

$$s^2_{amongGr} = \frac{MS_{amongGr} - MS_{amongSubgr}}{bn}$$

(5) Refraction can cause image distortion. Refraction is the bending of a ray of light as it passes from one medium (e.g. seawater) into another (e.g. air inside the underwater camera housing/laser shell) in a direction that is not perpendicular to the boundary between the two media (Feynman et al., 1963). Previous studies however demonstrated that: (i) when laser beams are set perpendicular to the camera lens there is no light refraction apparent to the camera when submerged (Muljowidodo et al., 2009); and (ii) there is no significant difference between above water and in-water measurement results (Jeffreys et al., 2013). Hence, in this study, image distortion was considered minimal and to have had only a negligible effect on the obtained measurements.

Although it is unlikely to completely eliminate the abovementioned errors during field data collection, it is possible to (1) mitigate for such errors (*i.e.* discarding the images that do not meet the criteria indicated above) and (2) account for them by means of ME quantification, thus increasing the accuracy of the measurements.

### 3.2.2 Morphological features

#### *Dorsal fin shape*

Dorsal fin shape was tested qualitatively and coded after Perrin (1991) as shown in Figure 3.4. When the overall shape of the fin was not

recognizable (e.g. the distal portion of the dorsal fin was entirely missing due to injury) the fin was not assigned to a category and not used in the analysis.

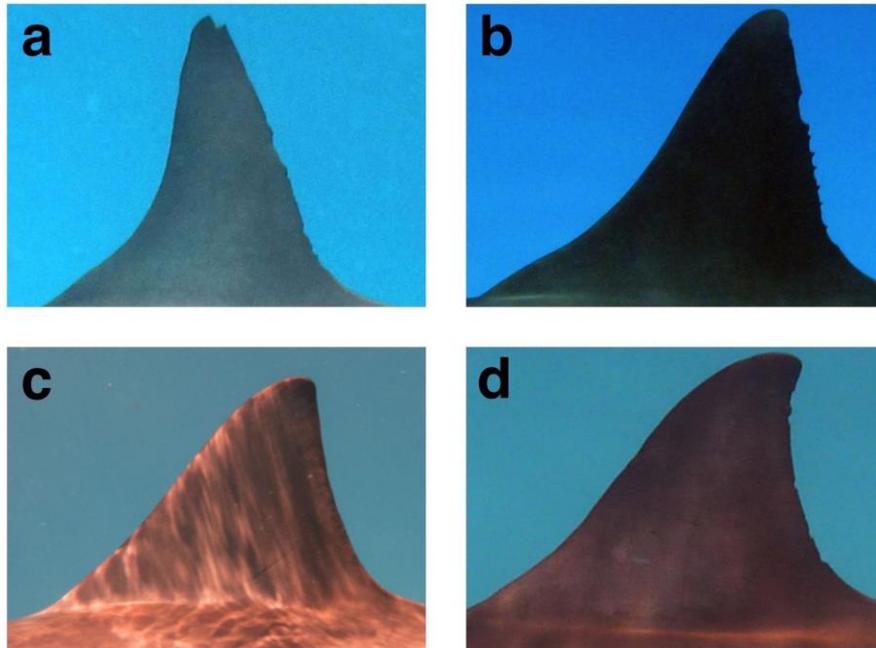


Figure 3.4. Dorsal fin shapes of Red Sea spinner dolphins (the leading edge is to the left for all fins): (a) Shape 1: canted - closest to a right triangle with hypotenuse posterior; (b) Shape 2: erect - isosceles triangle; (c) Shape 3: falcate - right triangle with hypotenuse anterior; (d) Shape 4: falcate and indented to varying degrees along the trailing edge. Shapes 1-3 after Perrin (1991).

### *Post-anal hump*

Size of post-anal hump represents a secondary sexual character in males of several small cetacean species (Jefferson, 1990; Jefferson et al., 1997; Neumann et al., 2002) including spinner dolphins (Perrin et al., 1991). In this study, photographed dolphins whose estimated age and sex were known, were graded for the depth of post-anal hump. Only photographs that displayed the entire dolphin body in one plane, not bent up or down (Figure 3.3b) and perpendicular to the camera were used. The terminology of Jefferson (1997) was used to describe the depth of post-anal hump, as listed in Table 3.1.

Table 3.1. Categories used to qualitatively describe the Red Sea spinner dolphin post-anal hump (*i.e.* increase in girth in the posterior portion of the body).

| Category           | Description of the depth of the post-anal hump in the Red Sea spinner dolphin | Image  |
|--------------------|---|--|
| <b>Non Present</b> | No ventral protuberance.  |    |
| <b>Slight</b>      | Slightly swollen behind the anal region.                                      |    |
| <b>Moderate</b>    | Evident protuberance in the post-anal region.                                 |   |
| <b>Large</b>       | Large ventral protuberance, thick peduncle.                                   |  |

### 3.2.3 Pigmentation pattern

The colouration of the Red Sea spinner dolphins was examined by analysing underwater photographs collected throughout the entire study, from October 2005 to August 2014 (Chapter 2). Only images with negligible light reflection on the dolphin body and good contrast were used for further analyses. To determine the ontogeny of the pigmentation pattern, the intensity of the pigmented eye-to-anus stripe (following terminology from Mitchell, 1970) was used as proxy (Table 3.2). This

stripe runs from the eye to the genital/anal region and may be sex and age related (e.g. Jefferson et al., 1997).

Table 3.2. Description of the eye-to-anus stripe categories used as proxy for the colouration pattern of Red Sea spinner dolphins.

| Category              | Description of the eye-to-anus stripe in the Red Sea spinner dolphin  | Image  |
|-----------------------|---|--|
| <b>Non Present</b>    | No stripe or dense pigmentation are visible. Two or three tone color phase.   |    |
| <b>Faint and thin</b> | Sparse pigmentation/light line usually starting off in the centre of the flank.   |    |
| <b>Moderate</b>       | Marked stripe running along the flank: either short and central or extending towards the eye but fades away before reaching it. |   |
| <b>Dark and thick</b> | Evident dark line along the flank that reaches the eye. Sparse pigmentation above and/or below the eye.                         |  |

### 3.2.4 Analytical approach

Sexual dimorphism was examined by conducting a multivariate analysis of variance (MANOVA). Morphometric measurements were collected for 61 adult individuals. However, individuals with missing measurements even for only one variable (either TL, DFW or DFH) were eliminated from the dataset, hence 24 males and 22 females were included in the MANOVA. Power analyses were conducted in G\*Power to evaluate the effect size (Faul et al., 2007). All measurements were tested for multivariate normality (Shapiro-Wilk test) and homogeneity of variance and covariance of matrices (Box's M test) between sexes. Univariate normality is a necessary condition for multivariate normality but does not guarantee multivariate normality. Univariate test of equality of variances between groups was performed first (Levene's test), then covariance matrices were compared between groups using Box's M test (non significant if the matrices are the same).

The differences in each character were then analysed with t-tests. To guard against Type I error, first the absence of multicollinearity was checked. Tabachnick and Fidell (2007) suggest that no correlation should be above  $r = 0.90$  (the morphometric data, *i.e.* TL, DFW and DFH, were significantly correlated to each other ( $p < 0.05$ ), but  $r$  was between 0.70 and 0.80 for all pairs). Secondly we considered an alpha value of 0.016 (Bonferroni correction =  $0.05/n$ , where  $n$  is the number of tests conducted and equals 3) as significant in the t-tests.

Dorsal fin canting index was calculated to determine if the shape of dorsal fins differed between sexes as:  $a/DFW = \text{canting index}$ , where  $a$  = length from posterior insertion of dorsal fin to a line perpendicular with the dorsal fin tip (Jefferson, 1990) (Figure 3.3). The difference between sexes was analysed with t-test (27 males, 23 females).

Dorsal fin shapes, degree of post-anal hump depth and pigmentation patterns were examined across age and sex classes. Chi-square tests

were used to test for statistical significance within age/sex classes (for  $n > 10$ ).

To evaluate the ontogeny of pigmentation in the Red Sea spinner dolphins, observations of individuals whose date of birth (DOB) was accurate to within a year were collated from across the 2005-06, 2010 and 2011-2014 surveys. Data for individuals whose minimum age estimation was based on literature (e.g. dolphins that were already adult when first encountered) were included and their DOB accuracy labelled as “Tentative year”.

Linear regressions were fitted to determine whether age and/or total body length could predict the Canting Index in females and males. To best visualize at what point (age and/or total body length) dorsal fins started to be more canted forward, locally weighted regression were fitted to the data (i.e. smoothing interpolation by function `loess` in R, R Core Team, 2014). A multinomial logistic regression was fitted to assess if age and/or total body length could predict the colouration pattern of the Red Sea spinner dolphin. Significance for all statistical tests was set at  $p < 0.05$ . All analyses were performed with the freely available software R (R Core Team, 2014).

### 3.3 Results

In total, 12 photogrammetric surveys were conducted during which 220 high quality images of 113 spinner dolphins were taken: 61 adults (33 females and 28 males) and 52 immature individuals. Mean values of morphometric measurements per age class are given in Table 3.3.

#### 3.3.1 Source of error

##### *Measurements variation within individual*

The CV of TL for all age/sex class individuals ( $N=113$ ) averaged 3.40% (range: 0.15 - 6.78%). DFW ranged from 0.35 to 8.16% with a mean value

of 4.42% and for DFH the mean value was 3.77%, with a range from <0.1% to 8.76%. CVs for each age/sex class are given in Table 3.3 whilst CVs by individual are listed in Appendix III.

Table 3.3. Summary statistics of morphometric measurements, total length (TL), dorsal fin width (DFW) and dorsal fin height (DFH) per age class and sex class (when available) of the Red Sea spinner dolphins. Age classes are defined as: NB: newborn <2months; C1: 1-year old calf; C2: 2-years old calf; C3: 3-years old calf; Juvenile: >4 years old, until adult; Adult: physically mature dolphin.

| Age/Sex Class    | n  | TL    |       |       | DFW  |      |      | DFH  |      |      |
|------------------|----|-------|-------|-------|------|------|------|------|------|------|
|                  |    | Mean  | SD    | CV    | Mean | SD   | CV   | Mean | SD   | CV   |
| <b>NB SexUnk</b> | 23 | 85.6  | 5.98  | 2.61% | 12.6 | 1.13 | 1.8% | 8.1  | 0.62 | 5.4% |
| <b>C1</b>        |    |       |       |       |      |      |      |      |      |      |
| <b>Males</b>     | 2  | 115.3 | 8.46  | 3.93% | 18.9 | 0.99 | 4.3% | 12.3 | 0.14 | 1.1% |
| <b>SexUnk</b>    | 5  | 124.7 | 8.01  | 4.68% | 19.3 | 2.08 | 3.0% | 13.0 | 0.23 | 1.4% |
| <b>C2</b>        |    |       |       |       |      |      |      |      |      |      |
| <b>Females</b>   | 4  | 134.3 | 3.39  | 4.57% | 18.9 | 0.95 | 5.3% | 13.4 | 1.14 | 5.9% |
| <b>Males</b>     | 1  | 146.4 | -     | -     | -    | -    | -    | -    | -    | -    |
| <b>SexUnk</b>    | 8  | 138.6 | 5.40  | 3.09% | 20.3 | 0.79 | 3.8% | 14.6 | 1.22 | 1.1% |
| <b>C3</b>        |    |       |       |       |      |      |      |      |      |      |
| <b>Males</b>     | 1  | 155.9 | -     | 3.16% | 20.5 | -    | 0.3% | 16.1 | -    | -    |
| <b>SexUnk</b>    | 1  | 148.1 | -     | 3.87% | 19.7 | -    | 5.7% | 15.5 | -    | 0.0% |
| <b>Juvenile</b>  |    |       |       |       |      |      |      |      |      |      |
| <b>Males</b>     | 6  | 156.3 | 13.06 | 5.14% | 22.2 | 1.14 | 6.5% | 16.7 | 1.32 | 2.0% |
| <b>SexUnk</b>    | 1  | 173.2 | -     | -     | 22.3 | -    | -    | 16.9 | -    | -    |
| <b>Adult</b>     |    |       |       |       |      |      |      |      |      |      |
| <b>Males</b>     | 28 | 183.4 | 7.53  | 2.2%  | 26.2 | 1.69 | 4.8% | 20.1 | 1.49 | 4.3% |
| <b>Females</b>   | 33 | 167.0 | 7.68  | 3.58% | 23.1 | 1.10 | 5.4% | 16.5 | 1.21 | 6.1% |

### *Measurement errors*

Results of the model II nested ANOVA are given in Table 3.4 and they show that variation among individual dolphins was significantly greater than among measurements of the same individual for all metrics and can be considered to be repeatable (Bailey and Byrnes, 1990). The mean among-photograph error was also greater than within-photograph error for all metrics, *i.e.* the variation between different photographs of the same individual significantly exceeded variation from repeated measurements of the same photograph. Repeated measurements of the same individual, when available, were averaged in all subsequent analyses.

Table 3.4. Summary of the Model II nested ANOVA and percentage Measurement Errors for total length (TL), dorsal fin width (DFW) and dorsal fin height (DFH) of the Red Sea spinner dolphins

|   | <b>SS</b> | <b>df</b> | <b>MS</b> | <b>F</b> | <b>p-value</b> | <b>Variance</b> | <b>%ME within</b> | <b>%ME among</b> |
|---|-----------|-----------|-----------|----------|----------------|-----------------|-------------------|------------------|
| <b>TL</b>                                   |           |           |           |          |                |                 | 0.05              | 4.37             |
| <b>Among individuals</b>                    | 182566    | 15        | 12171     | 66.50    | <0.001         | 799.20          |                   |                  |
| <b>Among photographs within individuals</b> | 5857      | 32        | 183       | 453.24   | <0.001         | 36.53           |                   |                  |
| <b>Within photographs</b>                   | 78        | 192       | 0         |          |                | 0.40            |                   |                  |
| <b>Total</b>                                | 188500    | 239       | 789       |          |                |                 |                   |                  |
| <b>DFW</b>                                  |           |           |           |          |                |                 | 0.12              | 5.73             |
| <b>Among individuals</b>                    | 4063      | 12        | 339       | 50.09    | <0.001         | 22.12           |                   |                  |
| <b>Among photographs within individuals</b> | 176       | 26        | 7         | 248.00   | <0.001         | 1.35            |                   |                  |
| <b>Within photographs</b>                   | 4         | 156       | 0         |          |                | 0.03            |                   |                  |
| <b>Total</b>                                | 4243      | 194       | 22        |          |                |                 |                   |                  |
| <b>DFH</b>                                  |           |           |           |          |                |                 | 0.08              | 5.04             |
| <b>Among individuals</b>                    | 2755      | 9         | 306       | 57.35    | <0.001         | 20.05           |                   |                  |
| <b>Among photographs within individuals</b> | 107       | 20        | 5         | 322.87   | <0.001         | 1.06            |                   |                  |
| <b>Within photographs</b>                   | 2         | 120       | 0         |          |                | 0.02            |                   |                  |
| <b>Total</b>                                | 2864      | 149       | 19        |          |                |                 |                   |                  |

### 3.3.2 Sex dimorphism in adult spinner dolphins

All morphometric measurements collected (TL, DFW, DFH, *a*) had normal distribution (Shapiro-Wilk test  $p > 0.05$ ) and their variance and covariance of matrices (Box's M test,  $p > 0.05$ ) were homogeneous between sexes (Figure 3.5).

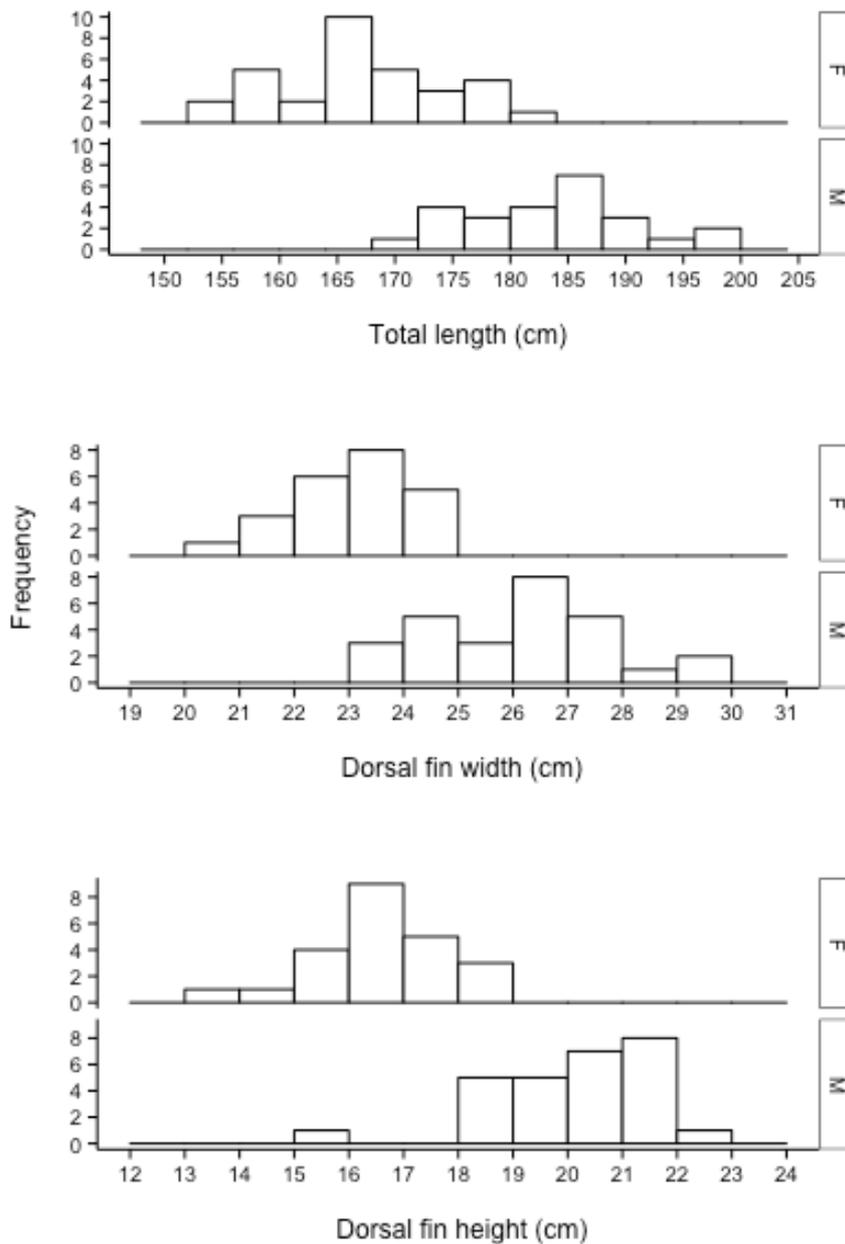


Figure 3.5. Morphometric measurements for 61 individual adult Red Sea spinner dolphins grouped by sex. F and M stand for Females and Males, respectively.

Forty-six individuals (22 adult females and 24 adult males) were included in MANOVA analysis and found to be significantly different between sexes ( $p < 0.0001$ ; Table 3.5). Power analyses for MANOVA ( $\alpha = 0.05$ ,  $\text{power} = 0.80$ ) indicated effect size ( $f = 0.26$ ) to be small, according to (Cohen, 1992) to medium, according to (Faul et al., 2007).

Table 3.5. Overall MANOVA tests of morphometric measurements of Red Sea spinner dolphins yielded significant differences between sexes.

|                         | <b>Test</b> | <b>F</b> | <b>Df</b> | <b>P</b> |
|-------------------------|-------------|----------|-----------|----------|
| <b>Pillai</b>           | 0.73142     |          |           |          |
| <b>Hotelling-Lawley</b> | 2.7233      | 38.126   | 3,42      | 4.65e-12 |
| <b>Roy</b>              | 2.7233      |          |           |          |
| <b>Wilks</b>            | 0.26858     |          |           |          |

Given the significance of the overall tests, the univariate main effects were examined and found significantly different (all  $p < 0.0001$ ; after the conservative Bonferroni correction). All morphometric measurements of adult males were significantly larger than those of adult females (Table 3.6).

Table 3.6. Summary statistics of morphometrics of adult Red Sea spinner dolphins grouped by sex.

|                      |             | Females | Males | t-test<br>p-values |
|----------------------|-------------|---------|-------|--------------------|
| <b>Morphometrics</b> |             |         |       |                    |
| <b>TL</b>            | <b>n</b>    | 32      | 25    |                    |
|                      | <b>mean</b> | 167.0   | 183.4 | <0.0001            |
|                      | <b>SD</b>   | 7.68    | 7.52  |                    |
|                      | <b>SE</b>   | 1.36    | 1.50  |                    |
| <b>DFW</b>           | <b>n</b>    | 23      | 27    |                    |
|                      | <b>mean</b> | 23.1    | 26.2  | <0.0001            |
|                      | <b>SD</b>   | 1.10    | 1.69  |                    |
|                      | <b>SE</b>   | 0.23    | 0.32  |                    |
| <b>DFH</b>           | <b>n</b>    | 23      | 27    |                    |
|                      | <b>mean</b> | 16.5    | 20.1  | <0.0001            |
|                      | <b>SD</b>   | 1.20    | 1.50  |                    |
|                      | <b>SE</b>   | 0.25    | 0.29  |                    |

The difference between the mean Canting Indices (CI) for adult males and females was found highly significant ( $t = -5.3706$ ,  $df = 45$   $p < 0.0001$ ; Figure 3.6).

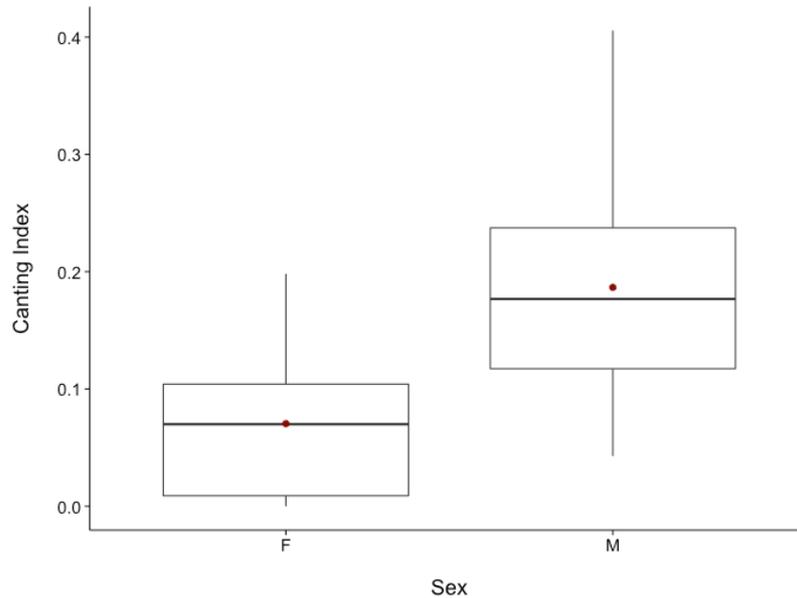


Figure 3.6. Box plot of Canting Indices (CI) values for females (F;  $n=23$ ) and males (M;  $n=27$ ) Red Sea spinner dolphins. Boxes show lower and upper quartile; whiskers represent minimum and maximum values; medians and means are represented by midlines and red dots, respectively.

The mean dorsal fin width/height ratio of adult females was significantly higher than that of males ( $t = 3.2998$ ,  $df = 47$ ,  $p < 0.01$ ; Figure 3.7). These results indicate that dorsal fins of adult males are proportionally taller and more canted forward than in females.

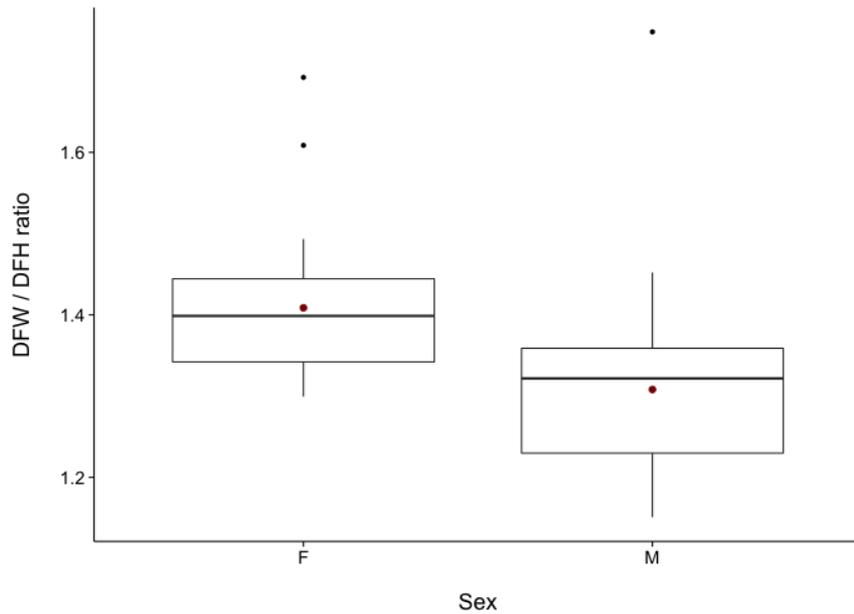


Figure 3.7. Box plot of dorsal fin width/height ratio values of female (F;  $n=23$ ) and male (M;  $n=27$ ) Red Sea spinner dolphins. Boxes indicate lower and upper quartile; whiskers represent minimum and maximum values; medians and means are represented by midlines and red dots, respectively.

### 3.3.3 Size by age class

The total length (TL) measurements were obtained for 109 spinner dolphins of different age classes. Mean dolphin size distribution per age class is shown in Figure 3.8.

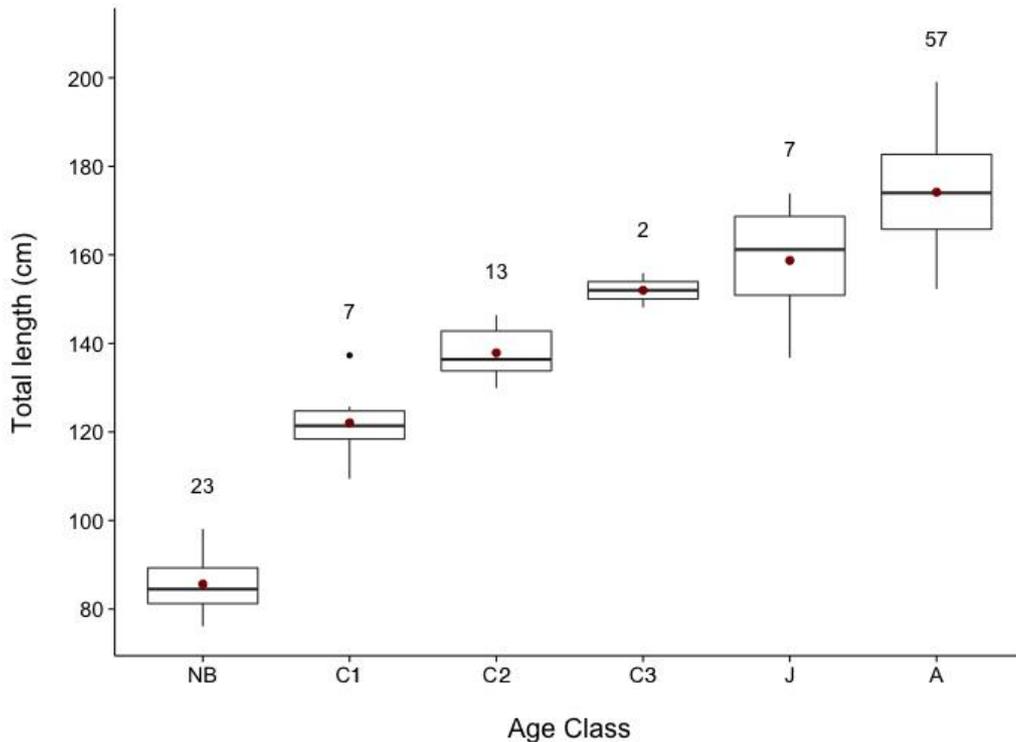


Figure 3.8. Mean body length of the Red Sea spinner dolphin by age class. Boxes show lower and upper quartile; whiskers indicate minimum and maximum values; medians and means are represented by midlines and red dots, respectively. Sample size for each age class is shown above each box. Age classes are defined as: NB: newborn (< 2months old); C1: 1-year old calf; C2: 2-years old calf; C3: 3-years old calf; J: juvenile (>4 years old, until adult); A: mature dolphin.

### 3.3.4 Ontogeny of phenotypic characters

Immature females and males have falcate or very falcate dorsal fins, which become significantly more erect with age in males only (Figure 3.9; see also further "Development of the dorsal fin shape"). The development of post-anal hump follows the same pattern; it is absent or slight in immature individuals and remains so in adult females, but in males it increases in size and volume with age.

One of the most peculiar features of the Red Sea spinner dolphins is a dark eye-to-anus stripe, which is age-related; it is absent or faintly expressed in immature dolphins, whereas in mature individuals it becomes darker with age. Adult females, however, displayed a variable intensity of pigmentation, ranging from faint to dark. All males were significantly darker (Figure 3.9).

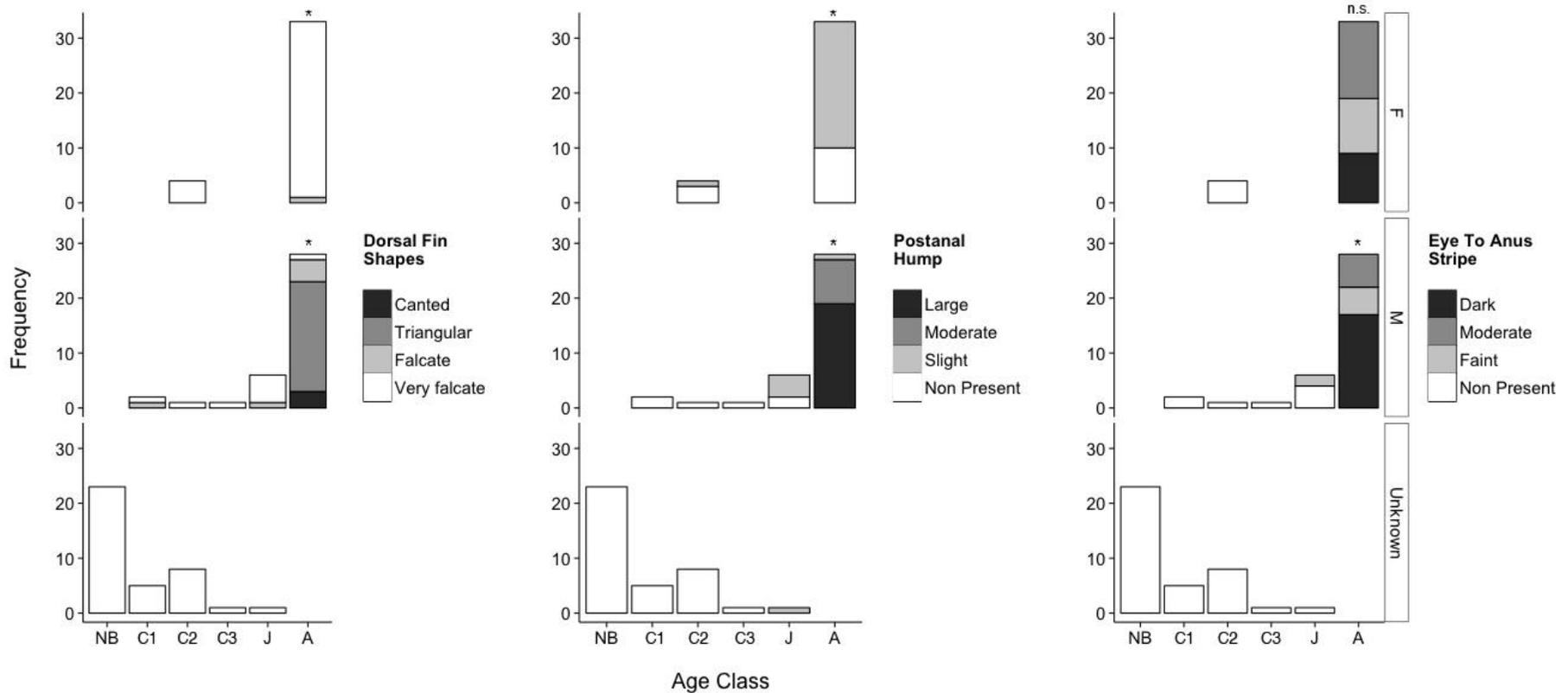


Figure 3.9. Frequency of three phenotypic characters, shape of the dorsal fin, depth of the post-anal hump, and eye-to-anus stripe, across age and sex classes of the Red Sea spinner dolphin. Age classes are defined as: NB: newborn <2months; C1: 1-year old calf; C2: 2-year old calf; C3: 3-year old calf; J: juvenile (>4 year old, until full-size adult); A: mature dolphin. F and M stand for Females and Males, respectively. Within age/sex class significance is indicated with \* and n.s. stands for non-significant.

### *Development of the dorsal fin shape*

Canting Index (CI) calculated at different age and different body length indicates that age and total body length can serve as good predictors of CI in male ( $p < 0.001$ ,  $R^2 = 0.39$  and  $p < 0.05$ ,  $R^2 = 0.20$  for age and total body length, respectively) but not female ( $p > 0.05$ ,  $R^2 = 0.09$  and  $p > 0.05$ ,  $R^2 = 0.004$ , respectively) Red Sea spinner dolphins (Figure 3.10). In males, after reaching the age of ~8 years and body length of ~160 cm, the dorsal fin undergoes a rapid development and becomes progressively more canted with age, as indicated by a rapid change of the CI (Figure 3.11; the lack of sexed newborns in the dataset and the ages being mostly assigned referentially likely contribute to the instability of the smoothed curves). From this point, males begin showing increasing signs of sexual dimorphism. No such changes occur in females.

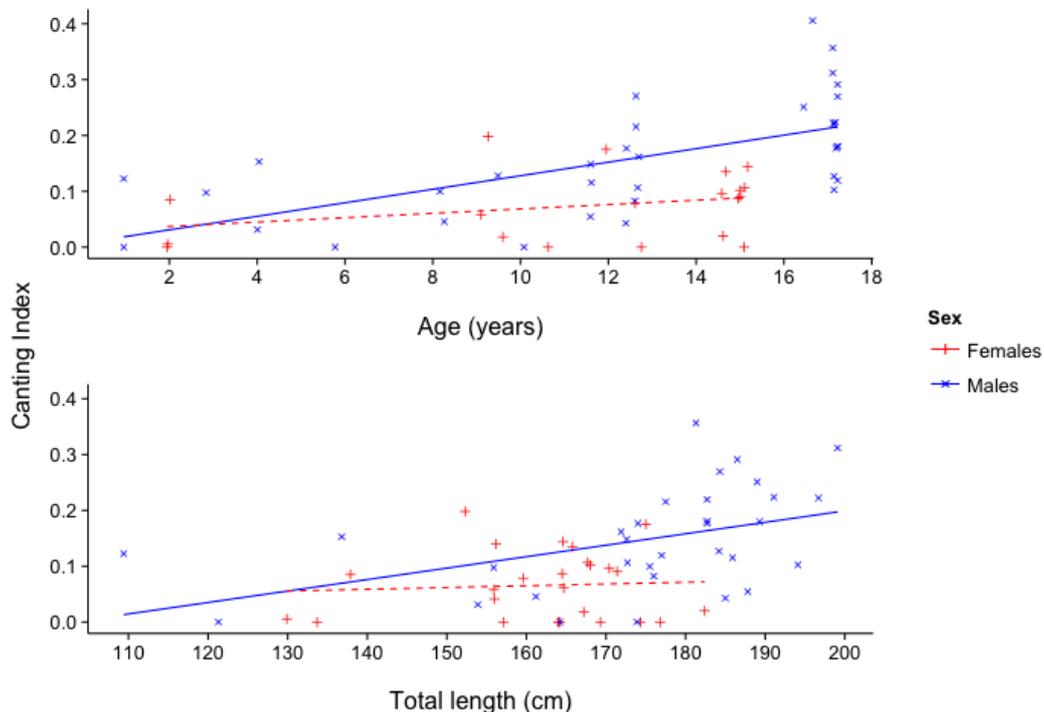


Figure 3.10. Relationship between Canting Index and age (top) and total body length (bottom) in male and female Red Sea spinner dolphins. Non significant relationships are indicated with dashed lines for reference only.

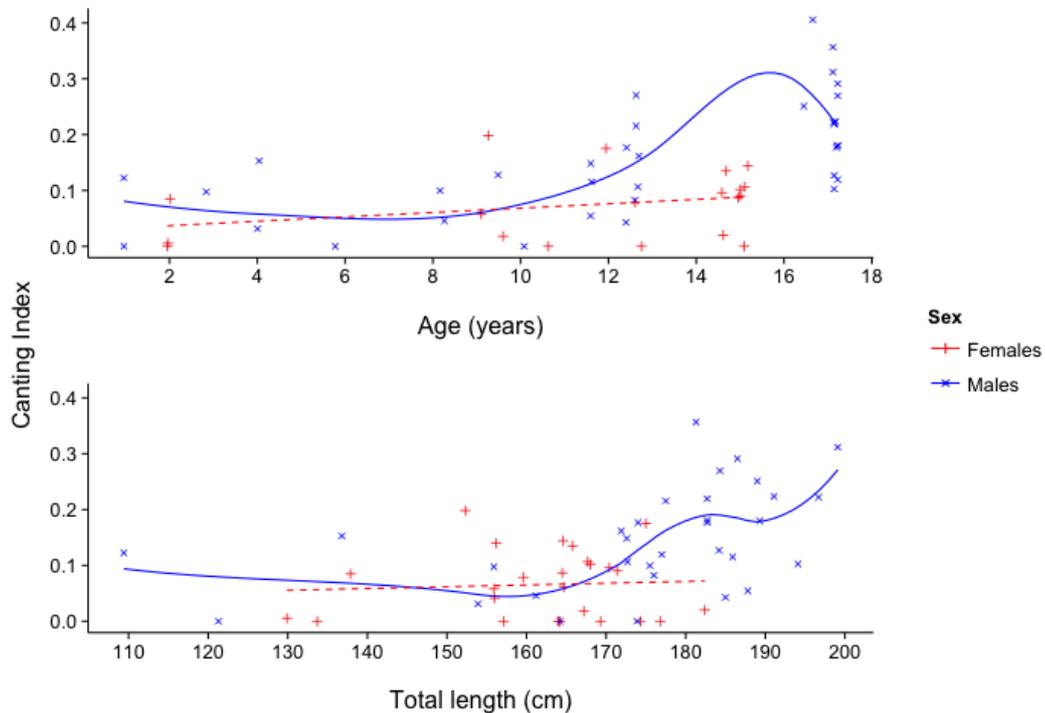


Figure 3.11. Development of the dorsal fin of male and female Red Sea spinner dolphins, as indicated by Canting Index in relation to age and total body length (smoothing interpolation by function `loess` in R).

#### *Development of the eye-to-genital stripe*

The Red Sea spinner dolphin age-related darkening varies greatly from individual to individual and overall pigmentation patterns of the eye-to-genital stripe overlap quite substantially across years (Figure 3.12). The dolphins are born with two or three tone countershading colouration, darker dorsally and progressively whiter towards the ventral region. The colouration of the eye-to-genital stripe along the flanks begins to darken slightly at 3-4 years of age but remains faint for several more years. At the age of *ca.* 10 years, this pigmented stripe is generally evident, from thin to moderate, and elongates in both directions, fading towards the eye and the genital region (Table 3.7).

The relatively short period of this study did not allow for an exact determination of the age at which dolphins display the well-defined thick eye-to-genital stripe along the flanks and a darker pigmentation above and/or below the eyes. However, by collating observations of dolphins

whose birth date was estimated to within 1-year accuracy with those whose minimum age was assigned referentially (based on other published studies; e.g. Whitehead and Mann, 2000; Perrin, 1998; see "Age estimation" Chapter 2), the eye-to-genital stripe appears to reach its darkest colouration at the age of ~15 years (Table 3.7).

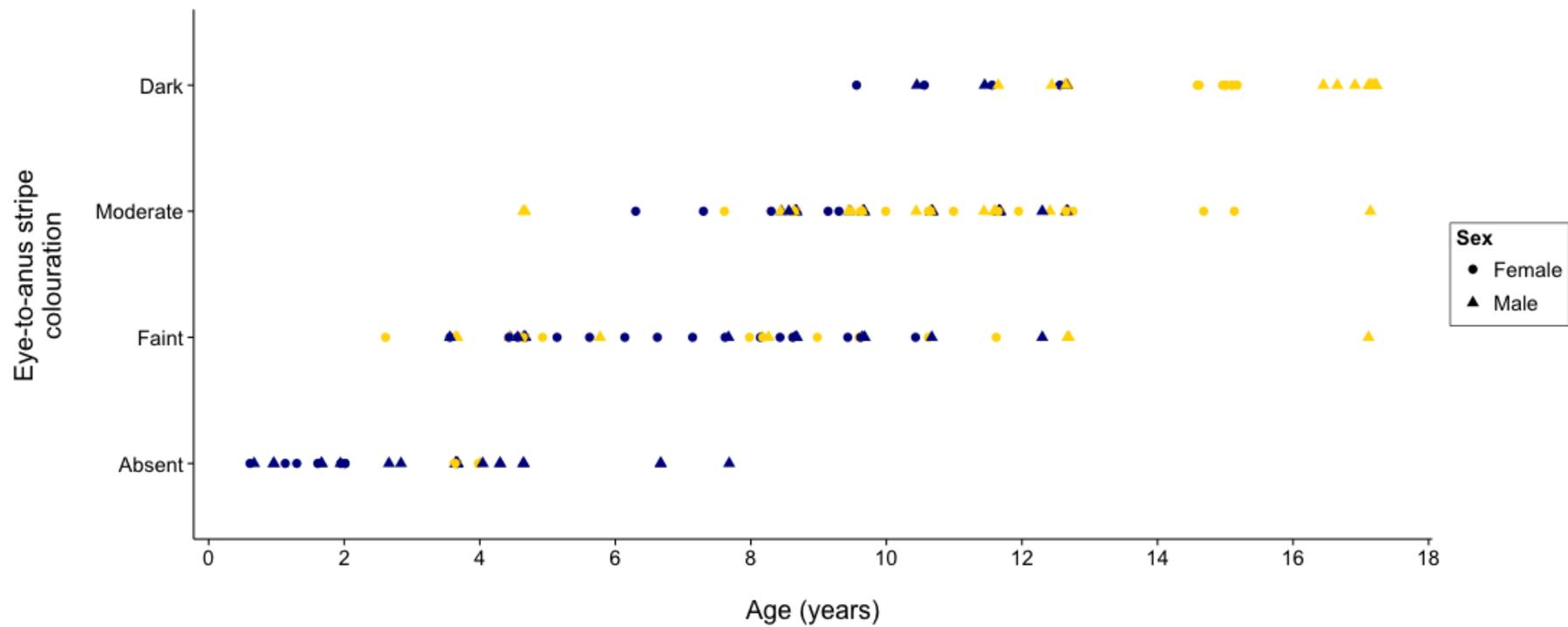


Figure 3.12. Ontogeny of the eye-to-anus stripe colouration patterns for the Red Sea spinner dolphin. Dolphins whose age was estimated to within 1-year accuracy (this study) are indicated in blue; referential age estimates are indicated in yellow.

Table 3.7. Mean age at each eye-to-anus stripe colouration category for the Red Sea spinner dolphin. Dataset A includes only dolphins whose age was estimated to within 1-year accuracy; Dataset B includes dataset A and dolphins whose minimum age was estimated referentially.

| Dataset | Eye to anus stripe colouration | Mean (yr) | SD (yr) | SE (yr) | Min (yr) | Max (yr) | Obs. (n) |
|---------|--------------------------------|-----------|---------|---------|----------|----------|----------|
| A       | <b>Absent</b>                  | 3.1       | 1.80    | 0.32    | 0.6      | 7.7      | 31       |
|         | <b>Faint</b>                   | 7.0       | 2.44    | 0.42    | 3.6      | 12.3     | 33       |
|         | <b>Moderate</b>                | 10.0      | 1.60    | 0.27    | 6.3      | 12.7     | 35       |
|         | <b>Dark</b>                    | 11.3      | 1.14    | 0.43    | 9.6      | 12.7     | 7        |
|         | <i>Tot. obs.</i>               |           |         |         |          |          | 106      |
| B       | <b>Absent</b>                  | 3.1       | 1.67    | 0.27    | 0.6      | 7.7      | 38       |
|         | <b>Faint</b>                   | 7.4       | 2.98    | 0.40    | 2.6      | 17.1     | 55       |
|         | <b>Moderate</b>                | 10.4      | 2.06    | 0.24    | 4.6      | 17.1     | 74       |
|         | <b>Dark</b>                    | 14.7      | 2.45    | 0.42    | 9.6      | 17.2     | 34       |
|         | <i>Tot. obs.</i>               |           |         |         |          |          | 201      |

Despite the considerable individual variability in the pattern of the eye-to-genital stripe, results of multinomial logistic regression (Pseudo- $R^2=0.61$ ) indicate that the patterns are determined by age ( $p<0.05$  for all colouration categories), not the body length ( $p>0.05$ ) (Figure 3.13).

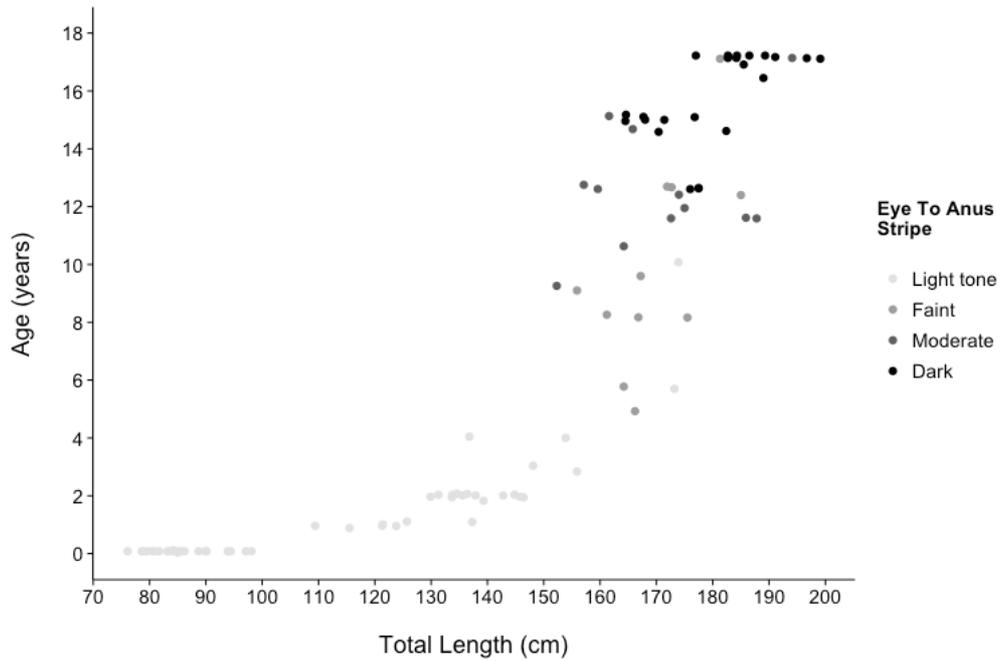


Figure 3.13. Ontogeny of the eye-to-anus colouration patterns in relation to body length and age in the Red Sea spinner dolphin.

For a pictorial depiction of the development of the eye-to-genital stripe along the flanks of the body, from immature to a mature individual, see Appendix II. A qualitative summary of age classes and relevant morphometric and morphological features is presented in Table 3.8.

Table 3.8. Age classes, mean body length (size), eye-to-anus stripe colouration and dimorphic features of the Red Sea spinner dolphins seen at Samadai reef. Young and old adults had similar body lengths but different degree of colouration.

| Age Class          | Approximate age interval | Mean size $\pm$ SD (min-max; n)   | Eye-to-anus stripe colouration              | Sexually dimorphic features  |
|--------------------|--------------------------|---|---|--|
| <b>Newborn</b>     | 1-8 weeks                | <b>85.7 <math>\pm</math> 5.98</b><br>(76.1-98.1; n=23)                      |   |  |
| <b>Calf 1</b>      | 1 year                   | <b>122.1 <math>\pm</math> 8.69</b><br>(109.4-137.3; n=7)                    | Absent<br>(Two-three tone body colouration) | Absent<br>(very falcate/falcate dorsal fin and no post-anal hump)  |
| <b>Calf 2</b>      | 2 years                  | <b>137.9 <math>\pm</math> 5.54</b><br>(129.9-146.4; n=13)                   |   |  |
| <b>Calf 3</b>      | 3 years                  | <b>152.0 <math>\pm</math> 5.52</b><br>(148.1-155.9; n=2)                    |   |  |
| <b>Juvenile</b>    | 4-9 years                | <b>158.7 <math>\pm</math> 13.52</b><br>(136.8-173.9; n=7)                   | Faint                                       | Females: absent.<br>Males: slightly visible post-anal hump   |
| <b>Young Adult</b> | 10-14 years              | <b>Females</b><br><b>167.0 <math>\pm</math> 7.68</b><br>(152.3-182.4; n=32) | Moderate                                    | Females: slight post-anal hump or distended mammarys in case of lactation.<br>Males: moderate post-anal hump and triangular dorsal fins. |
| <b>Old Adult</b>   | 15+ years                | <b>Males</b><br><b>183.4 <math>\pm</math> 7.52</b><br>(171.9-199.1; n=25)   |   | Dark   |

### *Lower lip pigmentation*

A unique feature that appears to be exhibited only by spinner dolphins of the Red Sea and in the contiguous waters of Gulf of Aden (Robineau and Rose, 1983) is the dark pigmentation of the lower lip that broadens in the posterior half of the lower jaw (Figure 3.14). This inverted bell-shaped black lip patch characterizes the Red Sea spinner dolphins of all age/sex classes.

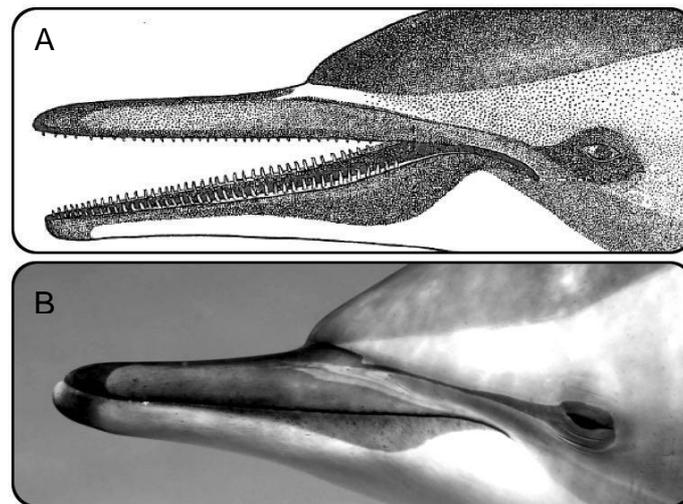


Figure 3.14. Lateral view of the spinner dolphin bridle: (A) immature male stranded in Gulf of Aden (illustrated in Robineau and Rose, 1983); (B) photographed in Samadai reef (this study).

## **3.4 Discussion**

### **3.4.1 Methodological considerations**

For cetaceans, morphometric data are usually obtained from stranded or by-caught specimens, with only a few exceptions (e.g., Tolley et al., 1995). The northern part of the Red Sea has a narrow shelf above which fringing reefs occur along the shore almost continuously (Sheppard et al., 1992). This coastal feature renders the retrieval of dead or live strandings unlikely and rare. Moreover, due to a lack of fisheries information and surveillance, by-catch is usually not reported in the region, although it is known to occur and attributed mostly to illegal fishing, thus usually discarded at sea

(Gladstone et al., 1999). Under these circumstances, the underwater paired-laser photogrammetry approach provided a valuable and effective means of collecting morphometric data of a little known population of spinner dolphins in the region where such data are meagre and hard to obtain.

Underwater laser-metrics methodology resulted with an average CV of 3.4% for total body length, 4.4% for dorsal fin width and 3.8% for dorsal fin height. These results are comparable to those obtained in other studies that employed photogrammetric techniques to estimate the size of cetaceans in the field (Gordon, 1990; Cubbage and Calambokidis, 1987; Best and R  ther, 1992; Perryman and Lynn, 1993; Dawson et al., 1995; Spitz et al., 2000; Cosens and Blouw, 2003; Jaquet, 2006; Rowe and Dawson, 2008; Webster et al., 2010). The low measurement errors had shown that the field procedure was robust and the approach gathered replicable data, not subject to type II error (Zuur et al., 2010).

In the course of processing the photographic data, particular attention should be given during the initial steps of selecting images. Photographs with dolphins that are not perpendicular to the photographer should be discarded. Mean among-photograph error greater than within-photograph error in fact indicates that orientation of the dolphin body and dorsal fin to the plane of the camera contributes much more error than the photograph measurement process.

When collecting measurements of live cetaceans, the flexibility of the highly mobile animals makes the underwater photogrammetric technique unlikely void of error. On the other hand, measurements of dead specimens, although more precise, may be biased and sometimes inaccurate as the relevant metrics vary post-mortem (Perrin, 1997), unless the carcasses are very fresh. In this study, by discarding photographs that did not meet the required quality criteria, the bias introduced by the inherent flexibility of the photographed target was minimized. To further mitigate the sources of error, several digital images per each individual

were collected and only the most perpendicular with the individual not bent were selected and retained for subsequent analyses.

An obvious advantage of analysing photographs of live animals resides in the reliability of the “true” colouration pattern captured on the photographs (Stockin and Visser, 2005; Rosso et al., 2008), which is known to darken post-mortem (Perrin, 1997). In overall, therefore, the quantification of errors, replicability of measurements, and the reliability of the photographic material plays an important role in this method in ensuring the analyses are biologically meaningful.

### 3.4.2 Sexual dimorphism

Sexual dimorphism in spinner dolphins has been found to vary geographically (Perrin and Mesnick, 2003), following an approximate east-west gradient from highly dimorphic forms, such as *S. l. orientalis*, to ecotypes displaying a moderate to weak dimorphism, such as *S. l. roseiventris* (see also Figure 3.1). In this study, adult Red Sea spinner dolphins were found to be highly sexually dimorphic, although not exaggerated as *S. l. orientalis* (Perrin, 1990), with males being significantly larger in all metrics measured (TL, DFH, DFW), having a more forward-canted and proportionally taller dorsal fin and a larger post-anal hump than females. Similarly to spinner dolphins elsewhere, the forward cant of the dorsal fin is related to the development of a post-anal hump in males (Perrin, 1998). In terms of colouration patterns, the intensity and thickness of the eye-to-anus stripe increased with age in both sexes, but in old adult males it became significantly darker and thicker than in females, similarly to Fraser’s dolphins (*Lagenodelphis hosei*, Jefferson et al., 1997).

In this study, dimorphism of flukes, known to have upturned tips in adult males in the eastern tropical pacific spinner dolphins (Perrin, 1975; Perrin, 1990; 2009b) was not evaluated nor tested between sexes or among age classes but seemed to be present in the Red Sea spinner dolphins as well (pers. obs.).

Varying degrees of sexual dimorphism are also found in other species of odontocetes, such as common dolphins (*Delphinus delphis*; Murphy and Rogan, 2006; supplemental material Murphy et al., 2006), bottlenose dolphins (*Tursiops truncatus*; Tolley et al., 1995; Rowe and Dawson, 2009), Dall's porpoises (*Phocoenoides dalli*; Jefferson, 1990; Amano and Miyazaki, 1996), pantropical spotted dolphins (*Stenella attenuata*; Schnell et al., 1985a) and killer whales (*Orcinus orca*; Clark and Odell, 1999). The degree of sexual dimorphism in a species is thought to be a result of the difference between the sum of natural selection and sexual selection pressures affecting the male and the sum of those affecting the female (Ralls and Mesnick, 2002); and these selective pressures are profoundly interconnected (Emlen and Oring, 1977). In spinner dolphins, there is evidence that sexual dimorphism is tightly related to the mating system and varies with a gradient from a more polygynous mating system in the eastern form (highly dimorphic) to a more open or polygynandrous mating system in the less dimorphic whitebelly form and the Hawaiian spinner dolphin (Perrin and Mesnick, 2003; Norris et al., 1994). By inference, the sexual dimorphism described for the Red Sea spinner dolphin (forward canted dorsal fin, deepened caudal peduncle and enlarged post-anal hump in adult males) can be considered indicative of a polygynous mating system.

The differences in mating systems seem to be driven by varying degrees of primary productivity (reviewed in Andrews et al., 2013), where higher levels of productivity favour a polygynous mating system whereas a promiscuous mating system seem to occur in less productive ecosystems (Perrin and Mesnick, 2003). The Red Sea is a relatively oligotrophic semi enclosed basin, particularly in the northern part and less so in proximity of the Gulf of Aden (DiBattista et al., 2015b). According to the productivity-driven hypothesis, this would suggest a promiscuous mating system for the Red Sea spinner dolphin.

This apparent contradiction may perhaps be explained by taking into account the circadian rhythms of spinner dolphins, *i.e.* resting during the

day and foraging at night. Assuming that productivity does not represent an environmental constraint on growth, the next most important resource for this species is the availability of resting areas (Tyne et al., 2015). Many of the Red Sea reefs have a characteristic structure of shallow flat tops, steep sloping sides and an elongated north–south axis (Dullo and Montaggioni, 1998). For resting and socializing, spinner dolphins generally visit reefs with a semi-circular shape that create a sheltered inner lagoon, but these are relatively rare. In the Southern Egyptian Red Sea, only six areas that represent such configuration (Figure 1.1, Chapter 1) are known to be frequented by spinner dolphins (Costa, 2015; Fumagalli, 2016); although some other areas in these largely uncharted waters, probably a small number, may potentially also function as resting coves for spinner dolphins.

Limited availability and spatial predictability of resources such as resting areas may enhance the probability of higher encounter rates between adult males who rival over the access to females, which in turn may favour larger, sexually dimorphic males who compete to exclude other males from mating. However, this does not explain why such dimorphism is not reported, for example, in the Hawaiian spinner dolphin that also uses sheltered bays during the day. Some other socio-ecological and behavioural mechanisms are probably at work here, and this calls for further investigations.

### **3.4.3 Colouration and size**

Variation in colouration patterns has been observed and documented extensively in spinner dolphins (Perrin, 1972; Perrin et al., 1991) ranging from a uniformly dark and extensive “dorsal field overlay” (Perrin, 1972) in the easternmost forms to a lighter tripartite pattern (dark grey cape, light grey sides and white or very light grey belly) in the Gray’s form (Figure 3.1). In the present study, the Red Sea spinner dolphins displayed the tripartite colouration pattern and the data show that colouration pattern variability is primarily determined by age. The eye-to-anus stripe

progressively thickened and darkened with age in both sexes, confirming the age-related colouration hypothesis proposed by Eyre and Frizzle (2012) for the species in the region.

Perrin (1997) extensively documented the spinner dolphins bridle colouration patterns (Perrin, 1972), but never reported the dark inverted bell-shaped lower lip patch described in this study, which appears to be unique to the Red Sea and Gulf of Aden spinner dolphins (Robineau and Rose, 1983).

The ontogeny of pigmentation has been described in details in the genus *Stenella* (Perrin, 1969; Perrin, 1972; Perrin et al., 1994; Herzing, 1997; Perrin and Hohn, 1994) and *Tursiops* (Smolker et al., 1992; Charlton-Robb et al., 2011; Krzyszczyk and Mann, 2012). The possible function(s) of pigmentation have been addressed in cetaceans (e.g. Mitchell, 1970; Caro et al., 2011; Krzyszczyk and Mann, 2012), and the theoretical framework suggests that countershading, i.e. dark dorsum and light ventrum, is not primarily a cryptic mechanism to avoid predation but rather to avoid being seen by the prey (Caro et al., 2011); the prominent markings are involved in intraspecific communication; white markings on several parts of the body are involved in the prey capture; and eye patches, bridle stripes, and lip patches serve to mask eyes, blowhole, and mouth (Mitchell, 1970; Caro et al., 2011).

In the Red Sea spinner dolphins, it is possible that the lighter two-three tone colouration characteristic to newborns and calves may work well in concealing young swimming in echelon formation (Mitchell, 1970). The white/light grey belly that does not darken with age (no ventral speckling is reported for spinner dolphins) is possibly for obliterative shading through countershading. The age-related eye-to-anus stripe seems likely an expression, or perhaps a by-product of sexual maturation. Several studies speculated that colour phase may be influenced by reproductive hormones, suggesting that an increase in the intensity of pigmentation could be correlated with the process of sexual maturation (Kasuya et al., 1974; Myrick et al., 1986; Chivers and Myrick Jr, 1993; Krzyszczyk and

Mann, 2012). This hypothesis would explain the significantly darker eye-to-anus stripe in sexually mature adult males but would not fully explain the greater variability in colouration found for adult females. Furthermore, seasonal hormonal cycles have been demonstrated for both sexes in spinner dolphins (Wells, 1984). Whether the pigmentation of Red Sea spinner dolphins also follows a more subtle hormone-driven seasonal pattern (e.g. slightly darker in certain months and in certain areas of the body) and, for example, provide information of female reproductive status (as it does for example in macaques, where males discern ovulating period in females from their facial luminance; Higham et al., 2011) is not known and would be difficult to assess in free-ranging dolphins. Similarly, it has been speculated for spinner dolphins (Perrin and Henderson, 1984) as well as for other delphinids (e.g. common dolphins; Murphy and Rogan, 2006) that the size of the post-anal hump may be more pronounced during the mating season. However, in the present study, the qualitative assessment of pigmentation and the size of post-anal hump was not sufficiently discriminative to detect and test any within-year variations.

Several studies (Caldwell & Caldwell, 1966; Perrin, 1969; Krzyszczyk and Mann, 2012) have used the degree of colouration in delphinids as a proxy to define age classes and infer socio-ecological factors to better estimate population parameters. Although we found moderate degree of individual variation in colour pattern, in general it was well possible to distinguish age classes based on colouration and, for males, the degree of dorsal fin canting and the size of post-anal hump. However, the downward biased age estimation of fully-grown old adults (in this study, based solely on referential estimates) is likely to have affected the age class interval. In other words, it is likely that fully-grown old individuals, especially males, may display greater sexually dimorphic features some years later than reported here.

According to Perrin (1998) both males and females undergo a growth spurt at about the onset of puberty (see Chapter 4) and males in particular undergo a sharp increase of testis weight (sexual maturity) at body length

of 160-180 cm. Although in the present study the weight of testis was not available, there was a striking consonance between the testis weight increase documented for the spinner dolphins in other regions and the sharp increase of the canting index at about the same body length for the Red Sea spinner dolphins. It is possible that the change in the dorsal fin shape (as indicated by high values of the Canting Index) in male Red Sea spinner dolphin represents a good indicator of attaining sexual maturity. Conversely, it is improbable to determine precisely the attainment of sexual maturity in females by merely assessing their colouration or any other morphological or morphometric characters.

Variations in colouration pattern in cetaceans may contribute to the recognition of new subspecies (Perrin et al., 2009a) and in some cases initially presupposed different forms were later recognized as different species (Heyning and Perrin, 1994). Intraspecific variability of colour patterns is known to be high in genera of *Stenella*, *Delphinus*, *Lagenorhynchus* and *Orcinus* (Perrin, 1972; Rosso et al., 2008; Amaha, 1994; Walker et al., 1986; Evans et al., 1982; Krahn et al., 2004). Consequently, for species in those genera, caution should be exercised when employing colour-patterns as taxonomic features (Fraser and Noble, 1970). Colouration patterns should be viewed in combination with other features, such as morphometric measurements of external and osteological characters, especially skull morphology, and genetic data (Reeves, 2004).

#### **3.4.4 Geographic variation**

The morphometric data obtained in this study were compared with published data for adult spinner dolphin ecotypes from other regions (Table 3.9).

The Red Sea spinner dolphin seems to be intermediate in length between the Central American or the “Tres Marias” ecotypes and the Dwarf form, displaying a comparable size to Gray’s and Whitebelly forms. However,

differently from the latter ecotypes, adult Red Sea spinner dolphins exhibit strong sexual dimorphism and some unique features of pigmentation.

Whether the Red Sea spinner dolphins are genetically different from other spinner dolphins is currently unknown, although Perrin et al. (2009a) suggested the likely existence of more forms in the region deserving a subspecies status. Efforts should be made in the future to collect tissue samples, so that genetic variation could be examined in parallel with studies of external morphology. Osteological metrics, skull morphometrics especially, would further add important information as they are less prone to measurement errors (*i.e.* they do not change post-mortem). All such information would greatly help to clarify the taxonomic status of the Red Sea spinner dolphin. However, much of this data is likely to remain scarce still for a long time as field studies are hampered by economic and political constraints and retrieval of carcasses is rare.

According to recent studies investigating distribution and richness of species in the Red Sea (DiBattista et al., 2013; DiBattista et al., 2015a; DiBattista et al., 2015b), endemism appears to be higher in the region than previously reported and the Red Sea is thought to represent an “evolutionary incubator”, similarly as regions such as the Hawaiian Archipelago and the Marquesas Islands, which implies that these are important peripheral areas that contribute unique genetic lineages to other regions of the Indo-Pacific. One of the factors leading to the higher rate of endemism in the Red Sea is thought to be the nutrient-rich cold upwelling that separates the Gulf of Aden from the rest of the Arabian Sea and the narrow Bab al Mandeb strait that physically separates the Red Sea from the Gulf of Aden; the latter barrier considered of a lesser importance and the Gulf of Aden is thought of as biogeographical extension of the Red Sea (DiBattista et al., 2015b). It is therefore possible that these isolating mechanisms apply also, at least to some extent to spinner dolphins inhabiting the Red Sea. Hence, some level of genetic differentiation from other spinner dolphin forms is possible or even likely.

Table 3.9. Comparison of the Red Sea spinner dolphins with published information of six known ecotypes of spinner dolphins (extracted from Andrews et al., 2013).

|                                | Central American | Tres Marias         | Eastern    | Whitebelly   | Gray's     | Dwarf      | Red Sea                                       |
|--------------------------------|------------------|---------------------|------------|--------------|------------|------------|---|
| <b>Morphometric characters</b> |                  |                     |            |              |            |            |   |
| <b>Female body length (cm)</b> | 193–211          | 186.2<br>(~165–210) | 171.3±5.99 | 175.6±6.82   | 180±10.95  | —          | 167.0±7.68 (n=32)                             |
| <b>Male body length (cm)</b>   | 212–216          | —                   | 176.1±6.12 | 179.8±7.31   | 186.7±4.23 | 144.8±7.88 | 183.4±7.52 (n=25)                             |
| <b>Colouration</b>             | Uniform          | Uniform             | Uniform    | Intermediate | Tripartite | Tripartite | Tripartite<br>(unique trait: black lip patch) |
| <b>Sexual dimorphism</b>       | Strong           | Strong              | Strong     | Intermediate | Weak       | Weak       | Strong  |

### 3.4.5 Taxonomic considerations

Reeves and colleagues (2004) recommended that in order to formally recognize a subspecies, there has to be at least one good line of either morphological or genetic evidence. It was also suggested that species' distribution, behaviour and ecology should be considered not as primary but as supporting evidence (Reeves, 2004). However, Perrin et al. (2009a) questioned whether or not a broad gap in distribution should be considered a strong line of evidence to recognize different geographic forms. Dizon (1992) proposed a phylogeographic approach that identifies Evolutionary Significant Units (ESU), suggesting that distribution of animals, phenotype and genotype all contribute to the recognition of an ESU. The more geographically separated and genetically diverged a group of organisms is from other groups of that taxon, the more likely to be an ESU (Category I). When genetic separation is clear but there is little geographic partitioning or when there is little genetic differentiation but the group is isolated geographically from other conspecifics, Category II and III of ESU, respectively, were suggested (Dizon et al., 1992). Appropriate identification of taxonomic groups and/or delineation of evolutionary significant units is critical to conservation efforts as it allows to design and implement more effective management programs.

The currently accepted ecotypes of spinner dolphins (as summarized earlier, after Andrews et al., 2013) were defined by their geographic distribution, colour pattern, body size, dorsal fin profile, post-anal hump, and skull osteology. The present study lacks cranial and other osteological metrics, but this does not differ much from photogrammetric data by Perryman and Westlake (1998) which was thought to be sufficient to propose a new geographic form. Another limitation of our study is that all data were collected in a single location in the Egyptian Red Sea, the Samadai reef, and may be considered not representative of the entire Red Sea population. However, observations carried out elsewhere in the region (pers. obs.) paired with previously published reports (Robineau and Rose, 1983; Robineau and Rose, 1984; Eyre and Frizell, 2012) suggest that the

morphological features and morphometric characteristics described in this study are also exhibited by spinner dolphins across the whole region. As new studies take place and further data are gathered, the morphometric data presented here may contribute to a more thorough evaluation of the taxonomic status of the Red Sea spinner dolphin.

## **Chapter 4. Growth pattern and sexual dimorphism of the Red Sea spinner dolphin**

### **4.1 Introduction**

The life history of an individual is defined by its pattern of allocation of resources into the processes of growth, survival and reproduction (Chivers, 2009). The life history parameters generally investigated in ecological studies in mammals include individual growth, mean age at reaching sexual maturity, pregnancy rates, calving interval and longevity. Compiling data from many individuals of both sexes allows for a broader pattern of the various parameters to be estimated, which in turns describes the life history strategy of a species (Chivers, 2009).

In studies of cetaceans, individual length estimates have been applied in the assessments of (1) taxonomic status and stock structure (Perryman and Lynn, 1993; Perryman and Lynn, 1994; Perryman and Westlake, 1998; Pitman et al., 2007; Baker et al., 2002; Jaquet, 2006), (2) health conditions (Perryman and Lynn, 2002) and levels of population exploitation (Martin, 1981), (3) group structure and size class segregation (Perryman and Lynn, 1994; Cubbage and Calambokidis, 1987), and (4) sexual size dimorphism (Amano and Miyazaki, 1993; Tolley et al., 1995). Individual age estimates, which are inherently related to individual body length estimates, are critical for estimating age-specific survival rates and deriving age-structured population models (Slooten and Lad, 1991). Length-at-age data allow to examine growth patterns (Perrin et al., 1977; Read et al., 1993; Larese and Chivers, 2009; Webster et al., 2010; Lubetkin et al., 2012) and estimate reproductive and demographic parameters (Perrin and Reilly, 1984; Read et al., 1993) that can be used in stock assessments and contribute to the informed management of species and local populations. Studies of free-ranging populations can be further enhanced if the sex of the studied individuals can be reliably identified,

facilitating considerably greater insights into socio-behavioural dynamics and reproductive strategies (Gowans et al., 2000).

Most of cetacean life history data are collected from dead specimens incidentally or intentionally taken during fishery operations or found stranded (Chittleborough, 1959; Perrin et al., 1976; Hohn et al., 1996; Siciliano et al., 2007; Garde et al., 2007; Lubetkin et al., 2008). When dead specimens are studied, a complete suite of biological and morphological data can be collected, including reproductive and physical maturity, individual sex and age. In baleen whales, the techniques for estimating age include the examination of ear plugs (Chittleborough, 1959; Lockyer, 1984) and ear bones (Christensen, 1981; but see: Kastelle et al., 2003) baleen plate isotopic analysis (Lubetkin et al., 2008), chemical analysis of eye lens nucleous (aspartic acid racemization - AAR; (George et al., 1999), ovarian corpora count (George et al., 2011) which is also used to assess the reproductive maturity in females (Perrin and Reilly, 1984), or a combination of some of these techniques (Lubetkin et al., 2012). The age of odontocetes can be determined by counting the growth layer groups (GLG) in tooth sections (Perrin and Myrick Jr, 1980; Myrick et al., 1984).

Although less commonly, such data are also gathered from animals studied in captivity (Clark et al., 2000) and, even less frequently, in the wild (Read et al., 1993; Fearnbach et al., 2011). In the majority of field studies of free-ranging cetaceans, however, the application of the above techniques is challenging and often impossible (Hohn et al., 1989). Photo-ID studies offer a less invasive method to collect age data (Stevick, 1999; Fortune et al., 2012) but this approach is not common as it requires long-term, regular and frequent field effort. The photographic technique relies on the individual recognition and, in odontocetes, it is usually based on the presence of natural marks on dorsal fins (see General Methodology in Chapter 2). These marks accumulate throughout an individual's life. Most calves and young individuals do not have many of such marks and thus are not individually distinctive. Consequently, unless the animal is already

well marked from early stages of life, the photo-ID approach provides estimates of the minimum age of an individual. Remote photogrammetric techniques have been employed increasingly frequently in field studies in recent years and proved to be successful in collecting accurate measurements (Best and Rüther, 1992; Bräger and Chong, 1999; Durban and Parsons, 2006; Durban et al., 2015; see also Chapter 3).

Current knowledge of the life history parameters of spinner dolphins is considerable and covers several regions and populations (e.g. Perrin et al., 1977; Perrin and Henderson, 1984; Barlow, 1984; Larese and Chivers, 2009). Much of the information gathered refers to *Stenella longirostris orientalis* by-caught in purse-seine fishery in the Eastern Tropical Pacific, and to a lesser degree other forms of spinner dolphins from other regions in the Pacific and Southeast Asian waters (Harrison et al., 1972; Perrin et al., 1989; Perryman and Westlake, 1998; Perrin et al., 1999; Perrin, 2009b). Never previously have such data been collected for the Red Sea spinner dolphin. The study presented in this chapter has aimed at filling in this knowledge gap. We use photo-identification dataset of individuals of known age, sex and body measurements obtained through underwater photographic techniques to construct individual growth curve models. We compare our results generated for the Red Sea spinner dolphin with other known ecotypes of the species. Furthermore, we assess the feasibility of using morphometric data for the identification of sex of free-ranging individuals. This work contributes novel information and advances the knowledge of the spinner dolphin life history parameters.

## **4.2 Materials and methods**

### **4.2.1 Data collection and processing**

Paired laser photogrammetric data were collected in June-August 2014 during 12 underwater photo-identification sessions carried out in Samadai reef. The study area, data collection and processing methods are described in Chapter 2 and Chapter 3. The morphometric data (TL: total

length; DFW: dorsal fin width; DFH: dorsal fin height; CI: Canting Index; see Chapter 3 and Figure 3.3) were collected for 113 individuals of different age and sex classes as summarized in Appendix III. In some cases, some of the morphometric data could not be obtained for some of the photographed individuals, and therefore different analyses described further may use different sub-sets of the data, as specified in the relevant sections of the next paragraphs.

## 4.2.2 Analytical approach

### *Growth functions*

The analysis of individual growth was carried out on a dataset of 96 individuals with complete records of known length and date of birth (DOB) (see Appendix III, Table A III.4 for DOB accuracy). Of these, 45 were physically mature individuals (hereafter adults) and 51 were physically (and likely sexually) immature individuals (23 newborns, seven 1-year old calves, thirteen 2-year old calves, two 3-year old calves, and six juveniles); 34 were identified as males, 24 as females, and 38 remained un-sexed. All un-sexed individuals were immature dolphins that were not yet sexually dimorphic (see Chapter 3) and could not be approached sufficiently close for an inspection of the genital area. To perform sex-specific analyses, we assumed no significant difference in length at birth and growth rate between sexes during the first few years of life (Perrin and Henderson, 1984). In the analyses, the 38 un-sexed immature dolphins were assigned to both sex classes.

### *Model fitting*

There have been several non-linear growth models proposed and some work better than others for mammalian species (Richards, 1959; Zullinger et al., 1984; Neuenhoff et al., 2011; Gaillard et al., 1997). For a greater accuracy of model projections, at least two or more growth curves should be compared to find the best fit (e.g. Larese and Chivers, 2009; Webster et al., 2010; Fortune et al., 2012; Lubetkin et al., 2012), but in various studies it is often not the case (Read and Tolley, 1997; Ferrero and

Walker, 1999; Ramos et al., 2000; Murphy and Rogan, 2006; Garde et al., 2007; Siciliano et al., 2007). In this study, average growth trends were investigated by fitting von Bertalanffy (von Bertalanffy, 1938), Richards (Richards, 1959), Gompertz (Gompertz, 1825) and Karkach (Karkach, 2006) logistic growth curves (Table 4.1) to the length-at-age data for all individuals and for each sex separately, using non-linear regressions available in the Fisheries Stock Analysis (FSA) package (Ogle, 2015) in R (R Core Team, 2014).

Table 4.1. Functions considered in this study for modelling the growth curve of the Red Sea spinner dolphin.

| Growth model       | Function   |
|--------------------|--|
| von Bertalanffy    | $L_t = L_\infty - (L_\infty - L_0)\exp(-Kt)$                         |
| Richards           | $L_t = L_\infty (1 - b\exp(-Kt))^M$                                  |
| Gompertz           | $L_t = L_\infty \exp(-\exp(b - Kt))$                                 |
| Logistic (Karkach) | $L_t = \frac{L_\infty L_0}{L_0 + (L_\infty - L_0)\exp(-K_\infty t)}$ |

Where  $L_t$  is the length at age ( $t$ ),  $L_\infty$  is the asymptotic length,  $L_0$  is the length at birth,  $b$  is a correction factor,  $K$  is a growth rate constant and  $M$  describes the relative position of the asymptote.

Bootstrap approach (999 simulations) was used to compute confidence intervals for parameters as it is considered the most useful for small datasets (Ritz and Streibig, 2008). An information-theoretic approach was used to select the best fitting model for length-at-age data. Models were compared on the basis of the value of Akaike's information criterion (AIC) (Akaike, 1998) that indicates the better fit using more parsimonious models. The most supported model scored the lowest AIC value. The best fitting growth model (von Bertalanffy) was then further analysed to describe growth differences between sexes. Eight nested models, all but

one representing a difference between sexes for at least one of the parameters, were compared and are shown in Table 4.2.

Table 4.2. Candidate models considered when examining differences in von Bertalanffy growth curves between sexes. The abbreviations denote which parameters differ between sexes for that model. No parameters differ between sexes for the simplest model ( $\Omega$ ).

| Abbreviation           | Model  |
|------------------------|--|
| $\{L_\infty, L_0, K\}$ | $L_t = L_\infty[Sex] - (L_\infty[Sex] - L_0[Sex])\exp(-K[Sex]t)$ |
| $\{L_\infty, K\}$      | $L_t = L_\infty[Sex] - (L_\infty[Sex] - L_0)\exp(-K[Sex]t)$      |
| $\{L_\infty, L_0\}$    | $L_t = L_\infty[Sex] - (L_\infty[Sex] - L_0[Sex])\exp(-Kt)$      |
| $\{L_0, K\}$           | $L_t = L_\infty - (L_\infty - L_0[Sex])\exp(-K[Sex]t)$           |
| $\{L_\infty\}$         | $L_t = L_\infty[Sex] - (L_\infty[Sex] - L_0)\exp(-Kt)$           |
| $\{K\}$                | $L_t = L_\infty - (L_\infty - L_0)\exp(-K[Sex]t)$                |
| $\{L_0\}$              | $L_t = L_\infty - (L_\infty - L_0[Sex])\exp(-Kt)$                |
| $\{\Omega\}$           | $L_t = L_\infty - (L_\infty - L_0)\exp(-Kt)$                     |

Where  $L_t$  is the length at age ( $t$ ),  $L_\infty$  is the asymptotic length,  $L_0$  is the length at birth and  $K$  is a growth rate constant.

The likelihood ratio and extra sum-of-squares tests were computed for comparing the most complex model ( $L_\infty, L_0, K$ ) and simplest model ( $\Omega$ ) to determine if there was evidence that at least one of the parameters differed between the sexes. All other models were subsequently evaluated with the Akaike's information criterion (AIC) and models with the lowest AIC values were considered best fitting the data and were used to identify the parameters of the growth curve that differed between the sexes.

#### *Total body length prediction*

To assess whether dorsal fin measurements could successfully be used to predict individual total body length, a subset of 32 males, 25 females and 14 un-sexed individuals for which all required measurements were

available, was selected for the analysis. As evidence of multicollinearity was found in the data, simple linear regressions were used to identify the best predictor for total body length (TL) between dorsal fin width (DFW) and dorsal fin height (DFH). Analysis of covariance (ANCOVA) was used to compare the regression lines and determine whether the regression line slopes were different from each other.

#### *Sex prediction in adult spinner dolphins*

A multivariate logistic regression was conducted to determine which of the morphometrics (TL, DFW, DFH and Canting Index CI), or combination thereof, best predicted the observed sex in adult spinner dolphins. This analysis was performed on 24 males and 22 females for which all required morphometric measurements were obtained. Another two logistic regressions were performed to (1) examine potential differences between the overall body shape of male and female dolphins and (2) determine if non size-related variables could be used to predict dolphins' sex in case only photographs of individual dorsal fins were available and photogrammetric data were not collected (such as it usually is in traditional boat-based photo-ID studies conducted above the water). In the first regression, dorsal fin width (DFW) and height (DFH) were divided by the total length (TL) to obtain standardized values. In the second, only dorsal fin proportional morphometrics (*i.e.* CI, and DFW divided by DFH) were considered and entered in the model. The predictions of sexes generated by these models were compared with known sexes and the accuracy of prediction of each model was assessed as the percentage of individuals for whom the prediction truly represented their known sex. Pearson  $\chi^2$  and Hosmer-Lemeshow Goodness-of-fit tests assessed the fit of the logistic models against the data.

Significance for all statistical tests was set at  $p < 0.05$ . All analyses were performed with the freely available software R (R Core Team, 2014).

## 4.3 Results

### 4.3.1 Growth models

Length-at-age data were available for 96 individuals, distributed across sex and age classes, as illustrated in Figure 4.1 (for age accuracy see Appendix III Table A.4).

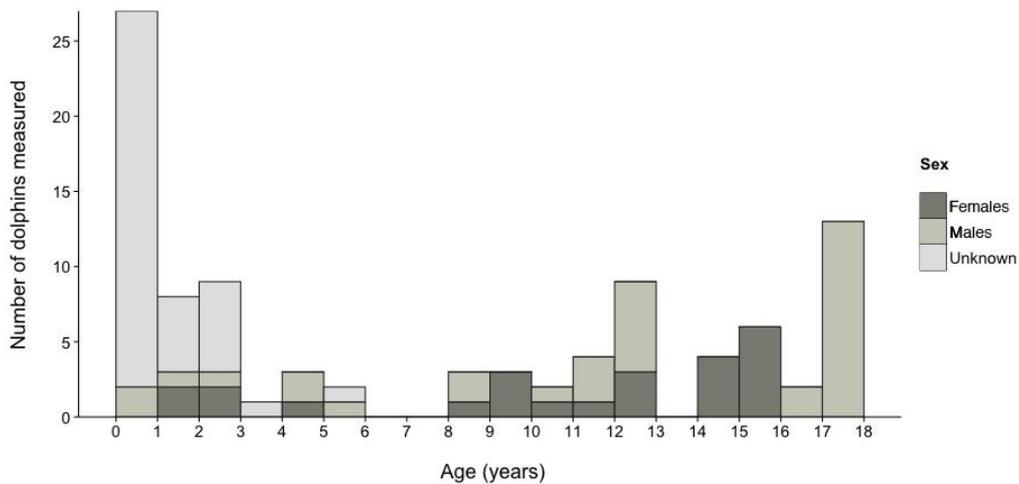


Figure 4.1. Age-frequency distribution of body lengths of 96 individuals of the Red Sea spinner dolphins obtained during 12 photogrammetric surveys at Samadai Reef.

Von Bertalanffy, Gompertz, Richards, and the Karkach logistic growth curves were fitted to these individual data, both considering all data combined and by sex. The estimation algorithm for the Richards model failed to achieve convergence and was not considered for further analyses. The AIC values (Table 4.3) indicated that von Bertalanffy growth function was the best fitting model for the Red Sea spinner dolphins, both when sexes were combined together and when considered separately. In general, however, all three growth functions, von Bertalanffy, Gompertz and Karkach, fitted the data well (Figure 4.2) and the estimates for the parameters were in fact similar (Table 4.4).

Table 4.3. Akaike's information criterion values for small sample sizes (AICc) for von Bertalanffy, Gompertz and Karkach's growth models for the Red Sea spinner dolphins.

| <b>Growth Model</b>    |                          |             |                   |                    |
|------------------------|--------------------------|-------------|-------------------|--------------------|
| <b>All Individuals</b> | <b>No. of parameters</b> | <b>AICc</b> | <b>Delta AICc</b> | <b>AICc Weight</b> |
| von Bertalanffy        | 4                        | 703.65      | 0                 | 0.91               |
| Gompertz               | 4                        | 708.54      | 4.89              | 0.08               |
| Logistic Karkach       | 4                        | 713.01      | 9.36              | 0.01               |
| <b>Males*</b>          |                          |             |                   |                    |
| von Bertalanffy        | 4                        | 507.17      | 0                 | 0.98               |
| Gompertz               | 4                        | 514.77      | 7.6               | 0.02               |
| Logistic Karkach       | 4                        | 521.64      | 14.47             | 0                  |
| <b>Females*</b>        |                          |             |                   |                    |
| von Bertalanffy        | 4                        | 418.36      | 0                 | 0.71               |
| Gompertz               | 4                        | 420.63      | 2.27              | 0.23               |
| Logistic Karkach       | 4                        | 423.24      | 4.88              | 0.06               |

\*Un-sexed immature individuals included.

Table 4.4. The estimated growth parameters and relative bootstrapped 95% confidence intervals for three growth functions (formulae shown in Table 4.1) where  $L_{\infty}$  is the asymptotic length,  $L_0$  is the length at birth,  $K$  is a growth rate constant and  $b$  is a correction factor.

| <b>Growth model</b> | <b>Parameter estim.</b> |       |              | <b>95% Confidence Intervals</b> |        |                    |       |                    |      |
|---------------------|-------------------------|-------|--------------|---------------------------------|--------|--------------------|-------|--------------------|------|
|                     |                         |       |              | <b>Lower Upper</b>              |        | <b>Lower Upper</b> |       | <b>Lower Upper</b> |      |
| von Bertalanffy     | $L_{\infty}$            | $L_0$ | $K$          | $L_{\infty}$                    |        | $L_0$              |       | $K$                |      |
|                     | 176.29                  | 83.50 | 0.44         | 173.49                          | 178.94 | 79.61              | 87.46 | 0.38               | 0.50 |
| Gompertz            | $L_{\infty}$            | $b$   | $K$          | $L_{\infty}$                    |        | $b$                |       | $K$                |      |
|                     | 175.70                  | -0.31 | 0.55         | 172.93                          | 178.33 | -0.38              | -0.25 | 0.48               | 0.63 |
| Logistic Karkach    | $L_{\infty}$            | $L_0$ | $K_{\infty}$ | $L_{\infty}$                    |        | $L_0$              |       | $K_{\infty}$       |      |
|                     | 175.31                  | 84.99 | 0.68         | 172.66                          | 178.04 | 81.11              | 88.73 | 0.59               | 0.78 |

Note: Richards growth model did not converge.

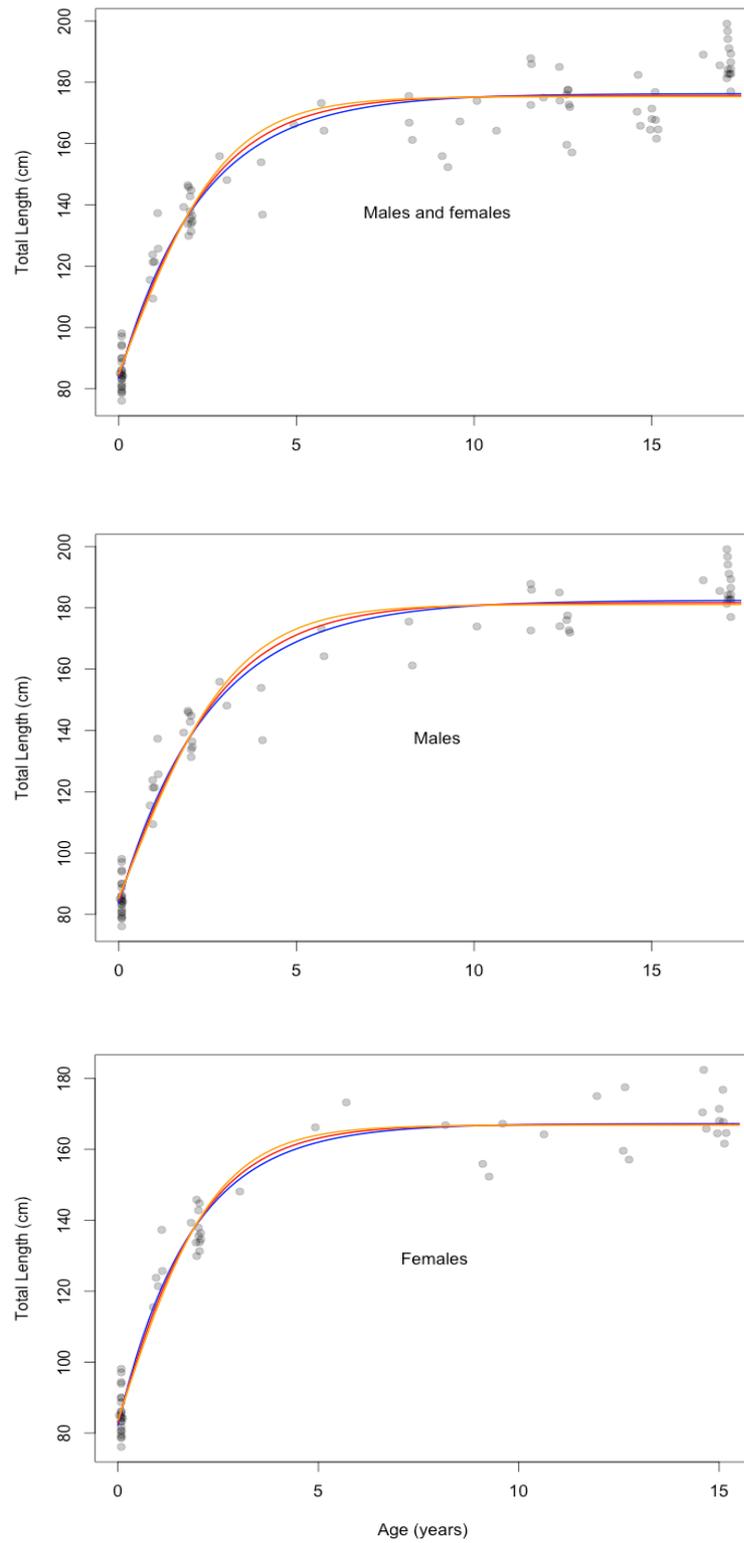


Figure 4.2. Models fitted to the von Bertalanffy (blue), Gompertz (red), and logistic (orange) growth functions generated for the Red Sea spinner dolphins.

The von Bertalanffy growth curve was consistently a better fit (Figure 4.3) and no systematic bias was evident in the residuals of the von Bertalanffy model fit (Figure 4.4). Von Bertalanffy growth model was therefore selected for further investigation of sex-specific growth differences.

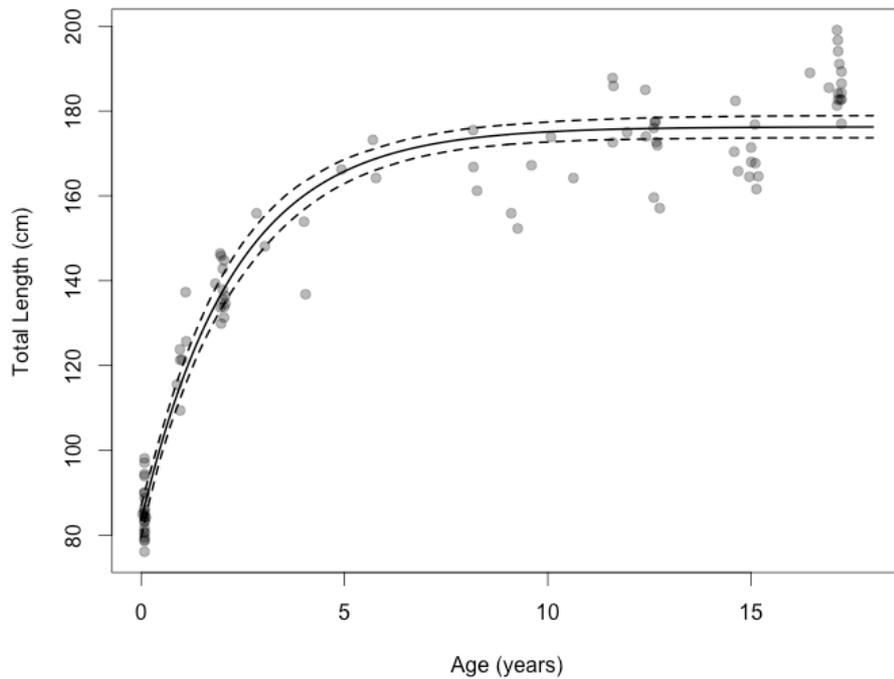


Figure 4.3. Length versus age with superimposed best-fit von Bertalanffy growth model and 95% bootstrapped confidence intervals (dashed lines) for Red Sea spinner dolphins.

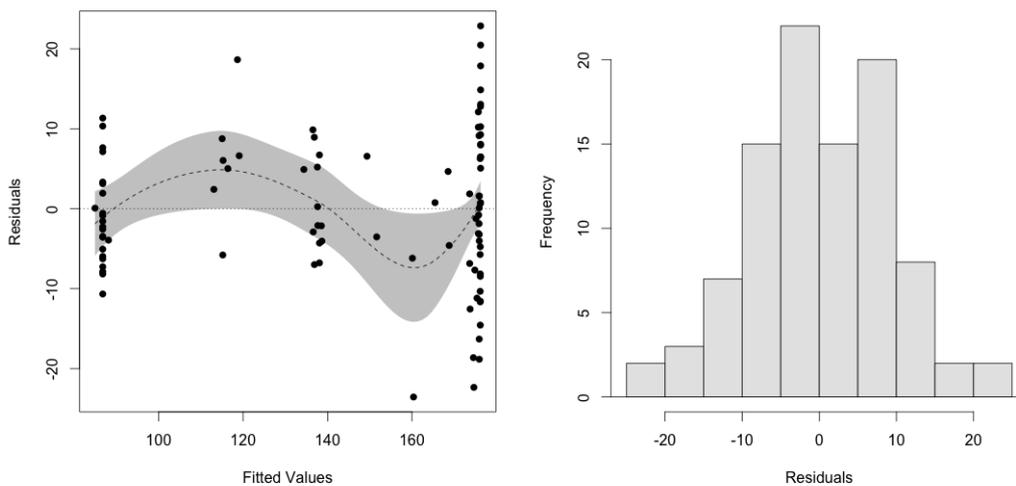


Figure 4.4. Residual plot (left) and histogram of residuals (right) from fitting the von Bertalanffy growth function to the Red Sea spinner dolphins data, showing a roughly normal distribution symmetric around 0.

Among the models considered to examine differences between sexes (see Table 4.2), the most complex candidate model ( $L_{\infty}, L_0, K$ ), was found to be significantly different from the simplest ( $\Omega$ ) (the likelihood ratio and extra sum-of-squares test both indicated a significant difference, with  $X^2=40.09$ ,  $p < 0.0001$  and  $F=14.883$ ,  $p < 0.0001$ , respectively). Thus, there is evidence of some difference in the von Bertalanffy growth curve parameters between female and male Red Sea spinner dolphins. The asymptotic length ( $L_{\infty}$ ) and the growth rate constant ( $K$ ) best explained the differences in growth patterns between sexes (Table 4.5, Figure 4.5).

Table 4.5. Akaike's information criterion (AIC; shown in ascending order from the most to the least supported model) and the related degrees of freedom (df) for the eight models considered for examining difference between sexes in the Red Sea spinner dolphins.

| <b>Model Abbreviation</b> | <b>df</b> | <b>AIC</b> | <b>Delta AIC</b> |
|---------------------------|-----------|------------|------------------|
| $\{L_{\infty}, K\}$       | 6         | 922.29     | 0                |
| $\{L_{\infty}, L_0, K\}$  | 7         | 923.89     | 1.60             |
| $\{L_{\infty}\}$          | 5         | 931.42     | 9.13             |
| $\{L_{\infty}, L_0\}$     | 6         | 932.43     | 10.14            |
| $\{\Omega\}$              | 4         | 957.99     | 35.70            |
| $\{K\}$                   | 5         | 959.88     | 37.59            |
| $\{L_0\}$                 | 5         | 959.97     | 37.68            |
| $\{L_0, K\}$              | 6         | 961.87     | 39.58            |

Where  $L_{\infty}$  is the asymptotic length,  $L_0$  is the length at birth and  $K$  is a growth rate constant.

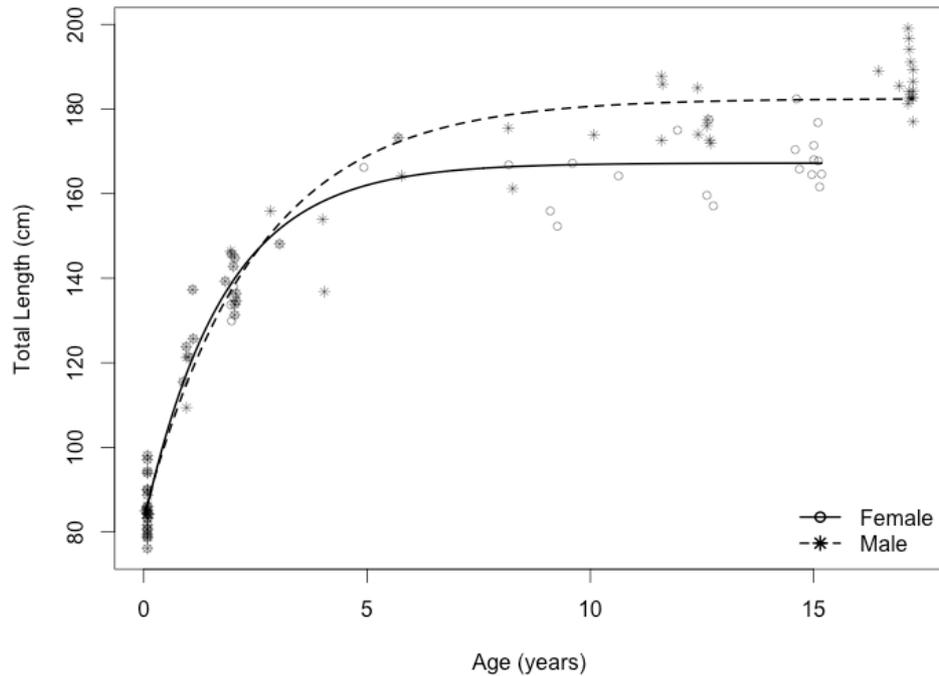


Figure 4.5. Length versus age with separate superimposed best-fit von Bertalanffy growth models for male and female Red Sea spinner dolphins.

The von Bertalanffy ( $L_{\infty}, K$ ) model was considered the best fitting model using the Akaike information criterion. The model estimated that female Red Sea spinner dolphins attained an asymptotic body length of 167.2 cm (95%CI: 164.61-170.24 cm) and males a larger asymptotic length of 182.5 cm (95%CI: 179.45-185.55 cm). Furthermore, the value of  $K$  was found higher for females ( $K_{\text{female}}=0.55 > K_{\text{male}}=0.40$ ). The larger the value of  $K$ , the faster the organism approaches its maximum size, indicating that females reached earlier their asymptotic length than males. In other words, the growth slowed down earlier in females than males, at approximately 5-6 years and 8-9 years, respectively. However, growth did not stop completely, especially in males.

#### 4.3.2 Total length prediction

Linear regressions were fitted to show the relationship between TL and DFW, and TL and DFH (Figure 4.6 and Figure 4.7). Overall, DFW was

found to be a better predictor for TL ( $R^2=84\%$ ,  $p<0.0001$ ). When examining the two sexes independently, DFW was confirmed a better predictor for females total length ( $R^2=74\%$ ,  $p<0.0001$ ), whereas DFH predicted males TL better ( $R^2=72\%$ ,  $p<0.0001$ ) then DFW ( $R^2=66\%$ ,  $p<0.0001$ ). Examination of the regression slopes provided no indication of differences between sexes.

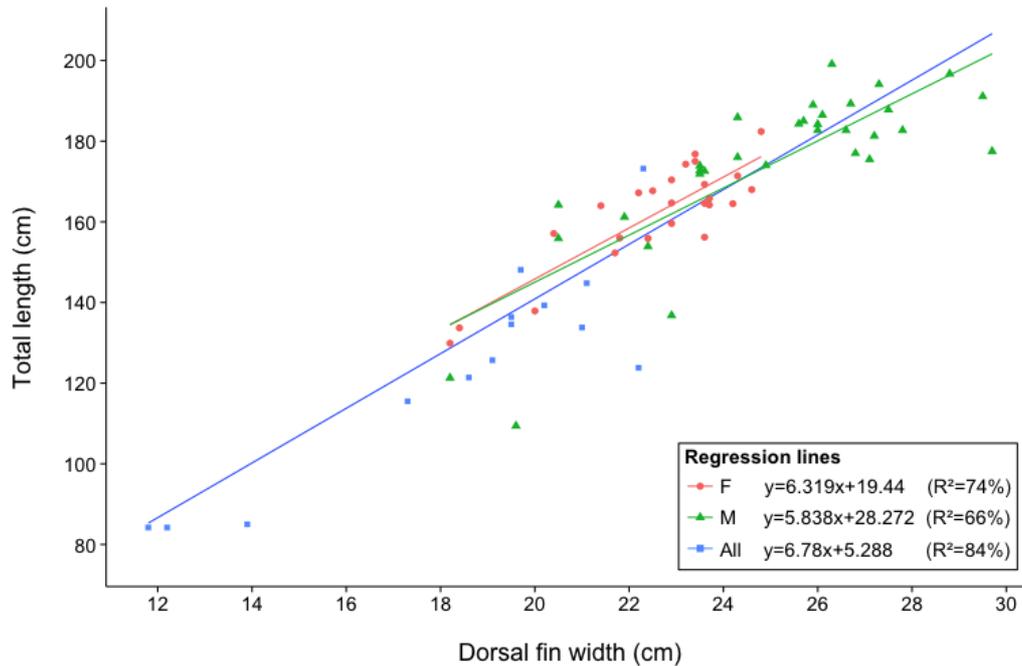


Figure 4.6. Relationships between the total length and dorsal fin width for male, female and all individuals of the Red Sea spinner dolphins. The regression line fitting the data is shown together with the regression equation and the  $R^2$  value.

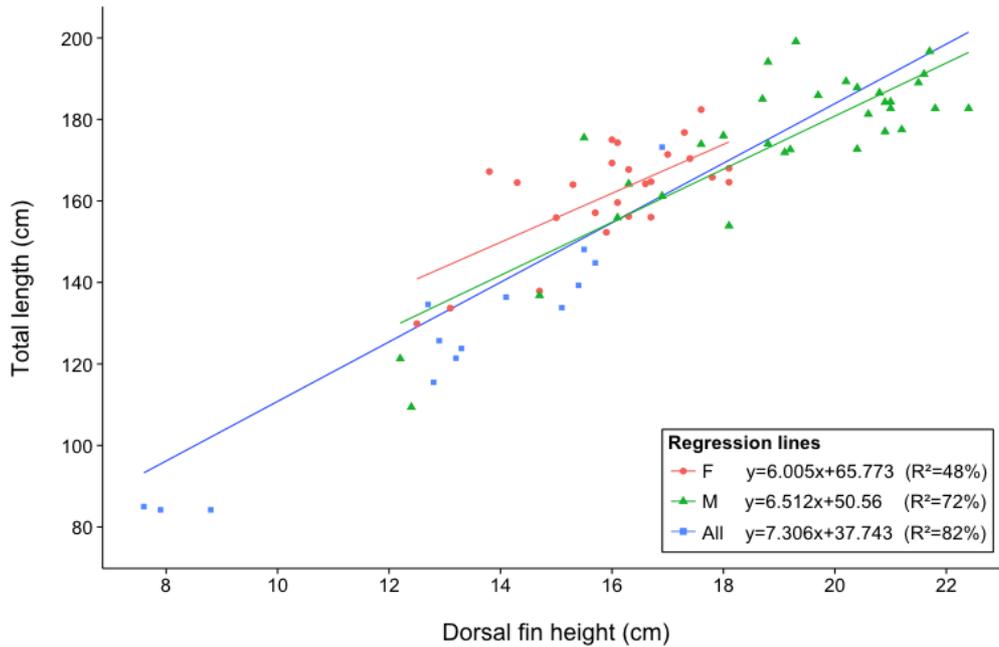


Figure 4.7. Relationships between the total length and dorsal fin height for male, female and all individuals of the Red Sea spinner dolphins. The regression line fitting the data is shown together with the regression equation and the  $R^2$  value.

### 4.3.3 Sex prediction

In the logistic regression analysis conducted on 46 adult spinner dolphins (22 females and 24 males) the algorithm did not converge, standard errors (SE) were unreasonably large and significance value  $p$  was equal to 1 for all variables. This outputs suggested that complete or quasi-complete separation (also known as perfect prediction) possibly occurred. A complete separation happens when the outcome variable separates a predictor variable or a combination of predictor variables completely (Albert and Anderson 1984). To verify whether the cause of such result was indeed that the predictors were “too good” and perfect prediction occurred, a test for separation was conducted (Konis, 2007) using the SafeBinaryRegression package in R (Konis, 2013). Results indicated that TL, DFW, DFH, and CI were all causing separation among the sample points. This confirmed that the logistic regression model indeed correctly predicted the sexes of all of the Samadai spinner dolphins included in the analysis. When complete or quasi-complete separation occurs there is no need for the logistic model (Peng and So, 2002).

Results of two logistic regression analyses applied to (1) all variables after standardization for TL, and to (2) dorsal fin variables only, are reported in Table 4.6. Goodness of fit (GOF) tests were all non-significant ( $p > 0.05$ ) indicating no evidence of lack of fit of the data. In Table 4.6, the applicability of our methodological approach to conditions typical of underwater and above water photo-ID conditions is also shown, with model (2) representing both conditions.

Table 4.6. Summary results of the logistic regression models. Each parameter estimated is reported with its standard error (SE) and significance value (p). Akaike Information Criterion (AIC) and the accuracy of prediction (in percentage) are also shown. (StDFW=DFW/TL; StDFH=DFH/TL; Canting Index=CI; x=DFW/DFH).

| Photo-ID approach                         | Parameter Estimate | SE       | p       | Pearson $\chi^2$<br>GOF statistics<br>(df; p-value) | Hosmer-Lemeshow<br>GOF statistics<br>(df;g; p-value) | AIC                        | Prediction<br>accuracy |       |
|---|--------------------|----------|---------|---|--|----------------------------|------------------------|-------|
| <b>(1)<br/>Underwater<br/>only</b>        | <b>(Intercept)</b> | -138.197 | 64.786  | 0.0329**  | 32.95724<br>(41; p=0.81)                             | 2.1987<br>(8; 10; p= 0.97) | 42.957                 | 84.8% |
|   | <b>StDFW</b>       | -905.513 | 488.415 | 0.0637*   |  |                            |                        |       |
|   | <b>StDFH</b>       | 1386.526 | 679.967 | 0.0414**  |  |                            |                        |       |
|   | <b>CI</b>          | 13.093   | 6.474   | 0.0431**  |  |                            |                        |       |
|   | <b>x</b>           | 88.254   | 45.515  | 0.0525*   |  |                            |                        |       |
| <b>(2)<br/>Underwater<br/>and surface</b> | <b>(Intercept)</b> | 5.601    | 5.63    | 0.3197  | 40.84342<br>(43; p=0.57)                             | 9.5595<br>(8; 10; p=0.30)  | 46.843                 | 80.4% |
|   | <b>CI</b>          | 17.716   | 6.282   | 0.0048**  |  |                            |                        |       |
|   | <b>x</b>           | -5.603   | 3.997   | 0.1609  |  |                            |                        |       |

Note: \*\*p<0.05; \*p<0.1

As depicted in Figure 4.6, model (1) produced some unusually large parameter estimates and standard errors for predictors, an indication of potential complete or quasi-complete separation. Tests performed with the SafeBinaryRegression package (Konis, 2013) confirmed that separation occurred. Model (2) did not show evidence of separation, hence, was chosen as more reliable. The discriminant function resulting from the logistic regression analysis for this model was:

$$\ln\left(\frac{p}{1-p}\right) = 5.601 + 17.716(\beta_1) - 5.603(\beta_2)$$

Where  $\beta_1$  is the Canting Index and  $\beta_2$  is the proportion DFW/DFH. The model correctly classified 80.4% of the adult dolphins, misclassifying five males and four females. The classification function rearranged as:

$$p = \frac{e^{5.601 + 17.716(\beta_1) - 5.603(\beta_2)}}{1 + e^{5.601 + 17.716(\beta_1) - 5.603(\beta_2)}}$$

can be used to yield the probability that a dolphin is a male ( $p > 0.5$ ) or a female ( $p < 0.5$ ), based on the Canting Index and the proportion DFW/DFH as measured on the ID images.

#### 4.4 Discussion

In the present study we used underwater laser photogrammetry paired with photo-ID technique to obtain length measurements from 45 sexed adult dolphins and 51 immature dolphins, of which 75% were un-sexed, to describe the growth patterns of spinner dolphins in the Red Sea.

The non-linear growth models most frequently used to describe various biological processes include Gompertz (Gompertz, 1825), von Bertalanffy (von Bertalanffy, 1938), Richards (Richards, 1959) and the sigmoidal logistic equations (Zullinger et al., 1984; Birch, 1999). In previous cetacean studies, whenever several growth models were compared, the Gompertz growth function resulted in the best fit in most cases (Clark et al., 2000; Di-Méglio et al., 1996; Fortune et al., 2012; Neuenhoff et al.,

2011; Stolen et al., 2002) or it was simply chosen as the most meaningful growth model as, for example, it was the best-fitting model for the initial growth spurt, despite other models, e.g. the von Bertalanffy, being a better fit overall (Webster et al., 2010). Usually, however, only a single growth curve was applied to describe the growth pattern of a species, typically based on previous studies (e.g. Calzada et al., 1997; Murphy and Rogan, 2006). This approach certainly makes within-species comparisons more coherent, but hampers the assessment of the appropriateness of the model choice and, consequently, the accuracy of the parameters obtained. Unarguably, a set of different growth models should be examined and compared, and the choice of the most suitable model should eventually be a trade-off between complexity, flexibility, accuracy and its biological meaning.

In the present study, the von Bertalanffy growth curves had only a slight but consistently better fit for the observed length-at-age data for the Red Sea spinner dolphins. The model projections generated in this study indicated a larger length at birth, but a smaller body size at the age of one and two years for the Red Sea dolphins compared to the eastern tropical spinner dolphin and the whitebelly hybrid (Table 4.7). However, the length at birth estimation can be affected by (i) the accuracy in the estimated date of birth (DOB), which in this study was 1-8 weeks (Chapter 1 and Chapter 5) and (ii) model performance (e.g. the von Bertalanffy equation consistently underestimates neonatal metrics; Zullinger et al., 1984). At present therefore, it cannot be concluded that newborn spinner dolphins in the Red Sea are larger than their conspecifics elsewhere.

Gaillard and colleagues (1997) suggested to study growth from the conception, instead of birth, whenever possible, and to include prenatal data in the analysis. By doing so, the length at birth may gain in precision by using in the model a more informative prior for length at birth  $L_0$ , typically resulting in a lower value of  $L_0$  (Neuenhoff et al., 2011; Chivers et al., 2015). Although valuable, this approach however is very challenging in studies of free-ranging cetaceans.

Table 4.7. The mean length (in cm) and 95% confidence intervals (in parentheses) of the Red Sea spinner dolphin extrapolated from the best-fit von Bertalanffy growth curves, (this study) compared with relevant published data.

|                                 | Red Sea             | Eastern                 |   | Whitebelly              |   |
|---------------------------------|---------------------|-------------------------|---|-------------------------|---|
|                                 | This study          | Larese and Chivers 2009 | Perrin et al. 1977;<br>Perrin and Henderson<br>1984 | Larese and Chivers 2009 | Perrin et al. 1977;<br>Perrin and Henderson<br>1984 |
| <b>Length at birth</b>          | 83.5 (79.6–87.5)    | 79.7 (78–84)            | 76.9  | 80.2 (79–82)            | 75.9  |
| <b>Length at age 1 year</b>     | 116.3 (113.4–119.5) | 121.5 (120.4–122.7)     | 132.5   | 122.5 (120.9–124.2)     | 137.2   |
| <b>Length at age 2 years</b>    | 137.5 (133.8–141.5) | 144.1 (143.2–145.0)     | —   | 146.1 (144.6–147.4)     | —   |
| <b>Length at age 3 years</b>    | 151.2 (147.5–155.0) | —                       | 156.6 <sup>a</sup>                                  | —                       | 159.9 <sup>a</sup>                                  |
| <b>Female asymptotic length</b> | 167.2 (164.5–170.5) | 171.5 (171.4–171.8)     | 170.9   | 177.1 (176.7–177.3)     | 174.9   |
| <b>Male asymptotic length</b>   | 182.5 (179.4–185.6) | —                       | 179.5   | —                       | 180.5   |

<sup>a</sup>Lengths at 4GLGs, approximately 3 yrs; GLGs are difficult to distinguish in 3-4 yrs old specimens (Hohn *et al.* 1989; Perrin *et al.* 1977).

A difference in the length at birth between sexes cannot be completely ruled out by the present study. Following Perrin and Henderson (1984), length measurements of un-sexed young dolphins were assigned to both sexes making it impossible to detect any sexual dimorphism in size at birth or to distinguish sex-specific differences in post-natal growth patterns. Furthermore, according to the results presented in this chapter, the length at birth did not contribute to explaining the differences observed in the growth curves of females and males.

Following an initial rapid growth spurt in the first three years, early in their fourth year females and males attained approximately 90% and 83% of their asymptotic length, which is *ca.* 151 cm for both. At that point, the growth trajectories of males and females begin to diverge which results with sexually dimorphic adults. The 99% of the asymptotic length is typically considered the age at physical maturity (Auttila et al., 2016; Read and Tolley, 1997). In our study, this corresponded to the length of 165.5 cm for females and 180.7 cm for males, attained at approximately 7 years of age in females and at 10 years in males.

As physically mature females and males in our study were assigned minimum ages referentially (see Chapter 2), they could possibly be a few years older than our referential estimates. This may have negatively biased the growth rate and, especially males may have grown for a longer period of time than our models indicate. Consequently, age can be predicted accurately from the growth curve for smaller/younger animals for which growth rate is still large compared with individual variation in length.

The data gathered in our study had a proportionally large number of either very young and old animals, but a smaller number of juveniles and there was a complete lack of data for individuals 6-8 years old (Figure 4.1). However, Larese and Chivers (2009) in their studies of spinner dolphins, indicated that the under-representation of juvenile individuals did not bias the growth curve fits, suggesting that our dataset was sufficiently robust to describe the growth pattern of the Red Sea spinner dolphins.

Growth trajectories studied in several animal taxa demonstrate several periods of rapid growth, best described by a combination of separate growth curves for each period (Karkach, 2006). Albeit a single-stage growth model is most often used to fit length-at-age data for cetaceans, many studies demonstrated that growth slows after weaning to increases again near sexual maturation, both in mysticetes (Fortune et al., 2012; Lubetkin et al., 2012) and in small odontocetes (Chivers et al., 2015; Ferrero and Walker, 1999; 1996; Gol'din, 2004; Mattson et al., 2006; Perrin et al., 1976). This applies also to the spinner dolphin; secondary growth spurts are known to consistently begin at approximately 4 and 6 years of age in female eastern and whitebelly spinner dolphins, respectively (Larese and Chivers, 2009) and after the age of 4 years in males (Perrin et al., 1977). It is therefore recommended that efforts be made, both in the Red Sea and elsewhere, to increase the data sample size and to apply the multiphasic form of the Laird-Gompertz model (Laird, 1969) which would likely facilitate a better fit of the length-at-age data than the monophasic models. This would facilitate a better estimation of length at birth and help identifying potential late growth spurts.

The asymptotic length of male Red Sea spinner dolphins appears to be similar, or possibly slightly larger than that of the eastern tropical Pacific form and the whitebelly ecotype (Table 4.7). Females had comparatively smaller asymptotic lengths instead, suggesting that the Red Sea spinner dolphin are more sexually dimorphic in size than the two other forms. However, our sample size was considerably smaller than that used by Perrin and Henderson (Perrin and Henderson, 1984) and Larese and Chivers (Larese and Chivers, 2009) and therefore our findings have to be viewed as preliminary.

According to Bergmann's rule (Bergmann, 1847; Blackburn et al., 1999), body size is inversely correlated with surface water temperature in many regions. It could be argued that Red Sea spinner dolphins follow such general pattern, as the Red Sea waters are warmer than oceanic waters

(Sheppard et al., 1992). Alternatively, another theory suggests that dolphins in enclosed or semi-enclosed seas, such as the Red Sea, would generally tend to adapt to their environment (habitat, prey type and availability) by being smaller in size than the same species in the open ocean (Perrin, 1984). Although these hypotheses are not mutually exclusive, they would only explain why females are comparatively smaller than in other ecotypes. Other selective forces may also be acting upon the animals and the characteristics described in our study likely reflect adaptations to the local environment as well as complex ecological and socio-ecological selective pressures (Gowans et al., 2008).

Sexual selection may have played a role in the evolution of sexual dimorphic characters in the Red Sea male spinner dolphins, just as it has been suggested for other mammalian taxa (Clutton-Brock et al., 1977; Shine, 1989). In the Egyptian Red Sea, limited resources such as resting areas and the access to females are spatially and temporally predictable (see also Chapter 5 and Chapter 6), enhancing the probability of higher encounter rates between male rivals. Selective pressures exerted on males, therefore, may act to maximize the investment in future reproduction through the development of secondary sexual characters and attain maturity at an older age. The prolonged period of growth and the greater size observed in males in this study may serve as an investment, as males may need to compete for access to receptive females and their individual size may determine the outcome (Weckerly, 1998). The observation of tooth rake marks on the bodies of both males and females (pers. obs., Figure 4.8), suggest that physical interactions, possibly aggressive, occur and may include pre-mating competition between males and/or sexual coercion as described elsewhere (Jefferson, 1990; Scott et al., 2005; see Chapter 5).



Figure 4.8. Tooth rake marks along the flanks of female (left) and male (right) Red Sea spinner dolphins (photo: Amina Cesario).

In the eastern tropical Pacific, the mating system of spinner dolphins has been found to vary geographically, with a gradient from a more polygynous mating system in the eastern form to a more promiscuous mating system in the whitebelly form (Perrin and Mesnick, 2003). Perrin and Mesnick (2003) theory, and other authors before them (Brownell and Ralls, 1986; Jefferson, 1990), suggests that cetacean species (or geographic forms, in this case) with relatively small testes and high degree of sexual dimorphism compete principally by monopolizing females and preventing other males from copulating with them. Species (or forms) with relatively large testes and moderate dimorphism, on the other hand, tend towards promiscuous mating systems in which males do not interact aggressively with other males and mate with as many females as possible.

The predictability of resources, strong sexual dimorphism, different attainment of physical maturity between sexes, and the signs of aggression (tooth rake marks) seen in the Red Sea spinner dolphin suggest that this form displays a polygynous mating system (Perrin and Mesnick, 2003; Gowans et al., 2008; Jefferson, 1990; Scott et al., 2005) see also Chapter 3 and Chapter 6). Although not available at present and unlikely to be available anytime soon, information on the testes size would be highly informative in further studies of the reproductive biology of Red Sea spinner dolphins.

The findings of the present study indicate a relationship between the total body lengths and dorsal fin metrics which could be used to estimate the length of free-ranging dolphins from photographs of their dorsal fins, making it applicable to traditional boat-based photo-ID studies. Once the individual length is estimated, approximate age information can be derived from the growth curve generated in this study, facilitating better assessment of the population age structure (e.g. Webster et al., 2010) and hence more accurate estimates of population demographic parameters. Examination of the regression slopes provided no indication of differences between sexes, likely because immature individuals, which are not sexually dimorphic (Chapter 3), were included in the analysis.

Similarly to other ecotypes of spinner dolphins (Perrin et al., 1991), adult dolphins in the Red Sea displayed a sexually dimorphic dorsal fin. In the present study, it was possible to reliably predict the sex of adult individuals from photo-ID images even with no photogrammetric data (Table 4.6). Future studies should endeavour to verify the prediction function found in this study, preferably with data from another population(s) of Red Sea spinner dolphins where sex of individuals is known from underwater observations (e.g. Satayah population; see Chapter 1 and Chapter 6; Fumagalli, 2016). This would then facilitate a greater confidence and broader application of this approach to other populations for which sex data are not available, benefiting future studies of spinner dolphin ecology and social structure across the Red Sea region. This sexing technique has been previously applied to bottlenose dolphins in Doubtful Sound, New Zealand (Rowe and Dawson, 2009) and Australian humpback dolphins (Brown et al., 2015). It represents a less invasive alternative to biopsy sampling (Gowans et al., 2000), and applicable in areas and regions where biopsy sampling may not be permissible under local regulation; yet can gather valuable information with a high degree of accuracy. However, as spinner dolphins exhibit great phenotypical variability and their sexual dimorphism seems to vary geographically (Perrin, 2009), the discriminant function proposed in this study may apply successfully only to the Red Sea spinner dolphins and probably not other geographic forms elsewhere.

## **Chapter 5. Reproductive parameters of the Red Sea spinner dolphin**

### **5.1 Introduction**

Reproductive parameters, including calving interval, crude birth rate, calf survivorship, annual recruitment rate, female age at first reproduction and fecundity represent an integral component of species' life history. The knowledge of these parameters is essential to understanding the demography and viability of wild animal populations (Perrin and Reilly, 1984; Lockyer, 2007), especially when their conservation status is threatened or endangered, or yet undetermined (Currey et al., 2009). Comparing reproductive parameters among populations may reveal, for example, adaptation to local habitats or resilience (or lack thereof) to anthropogenic pressures (Urian et al., 1996; Chivers et al., 2015; Wade et al., 2012). In cetaceans, these life history parameters can be estimated through the examination of gonadal tissue of stranded, intentionally or incidentally captured specimens (Perrin and Reilly, 1984; Whitehead and Mann, 2000). Such cross-sectional data consist of the distribution of reproductive states among females within a population. The benefit of a cross-sectional study is that it allows comparing and recording different variables at the same time; however, it only provides information at a single point in time, with no assessment of individual and temporal variability. Alternatively, reproductive parameters can be estimated through a longitudinal study of free-ranging populations using photo-identification techniques (Wells and Scott, 1990; Mann et al., 2000a; Henderson et al., 2014; Chang et al., 2016). Longitudinal data are the most revealing type of information, as they allow to describe the reproduction patterns over time and permit to investigate individual heterogeneity in reproductive rates, which is rarely addressed in cetacean studies (Wells, 2014; Brough et al., 2016).

Currently, most of the knowledge of spinner dolphin reproductive parameters comes from the examination of more than 6000 female specimens incidentally killed between 1968 and 1994 in the yellowfin tuna (*Thunnus albacares*) purse-seine fishery in the eastern tropical Pacific Ocean (Larese and Chivers, 2009). Two forms of the spinner dolphin, the eastern subspecies (*Stenella longirostris orientalis*) and the whitebelly hybrid, were estimated to have their populations reduced to less than 50% and between ca. 60% and 70% of their pre-exploitation sizes, respectively (Smith, 1983; Gerrodette et al., 2008). Despite the management actions by the USA and international fishing agencies, that have reduced dolphin by-catch by two orders of magnitude across the past 30 years, neither of the two forms of spinner dolphins has shown signs of recovery (Gerrodette and Forcada, 2005; Wade et al., 2007; Wade et al., 2012) as their reproductive output is declining (Cramer et al., 2008). Life history studies of these two forms revealed a diffused reproductive seasonality, gestation time between 10 and 11 months, calving interval of about 3 years, lactation length of 1-2 years and life span of 20-25 years (summarized in Perrin and Gilpatrick Jr, 1994).

While a substantial body of information on the reproductive parameters of the heavily exploited eastern tropical Pacific “pelagic” forms has been gathered, very little is known of the more “coastal” ecotype, the Gray’s spinner dolphin (*S. l. longirostris*) (see Chapter 3 for taxonomic status), which may be subject to different types of anthropogenic pressures, such as commercial dolphin-watching operations (Lammers, 2004; Tyne et al., 2015) or direct killing, either recent, as in some regions, e.g. the Caribbean, the Philippines, Sri Lanka (Perrin and Gilpatrick Jr, 1994 and references therein; Bearzi et al., 2012) or still ongoing (e.g. Oremus et al., 2015).

The Red Sea spinner dolphins are frequently exposed to swim-with-dolphins tourism, which is currently regulated in Samadai reef, the research site of this study (Notarbartolo di Sciara et al., 2009), but nowhere else in the Egyptian Red Sea. Recent study (Fumagalli, 2016)

indicates the impact of such tourism activities is considerable and their sustainability has to be viewed cautiously. A better understanding of the dolphin natural history and population ecology can be informative for the delineation of future management strategies.

In this study, the life history traits of female Red Sea spinner dolphins were evaluated using five years of photo-identification data collected across nine years of field research in Samadai reef. Reproductive parameters calculated included the calving season, calving interval, crude birth rate, calf survivorship, annual recruitment rate and age at first reproduction. The individual heterogeneity in female reproductive success was also investigated. The results presented in this chapter provide information that is instrumental for the evaluation of the effectiveness and sustainability of the management measures currently in place in Samadai reef.

## **5.2 Materials and methods**

### **5.2.1 Data collection and underwater photo-identification**

Samadai reef was surveyed from October 2005 to September 2006 (Costa et al., *in preparation*), in April 2010, and from May 2011 to August 2014. In 35 months fieldwork, 208 sightings were recorded and photo-ID data were collected during 198 sightings. The study area, data collection, age/sex composition and photo-processing methods have been presented in detail in Chapter 2.

Longitudinal data, such as the reproductive histories of individual females are considered the most revealing and least biased type of information (Whitehead and Mann, 2000; Clutton-Brock and Sheldon, 2010) and were used in this study. Identifiable females of all age classes (Distinctiveness category 1 to 4, whose photographs had excellent to fair quality, *i.e.* Q1 to Q4; see Appendix I), photo-captured between 2005 and 2014 were included in the analyses. Including all sightings of known individuals

collected since 2005 allowed to fill in gaps in individual sighting histories, facilitated a more comprehensive assessment of the reproductive parameters and allowed to investigate individual variation (e.g. females' age; see below).

Underwater photo-ID provided the opportunity to determine the sex of individuals and the female reproductive status (Herzing, 1997; Mann et al., 2000a). The sex of the individuals was identified by: (a) direct observations of the genital area (e.g. the presence of mammary slits for females and extruded penis or evident sexually dimorphic post-anal hump for adult males), (b) persistent association with a newborn/calf that regularly swam in echelon position (in contact, under the presumed mother), or (c) evident pregnancy status.

Female reproductive status was categorized as: (1) early visually detectable stage of pregnancy (hereafter defined as "early pregnancy"), *i.e.* slightly swollen, approximately midterm pregnancy; (2) late pregnancy, *i.e.* visibly swollen, from approximately the eighth-ninth month of pregnancy; or (3) postpartum, *i.e.* distended mammaries for a few (~2-4) weeks after delivery, recognizable regardless of the association with a newborn (Figure 2.2, Chapter 2). Underwater photo-identification allowed to detect instances of perinatal mortalities (*i.e.* females seen pregnant and re-sighted in a postpartum status with no calf) and to incorporate these data into analyses.

Individual identification of newborns and calves was based on the consistent association with an identifiable adult, presumed to be the mother. Their age was estimated by their external appearance and body size relative to that of adult. All newborns and calves displayed the light tripartite coloration (Chapter 3). Newborn animals were identified by the presence of features such as visible foetal folds and size less than half the length of a larger accompanying animal presumed to be the mother (approximately up to 6-8 weeks old; Chapter 3). Calves 2-6 months old were approximately half the size of the accompanying adult, without foetal

fold marks. Calves around 1 year of age were approximately 2/3 the length of an adult, calves of 2 and 3 year of age were >3/4 of adult body size, with body shape similar to that of adult but slender and light in colour.

The date of birth (DOB) of newborns and calves 2-6 months old whose mother was seen pregnant, was estimated from the photo-ID data based on last sighting of the mother seen pregnant and the first sighting of the mother-calf pair. For all other calves, the month of birth was estimated backward from the date when the mother-calf pair was first sighted by subtracting the estimated age of calves. DOB accuracy was classified as: "Exact":  $\pm 3$  days; "Best":  $\pm 1$  week; "Good":  $\pm 2$  weeks; "Fair":  $\pm 1.5$  month; "Year":  $\pm 3-6$  months; and "Tentative year":  $> 6$  months.

### 5.2.2 Reproductive parameters

The reproductive parameters of the Red Sea spinner dolphin, including birth rate, annual recruitment rate, fecundity rate, calf survivorship, calving interval, weaning age and age at first birth were calculated based on the inferred age and birth dates of calves.

Calving seasonality was defined as higher number of births (*i.e.* number of newborns and calves 2-6 months old) in a particular month or season (Caughley, 1977). All known births that could be estimated with 3-month accuracy were used in this analysis (Mann et al., 2000a).

Crude birth rate was estimated assuming a sex ratio of 1:1, reported for spinner dolphins (Perrin and Reilly, 1984) and using longitudinal Photo-ID data: the number of births (inclusive of females in post-partum status with no accompanying neonate) was divided by the estimated total population (Wells and Scott, 1990; Clapham and Mayo, 1990). The annual total population was obtained by summing the number of calves (equal to the number of mother-calf pairs or females seen pregnant) to twice the number of mature females (doubled to adjust for the sex ratio).

The annual recruitment rate was calculated by dividing the number of calves surviving to the age 1-year by the annual total population, excluding the number of births (Wells and Scott, 1990). The fecundity rate was calculated as the ratio of the number of calves surviving to age 1-year to the number of mature females (Wells and Scott, 1990).

The calf survival analysis was performed using the Kaplan-Meier method (Kaplan and Meier, 1958), which is a non-parametric statistic suitable for small datasets with precisely measured event times and has the advantage of taking into account censored data, *i.e.* when the calf fate (survival or death) is unknown (Kaplan and Meier, 1958; Hosmer Jr and Lemeshow, 1999). The Kaplan-Meier survival curve is defined as the probability of surviving in a given length of time while considering time in many small intervals (Altman, 1991). The Kaplan-Meier estimator is the nonparametric maximum likelihood estimate of the survival probability  $S$  of an individual to survive until time  $t$ , and it is calculated as:

$$\hat{S}(t) = \prod_{t_i < t} \frac{n_i - d_i}{n_i}$$

where  $n_i$  is the number of individuals alive at time  $i$ , and  $d_i$  is the number of individuals that died or are censored. In other words, for each time interval  $i$ , survival probability is calculated as the number of individuals surviving by the number of individuals still alive, whose fate is known and that may die. Individuals who have died, or whose fate is unknown are not included in the denominator. If mothers were sighted repeatedly without their calf when the calf was < 2 years old, the calf was presumed dead.

For females that were photo-identified in both 2005-2006 and 2011-2014, Wilcoxon test (Gehan, 1965) was used to compare the survival of calves born to younger females (*i.e.* individuals that were physically and likely sexually immature, either calves or juveniles, when first photo-identified in 2005-2006) with calves born to older females (*i.e.* individuals that were sexually mature when first photo-identified in 2005-2006). The survival analyses were performed using the Survival package (Therneau, 2015;

Therneau and Grambsch, 2000) in program R (R Core Team, 2014). Female reproductive success was defined as the number of calves surviving until weaning. Censored calves (whose fate was unknown) were excluded (Mann et al., 2000a).

Calving interval was defined as the interval in years between the estimated birth months of successive calves of an identified female (Clapham and Mayo, 1990).

Weaning was assumed to have occurred when a calf was no longer associated consistently with its mother. For calves that survived until their second year, weaning age was determined by taking the time midpoint between the last sighting of a calf associated with the mother and the first sighting of the mother without the calf (Mann et al., 2000a).

Age of first birth was defined as the age (in years) at which an immature female ( $\leq 3$  years) photo-identified in 2005-2006 was observed with her first calf in Samadai reef in later years. Considering that spinner dolphin gestation period last between 10.5 and 10.9 months (Perrin and Gilpatrick Jr, 1994; Whitehead and Mann, 2000; Larese and Chivers, 2009), the age at reaching sexual maturity was assumed to be approximately one year before the age at first birth.

Females that were mature in 2005 and 2006 and were repeatedly seen in later years with neither calf nor pregnant were considered in postreproductive status (Perrin et al., 1977; Marsh and Kasuya, 1986).

### **5.2.3 Tooth rake scarring and indication of alloparental care**

The presence of tooth rakes on females was assumed to be a result of interaction with adult males, as in Scott et al. (2005). The presence of fresh tooth rakes was examined only on excellent or very good quality photographs (Q1 and Q2) and each photograph was scored by the presence or absence of tooth rake marks. To examine whether tooth rake marks may represent a predictor of cycling events (*i.e.* an observed

pregnancy the following year) the reproductive status of females with tooth rakes was compared to their status the following year.

On a few occasions, newborns were seen temporarily associated in echelon position (swimming under a larger individual, lightly touching the adult's abdomen) (Mann et al., 2000a) with an individual other than the mother, as determined by the absence of typical postpartum features. This behaviour, observed also in the Hawaiian spinner dolphin (Johnson and Norris, 1994), was defined in this study as "babysitting", although generally such term "refers to remaining with young during the absence of the mother" (pg. 354, Kleiman and Malcolm, 1981), whereas in this study the mother was usually resting nearby.

## **5.3 Results**

### **5.3.1 Calving seasonality**

Between October 2005 and August 2014, 84 Red Sea spinner dolphins were identified as adult females, of which 75 had at least one calf during that period. A total of 153 calves were seen and the fate of 120 of them is known until their first year of life. Out of the 80 births recorded, 52 had an estimated Date of Birth (DOB) accurate within 3 months (calves with DOB: "Exact" n=1, "Best" n=8, "Good" n=28, "Fair" n=15) and were included in calving seasonality analysis.

Reproductive histories of 75 females indicated that the birth season extended from June to August, accounting for 92% of all births (n=52) and peaked in July, when 43% (n=37) of calves with the birth date estimation accurate to one month were born (Figure 1). This pattern corresponds to the annual pattern of the mean Sea Surface Temperature (SST) in the area (Figure 5.1a). Pregnant females were seen mostly up until July and increasingly less so in the following months (Figure 5.1b). Furthermore, fresh signs of tooth rakes were observed primarily in July, August and September on females accompanied by dependent calves of 2 years of age or older (45%) or on females without dependent calf (52%).

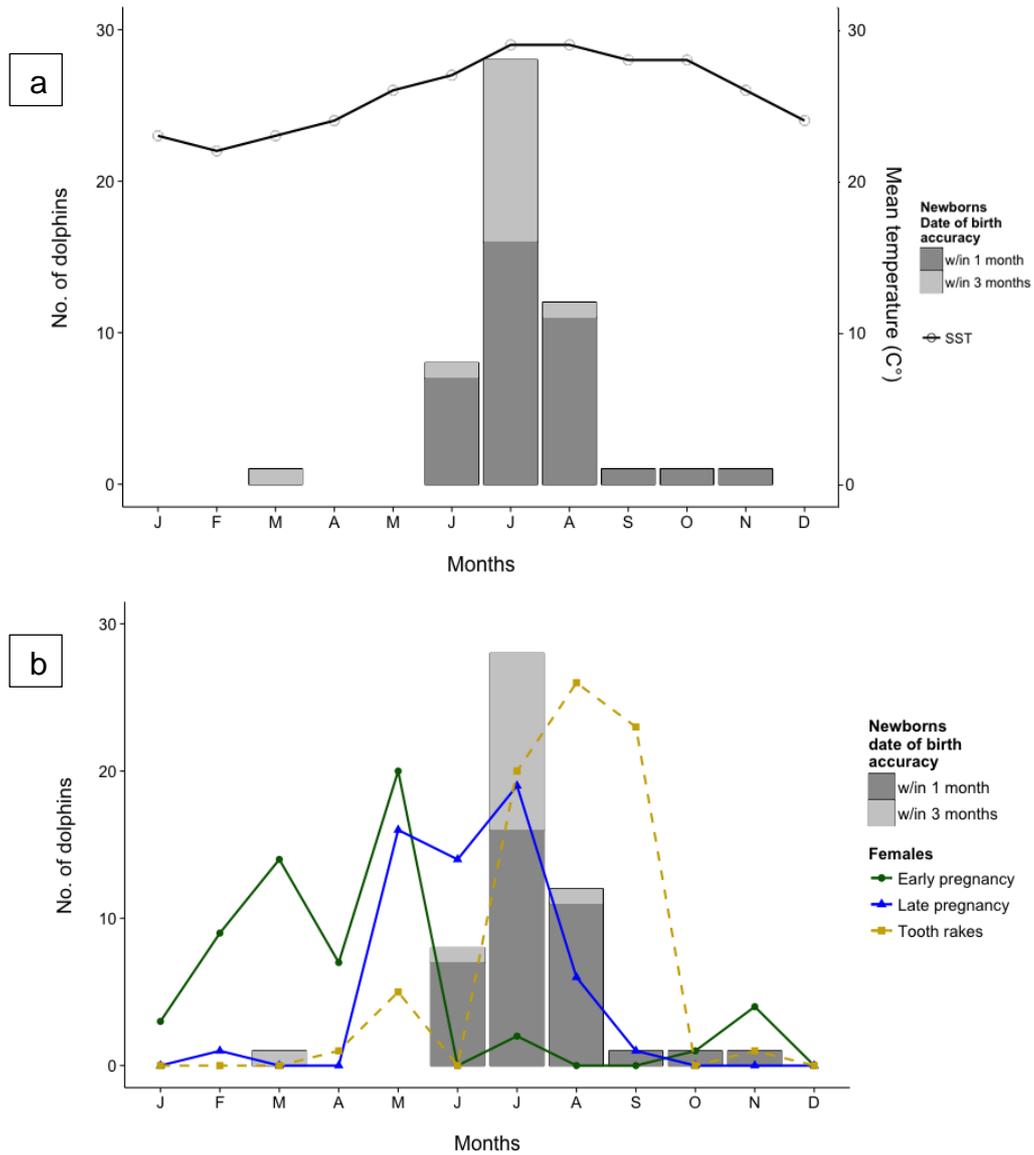


Figure 5.1. Distribution of the estimated month of births of 52 Red Sea spinner dolphin calves in Samadai reef between 2005 and 2014. (a) Mean monthly sea surface temperature (SST) was acquired using the GES-DISC Interactive Online Visualization ANd aNalysis Infrastructure (GIOVANNI) as part of the NASA's Goddard Earth Sciences (GES) Data and Information Services Center (DISC). (b) Monthly numbers of females seen in early (n=42) and late (n=36) pregnancy, and females with fresh tooth rakes (n=29) are also shown.

Of the 29 females showing fresh scarring (tooth rakes), 13 were resighted in two consecutive years, and 11 of them (85%) gave birth the following year. The other two females were young individuals, never seen in association with calf or pregnant, and they both showed signs of tooth

rakes in the subsequent year. The mean number of months between the observation of tooth rakes on a female and the birth of her calf was 10.8 months (SD=0.7, n=8), with 1-month accuracy of the estimated DOB, which resembles closely the gestation time of this species (range 10.5 - 10.9 months; Perrin et al., 1977; Perrin and Gilpatrick Jr, 1994; Whitehead and Mann, 2000; Larese and Chivers, 2009).

### 5.3.2 Annual reproductive parameters

Of the 75 mothers, nine were seen with successive calves, of which seven were “older females” and two were “younger females”. Two-year calving interval was most typical (n=6) compared to three-year interval (n=3). Given the skewed distribution, the median calving interval was calculated and approximated 2.06 years (IQR 0.99; n=9; Table 5.1). Females that were not seen with their calves anymore before the calves reached the age of 2-years were excluded from this analysis, as these calves were presumed to be dead.

Table 5.1. Central tendencies of calving interval for female Red Sea spinner dolphins seen at Samadai reef. Given the skewed distribution of calving interval, the median value is considered more representative than the mean (also given here for comparison with other studies).

|                                 | Calving interval |                |
|---------------------------------|------------------|----------------|
|                                 | 2-year           | 3-year         |
| <b>No. of older females</b>     | 4                | 3              |
| <b>No. of younger females</b>   | 2                | 0              |
| <b>Mean<br/>(SD)</b>            | 2.01<br>(0.11)   | 3.04<br>(0.09) |
| <b>Overall median<br/>(IQR)</b> | 2.06<br>(0.99)   |                |
| <b>Overall mean<br/>(SD)</b>    | 2.35<br>(0.53)   |                |

Twenty-one calves were seen weaned during the study period, of which 13 and eight were approximately two and three years of age, respectively. For five of them the DOB estimation was accurate to 1 month and it was possible to estimate the weaning age. Four calves were weaned at the age of 2-years (mean =  $2.05 \pm 0.10$  SD) and one at the age of 3-years (overall median=2.1, IQR=0.01, n=5). At the time of weaning, all five mothers were in their “late pregnancy,” indicating that mothers usually disassociated with their calf only shortly before their new calf has born.

Between 2006 and 2014, the crude birth rate estimates averaged 0.104 ( $\pm$  SD 0.016, Table 5.2). The mean annual recruitment rate was 0.080 (SD=0.007). Annual proportion of censored cases, estimated as the ratio of the calves whose fate remained unknown to the number of births, was 0.05, 0.26 and 0.25, in 2011, 2012 and 2013 respectively. Hence, the bias due to censored instances was assumed to be negligible. The mean fecundity rate was estimated at 0.196 (SD=0.018).

Table 5.2. Annual reproductive parameters of the Red Sea spinner dolphins in Samadai reef. The crude birth rate represents the ratio of the number of births to the sum of the number of identified individuals in a given year. The number of identified individuals represent the total number of photographically identified mature females (doubled to adjust for the sex ratio) plus the number of mother-calf pairs, which corresponds to the number of calves in a given year (including the number of births). The recruitment rate represents the ratio of the number of calves of Age 1 to the number of identified individuals (excluding the number of births) and the fecundity rate corresponds to the ratio of the number of calves of Age 1 to the number of mature females in any given year.

| Parameters                       | 2006         | 2011         | 2012         | 2013         | 2014         | Weighted mean | Weighted SD  |
|----------------------------------|--------------|--------------|--------------|--------------|--------------|---------------|--------------|
| No. of mature females            | 43           | 54           | 71           | 54           | 52           |               |              |
| No. of mother-calf pairs         | 39           | 39           | 58           | 44           | 43           |               |              |
| No. of identified individuals    | 125          | 147          | 200          | 152          | 147          |               |              |
| No. of births                    | 7            | 20           | 27           | 16           | 10           |               |              |
| No. of surviving calves to Age 1 |              | 9            | 16           | 10           |              |               |              |
| No. of not surviving calves      |              | 10           | 4            | 2            |              |               |              |
| <b>Crude birth rate</b>          | <b>0.056</b> | <b>0.136</b> | <b>0.135</b> | <b>0.105</b> | <b>0.068</b> | <b>0.104</b>  | <b>0.016</b> |
| <b>Recruitment rate</b>          | -            | <b>0.071</b> | <b>0.092</b> | <b>0.074</b> | -            | <b>0.080</b>  | <b>0.007</b> |
| <b>Fecundity rate</b>            | -            | <b>0.167</b> | <b>0.225</b> | <b>0.185</b> | -            | <b>0.196</b>  | <b>0.018</b> |

### 5.3.3 Calf survival

Survival analysis (Kaplan and Meier, 1958) across the initial three years of life returned a calf survivorship of 0.85 (95%CI 0.79-0.91) at the age of 6 months, 0.79 (95%CI 0.73-0.87) at 1-year of age and 0.77 (95%CI 0.70-0.85) between 1.25 and 3-year of age (Figure 5.2a). A comparison of calves born to older (*i.e.* individuals that were adults when first photo-identified in 2005-2006) *versus* younger females (*i.e.* individuals that were immature, either calves or juveniles, when first photo-identified in 2005-2006) (Figure 5.2b) revealed a significant difference in calf survival (Wilcoxon  $X^2=4.8$ ,  $df=1$ ,  $p= 0.0281$ ), showing a lower survivorship of the calves born to younger females. Calf survival was 0.67 (95%CI 0.49-0.91) at the age of 6 months, 0.61 (95%CI 0.43-0.87) between 1 and 3-year of age, for younger females, whereas older females had a calf survivorship of 0.89 (95%CI 0.82-0.96), 0.84 (95%CI 0.76-0.92) and 0.80 (95%CI 0.71-0.90), at the age of 6 months, 1 year and between 1.25 and 3-year of age, respectively. Underwater photo-identification allowed these results to be inclusive of perinatal mortality (*i.e.* females seen pregnant and re-sighted in a postpartum status with no calf).

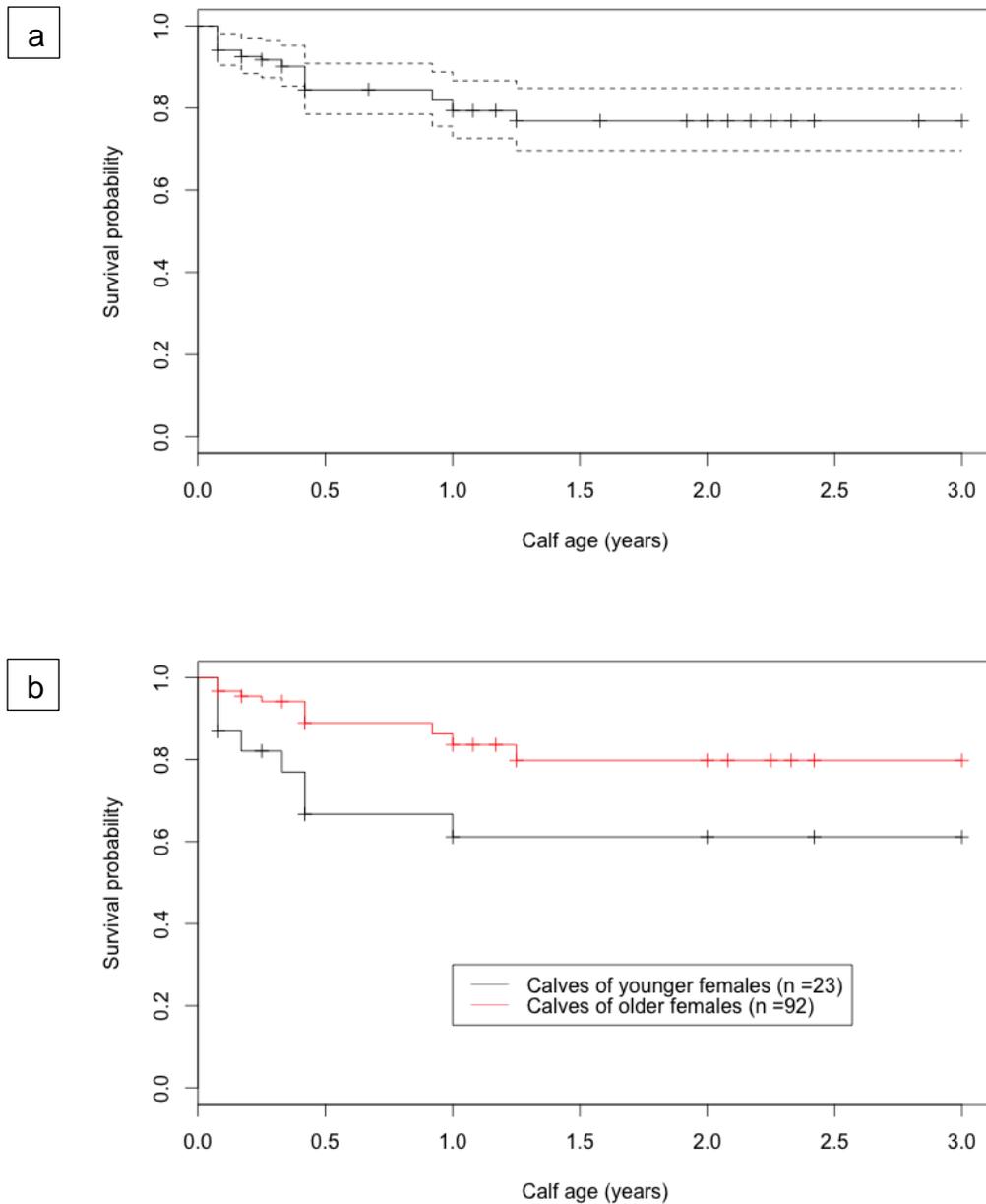


Figure 5.2. The Red Sea spinner dolphin calf survivorship from birth to 3-years of age. (a) Kaplan-Meier survival analysis is shown for all calves grouped together ( $n=153$  born to 75 females; dashed lines represent Confidence Intervals) and (b) for calves born to younger and older females ( $n=23$  and  $n=92$  respectively, born to 51 females). Crosses represent censored instances, *i.e.* when the calf fate (survival or death) is unknown.

The female reproductive success, measured as the number of surviving calves, was relatively high; 63% of females had all calves surviving, 23% had either half or two-thirds of the calves surviving and only 14% of females had no surviving calf. Among the 84 females included in this study, two (2.4%) were found to be likely postreproductive.

#### **5.3.4 Age at first birth and age at sexual maturity**

Four females that were calves when first seen in 2005-2006, were observed with calves of their own in later years. Data from these individuals suggested that females have their first calf when 9-11 years old and reach sexual maturity at the age of 8-10 years. Young females were most commonly seen temporarily “babysitting” calves. Of the 17 observed cases, 12 times (70%) the “babysitter” was a young female, four times an adult female and on 1 occasion an old individual, possibly postreproductive.

### **5.4 Discussion**

#### **5.4.1 Uncertainty of parameter estimation**

Estimating the reproductive parameters for wild cetaceans can prove challenging, as data collection is intrinsically restrained by the animals’ limited time at the surface and because it is frequently affected by external factors such as atmospheric and sea conditions.

The most commonly recognized bias is related to the uncertainty associated with calf survival due to undocumented birth events (e.g, Mann et al., 2000a). In case of an unrecorded calving event, in which the calf dies soon after birth, calf survival rate would be biased upwards, while the annual birth rate would be biased downwards. In the present study, however, the optimal working conditions in Samadai reef (*i.e* underwater observation and data collection), allowed to document both pregnancy and postpartum status, allowing to account for perinatal mortality, hence

decreasing such potential biases. Moreover, gathering data within the sheltered and clear water of the lagoon, even when sea conditions would have not permitted data collection (e.g. Beaufort scale  $\geq 3$ ), allowed the research team to overcome most of the limitations dictated by the open-water field conditions.

The estimates were found to be within a comparable range to conspecific and congeneric species as well as species with similar life histories. The estimated median calving interval of 2.06 years for the Red Sea spinner dolphin is comparable to the estimate first calculated for the eastern tropical Pacific spinner dolphin (range 2.11-2.22 years; Perrin et al., 1977) but shorter than the averaged estimates revised for the same subspecies and for the whitebelly hybrid in later studies (range 2.84-3.04 years; Perrin and Gilpatrick Jr, 1994; Larese and Chivers, 2009). Common dolphins (*Delphinus delphis*) are reported to have a similar inter birth interval (2.1 years, Danil and Chivers, 2007) whereas it appears to be longer, approximately three years, in some congeners such as Atlantic spotted dolphin (*Stenella frontalis*) and pantropical spotted dolphin (*Stenella attenuata*) (Herzing, 1997; Perrin and Hohn, 1994).

The median age of calves at weaning was 2.1 years, which was very close (2 years, Cramer et al., 2008) or well within the range (*circa* 1-3 years, Perrin and Henderson, 1984; Perrin and Reilly, 1984) to that reported for spinner dolphins in the eastern tropical Pacific. Although lactation in spinner dolphins generally lasts about 11-19 months (Henderson et al., 1980; Larese and Chivers, 2009), in this study calves were seen associated with their mother in infant position until the subsequent birth of a sibling (similar to *Stenella frontalis*, Herzing, 1997; and *Tursiops aduncus*, Mann et al., 2000a) suggesting that they undergo a gradual weaning (*i.e.* shift in diet based on a mixture of milk and solid food) during their second year of life, as reported for other species of cetaceans (e.g. Matthews and Ferguson, 2015; Archer and Robertson, 2004). Perrin and colleagues (1977) found that only 1.44% of lactating spinner dolphin females were also simultaneously pregnant, whereas a higher percentage

(30.4%) was found for the short-beaked common dolphins (*Delphinus delphis*, Danil and Chivers, 2007). Although there are observations of > 2-years old calves Red Sea spinner dolphins still suckling their mothers (pers. obs.), it is unclear whether this was due to the nutritional or social needs of the younger animal (e.g. Karczmarski, 1999). For example, in one instance, a female accompanied by her calf during her new pregnancy, resumed nursing the previous calf shortly after she lost her newborn.

Red Sea spinner dolphins showed signs of tooth rakes along the flanks. In a population of bottlenose dolphins where sexual coercion is known to occur, cycling females were significantly more likely to have tooth rakes marks than non-cycling females (Scott et al., 2005). In this study, the mean number of months between the observation of tooth rakes on a female and the birth of her calf (10.8 months) resembled closely the gestation time of this species (range 10.5-10.9 months; Perrin et al., 1977; Perrin and Gilpatrick Jr, 1994; Whitehead and Mann, 2000; Larese and Chivers, 2009), suggesting that the presence of tooth rakes on females' body can be an indication of sexual behaviour and cycling in females.

The mean crude birth rate (~0.10) was slightly higher than those reported for spinner dolphins in the Tropical Pacific (range: 0.067-0.094; Perrin and Henderson, 1984; Perrin and Reilly, 1984) and Atlantic spotted dolphins, *S. frontalis* (0.08; Herzing, 1997), close to those reported for two species of common dolphins, *Delphinus capensis* and *D. delphis* (0.09 and 0.138, respectively; Chivers et al., 2015) and substantially higher compared to bottlenose dolphins', *Tursiops* spp. (range 0.049-0.07, Wells and Scott, 1990; Bearzi et al., 1997; Kogi et al., 2004). The average annual recruitment rate estimated in this study (0.08) was generally higher than those reported for other species (e.g. 0.06 for Atlantic spotted dolphin, *S. frontalis*, Herzing, 1997; 0.048 for common bottlenose dolphin, *T. truncatus*, Wells and Scott, 1990; 0.068 for Indo-Pacific bottlenose dolphin, *T. aduncus*, Kogi et al., 2004). The fecundity rate (circa 0.20) was

similar to other studies (0.23, Herzing; 0.144, Wells and Scott, 1990; 0.24, Kogi et al., 2004).

Two females seen at Samadai reef (2.4%) were considered senescent. Other studies of spinner dolphins found comparable evidence of senescence, e.g. 1% (Perrin et al., 1977; Perrin, 1998) and 0.7% (Larese and Chivers, 2009). In this study, however, females were defined as postreproductive if they were not seen pregnant or repeatedly associated with a calf (*sensu*, Marsh and Kasuya, 1986), and this is only one of the criteria usually used in the literature to assess evidence of senescence (Perrin et al., 1977). The other criteria can be met only when dead specimens of mature females are available and the ovaries, that bear the marks of ovulations, examined (Perrin et al., 1977). Therefore, the proportion of postreproductive females reported in this study should be considered with caution.

Some of the differences indicated above are likely due to different sampling methods, *i.e* live animal sightings versus by-caught specimens. In general, however, these differences are minor and the parameters estimated in this study appear consistent with other similar studies and therefore likely well representative of the spinner dolphins in the northern Red Sea.

#### **5.4.2 Calving seasonality**

The calving season in the Red Sea had one pronounced annual peak, with 92% of the births recorded between June and August. In eastern and whitebelly spinner dolphins, births occur throughout the year, although the former usually shows a single broader annual peak between January and June whereas the latter display a bimodal pattern with peaks in January through March and June through August (Larese and Chivers, 2009; Barlow, 1984). Perrin and Henderson (1984) reported a seasonal fluctuation in testis weight (which they assumed to be representative of male fertility) which in the eastern spinner dolphin increased in March-

June and in the whitebelly form peaked in July-August and February and decreased between September and January in both forms. This pattern well predicted the broader calving peak for the eastern spinner dolphins and the bimodal distribution of birth dates for the whitebelly hybrid form. Hawaiian spinner dolphins were also reported to display a bimodal pattern, with two calving peaks during the year, in August and February (Östman-Lind et al., 2004). Serum hormone levels in spinner dolphins in a captive facility in Honolulu (Hawaii) showed one male having peak testosterone levels in June and July, and two females having elevated estradiol levels in June and October, respectively (Wells, 1984). Hormone levels in females suggested that those two individuals might only give birth at one time of the year, similarly as seen at Samadai reef.

In tropical and subtropical regions, a diffuse reproductive seasonality is generally expected (Whitehead and Mann, 2000); however, adaptations to local environmental conditions may have a strong influence on the seasonality of reproduction (Urian et al., 1996). The calving season in the Red Sea corresponds with warmer water temperatures, which may represent one of the proximate causes of the observed birth seasonality. The parturition rate in odontocetes often increases during the highest surface water temperature (e.g., Bearzi et al., 1997; Kogi et al., 2004; Wells, 2014; Mann et al., 2000a) as it likely helps the survival of newborn calves, which have a small volume-to-surface-area ratio and poor insulation (*i.e.* thin blubber layer) (Whitehead and Mann, 2000). Calving seasonality also often coincides with increased prey abundance (Whitehead and Mann, 2000), which is crucial in securing energy for lactation (Lockyer, 2007). Findings related to the Red Sea spinner dolphin feeding ecology suggest that dolphins forage mostly on the same prey species year-round (Appendix VII); however, it is unknown whether there is any seasonal variation in the prey abundance. Recent studies on the phytoplankton seasonal succession in the Red Sea showed, however, that the period between mid-May and mid-September (which includes the calving season reported here) represents the most oligotrophic time (Raitsos et al., 2013), suggesting it may not coincide with highest prey

abundance. Therefore, whether prey abundance dictates seasonality of breeding in the Red Sea spinner dolphins remains yet to be determined.

An alternative ultimate explanation to the female synchronous reproductive peak observed in Samadai reef may be related to (1) an anti-predator strategy, where a newborn may be safer from predators if there are other calves in the group (*i.e.* dilution effect) and where the formation of nursery groups may facilitate a greater cover and communal defence (Norris and Schilt, 1988; Whitehead and Mann, 2000; see also the “predation risk hypothesis” discussed in Chapter 6); (2) allomaternal care of calves (“babysitting”), which may be more efficient if calves within a group are of the same age (Whitehead and Mann, 2000).

#### **5.4.3 Calf survivorship and heterogeneous reproductive success**

In the present study, calf survivorship for an individual younger than 1-year was estimated at 0.85 and was comparable, and generally higher, to published estimates of other odontocetes, *e.g.* circa 0.8 for *T. truncatus* (Wells and Scott, 1990; Haase and Schneider, 2001), 0.76 for *S. frontalis* and *T. aduncus* (Herzing, 1997; Mann et al., 2000a). A slightly higher value (0.87) was reported for *T. aduncus* in Kimura Island, Japan, but the authors cautioned that the value may have been overestimated (Kogi et al., 2004).

Shark predation is certainly among the extrinsic causes of mortality (Heithaus, 2001) (see Figure 6.5, Chapter 6), but it is difficult to evaluate to what extent. Other concurrent causes may be of anthropogenic origin. Cetaceans are commonly affected by incidental entanglement in fishing gear (Reeves et al., 2005; Read et al., 2006) and although the magnitude of the impact of commercial and artisanal fisheries in the area is unknown, only few scars caused by fishing gears were observed on spinner dolphins in Samadai reef (on two individuals, pers. obs.) and, at least in one case, were not fatal (a dolphin entangled with fishing line and hooks was re-

sighted freed of the entanglement), suggesting incidental by-catch in the area is limited. Conservation concerns have instead emerged in relation to the rapid development of tourism activities in the region (PERSGA, 1998), which includes dedicated commercial dolphin watching operations in spinner dolphins' resting areas. There is evidence that spinner dolphins engage in resting behaviour predominantly in well-defined preferred resting habitats (Tyne et al., 2015), which make them particularly vulnerable to disturbance caused by tourism operations (e.g. Courbis and Timmel, 2009; Lammers, 2004; Danil et al., 2005; Timmel et al., 2008). One of the potential indicators of a stressed population is represented by low calf survival and reproductive success (Orams, 2004). The results reported in this chapter, however, did not raise concern for Samadai reef population, where a management plan in place since 2004 (Notarbartolo di Sciara et al., 2009; Chapter 2) regulates tourist access to the resting area, limiting spatially and temporally the tourists' interactions with dolphins.

Although the overall calf survival appears to be relatively high for this population, calves born to younger females showed a significantly lower survival (0.67) than older females (0.89), indicating heterogeneity in female reproductive success. Few studies have addressed which intrinsic factors influence calf survival, although high variance in reproductive success seems likely to be a feature of many dolphin populations (e.g. Wells, 2014; Henderson et al., 2014; Brough et al., 2016). At Sarasota, Florida, female reproductive success of bottlenose dolphins (*T. truncatus*) appears to be related to several factors, including the mother's age, where older, more experienced mothers are more successful in rearing young over the typical 3- to 6-year period of association (Wells, 2014). Age has been correlated with reproductive success in other bottlenose dolphin populations (Mann et al., 2000a; Frère et al., 2010a). In Doubtful Sound, New Zealand, Brough et al. (2016) demonstrated that birth timing and mother size are correlated with female reproductive success, whereas minimum mother age did not appear to be a significant predictor of calf survival, although the authors stated that some lack of accuracy in the

parameterisation of age may have impacted the ability to establish age-related effects.

The considerable variation in reproductive success of Samadai reef females seemed to be related to the mother's age, conforming to what is generally known for mammals, *i.e.* first-born calves are more likely to die than later-born calves (Clutton-Brock, 1984; Promislow and Harvey, 1990). The proximate causes may be physiological and/or related to maternal inexperience in parenting (Whitehead and Mann, 2000). Younger mothers may have a higher relative energetic cost of gestation and lactation during a period in which they are still investing in their own somatic growth (*e.g.* Reiter and Le Boeuf, 1991; Wells, 2014). Older females may have more experience at parenting, possibly raising their calves in larger groups (Wells, 2000; but see Mann et al., 2000a), likely providing higher protection against predation (Wells, 2014). The observed allomaternal care mostly displayed by younger females in the present study, suggests their urge to practice the maternal skills needed in later years, supporting the experience-related hypothesis.

At Samadai reef, calves and juveniles were seen interacting with tourists more frequently than adults (observed but not quantified). Constantine (2001) reported that juvenile common bottlenose dolphins were significantly more likely to interact with tourists than adult dolphins and that juveniles were more likely to swim in close proximity with an adult when tourists were not in the water. Although mothers may not perceive swimmers as a threat to their offspring (Constantine, 2001), it has been demonstrated that experienced mothers increase control over their calf's environment as compared to first-time mothers, by maintaining greater synchrony and keeping calves closer (Owen, 2001). It cannot be ruled out that lower control over their offspring by younger mothers and the subsequent higher interaction with tourists in Samadai reef, may disrupt calves' rest and sleep phases, reducing their functional abilities and alertness (Cirelli and Tononi, 2008) and ultimately enhancing the chance

of predation during night-time forays. However, there are no data available or means of testing such a hypothesis.

#### **5.4.4 Calving interval and age at sexual maturity**

Spinner dolphins at Samadai reef showed individual heterogeneity in the length of calving interval. Danil and Chivers (2007) found that younger adult females tend to have relatively shorter calving interval compared to the older. Similarly, Perrin et al. (1977) hypothesized that older females of the eastern tropical spinner dolphin (*S. l. orientalis*) have fewer calves, which they nurse longer. In the current study, females with 3-year interbirth interval were older females (n=3), supporting Perrin et al. (1977) and Danil and Chivers (2007) hypothesis. However, most of the females with 2-year calving interval were also older individuals (67%, n=4). Although the sample size in this study was small and skewed towards older females, the preliminary result seems to support Larese and Chivers (2009) work on eastern spinner dolphins, that did not detect any age-related change in the reproductive output.

The estimated mean calving interval at Samadai reef (approximately 2 years) was shorter than that estimated for the conspecifics elsewhere (Larese and Chivers, 2009). Danil and Chivers (2007) suggested that such difference may reflect a compensatory response to low population density. Under this assumption, shorter calving intervals and earlier age at reaching sexual maturity are expected as a response in stressed or exploited populations (Fowler, 1984). In an earlier study, however, Perrin and Reilly (1984) compared the reproductive parameters of two spinner dolphin populations with different level of exploitation and noticed that the estimates did not behave entirely as would be predicted by the assumption of density-dependent response. The length of lactation was longest in the most exploited population and shortest in the least-exploited population. Assuming that duration of lactation may be proportionally related to the length of calving interval, the shorter-than-expected interbirth interval found in the present study should not necessarily be a cause of concern.

Females at Samadai reef appeared to attain sexual maturity at 8-10 years. Given that no data were collected between 2007 and 2010, it cannot be completely excluded that the age at sexual maturity was somewhat overestimated, as females might have given birth, and subsequently lost their calf when no data were collected. This is not highly likely, however, as their age between 2007 and 2010 would have ranged between 3 and 6 years (*i.e.* juvenile age class).

In the Red Sea spinner dolphin, the age at reaching sexual maturity (ASM) of 8-10 years appears to be later than that reported in female spinner dolphins of the eastern tropical Pacific (ETP) (4-7 years; Perrin and Gilpatrick Jr, 1994), but comparable with the updated estimate for the same ETP populations (9-10 years; Larese and Chivers, 2009). Differences in the ASM are thought to correspond to longevity (Larese and Chivers, 2009). When compared to species with comparable longevity, the ASM estimate reported here for the Red Sea spinner dolphins is similar to that of common dolphins (Danil and Chivers, 2007) and spotted dolphins (Herzing, 1997). Although further investigation is needed, the current ASM estimate, along with the observed calving interval of ~2 years, and relatively high calf survival and annual recruitment rate suggest a healthy population not subjected to any considerable natural or anthropogenic stressors.

## Chapter 6. Population parameters of spinner dolphins at Samadai reef

### 6.1 Introduction

Population parameters, such as abundance, survival, recruitment, connectivity and individual geographic fidelity constitute a fundamental component of species' population ecology. Accurate estimation of these parameters is important to understand ecological and biological processes (McCallum, 2000) and allows to identify potential impacts of natural and/or anthropogenic pressures (Hammond et al., 2013). Ultimately, this knowledge is critical in developing adequate management plans or refining existing approaches to make them more effective (Evans and Hammond, 2004). Population parameters are affected by the natural environmental variability (Forney, 2000) and may vary as a function of individual attributes and states, such as sex, age and reproductive status (Lebreton et al., 1992; Härkönen et al., 1999; Cameron and Siniff, 2004; Sprogis et al., 2016). In order to obtain accurate parameters it is crucial to integrate such variability into population analysis whenever possible (Eberhardt, 1985; Nichols et al., 2004; Pradel et al., 2008; Baird et al., 2015).

In cetaceans, various degrees of sexual segregation are not uncommon (e.g. Fury et al., 2013; Martin and Silva, 2004; Laidre et al., 2009; Webster et al., 2009). However, sex-specific studies are hampered by the intrinsic difficulty of differentiating between sexes in the wild, either because no obvious dimorphism is present (*i.e.* monomorphic species) or because it is challenging to assess such difference in the field even when species are sexually dimorphic (Ralls and Mesnick, 2002). Sexual dimorphism in spinner dolphins has been found to vary geographically (Perrin and Mesnick, 2003) and the Red Sea spinner dolphins exhibit a strong sexual dimorphism when fully grown adults (Chapter 3). Studies of socio-demographic dynamics of spinner dolphins also revealed a great intraspecific variability. These aspects have been studied in detail in the

Hawaiian Archipelago and in the Society Islands (French Polynesia). Off the Main Hawaiian Islands, spinner dolphins have generally a fission-fusion social structure (Norris and Dohl, 1980; Norris et al., 1994; Tyne et al., 2014) in which most animals associate with a number of other animals at different times, but associations form and break over a range of time scales. Group sizes are relatively small and comparable to those reported in the Society Archipelago. However, in the South Pacific, discrete insular communities appear to be connected through male and female gene flow which leads to a broader metapopulation structure (Oremus et al., 2007). Another scenario is reported in remote atolls in the far-western Hawaii, Midway and Kure atolls, where spinner dolphins form much larger groups with long-term social bonds, philopatry of both sexes, and parallel dispersal of mixed-sex groups that move between otherwise stable, resident and socio-behaviourally discrete dolphin communities (Karczmarski et al., 2005; Andrews et al., 2010).

The current knowledge of ecology and behaviour of spinner dolphins in the Red Sea is mostly based on data collected at Samadai reef during a 2-year monitoring project carried out in 2004-2005 (Notarbartolo di Sciara et al., 2009), a 1-year research project in 2005-2006 (Costa et al., 2012) and the findings of three concurrent projects conducted between 2010 and 2014 in the Southern Egyptian Red Sea (Costa, 2015; Fumagalli, 2016), including the study at Samadai reef presented here. Earlier research at Samadai reef indicated that a population of about 400 individuals use the area for resting and socializing and that some of these individuals preferentially choose this area year-round (Notarbartolo di Sciara et al., 2009; Costa et al., 2012). Studies conducted in two other resting areas, Satayah reef and Abu Tess reef, located 120 km and 380 km south of Samadai reef, respectively (Figure 1.1, Chapter 1), highlighted a great similarity with previous findings obtained at Samadai reef (Fumagalli, 2016; Costa et al., 2012; Costa et al., *in preparation*).

A recent line transect abundance estimate calculated across the southern Egyptian Red Sea (approximately 400 km of coastline, Figure 1.2, Chapter

1) indicated a population of spinner dolphins of about 7000 individuals (Costa, 2015). Given the inshore diurnal distribution of the species (Chapter 1), this estimation is likely negatively biased as it is exclusive of the reef-associated dolphins (*i.e.* the “resting area trapping effect”; Costa, 2015).

Among the several resting areas known to exist in the Egyptian Red Sea and exposed to commercial dolphin-watching operations (see Chapter 1), Samadai reef represents the only site where a management plan regulates tourist visits and activities (Notarbartolo di Sciara et al., 2009). A recent study by Fumagalli (2016) revealed that the exposure to tourism and research operations has an effect on the behavioural responses of the reef-associated dolphins, calling for a revision and implementation of site-specific management regulations. Previous population estimates calculated for the dolphins at Samadai reef were based on a short, 1-year study, which prevented any evaluation of the present management plan. As pointed out by Costa et al. (*in preparation*), further research was needed to provide a crucial multi-year data that could facilitate a thorough assessment of the effectiveness and methodological refinement of current management actions. For example, systematic abundance estimates and information on spatial and temporal distribution can indicate whether there are predictable areas and times of concentrated occurrence and behaviour that can be used to manage human activities (*e.g.* tourism) so that they coexist and not compete with the needs of dolphins (Evans and Hammond, 2004).

This study examines sex-specific geographic fidelity, abundance and population parameters in a reef-associated population of spinner dolphins in the Egyptian Red Sea. These estimates are compared with the limited information available for the Red Sea region as well as other spinner dolphin populations studied elsewhere. This work contributes to the assessment of the management plan that is currently in place at Samadai reef and furnishes a solid quantitative basis for further, long-term and potentially comparative study.

## 6.2 Materials and methods

### 6.2.1 Data collection and processing

The study area, data collection, age/sex composition and photo-processing methods have been described in detail in Chapter 2. Underwater photo-identification data were collected at Samadai Reef from May 2011 to August 2014 and, subsequently, capture-recapture techniques were applied to estimate the dolphin abundance, population parameters and movement patterns. Photo-identification data collected during an earlier study, from October 2005 to September 2006 were used to investigate individual residency patterns and examine potential long-term site fidelity.

From May 2011 to November 2012, surveys at Samadai reef were conducted for five consecutive days each month, weather permitting. In 2013 and 2014 data collection was limited to three summer months (June, July, August) but the monthly field effort intensified. Every one-day in the field at Samadai reef was defined as a 'survey', with each dolphin group encountered during a survey termed as a 'sighting'. A group is defined here as an aggregation of individuals within the waters of the lagoon, typically engaging in the same behaviour and usually with no changes in group membership throughout the survey day (see Chapter 2). Consequently, each survey day in which dolphins were present in the study area corresponds to one sighting. A sighting began when dolphins were spotted in the lagoon and ended when dolphins or the research team left, whoever first.

During each underwater session a large number of photographs were taken of as many individuals as possible, irrespective of distinctive marks. Attempts were made to attain an even photographic coverage of the group and to collect at least one high quality picture of the entire body for each individual. Pictures were usually taken at the distance of 2-10m from the

dolphins. Throughout the study, photographs were taken using a Canon G10, a Panasonic Lumix tz7, a Canon PowerShot S110 and a Canon PowerShot D10 all equipped with 10 bar underwater housings. All cameras ensured high standards of photographic quality.

Group sizes varied considerably throughout the study and the probability of photo-capturing all members of a group decreased with larger groups. Sightings in which the number of photographs containing at least one dorsal fin was less than three times the number of dolphins recorded, were excluded from all further analyses, assuming an incomplete photographic coverage (*sensu* Urian et al., 2015; see Appendix V for details). The quality of the photographs containing at least one dorsal fin was first assessed based on four characteristics: focus/clarity, contrast, angle and dorsal fin visibility. Only images of excellent (Q1) and very good (Q2) quality were used for analysis (Appendix I). Individual dolphins were identified based on any distinctive feature visible from both sides (e.g. notches, nicks and scars along the dorsal fin edges or the body profile). Secondary markings, such as tooth rakes, scrapes, scars, peculiar pigmentation patterns and marks on the pectoral fin edges, that were visible only from one side, were not considered suitable for identification purposes. Individual animals were considered “highly marked” (D1 and D2), “marked” (D3) or “non-distinctive” (D4 and D5) according to the number and size of notches, nicks and/or deformation observed on their dorsal fins or body profiles (Würsig and Jefferson, 1990) (Appendix I). The annual rate of mark acquisition was estimated across 9 years (2005-2014) as the probability of an individual dolphin acquiring a new reliable mark, following the methods of Default and Whitehead (1995). The yearly proportion of individuals transitioning from the less distinctive categories (D3 and D4) to any of the highly distinctive categories (D1 or D2) was calculated. Before an individual was assigned a unique identification number and included in the catalogue, it was compared with all other individuals in the photo-ID catalogue. One other experienced researcher periodically checked the catalogue.

The sex of the individuals was based on observations of the genital area, association with a newborn/calf or evident pregnancy status (see Chapter 2 and Chapter 5). Individuals were broadly divided into two mutually exclusive age classes: dependent calves (including newborns and calves up to their third year of age) and non calves (including juveniles and physically mature individuals; hereafter referred to as adults) (Perrin and Gilpatrick Jr, 1994). Dolphins were considered dependent calves when their size was estimated at less than 3/4 of the average adult length and swam in close association with an adult presumed to be the mother. All other larger individuals were assigned to the adult class. In this chapter, juveniles were included in the adult class as they were sufficiently marked to be photographically re-captured. Estimates of population parameters, abundance and movements patterns presented in this chapter refer to all highly marked (D1 and D2) non calves of both sexes combined and each sex separately.

## **6.2.2 Analytical approach**

### *6.2.2.1 Geographic fidelity and residence time*

To investigate the dolphin movement pattern in and out the study area, lagged identification rates were calculated. The lagged identification rate (LIR) indicates what is the probability that if an individual is seen in the area at some point in time, it can be re-sighted again in this area at some time lag later (Whitehead, 2001). In other words, LIR illustrates how individual residence within an area changes with time. To estimate the amount of time dolphins resided within and outside the study area throughout both warm and cold seasons, the data collected year-round between May 2011 and November 2012 (across 19 months, with mean interval between sightings =  $10 \pm 16.8$  days; range: 1-64 days) were used. Each sampling day corresponded to one group of dolphins, ensuring data independence. Lagged identification rates were calculated for all highly marked adult dolphins (D1 and D2) and for each sex separately (Table 6.1) and, subsequently, demographic models were fitted to the data.

Table 6.1. Mathematical models of lagged identification rates (Whitehead, 2001) fitted to the observed data of the Red Sea spinner dolphins at Samadai reef, Egypt.

| Model  | Function  | Parameter explanation  |
|--|---|--|
| <b>Closed</b><br><i>(No changes in the individuals present in the study area)</i>  | $1/a_1$   | $a_1$ = No. of individuals   |
| <b>Emigration + mortality</b><br><i>(Individuals could leave the study area but never return)</i>                                | $(1/a_1) \cdot \exp(-td/a_2)$   | $a_1$ = No. of individuals<br>$a_2$ = mean residence time  |
| <b>Emigration + reimmigration</b><br><i>(Individual could enter, leave and re-enter the study area)</i>                          | $(1/a_1) \cdot ((1/a_3) + (1/a_2) \cdot \exp(-(1/a_3 + 1/a_2) \cdot td)) / (1/a_3 + 1/a_2)$                     | $a_1$ = No. of individuals<br>$a_2$ = mean time in study area<br>$a_3$ = mean time out of study area                           |
| <b>Emigration + reimmigration + mortality</b><br><i>(Individual could enter, leave, re-enter the study area or never return)</i> | $(\exp(-a_4 \cdot td) / a_1) \cdot ((1/a_3) + (1/a_2) \cdot \exp(-(1/a_3 + 1/a_2) \cdot td)) / (1/a_3 + 1/a_2)$ | $a_1$ = No. of individuals<br>$a_2$ = mean time in study area<br>$a_3$ = mean time out of study area<br>$a_4$ = mortality rate |

*td*: time lag in days.

Residence time within and outside the study area was used to quantify the diel utilization of the lagoon by the dolphins rather than the actual residence inside the lagoon. Spinner dolphins usually enter Samadai reef in the morning for resting and leave for foraging later in the day (Notarbartolo di Sciara et al., 2009).

Bootstrap techniques were used to calculate 95% confidence interval error bars and standard errors for each model parameter, providing confidence spans closest to the true values and with least variation (Whitehead, 2007). The best fitting models were selected using the Quasi Akaike Information Criterion (QAIC) (Whitehead, 2007). The model with the lowest QAIC was selected as the best-fitting model and models with  $\Delta\text{QAIC} < 2$  were considered supported (Burnham and Anderson, 2002). Computation of lagged identification rates and model fitting was implemented using the software SOCPROG 2.6 (Whitehead, 2009).

#### 6.2.2.2 *Capture-recapture analysis*

The Robust Design approach (Pollock et al., 1990; Kendall et al., 1995; Kendall et al., 1997), which combines the use of open and close population models within one sampling design, was implemented to estimate annual abundance, survival rate and temporary emigration of spinner dolphins frequenting Samadai reef. The Robust Design stipulates open primary samples (capture occasions), with time intervals long enough to allow for population changes (*i.e.* gains and losses), within which are nested secondary capture samples distributed over short intervals, during which the population is assumed to be closed. Specifically, the Robust Design allows to estimate survival and temporary emigration between primary samples under the open population model, and population size within each primary sample through a closed population model (Pollock et al., 1990; Kendall et al., 1995; Kendall et al., 1997).

*Robust Design structure and assumptions*

As the Robust Design cannot estimate temporary emigration parameters when the time intervals are unequal between primary samples, a systematic survey design was resampled and the capture–recapture analysis were limited to the warm seasons (May–September; Sheppard et al., 1992; Edwards and Head, 1987). This ensured the estimability and comparability of all parameters. To obtain adequate sample sizes, individual capture histories were pooled by 6-day intervals. In total, during this 4-year study, there were 4 primary periods (warm seasons) separated by one-year time intervals and 25 six-day long secondary periods (see Results, Table 6.5).

The assumptions under the closed Robust Design are a combination of the assumptions for closed and open population methods, namely: (1) all individuals present in the population in a sampling occasion have equal probability of capture; (2) capture and recapture probabilities are equal; (3) marks are unique, permanent and correctly identified; (4) all individuals have equal survival probabilities; (5) all secondary samples are instantaneous; (6) the population is closed within primary periods, and (7) probabilities of capture are independent between individuals (Pollock, 1982; Pollock et al., 1990; Williams et al., 2002).

To reduce departure from the assumptions, several validations were implemented: (1) to minimise heterogeneity in capture probabilities, only high quality images (Q1 and Q2) and highly marked individuals (D1 and D2) were used in the analysis; (2) capture and recapture probabilities were assumed to be homogeneous and were set equal ( $p=c$ ) on all fitted models (photo-identification protocols should not elicit a behavioural response as they do not require physical removal and release of animals); (3) to ensure correct identification, only highly marked individuals were retained for further analyses and every individual image added to the photo-ID catalogue was verified by another experienced researcher to minimise misidentifications; (4) probability of survival can vary by several factors, including age and/or sex: to ensure equal survival probabilities,

dependent calves were excluded from all analyses and the effect of sex was investigated; (5) secondary periods were considered instantaneous as they were relatively short in duration (one season) in comparison with dolphin life span; (6) the assumption of closure within primary periods was tested using the program CloseTest (Stanley and Richards, 2005; Stanley and Burnham, 1999; Otis et al., 1978); (7) the assumption of the independence of captures is likely to be violated as Samadai spinner dolphins appeared to be socially structured and to have preferred associates (Appendix VI). This does not bias the estimates, but may inflate the corresponding standard errors (Williams et al., 2002).

Homogeneity of capture and survival probability and absence of behavioural response, *i.e.* assumptions (1), (2) and (4), were additionally assessed through goodness of fit tests (GOF) run on the data previously pooled into primary periods (*i.e.* the Cormack-Jolly-Seber model, CJS) using the program U-CARE (Choquet et al., 2009). The median variance inflation factor ( $\hat{c}$ ) (White and Burnham, 1999) was calculated and used to adjust for overdispersion in the data.

#### *Robust Design parameters estimation*

Robust Design analyses were run on two datasets: (1) all adult dolphins (including individuals of unknown sex); and (2) adult individuals for which sex had been determined. The sex-specific analyses were run on this latter dataset, excluding nine un-sexed individuals, to avoid incurring in positively and negatively biased survival estimates of known-sex and unknown-sex animals (Nichols et al., 2004).

Parameters estimated under the Robust Design structure included: number of animals in the study area for each primary sample ( $N$ ), the probability of apparent survival (product of true survival and fidelity to the study area) between primary periods ( $\phi$ ), the probability of temporary emigration given that an individual was absent ( $\gamma'$ ) or present ( $\gamma''$ ) in the previous primary sample, the probabilities of capture ( $p$ ) and recapture ( $c$ ).

*Robust Design model selection*

A step-down model selection approach (Lebreton et al., 1992) was adopted to estimate each demographic parameter. This procedure starts with a fully parameterized model that fits the data and decreases the dimensionality toward a more parsimonious model that is supported by the data. First, capture and recapture probabilities were constrained to be equal ( $p=c$ ) as photo-identification did not require handling of animals and therefore should have not affected the recapture probabilities (Parra et al., 2006). Capture probabilities were modelled as time varying between and within primary samples  $p=c(t,s)$ , as constant within primary samples  $p=c(t,.)$  and as constant between and within primary samples  $p=c(.,.)$ . The dimensionality of the apparent survival and temporary emigration probabilities was kept constant  $\phi(.)$  and simple (no-emigration model:  $\gamma'=\gamma''=0$ ) (Lebreton et al., 1992; Silva et al., 2009; Pérez-Jorge et al., 2016). Secondly, survival probabilities were modelled as constant over time  $\phi(.)$ , varying by time  $\phi(t)$ , and including time-since marking or “age dependence” effect (*i.e.* presence of transients and residents)  $\phi(a2)$ ; the best fitting model of capture probability previously estimated and the no-emigration model were used in this step. Lastly, temporary emigration parameters were modelled as random ( $\gamma'=\gamma''$ ), where the probability of an individual being present in the study area was independent on whether or not it was present in the study area in the previous sampling period; and as Markovian ( $\gamma'\neq\gamma''$ ), where the probability of an individual being present in the study area was conditional on whether it was present or not in the study area in the previous sampling occasion (Kendall et al., 1997). Both constant and time varying effects were tested on random and Markovian temporary emigration parameters, while using the best fitting models of survival and capture probability determined in previous steps.

The same procedure was followed for both datasets. In the analyses run on the dataset that included only sexed individuals, the sex ('sex') was additionally integrated in the candidate models set to investigate whether it had an effect on the demographic parameters.

The proportion of transient individuals was estimated for all adult individuals as  $1-\phi'/\phi$  (Pradel et al., 1997), where  $\phi'$  is the survival probability of newly marked individuals and  $\phi$  is the estimated survival of individuals previously encountered. Finally, parameter estimates of highly marked individuals (D1 and D2) were averaged across models based on the normalized Akaike weights (White et al., 2001; Burnham and Anderson, 2002) for all adults and for each sex separately.

The Quasi Akaike Information Criterion (QAICc) was used to evaluate model fit, as this Akaike Information Criterion accounts for overdispersion (Quasi) and small sample sizes ( $c$ ), and the best fitting model was identified as having the lowest QAICc (Burnham and Anderson, 1998; Burnham and Anderson, 2002; 2004). Robust Design analyses were implemented using program MARK (White and Burnham, 1999).

*Proportion of marked individuals and total abundance estimate*

Abundance estimates from mark-recapture models depend on the proportion of highly marked individuals (distinctive: D1 and D2) in the population ( $N$ ). In the current study, the terms abundance and population size are used synonymously, similarly as in Parra et al. (2006). To estimate the total abundance of the population ( $N_{total}$ ), estimates were adjusted based on the proportion of individuals that were not highly marked (less/non-distinctive: D3, D4 and D5). A mark rate was calculated using only excellent (Q1) and very good (Q2) photographs of distinctive and less/non-distinctive individuals (excluding calves) (Williams et al., 1993; Tyne et al., 2014):

$$\hat{\theta} = \frac{\text{number of high quality photographs with distinctive fins}}{\text{total number of high quality photographs with distinctive and non distinctive fins}}$$

It was not possible to estimate the mark rate for males and females separately as the sex of some members of a group, marked and unmarked, remained unknown.

The Samadai spinner dolphins appeared to have the sex ratio skewed towards males (see further). However, this is very likely due to males being usually more marked than females (e.g. Tolley et al., 1995; Scott et al., 2005) rather than a true skewed sex ratio in the population. Consequently, the mark rate calculated was not applied to the sex-specific averaged abundance estimates, as this could have had introduced a bias, and only the population size (N) was reported for those estimates. To obtain the total population size for each year, the averaged abundance estimates for all adults were scaled by the mark rate ( $\theta$ ) (Burnham et al., 1987) as:

$$\hat{N}_{\text{total}} = \frac{\hat{N}}{\hat{\theta}}$$

Where  $\hat{N}$  is the estimated number of distinctive individuals. The variance for the total population size was calculated using the delta method (Wilson et al., 1999; Urian et al., 2015):

$$\text{var}(\hat{N}_{\text{total}}) = \hat{N}_{\text{total}}^2 \left( \frac{\text{var}(\hat{N})}{\hat{N}^2} + \frac{\text{var}(\hat{\theta})}{\hat{\theta}^2} \right)$$

Log-normal 95% confidence intervals were calculated with lower and upper limits of  $N_{\text{total}} = N_{\text{total}}/C$  and  $N_{\text{total}} = N_{\text{total}} * C$ , respectively (Burnham et al., 1987), where:

$$C = \exp \left( 1.96 \sqrt{\ln \left( 1 + (CV(\hat{N}_{\text{total}}))^2 \right)} \right)$$

## 6.3 Results

### 6.3.1 Rate of discovery and sighting frequency

Between May 2011 and August 2014, 159 surveys were conducted at Samadai reef, resulting with 121 sightings of dolphin groups and an average dolphin occurrence of 76%. Photo-identification data were collected during 114 sightings (ca. 36 000 photographs taken) and a total of 105 sightings were considered suitable for mark recapture analysis (Table 6.2 and Appendix V). Underwater estimates of the group size varied between 3 and 140 individuals, with a mean of 50 (n=114,

SD=34.9). In total, 257 distinctive animals were identified (D1, D2 and D3), of which 203 were highly marked (D1 and D2) (Figure 6.1). The pattern of discovery curve indicated that new individuals continued to be identified throughout the study. However, 55% of the highly distinctive individuals were identified in the first year, 27% in the second year and only 9% in each of the following two years, suggesting a semi-saturated population (Figure 6.1). The annual rate of mark acquisition was estimated at 12.3%, *i.e.* of the 293 identified dolphins (D1 to D4) that were seen more than once from 2005 to 2014, 87 dolphins acquired at least one new distinctive mark (a total of 178 mark changes or new marks). However only 1.1% of these individuals transitioned to a distinctive category (D1 or D2) each year, while others were either already part of the highly marked population or did not gain in distinctiveness despite gaining a mark.

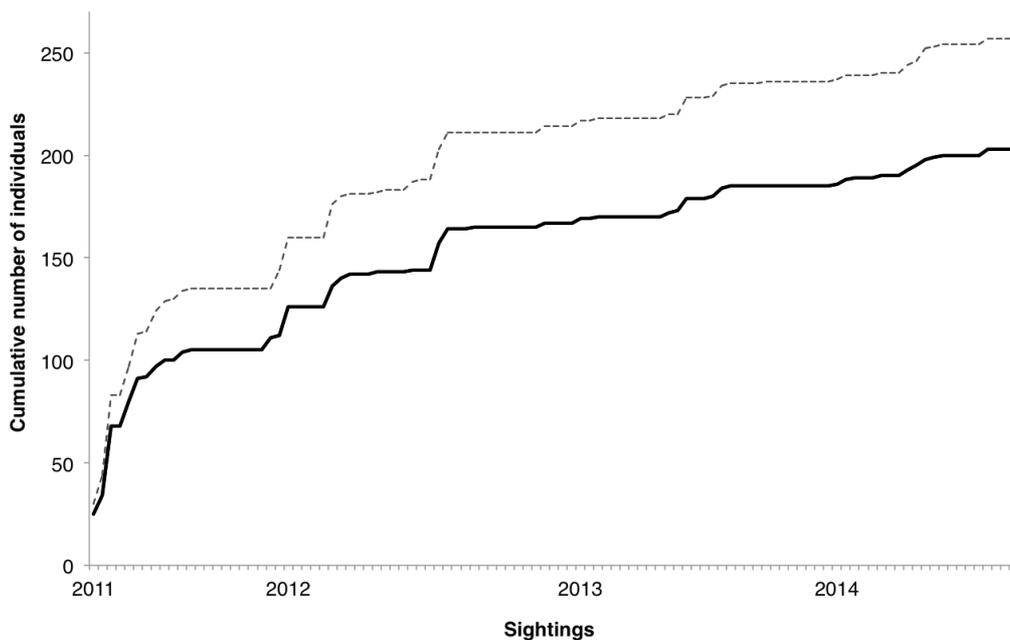


Figure 6.1. Rate of discovery of highly marked (D1 and D2; continuous line) and marked (D1, D2 and D3; broken line) adult spinner dolphins identified at Samadai reef between May 2011 and August 2014.

Table 6.2. Summary of research effort carried out in Samadai reef between May 2011 and August 2014. The number of photo-identification sessions used in the analysis is indicated. Dolphin occurrence is calculated as the number of time dolphins were found at Samadai over the number of time the team visited the site (Sightings/Survey days) and is reported in percentage. Subtotals per year are given in *italics*.

| Year               | Month | Survey days<br>(n) | Sightings<br>(n) | Photo-ID<br>(n) | Dolphin<br>occurrence<br>(%) |
|--------------------|-------|--------------------|------------------|-----------------|------------------------------|
| <b>2011</b>        |       | <b>30</b>          | <b>22</b>        | <b>22</b>       | <b>73</b>                    |
|                    | May   | 5                  | 5                | 5               | 100                          |
|                    | Jul   | 5                  | 3                | 3               | 60                           |
|                    | Aug   | 5                  | 3                | 3               | 60                           |
|                    | Sep   | 5                  | 3                | 4               | 60                           |
|                    | Oct   | 5                  | 4                | 3               | 80                           |
|                    | Dec   | 5                  | 4                | 4               | 80                           |
| <b>2012</b>        |       | <b>49</b>          | <b>34</b>        | <b>32</b>       | <b>69</b>                    |
|                    | Jan   | 8                  | 5                | 4               | 63                           |
|                    | Feb   | 3                  | 3                | 3               | 100                          |
|                    | Mar   | 4                  | 4                | 4               | 100                          |
|                    | Apr   | 4                  | 3                | 3               | 75                           |
|                    | May   | 6                  | 4                | 4               | 67                           |
|                    | Jul   | 7                  | 4                | 4               | 57                           |
|                    | Aug   | 3                  | 3                | 3               | 100                          |
|                    | Sep   | 4                  | 2                | 2               | 50                           |
|                    | Oct   | 5                  | 2                | 2               | 40                           |
|                    | Nov   | 5                  | 4                | 4               | 80                           |
| <b>2013</b>        |       | <b>43</b>          | <b>36</b>        | <b>29</b>       | <b>84</b>                    |
|                    | Jun   | 14                 | 12               | 9               | 86                           |
|                    | Jul   | 13                 | 12               | 10              | 92                           |
|                    | Aug   | 16                 | 12               | 10              | 75                           |
| <b>2014</b>        |       | <b>37</b>          | <b>29</b>        | <b>21</b>       | <b>78</b>                    |
|                    | Jun   | 9                  | 9                | 7               | 100                          |
|                    | Jul   | 17                 | 13               | 10              | 76                           |
|                    | Aug   | 11                 | 7                | 4               | 64                           |
| <b>Grand Total</b> |       | <b>159</b>         | <b>121</b>       | <b>105</b>      | <b>76</b>                    |

The sighting frequency ranged from one to 41, with a mean of 8.9 ( $\pm 0.61$  SE); with 77% of highly marked individuals seen more than once (Figure 6.2 and Table 6.3). In overall, female dolphins were sighted more frequently than males, both when all sightings were included and when the dataset was restricted to the warm seasons only (Table 6.3).

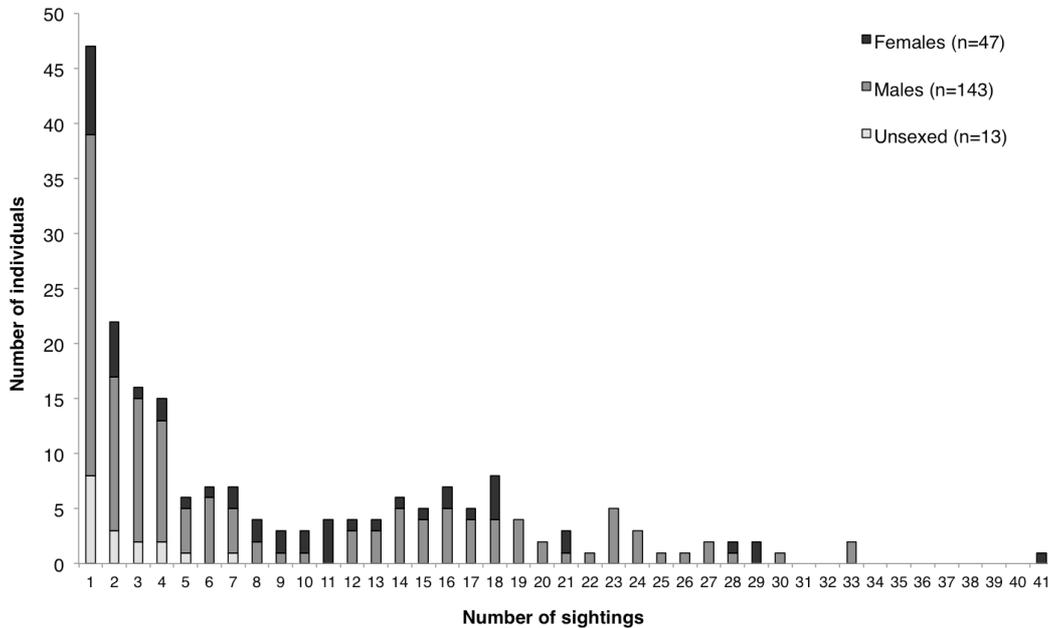


Figure 6.2. Sighting frequency of highly marked adult spinner dolphins (D1 and D2) at Samadai reef, from May 2011 to August 2014.

Table 6.3. Mean number of sightings ( $\pm$  SE) for all adult individuals combined and each sex separately, pooled by year.

|                           | 2011               | 2012               | 2013               | 2014               | Overall             |
|---------------------------|--------------------|--------------------|--------------------|--------------------|---------------------|
| <b>All adults (n=203)</b> | 3.6 ( $\pm 0.27$ ) | 4.2 ( $\pm 0.25$ ) | 3.6 ( $\pm 0.31$ ) | 3.0 ( $\pm 0.2$ )  | 8.9 ( $\pm 0.61$ )  |
| <b>Females (n=47)</b>     | 4.5 ( $\pm 0.48$ ) | 3.8 ( $\pm 0.4$ )  | 3.8 ( $\pm 0.66$ ) | 3.2 ( $\pm 0.38$ ) | 10.6 ( $\pm 1.33$ ) |
| <b>Males (n=143)</b>      | 3.4 ( $\pm 0.33$ ) | 4.5 ( $\pm 0.31$ ) | 3.7 ( $\pm 0.36$ ) | 3.0 ( $\pm 0.25$ ) | 8.9 ( $\pm 0.72$ )  |
| <b>Warm seasons only</b>  |                    |                    |                    |                    |                     |
| <b>Females (n=45)</b>     | 4.1 ( $\pm 0.42$ ) | 2.8 ( $\pm 0.34$ ) | 3.8 ( $\pm 0.66$ ) | 3.2 ( $\pm 0.38$ ) | 9.0 ( $\pm 1.23$ )  |
| <b>Males (n=131)</b>      | 3.3 ( $\pm 0.34$ ) | 2.3 ( $\pm 0.17$ ) | 3.6 ( $\pm 0.34$ ) | 3.0 ( $\pm 0.25$ ) | 7.0 ( $\pm 0.59$ )  |

Of the highly marked individuals seen at Samadai reef during the 2011-2014 study period, 47% were also seen during the 2005-2006 surveys.

### 6.3.2 Residence at Samadai reef

The three datasets (all adults combined and each sex separately) were best described by a population model that accounts for emigration and reimmigration, indicating that, across 19 months, individuals may visit, leave and re-visit Samadai reef (Table 6.4). The emigration and reimmigration and mortality model (which includes permanent emigration from the study area) was also supported ( $\Delta\text{QAIC} < 2$  for all three datasets). The two models yielded very similar parameter estimates (Table 6.4). The lagged identification rates, following an initial fall, have levelled off above zero at longer time lags (Figure 6.3), suggesting that some animals are permanent residents and/or others reimmigrate into the study area after longer time lags.

Table 6.4. Residency parameters ( $\pm$ SE) for highly marked adults (all combined and each sex separately) seen from May 2011 to November 2012 at Samadai reef. Best fitting models and supported models based on Quasi Akaike Criterion (QAIC) are indicated and best-fit model parameters are given in italics. Bootstrapped 95% CI are reported in parentheses.

| Dataset                            | Model                                  | No. of individuals at any given time             | Mean residence time in                           | Mean residence time out                          | Mortality                                   | QAIC    | $\Delta$ QAIC |
|------------------------------------|--|--|--|--|---|---------|---------------|
| <b>All adults combined (n=167)</b> |  |  |  |  |   |         |               |
|                                    | Closed                                 | 107 $\pm$ 5.1<br>(99.7- 118.3)                   |  |  |   | 23816.8 | 41.2          |
|                                    | Emigration + mortality                 | 96 $\pm$ 4.8<br>(87.2 - 105.7)                   | 1785 $\pm$ 1168.9<br>(1156.4 - 4549.3)           |  |   | 23805.0 | 29.4          |
| <i>best model</i>                  | <i>Emigration + reimmigration</i>      | <i>52 <math>\pm</math> 4.4<br/>(44.5 - 59.8)</i> | <i>6 <math>\pm</math> 17.8<br/>(3.2- 12.1)</i>   | <i>7 <math>\pm</math> 13.1<br/>(4.8- 12.8)</i>   |   | 23775.6 | 0             |
| <i>supported model</i>             | Emigration + reimmigration + mortality | 51 $\pm$ 4.7<br>(37.9 - 59.5)                    | 6 $\pm$ 2.6<br>(2.3 - 13.7)                      | 6 $\pm$ 2.0<br>(3.5 - 11.0)                      | 0.0002 $\pm$ 0.0002<br>(-0.0002 - 0.0006)   | 23776.1 | 0.5           |
| <b>Males (n=117)</b>               |  |  |  |  |   |         |               |
|                                    | Closed                                 | 73 $\pm$ 4.3<br>(66.0 - 82.1)                    |  |  |   | 14132.8 | 16.1          |
|                                    | Emigration + mortality                 | 66.3 $\pm$ 4.1<br>(58.2 - 74.8)                  | 2186 $\pm$ 2.23e12<br>(1019.6 - 14322.3)         |  |   | 14128.9 | 12.1          |
| <i>best model</i>                  | <i>Emigration + reimmigration</i>      | <i>30 <math>\pm</math> 4.7<br/>(21.4 - 41.3)</i> | <i>3 <math>\pm</math> 25.0<br/>(1.3 - 7.2)</i>   | <i>4 <math>\pm</math> 18.5<br/>(3.0 - 7.2)</i>   |   | 14116.7 | 0             |
| <i>supported model</i>             | Emigration + reimmigration + mortality | 29 $\pm$ 6.4<br>(19.4 - 44.6)                    | 2 $\pm$ 2.4<br>(1.1 - 10.8)                      | 3 $\pm$ 1.2<br>(2.5 - 7.4)                       | 0.0002 $\pm$ 0.0002<br>(-0.0003 - 0.0006)   | 14117.8 | 1.1           |
| <b>Females (n=41)</b>              |  |  |  |  |   |         |               |
|                                    | Closed                                 | 31 $\pm$ 2.6<br>(26.4 - 36.0)                    |  |  |   | 6843.9  | 21.0          |
|                                    | Emigration + mortality                 | 28 $\pm$ 2.1<br>(24.1 - 32.9)                    | 1963 $\pm$ 1383.7<br>(1076.0 - 6802.2)           |  |   | 6841.9  | 19.0          |
| <i>best model</i>                  | <i>Emigration + reimmigration</i>      | <i>16 <math>\pm</math> 2.6<br/>(11.6 - 21.0)</i> | <i>11 <math>\pm</math> 16.4<br/>(3.1 - 69.3)</i> | <i>11 <math>\pm</math> 12.7<br/>(5.4 - 49.1)</i> |   | 6822.9  | 0             |
| <i>supported model</i>             | Emigration + reimmigration + mortality | 16 $\pm$ 2.7<br>(11.9 - 21.4)                    | 11 $\pm$ 24.7<br>(2.8 - 110.7)                   | 12 $\pm$ 49.1<br>(4.8 - 156.3)                   | -8.78e-05 $\pm$ 0.0004<br>(-0.001 - 0.0003) | 6824.8  | 1.9           |

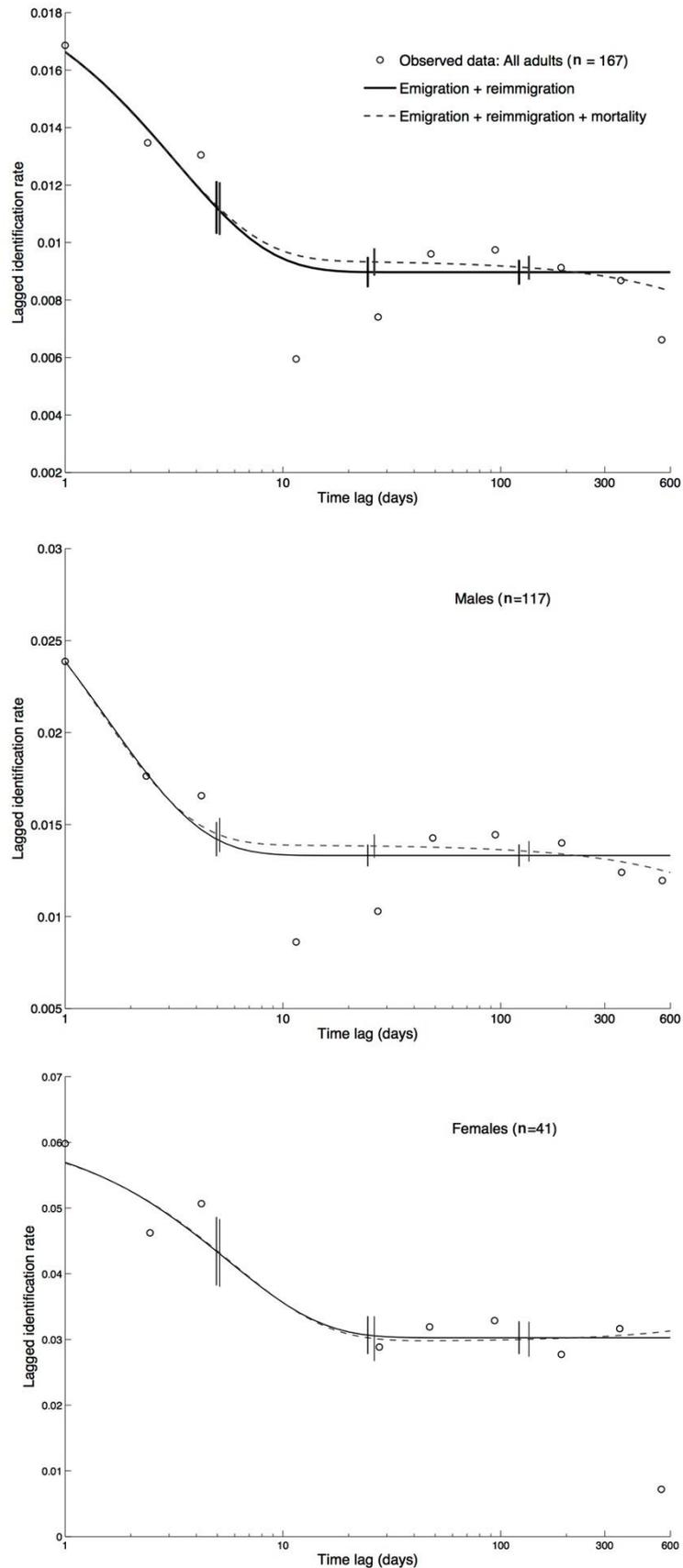


Figure 6.3. Lagged identification rate against time lag (days) of highly marked spinner dolphins seen at Samadai reef from May 2011 to November 2012 (all adults combined, including nine non-sexed individuals - top; males - middle; and females - bottom). Vertical lines indicate bootstrapped error bars.

On average, there were 52 (SE=4.4, 95% CI = 44.5-59.8) individuals in the study area at any given time and individuals utilized Samadai reef for approximately 6 days (SE=17.8, 95% CI = 3.2-12.1), before re-entering the area after a comparable period (7 days) outside the reef (SE=13.1, 95% CI = 4.8-12.8). When sex specific datasets were investigated, the lagged identification rate showed a similar pattern but different residence times for males and females. Estimates of mean community size indicated that approximately 30 males (SE = 4.7, 95% CI = 21.4-41.3) and 16 females (SE = 2.6, 95% CI = 11.6-21.0) were in the study area at any given time. Male dolphins appeared to utilize the study area for periods of 3 days (SE= 25.0, 95% CI = 1.3-7.2), and spend on average 4 days outside the study area (SE = 18.5, 95% CI = 3.0-7.2) before returning. Females had longer residence times of 11 days both inside the study area (SE = 16.4, 95% CI = 3.1-69.3), and outside (SE = 12.7, 95% CI = 5.4-49.1). In other words, males tended to visit Samadai reef for shorter time lags than females and appeared to be more transient than females. This tendency was supported by the models best fitting the 2011 - 2014 data (See Appendix IV) as well as the emigration-remigration-mortality model that best describes the May-2011 to November-2012 subset of data, suggesting that permanent emigration over periods of years could be mostly a prerogative of males.

### 6.3.3 Closure test

To ensure the estimability and comparability of all parameters, the sampling period was restricted to the warm seasons, decreasing the number of sighting from 105 to 75 and reducing the number of highly marked individuals from 203 to 185 (131 males, 45 females and nine un-sexed individuals).

The assumption of closure within primary sampling periods (*i.e.* years) was supported by the results of the Otis et al. (1978) test in all years but 2013 (Table 6.5). Primary samples corresponded to the warm seasons from 2011 to 2014 and secondary samples to the number of 6-day

intervals in which dolphins were seen at least once (73 total sightings; on average  $3 \pm 0.5$  SD sightings per secondary sample).

Table 6.5. Summary of the Robust Design structure and closure test results. CloseTest p-values are italicized if they did not satisfy the closure assumption ( $p < 0.05$ ).

| Primary samples (Year) | Secondary samples | Test Statistic (z) | p-value       |
|------------------------|-------------------|--------------------|---------------|
| 2011                   | 4                 | -0.345             | 0.3649        |
| 2012                   | 4                 | 4.620              | 1.0000        |
| 2013                   | 9                 | -2.689             | <i>0.0036</i> |
| 2014                   | 8                 | -0.564             | 0.2864        |

The goodness of fit test for the fully time-dependent Cormack Jolly Seber model (CJS) provided a poor fit to the data ( $\chi^2_{4} = 59.9$ ,  $p < 0.001$ ). The only significant subcomponent of the goodness-of-fit test was Test 3.Sr ( $Z = 6.53$ ,  $p < 0.001$ ) indicating a significant “transience” effect (Pradel et al., 1997). A time since marking or “two age-class” structure for survival (‘a2’) was consequently incorporated in the models (Pradel et al., 1997). The variance inflation factor (median  $\hat{c}$ ) estimated for this model was  $1.46 \pm 0.06$  SE and was used to adjust for the remnant lack of fit.

#### 6.3.4 Model selection

*All adults dataset* -The models with time variation (both between and within primary samples, *i.e.* ‘ $p=c(t,s)$ ’) in capture probabilities and with a “two age-class” effect (time varying for “transients” and time varying or constant for “residents”, *i.e.* ‘ $\phi(a2 t-t)$ ’ and ‘ $\phi(a2 t-.)$ ’, respectively) in survival probabilities were the best fitting models when no temporary emigration was included, *i.e.* ‘ $\gamma(0)$ ’ (Models 9 and 10 in Table 6.6). These models were used to investigate a suitable emigration model. Constant and time varying random and Markovian emigration models were fitted to the data, and the survival parameter was modelled again with the “two

age-class” effects incorporated. Eventually the best fitting model identified survival probabilities as time specific for transients and constant for residents, a constant random emigration model and a different capture probability for each sampling occasion (Model 1, Table 6.6). This Model 1 fitted the data about twice as well as Model 2 (with time varying random emigration) and Model 3 (with Markovian emigration) (Table 6.6).

Table 6.6. Robust Design candidate models set for the adults dataset. Models are in decreasing order of the  $\Delta QAIc_c$ , displaying apparent survival probability ( $\phi$ ), probability of capture ( $p$ ) and recapture ( $c$ ), and random ( $\gamma''=\gamma'$ ; notation  $\gamma()$ ), Markovian ( $\gamma''\neq\gamma'$ ; notation  $\gamma()Y()$ ) and no emigration ( $\gamma''=\gamma'=0$ ; notation  $\gamma(0)$ ) models. Constraints were applied to ensure parameters estimability to selected models.

|    | Model  | Constraints   | QAICc  | $\Delta QAICc$ | AICc Weights | Model Likelihood | No. Parameters | QDeviance |
|----|--|---|--------|----------------|--------------|------------------|----------------|-----------|
| 1  | $\phi(a2\ t-.)\ \gamma(.)\ p=c(t,s)$               |   | 373.26 | 0              | 0.33         | 1.00             | 34             | 1336.22   |
| 2  | $\phi(a2\ t-.)\ \gamma(t)\ p=c(t,s)$               | $\gamma''_k=\gamma''_{k-1}$ and $\gamma'_k=\gamma'_{k-1}$ | 374.53 | 1.27           | 0.18         | 0.53             | 35             | 1335.33   |
| 3  | $\phi(a2\ t-.)\ \gamma''(.)\ \gamma'(.)\ p=c(t,s)$ |   | 374.82 | 1.56           | 0.15         | 0.46             | 35             | 1335.62   |
| 4  | $\phi(a2\ t-t)\ \gamma(.)\ p=c(t,s)$               |   | 375.38 | 2.11           | 0.12         | 0.35             | 35             | 1336.17   |
| 5  | $\phi(a2\ t-.)\ \gamma''(t)\ \gamma'(.)\ p=c(t,s)$ | $\gamma''_k=\gamma''_{k-1}$ and $\gamma'_k=\gamma'_{k-1}$ | 376.21 | 2.95           | 0.08         | 0.23             | 36             | 1334.85   |
| 6  | $\phi(a2\ t-t)\ \gamma(t)\ p=c(t,s)$               | $\gamma''_k=\gamma''_{k-1}$ and $\gamma'_k=\gamma'_{k-1}$ | 376.69 | 3.43           | 0.06         | 0.18             | 36             | 1335.33   |
| 7  | $\phi(a2\ t-t)\ \gamma''(.)\ \gamma'(.)\ p=c(t,s)$ |   | 376.77 | 3.51           | 0.06         | 0.17             | 36             | 1335.41   |
| 8  | $\phi(a2\ t-t)\ \gamma''(t)\ \gamma'(.)\ p=c(t,s)$ | $\gamma''_k=\gamma''_{k-1}$ and $\gamma'_k=\gamma'_{k-1}$ | 378.12 | 4.86           | 0.03         | 0.09             | 37             | 1334.59   |
| 9  | $\phi(a2\ t-.)\ \gamma(0)\ p=c(t,s)$               |   | 391.18 | 17.92          | 0            | 0                | 33             | 1356.29   |
| 10 | $\phi(a2\ t-t)\ \gamma(0)\ p=c(t,s)$               |   | 391.23 | 17.97          | 0            | 0                | 34             | 1354.19   |
| 11 | $\phi(a2\ .-.)\ \gamma(0)\ p=c(t,s)$               |   | 402.56 | 29.30          | 0            | 0                | 31             | 1371.96   |
| 12 | $\phi(.)\ \gamma(0)\ p=c(t,s)$                     |   | 415.30 | 42.04          | 0            | 0                | 30             | 1386.84   |
| 13 | $\phi(t)\ \gamma(0)\ p=c(t,s)$                     |   | 418.26 | 45.00          | 0            | 0                | 32             | 1385.51   |
| 14 | $\phi(.)\ \gamma(0)\ p=c(t,..)$                    |   | 531.70 | 158.43         | 0            | 0                | 9              | 1547.08   |
| 15 | $\phi(.)\ \gamma(0)\ p=c(..,)$                     |   | 550.82 | 177.55         | 0            | 0                | 6              | 1572.30   |

Note:  $\gamma''(t)\ \gamma'(t) = \gamma''(t)\ \gamma'(.)$  when constraints  $\gamma''_k=\gamma''_{k-1}$  and  $\gamma'_k=\gamma'_{k-1}$  are applied as in this study there are only four primary occasions.

Parameter estimates were very similar across the supported models. Because of the uncertainty in the model selection, model averaging was used to generate parameter estimates (weighted across the 8 supported models). Model averaged parameter estimates returned a high survival probability of  $0.993 \pm 0.022$  SE for residents and a lower time specific survival probability of  $0.847 \pm 0.044$  SE,  $0.499 \pm 0.116$  SE and  $0.530 \pm 0.149$  SE for transients in 2012, 2013, 2014 respectively. The corresponding proportion of transient individuals was estimated as 14.7%, 49.7% and 46.6%. Capture probabilities varied greatly within primary periods, ranging from 0.06 to 0.71, but they were generally high and constant between primary periods (CJS annual capture estimates were high and ranged from  $0.786 \pm 0.028$  SE to  $0.792 \pm 0.033$  SE). The first two best fitting models identified a random temporary emigration structure, where the probability for an individual to be present in the study area in any given year was independent of whether or not it was present in the study area the previous year. However the model that had constant Markovian temporary emigration was also highly supported (Model 3, Table 6.6). The averaged estimated probability of temporary emigration ( $\gamma$ ) was low at  $0.147 \pm 0.004$  SE. The averaged probability of being absent given that a dolphin was present in the previous year ( $\gamma''$ ) was  $0.153 \pm 0.04$  SE; and the probability of being absent given that a dolphin was also absent in the previous year ( $\gamma'$ ) was slightly lower at  $0.106 \pm 0.079$  SE. Although the precision of  $\gamma'$  was moderately low, a generally high return rate of temporary emigrants to the study area (*i.e.*  $1-\gamma'=0.894$ ) was evident.

*Males and females dataset* - The effect of sex was evaluated by excluding from the dataset the individuals whose sex had not been determined ( $n=9$ ), decreasing the number of highly marked individuals from 185 to 176 (131 males and 45 females). Models including a multiplicative ('sex\*t'), additive ('sex+t') or constant ('sex') sex effect in capture probabilities were not supported (Model 16, 17 and 18 respectively in Table 6.7). Similarly, the model incorporating the sex covariate in survival probability

(‘sex\*a2t.’) received little support (Model 15). Although the best fitting model was a constant random emigration model (Model 1, Table 6.7), a model of random temporary emigration that varies between sexes (Model 4, Table 6.7) also received a considerable support ( $\Delta\text{QAICc} \sim 2$ ). This model estimated a probability of temporary emigration slightly higher for males ( $0.143 \pm 0.041$  SE), than for females ( $0.118 \pm 0.072$  SE). Parameters estimates for the best-fitting model were not substantially different from those reported for the all adults dataset.

Table 6.7. Robust Design candidate models set for male and female dataset. Models are in decreasing order of the  $\Delta\text{QAICc}$ , displaying apparent survival probability ( $\phi$ ), probability of capture ( $p$ ) and recapture ( $c$ ), and random  $\gamma''=\gamma'$ ; notation  $\gamma()$ , Markovian  $\gamma''\neq\gamma'$ ; notation  $\gamma() \gamma()$  and no emigration  $\gamma''=\gamma'=0$ ; notation  $\gamma(0)$  models. The covariate sex was also tested in this set of models. Constraints were applied to ensure parameters estimability to selected models.

|    | Model  | Constraints  | QAICc  | $\Delta\text{QAICc}$ | QAICc Weights | Model Likelihood | No. Parameters | QDeviance |
|----|--|--|--------|----------------------|---------------|------------------|----------------|-----------|
| 1  | $\phi(a2\ t-.)\ \gamma(.)\ p=c(t,s)$                                       |  | 722.41 | 0                    | 0.26          | 1.00             | 38             | 1447.00   |
| 2  | $\phi(a2\ t-.)\ \gamma''(.)\ \gamma'(.)\ p=c(t,s)$                         |  | 723.41 | 1.00                 | 0.16          | 0.61             | 39             | 1445.82   |
| 3  | $\phi(a2\ t-.)\ \gamma(t)\ p=c(t,s)$                                       | $\gamma''_k=\gamma''_{k-1}\ \text{and}\ \gamma'_k=\gamma'_{k-1}$ | 723.42 | 1.01                 | 0.16          | 0.60             | 39             | 1445.83   |
| 4  | $\phi(a2\ t-.)\ \gamma(\text{sex})\ p=c(t,s)$                              |  | 724.49 | 2.08                 | 0.09          | 0.35             | 39             | 1446.90   |
| 5  | $\phi(a2\ t-t)\ \gamma(.)\ p=c(t,s)$                                       |  | 724.52 | 2.11                 | 0.09          | 0.35             | 39             | 1446.93   |
| 6  | $\phi(a2\ t-.)\ \gamma''(t)\ \gamma'(.)\ p=c(t,s)$                         | $\gamma''_k=\gamma''_{k-1}\ \text{and}\ \gamma'_k=\gamma'_{k-1}$ | 724.82 | 2.41                 | 0.08          | 0.30             | 40             | 1445.04   |
| 7  | $\phi(a2\ t-.)\ \gamma''(\text{sex})\ \gamma'(.)\ p=c(t,s)$                |  | 725.29 | 2.88                 | 0.06          | 0.24             | 40             | 1445.51   |
| 8  | $\phi(a2\ t-t)\ \gamma''(.)\ \gamma'(.)\ p=c(t,s)$                         |  | 725.33 | 2.92                 | 0.06          | 0.23             | 40             | 1445.56   |
| 9  | $\phi(a2\ t-.)\ \gamma''(\text{sex})\ \gamma'(\text{sex})\ p=c(t,s)$       |  | 727.47 | 5.06                 | 0.02          | 0.08             | 41             | 1445.51   |
| 10 | $\phi(a2\ t-.)\ \gamma(\text{sex}^*t)\ p=c(t,s)$                           | $\gamma''_k=\gamma''_{k-1}\ \text{and}\ \gamma'_k=\gamma'_{k-1}$ | 727.65 | 5.24                 | 0.02          | 0.07             | 41             | 1445.68   |
| 11 | $\phi(a2\ t-.)\ \gamma''(\text{sex}^*t)\ \gamma'(\text{sex}^*t)\ p=c(t,s)$ | $\gamma''_k=\gamma''_{k-1}\ \text{and}\ \gamma'_k=\gamma'_{k-1}$ | 730.39 | 7.98                 | 0             | 0.02             | 43             | 1444.03   |
| 12 | $\phi(a2\ t-t)\ \gamma''(\text{sex}^*t)\ \gamma'(\text{sex}^*t)\ p=c(t,s)$ | $\gamma''_k=\gamma''_{k-1}\ \text{and}\ \gamma'_k=\gamma'_{k-1}$ | 732.39 | 9.98                 | 0             | 0.01             | 44             | 1443.83   |
| 13 | $\phi(a2\ t-.)\ \gamma(0)\ p=c(t,s)$                                       |  | 739.79 | 17.38                | 0             | 0                | 37             | 1466.56   |
| 14 | $\phi(a2\ t-t)\ \gamma(0)\ p=c(t,s)$                                       |  | 740.14 | 17.73                | 0             | 0                | 38             | 1464.73   |
| 15 | $\phi(\text{sex}^*a2\ t-.)\ \gamma(0)\ p=c(t,s)$                           |  | 746.26 | 23.85                | 0             | 0                | 41             | 1464.29   |
| 16 | $\phi(a2\ t-t)\ \gamma(0)\ p=c(\text{sex}+t)$                              |  | 747.31 | 24.90                | 0             | 0                | 42             | 1463.15   |
| 17 | $\phi(a2\ t-t)\ \gamma(0)\ p=c(\text{sex}^*t)$                             | $\gamma''_k=\gamma''_{k-1}\ \text{and}\ \gamma'_k=\gamma'_{k-1}$ | 770.35 | 47.94                | 0             | 0                | 63             | 1438.93   |
| 18 | $\phi(a2\ t-t)\ \gamma(0)\ p=c(\text{sex})$                                |  | 852.22 | 129.81               | 0             | 0                | 16             | 1623.55   |

Note:  $\gamma''(t)\gamma'(t) = \gamma''(t)\gamma'(.)$  when constraints  $\gamma''_k=\gamma''_{k-1}$  and  $\gamma'_k=\gamma'_{k-1}$  are applied as in this study there are only four primary occasions.

### 6.3.5 Total population size

The averaged annual total number of adult individuals using Samadai reef was generally stable throughout the four-year study, varying between 200  $\pm$ 4.4 SE and 227  $\pm$ 4.7 SE (Table 6.8). The ID ratio ( $\theta$ ) was 0.55  $\pm$ 0.17 SE. Averaged abundance estimates for males and females suggested that the slight variation in population size might be ascribed to males rather than females, whose estimates were almost constant between years (Table 6.8, Figure 6.4).

Table 6.8. Annual abundance estimates of spinner dolphins at Samadai reef between 2011 and 2014.

|                   | Highly marked individuals |     |     |           | Total population size |     |           |
|-------------------|---------------------------|-----|-----|-----------|-----------------------|-----|-----------|
|                   | Year                      | N   | SE  | 95%CI     | N <sub>total</sub>    | SE  | 95%CI     |
| <b>All adults</b> |                           |     |     |           |                       |     |           |
|                   | 2011                      | 113 | 4.4 | 104 - 121 | 203                   | 4.4 | 195 - 212 |
|                   | 2012                      | 114 | 7.2 | 100 - 128 | 205                   | 4.5 | 196 - 214 |
|                   | 2013                      | 111 | 2.9 | 105 - 117 | 200                   | 4.4 | 192 - 209 |
|                   | 2014                      | 126 | 3.8 | 118 - 133 | 227                   | 4.7 | 218 - 237 |
| <b>Females</b>    |                           |     |     |           |                       |     |           |
|                   | 2011                      | 32  | 2.0 | 28 - 35   |                       |     |           |
|                   | 2012                      | 29  | 2.9 | 24 - 35   |                       |     |           |
|                   | 2013                      | 31  | 1.4 | 28 - 33   |                       |     |           |
|                   | 2014                      | 30  | 1.7 | 27 - 33   |                       |     |           |
| <b>Males</b>      |                           |     |     |           |                       |     |           |
|                   | 2011                      | 77  | 3.3 | 70 - 83   |                       |     |           |
|                   | 2012                      | 81  | 5.4 | 71 - 92   |                       |     |           |
|                   | 2013                      | 75  | 2.2 | 71 - 79   |                       |     |           |
|                   | 2014                      | 89  | 3.0 | 83 - 95   |                       |     |           |

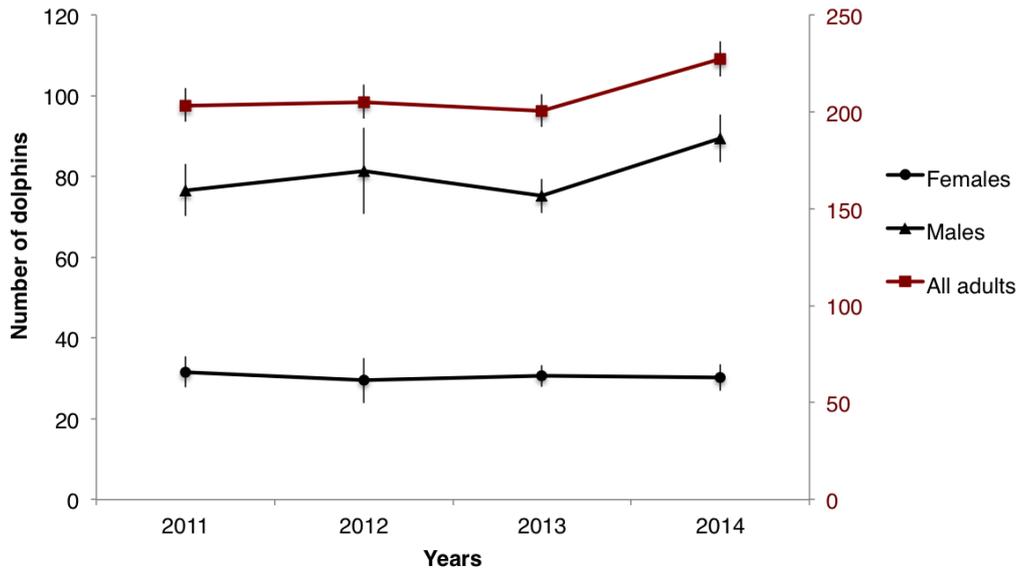


Figure 6.4. Annual abundance estimates for marked adult females and males (N), and annual total population sizes ( $N_{total}$ ) for adult spinner dolphins (in red - secondary axis) frequenting Samadai reef. Vertical lines indicate 95% confidence intervals.

## 6.4 Discussion

With the application of individual identification and mark-recapture techniques, this study provided an insight into the sex-specific movement patterns, demographic parameters and abundance of spinner dolphins frequenting an offshore resting habitat, the Samadai reef in the Egyptian Red Sea. The results indicate that (1) the Samadai dolphin population consists of long-term year-round resident individuals of both sexes as well as individuals that appear to be transient; (2) females exhibit stronger site fidelity than males, especially in the warm season; and (3) the population figures of a few hundred appear to be stable across recent years.

### 6.4.1 Residency, transience and immigration

Between 2011 and 2014 spinner dolphins were encountered in Samadai reef on 76% of the days the research team visited the reef, which is consistent with similar pattern observed in other resting areas elsewhere (e.g. Kealake'akua Bay, Norris and Dohl, 1980; French Polynesia, Gannier, 2002; Oahu Island, Lammers, 2004). Almost half of the highly

marked individuals using Samadai reef during the study period were first seen during the 1-year research project in 2005-2006 (Notarbartolo di Sciara et al., 2009; Costa et al., *in preparation*), indicating a long-term use of the resting area by a considerable part of the population; similarly as known for spinner dolphins elsewhere (e.g. Lammers, 2004). This is further supported by the lagged identification rates (LIR) which quantify individual site fidelity across a temporal scale. The model that best fitted the LIR suggests that across approximately two years, the dolphins were moving in and out of the study area. The short residence time and similarly short emigration time, both estimated to approximate one week, are consistent with an overall long-term utilization of the reef, at least by a portion of the population.

Arguably, the LIR is best understood as representing a period of regular and constant utilization of the reef by a resident community and a period of more discontinuous use by other more transient individuals. When the sampling period was restricted to warm seasons only (*i.e.* excluding the cold seasons and reducing the effort by approximately 30%), the number of highly marked individuals decreased only by 9% (18 individuals). This denoted continuity in reef use for most of the highly marked individuals during both seasons. However, during the 4-year study, the field effort during colder months was substantially lower than in warmer months, possibly reducing the number of highly marked individuals seen during the cold seasons. Evidence of transience was supported by the resighting frequencies showing that 33% of the individuals were captured only once and never again.

In a process of cataloguing the individually identified dolphins, a relatively small but constant number of new individuals were added to the catalogue each year. Part of these individuals were previously categorized as non distinctive who became distinctive through mark gain. The mark change rate calculated in this study (12.3%) was not dissimilar from those found for other cetaceans species (e.g. Dufault and Whitehead, 1995; Gowans and Whitehead, 2001; Baird et al., 2008) and can be used to assess

whether evolution of marks might have affected estimates of abundance (Urian et al., 2015). The mark acquisition rate could be sufficient to account for most of the immigration observed, indicating that the Samadai population of marked individuals could have been recruiting from within non-distinctive individuals only (which would then be an indication of population closure). However the annual rate of individuals transitioning from a less\non-distinctive status to a distinctive one was found to be 1.1%, suggesting instead that part of the immigration recorded was due to “real” new immigrants (which in such a case indicate “openness” between years). Cumulatively, this further supports the notion that the Samadai spinner dolphin population consists of long-term resident individuals, some of which transition from unmarked to marked each year, and occasional visitors (transients) that use Samadai once or a few times and leave soon after.

#### **6.4.2 Sex-specific site fidelity**

The two components of the population delineated in this study, residents and transients, included both males and females. Nevertheless, the lagged identification rates calculated for males and females separately highlighted two main differences between sexes: 1) a longer residence time for females than for males; and 2) higher site fidelity among females (especially during summer months) than males, which conversely displayed a generally higher transience. Also, permanent emigration seemed to be predominantly a prerogative of males.

*Site fidelity* - According to Norris and Dohl (1980), spinner dolphins seek sheltered and shallow waters to rest in order to minimize the shark predation risk that would be greater offshore. The higher residency of females is likely linked to their greater vulnerability. For example, by examining individual likelihood to be scarred, Urian and colleagues (1998) provided evidences that females were less willing to risk shark predation. Even unsuccessful predation attempts may in fact entail subsequent detrimental effects on their capability of rearing a calf or being able to

invest into reproduction (Heithaus, 2001). The “predation risk hypothesis” predicts that females use relatively predator-safe habitats, while males are thought to risk using habitats with higher predation but also with better food quality (e.g. Ruckstuhl and Neuhaus, 2002; see also below). This was observed in several locations, e.g. for the females bottlenose dolphins in the Sarasota community, Florida, that use the waters of shallow bays more than the males (Wells et al., 1980); in Shark Bay, Australia, where calf mortality has been found to be lower for females that spend more time in shallow waters than for females that range further offshore (Mann et al., 2000a); and in the Clarence River estuary, Australia, where shallow tributaries may provide safer conditions from predation as well as aggressive males (Fury et al., 2013).

The higher sighting frequency of females found especially during warm seasons is well explained in the context of the predation risk hypothesis, especially considering that this time of the year corresponds to the calving season (Notarbartolo di Sciara et al., 2009; Chapter 5). Predation pressure may favour movement of females with calves to safer habitats. Red Sea spinner dolphins are certainly subject to shark predation, as proven by the catalogued scarred individuals: approximately 7% of dolphins of all ages identified at Samadai reef showed evidence of shark attack. Reproductively mature females, especially if accompanied by a dependent calf during a reproductive season, are therefore more susceptible to predation. A non-fatal attack documented in 2013, directed at a resident female accompanied by her newborn, resulted not only in the calf loss, but also in a loss of 2 years of reproduction (*i.e.* the individual was seen with a new neonate in 2015) (Figure 6.5).

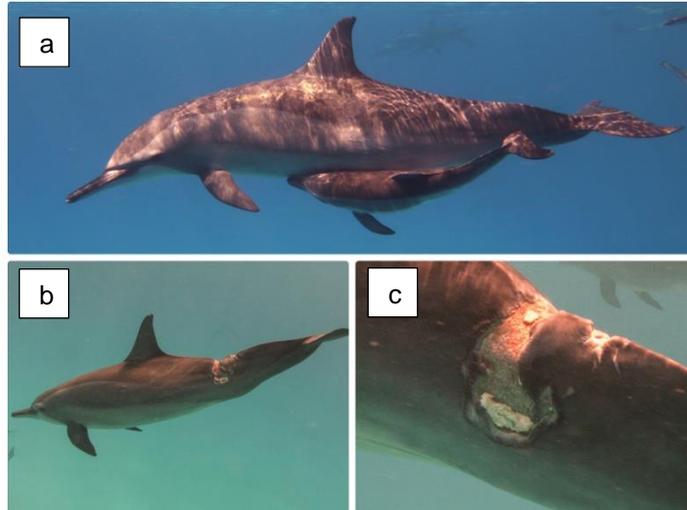


Figure 6.5. A resident young mother spinner dolphin who survived a shark attack. The neonate born in July 2013 (a) did not survive the attack which happened in August the same year (b, c).

In his review of sex segregation in odontocetes, Michaud (2005) suggested that differential vulnerability or tolerance to predation risk plays an important role in driving males and females to adopt different habitat selection strategies. In the current study, females and males did not segregate but rather varied in the sex-specific movement patterns inside and outside the resting habitat, suggesting that the higher vulnerability of females, especially during the calving months, might have driven the higher site residency.

*Transience* - Variation in habitat selection may be due to sexual dimorphism (e.g. Ruckstuhl and Clutton-Brock, 2005) with males ranging further than females in search of better food sources. Differences in body size could in fact result in divergent nutritional requirements, as larger individuals would require and be able to exploit more energetic and/or different food sources (e.g. sexually dimorphic male killer whales can dive deeper, Baird et al., 2005). However, the degree of sexual dimorphism described in the Red Sea spinner dolphin (Chapter 3 and Chapter 4) is unlikely to require sex-specific nutritional requirements; moreover, previous data collected in Samadai reef (Cesario, 2008) did not support such hypothesis as preys seemed not to vary qualitatively between sexes

(Appendix VII). Males and females appeared to exploit the same source of food (squids and mesopelagic fish), although possibly in different quantity. Males may display higher transience than females as a reproductive strategy, ranging further in search of receptive females (Whitehead, 1990; Connor et al., 2000). Other factors need to be explored further to fully understand the higher transience found in males.

In their recent studies in the Egyptian Red Sea, Fumagalli (2016) and Costa (2015) conducted research in other neighbouring resting habitats (e.g. Satayah reef, ca. 120 km South of Samadai reef) and offshore waters. A cross-matching conducted between the Samadai and Satayah dolphin catalogue found only five positive matches. The five individuals were seen in Samadai reef only once, four of them in the same sampling occasion. These five individuals were instead all recurrent adult males in Satayah reef where they have been encountered since 2006 through 2014. This finding suggests that there is some degree of interchange between the dolphin communities in these two reef habitats and that males may function as a vector of genetic connectivity (Fumagalli, 2016). This is in agreement with what has been found for spinner dolphins in French Polynesia (Oremus et al., 2007) but in contrast with spinner dolphins throughout the Hawaiian Archipelago (Andrews et al., 2010), which instead showed equal levels of dispersal for both sexes. It is therefore possible that some of the transient individuals seen at Samadai reef could be resident in other resting areas (“reef-associated” community). It seems plausible, however, that most of the transient individuals are likely part of an “offshore” population that visits resting areas less frequently than the resident conspecific. These offshore spinner dolphins in the Southern Egyptian Red Sea were recently estimated to number almost 7000 individuals (95%CI 4176-11605; Costa, 2015). When encountered offshore, they usually rest in association with the congener pantropical spotted dolphins (*Stenella attenuata*) (Costa, 2015), possibly relying on this species alertness to avoid deep-water shark predation (Norris and Dohl, 1980).

### 6.4.3 Robust Design parameters

As the spinner dolphins frequenting Samadai reef were engaged in emigration and remigration, therefore the capacity for the Robust Design to allow for temporary emigration was considered suitable to estimate abundance. The Robust Design assumes demographic closure within primary samples, assumption that held in most of the samples.

*Survival* - As expected from the Cormack Jolly Seber (CJS) parameterisation results, integrating age dependence on survival probability improved greatly the fit of the models, confirming the presence of transient dolphins in the Samadai population. Transience affected the survival probabilities of both sexes, as indicated by the poor fit of the model with sex effect on the age dependence. Robust Design estimates apparent survival, *i.e.* the product of true survival and site fidelity (White and Burnham, 1999). For the resident individuals it can be assumed that site fidelity is constant and high, meaning that the apparent survival estimated effectively corresponded to true survival. The resulting true survival for the Samadai resident population was found to be close to unity ( $0.99 \pm 0.02$  SE), only slightly higher than to the one estimated for the Hawaiian spinner dolphins during a 1-year study along the Kona Coast of Hawai'i Island (Tyne et al., 2014). However, Tyne and colleagues (2014) did not find evidence of permanent emigration, possibly because of the limited length of their study or because it is actually not present in the Kona Coast population for other social and/or ecological reasons.

*Temporary emigration* - The model selection indicated that temporary emigration was occurring across primary samples and was generally low (either random or Markovian), confirming the high fidelity of the animals to the site. Dolphins had a very high return rate (~90%) from one warm season to the next. Warm season was found to correspond to the reproductive peak (Chapter 5; Notarbartolo di Sciara et al., 2009) and the high return rate could be possibly explained by temporary emigrants entering the study area during the reproductive season to seek mating

opportunities (Smith et al., 2013). As previously indicated, however, some of the individuals are year-round resident and this might have inflated the return rate estimate.

Temporary emigration seemed to vary between sexes: slightly higher for males than for females. This finding was consistent with previous results of this study but given the relatively low precision of these estimates and the similar values estimated for each sex, it has to be viewed cautiously. Nevertheless, both females and males moved in and out of the study area, indicating that temporary emigration (and transience) have to be factored in during abundance estimations (Silva et al., 2009).

*Captures probabilities* - Captures probabilities were highly variable within primary samples and generally high and constant between years (CJS estimates *ca.*  $0.79 \pm 0.03$  SE). Given the great variability in group sizes from one day to another, such variability was expected even after data pooling was performed.

*Population size* - Estimated population numbers of Samadai spinner dolphins were generally stable across the 4-year study at about 200+ individuals (excluding calves). The small increase observed in 2014 appeared to be related to an influx of males rather than females, which instead showed almost no variation in their numbers throughout the study period. The abundance estimates for adult males were more than double that of females. Very likely this is not representative of a skewed sex ratio but it is due to males being more marked than females (see below).

Stability of the population size might be a by-product of the high predictability of resources, in terms of foraging grounds, resting areas and reproductive seasonality. Gowans and colleagues (2008) proposed a conceptual framework in which the predictability of resources would influence the movement patterns of individuals as well as their socio-ecology. This framework predicts that when resources are predictable in space and time, dolphins should remain resident in small areas and form

relatively small communities. Conversely, when resources are unpredictable individuals will range further and form large groups. The distribution of foraging grounds for spinner dolphins in the Red Sea is unknown. The year-round presence of apparently long-term resident individuals at Samadai reef would suggest that prey availability (mostly squid and mesopelagic fish associated with the mesopelagic boundary community (Benoit-Bird et al., 2001), see Appendix VII) is sufficiently predictable to sustain at least the resident population during the night-time forays in nearby deeper water. Similarly on a spatial scale, the relatively low number of suitable resting habitats nearby Samadai reef makes the distribution of safe habitats (*i.e.* resting areas, see Chapter 1) both limited and predictable. Finally, Samadai population showed a unimodal calving peak during the summer months (Chapter 5) and females were predictably found within the safe waters of Samadai during those months. The predictability of these resources, spatially and temporally, likely contributed to the high stability of abundance estimations and the high residency. The model proposed by Gowans et al. (2008) for resident population also predicts that females would form nursery groups, whereas males would form long-term associations with other males in order to sequester females. These features have also been observed for the Samadai population (Chapter 5; Cesario et al., 2013), confirming the validity of the model proposed.

The high long-term site fidelity of a relatively small population of spinner dolphins described for Samadai reef was similar to the one depicted for Satayah reef, a larger reef located approximately 120 km South of Samadai (Chapter 1). Fumagalli (2016) found that part of the individuals frequenting Satayah reef made regular, frequent and long-term use of the reef as a preferred site, whereas others were occasional visitors (transients). Abundance estimates ranged from 200+ individuals, under open model assumptions, and 292 (95%CI 228-374) under closure assumptions. The line-transect survey conducted on the pelagic population indicated that the area surrounding Samadai reef supported fewer individuals compared to that further south where Satayah reef is

located, possibly due to its more oligotrophic waters, small number of reefs present and less physiographic variability (Costa, 2015). Satayah reef is also much larger than Samadai reef and it could be possibly expected to have a higher carrying capacity. Despite such differences between Samadai and Satayah reefs, the mark recapture abundance estimates yielded very similar results, suggesting that other, possibly socio-ecological, mechanisms might play a role in explaining the demography of reef-associated spinner dolphins populations in the Red Sea.

On a regional scale, estimates found for Samadai population were similar to those found for the closed community at Midway Atoll (Karczmarski et al., 2005). Differently from the Midway, however, Samadai reef is not geographically isolated. Albeit being surrounded by a very few other ideal resting areas (“primary resting site”, see Chapter 1), the reef is only 7 km away from the coastline and in relatively close reach from other offshore reefs that can be considered as “secondary resting site”. Deep-water shark predation is assumed to be reduced in such environments and consequently spinner dolphins are relatively safe to move in these waters.

This current study seems to position the Red Sea spinner dolphins closer to the metapopulation scenario described by Oremus and colleagues (2007) in the Society Archipelago of French Polynesia, where a photo-identification study indicated low levels of demographic interchanges (*i.e.* small and relatively closed communities) and the presence of temporary immigrants, but no evidence of permanent immigration. Genetic data suggested low male biased dispersal and greater female philopatry, although it was not significant (Oremus et al., 2007). By combining a demographic approach with molecular evidence, Oremus and colleagues (2007) concluded that spinner dolphins population at the Society Archipelago might follow the metapopulation model proposed by Levins (1968), where spatially isolated patches of suitable habitats are positioned within a continuum of unsuitable habitat that individuals can traverse but within which they cannot breed. According to the findings of this study,

paired with Fumagalli's (2016) and Costa's (2015) results, it appears that the Egyptian Red Sea spinner dolphins would follow a metapopulation model where individuals showed high site fidelity and social stability (Appendix VI) within a preferred study area, but, with a high chance of gene flow occurring with a more transient component of the "offshore" population. Reef-associated populations in the Red Sea would then be best referred as communities, a regional assemblage of animals that share ranges, interact socially, but do not represent closed reproductive units (Wells et al., 1999).

#### **6.4.4 Limitations of the study**

The estimated occurrence of dolphins at Samadai reef (*i.e.* presence/absence ratio) may be biased downward, as it included an uncertainty for those days where the research team was forced to leave the area early in the day although dolphins could have had potentially visited the reef later on. The sex ratio of the Samadai population seemed to be skewed towards males. This is probably due to adult males being more heavily scarred and tattered than adult females (Scott et al., 2005; Rowe and Dawson, 2009; Marley et al., 2013). This might have affected negatively the female abundance estimates, but was accounted for in the total abundance estimates since they were adjusted for the mark ratio. The population size estimates were run across warm seasons only and therefore a seasonal pattern of temporary emigration cannot be excluded; although spinner dolphins appeared be reliant on Samadai reef throughout the whole year, it cannot be excluded that incorporating seasonal movements within the analytical design might have revealed different patterns of temporary emigration between cold and warm seasons. Finally, the total number of spinner dolphins that use Samadai reef throughout the year (super-population) may be larger than the one estimated in this study, as a 1-year previous study suggests (Costa et al., 2012; Costa et al., *in preparation*).

## Chapter 7. Conclusions

### 7.1 Summary results

Life history traits and demographic parameters are essential in modelling population dynamics, assessing the conservation status of a population and informing management decisions (Chivers, 2009; Evans and Hammond, 2004; Hammond et al., 2013). This thesis advances the knowledge of cetacean biology and ecology by providing information on morphology, individual growth, and reproductive parameters of spinner dolphins in the Red Sea, and mark-recapture estimates of population parameters at one of their primary resting habitats.

The findings of this study confirmed that Samadai reef represents a critical habitat for spinner dolphins in the region for several reasons. It is of paramount importance for resting purposes: the calm, shallow and sheltered waters of its internal lagoon are the perfect place where to rest, socialize and nurse calves with a very low risk of predation (Chapter 5 and Chapter 6; Notarbartolo di Sciara et al., 2009; Costa et al., 2012). It represents a crossroads for dolphins displaying sex-specific movement patterns and different levels of residency. The dolphins frequenting Samadai reef consist of both long-term year-round residents of both sexes and apparent transients, both exhibiting high survival rate; they form a relatively stable unit that cumulatively numbers ~200 individuals (excluding calves). The occasional interchange of individuals between different reef-associated communities may be related to male-biased dispersal. The presence of transient individuals and the observation of low connectivity between reefs suggest the existence of several reef-associated communities and a larger offshore population which might contribute to gene flow (Chapter 6).

The calving season in the Red Sea had one pronounced annual peak between June and August, and coincided with warmer water

temperatures. The crude birth rate, annual recruitment rate, fecundity rate and calf survivorship were all comparable to, or generally higher than, those reported for the species elsewhere (see below). However, calves born to younger females showed a significantly lower survival than older females, indicating heterogeneity in female reproductive success. Heterogeneity was also found in the calving interval and weaning time, which vary between 2 and 3 years; but, at the moment, it is unclear which are the proximate causes. Female spinner dolphins seem to attain sexual maturity at 8-10 years, when they likely begin to accumulate tooth rake marks, observed about 10.8 months before the birth of a calf (a time span which corresponds to the gestation period). The presence of such marks suggests that coercive sexual behaviours may be part of male reproductive strategy (Chapter 5).

Adult Red Sea spinner dolphins were found to be sexually dimorphic (Chapter 3 and Chapter 4). The study of the individual growth showed that female and male growth begins to diverge at the length of ~151 cm, after the initial rapid growth spurt in the first 3 years. Physical maturity is then attained at the length of ~165 cm for females and ~180 cm for males, at approximately 7 and 10 years of age, respectively (Chapter 4). Adult males were not only significantly larger in size, they also displayed a more forward-canted and proportionally taller dorsal fin and a larger post-anal hump than females. The change in the dorsal fin shape, that begins showing signs of sexual dimorphism at the age of ~8 years in the male Red Sea spinner dolphin, and the moderately marked eye-to-anus stripe, that begins to be evident at ~10 years of age, likely represent two good indicators of attaining sexual maturity. The intensity and thickness of the eye-to-anus stripe increase with age in both sexes, but in old adult males (~15 years of age) the stripe becomes significantly darker and thicker than in females. The inverted bell-shaped lower lip patch described in this study for both sexes and all age classes appeared to be a unique feature (Robineau and Rose, 1983; Chapter 3). These results indicate that the pigmentation pattern of the Red Sea spinner dolphins, along with their morphological and morphometric characteristics can be used for age class

determination, sex identification in adults, and estimates of sexual maturation in males, which ultimately enhance the potential of exploring sex-specific and age-based demographic models (Chapter 3 and Chapter 4).

## 7.2 Broader comparative context

Among cetaceans, the spinner dolphin is one of the most studied species globally that best exemplify geographic variability (Perrin, 1972; Perrin et al., 1991; Douglas et al., 1992; Perrin et al., 2007). Its morphology, population ecology and the life history traits are highly variable, for intrinsic as well as extrinsic causes (Chapter 1).

Morphometric and pigmentation features of the Red Sea spinner dolphins appear to differ from those displayed by other ecotypes, which corresponds to the elevated degree of endemism reported for the Red Sea bioregion (DiBattista et al., 2015). The Red Sea spinner dolphin seems to be intermediate in length between the Central American or the “Tres Marias” ecotypes and the Dwarf form, displaying a comparable size to Gray’s and whitebelly forms (Chapter 3). The latter ecotypes, however, do not exhibit the strong sexual dimorphism typical of the adult Red Sea spinner, which remains less pronounced than that of eastern spinner dolphin *S. l. orientalis* (Perrin, 1990). Variation in colouration patterns has been observed and documented extensively in the spinner dolphin (Perrin, 1972; Perrin et al., 1991) and the Red Sea spinner dolphins displayed the tripartite colouration pattern similar to the Gray’s form, *S. l. longirostris* (Perrin, 1972), with the exception of the presence of an eye-to-anus stripe that progressively thickens and darkens in elder individuals of both sexes, and in old adult males becomes significantly darker and thicker than in females, similarly to Fraser’s dolphins (*Lagenodelphis hosei*, Jefferson et al., 1997). Perrin (1997) extensively documented spinner dolphins bridle colouration patterns (photographs of specimens were collected from the eastern tropical Pacific, Hawaii, Gulf of Mexico, the U.S. east coast, Africa, and Japan; Perrin, 1972) but never reported the dark inverted bell-shaped

lower lip patch described in this study, which appears to be unique to the Red Sea and Gulf of Aden spinner dolphins (Robineau and Rose, 1983).

Reproductive parameters reported in this study were generally higher than those reported for the spinner dolphins elsewhere. The mean annual birth rate of  $\sim 0.10$  was slightly higher than those reported for the Eastern Tropical Pacific (ETP) spinner dolphins (Perrin and Reilly, 1984) and spotted dolphins (*Stenella frontalis*, Herzing, 1997), and substantially higher compared to bottlenose dolphins' (*Tursiops* spp., Wells and Scott, 1990; Bearzi et al., 1997; Kogi et al., 2004). The mean annual recruitment rate estimated in this study (0.08) was also generally higher than those reported for other species (*Stenella frontalis*, Herzing, 1997; *Tursiops truncatus*, Wells and Scott, 1990; *Tursiops aduncus*, Kogi et al., 2004). The fecundity rate ( $\sim 0.20$ ) was instead similar to other studies (Herzing, 1997; Wells and Scott, 1990; Kogi et al., 2004). The estimated median calving interval of  $\sim 2$  years for the Red Sea spinner dolphin is shorter than the estimates revised by Larese and Chivers (2009) for the ETP spinner dolphin and for the whitebelly hybrid, which are closer to the congeners that have a calving interval of about three years (*Stenella frontalis*, Herzing, 1997; *Stenella attenuata*, Perrin and Hohn, 1994). Calf survivorship for individuals younger than 1-year of age was estimated at 0.85 for the Red Sea spinner dolphins and was higher than published estimates of other odontocetes (*Tursiops truncatus*, Wells and Scott, 1990; Haase and Schneider, 2001; *Stenella frontalis*, Herzing, 1997; *Tursiops aduncus*, Mann et al., 2000). The age at sexual maturity (ASM) reported here is similar to the updated estimate for the same ETP populations (Larese and Chivers, 2009) as well as to those of species with comparable longevity such as common dolphins (*Delphinus delphis*, Danil and Chivers, 2007) and spotted dolphins (*Stenella frontalis*, Herzing, 1997). Eastern and whitebelly spinner dolphins give birth throughout the year (Larese and Chivers, 2009; Barlow, 1984) and Hawaiian spinner dolphins display a bimodal pattern, with two calving peaks during the year, in August and February (Östman-Lind et al., 2004). Differently, the calving

season in the Red Sea had one pronounced annual peak during the boreal summer months.

This study is unarguably shorter than the decades-long studies of bottlenose dolphins (*Tursiops* sp.) in Sarasota, Florida (Wells and Scott, 1999) or Shark Bay, Western Australia (Mann et al., 2000). However the spinner dolphin's longevity is considered to be ~25 years (Perrin and Gilpatrick Jr, 1994), and this study, that, cumulatively with previous shorter projects, spans over ~10 years, is likely sufficiently representative of reproductive parameters of the species in the Red Sea which suggest that the population is doing well.

Abundance and high long-term site fidelity of the Samadai reef population are similar to those found for the closed community at Midway Atoll (Karczmarski et al., 2005); however, strong evidence of emigration and reimmigration positions Samadai reef population closer to the spinner dolphins of the Society Archipelago in French Polynesia (Oremus et al., 2007), although the local community size was found slightly smaller (~150 individuals) than the one reported in this study. Samadai reef population size is substantially smaller than that estimated for the Kona coast of the Hawai'i Island stock (~630 individuals) (Tyne et al., 2014), but the annual apparent survival rate is high and comparable. Therefore, the population parameters estimated for Samadai reef do not, at the moment, represent a cause of concern.

### **7.3 Conservation management implication**

Cetaceans are affected globally by numerous human activities, including the direct impacts of hunting, incidental entanglement in fishing gear, vessel collision, and the indirect impacts of coastal development and habitat destruction, tourism, chemical pollution and noise pollution (e.g. offshore drilling, military sonar and seismic exploration), prey depletion and the effects of climate change (Harwood, 2001; Reeves et al., 2005; Read et al., 2006; Hammond et al., 2013). Compared to other regions in

the world, the Red Sea can be still considered as one of the least impacted seas (Sheppard et al., 1992). Nevertheless, the relatively recent increase in human activities along its coasts has resulted in an overexploitation of the marine resources in the region (PERSGA, 1998; Shaalan, 2005; Gladstone et al., 1999). Among the several recognized threats to the marine ecosystem, the rapid coastal tourism development brings along many conservation concerns for the Egyptian Red Sea (e.g. Hawkins and Roberts, 1994). Studies addressing the magnitude of the impact of these activities on cetaceans are still scarce (Fumagalli, 2016).

Gray's spinner dolphins diel pattern of behaviour (Chapter 1) renders this species particularly vulnerable to anthropogenic disturbance: harassment by dolphin watching boats and swim-with activities are emerging as a new threat worldwide (Bearzi et al., 2012); the Red Sea is no exception. Previous (Notarbartolo di Sciara et al., 2009) and current (Fumagalli, 2016) research carried out in the Egyptian Red Sea confirmed that spinner dolphins are subject to great pressure by dolphin-based tourism operations especially in the resting areas (Chapter 1). Samadai reef represents a well know tourist attraction for swim-with-dolphins activities (Notarbartolo di Sciara et al., 2009) and since January 2004 a management plan regulates touristic activities, capping the number of people in the water, the accessible areas and the time (Chapter 1 and Chapter 2). However this management plan was provisional as based on the scant knowledge available at the time and on a principle of precautionary approach (Notarbartolo di Sciara, 2003; Notarbartolo di Sciara et al., 2009).

Among the goals of this study was to assess the effectiveness of the management plan after approximately ten years from its implementation and to evaluate whether modifications were needed. Despite the lack of baseline population and reproductive parameter estimations for Samadai population before the implementation of the management plan (which makes impossible to assess whether the population has been stable, increasing or decreasing since the earlier 2000s), no decreasing trends

have been detected for this population for the duration of this study, suggesting that the current management measures are effective.

The duration of the study and the complex population dynamics described pose, however, some challenges from a conservation perspective. Firstly, the high site fidelity and relatively small but stable community size with low interchange with other communities could possibly raise concerns. Small populations usually experience reduced viability and fecundity and are therefore more prone to extirpation than large stable populations (Lande, 1988). The fecundity rate reported in this study, however, did not appear to be reduced. Moreover, evidence of a transient component may possibly represent the existence of a larger (in the order of thousands ~6700; Costa, 2015), offshore population with whom gene flow may occur (e.g. Wells, 2003). In such case the Samadai population would not be genetically depauperate, unless there are other socio-ecological constraints. It still remains to be further investigated whether the resident male alliances detected by Cesario et al. (2013) play a role in diminishing such gene flow by excluding other males from accessing resident receptive females. Secondly, the observed short and unimodal breeding season likely limits the rate at which females can be inseminated after an aborted pregnancy, calf death, or weaning (Barlow, 1984). And thirdly, the high residency of individuals increases their exposure to anthropogenic pressures. The cumulative exposure of spinner dolphins to tourist activities may alter their energetic budget (Williams et al., 2006) and their state of rest (*i.e.* sleep deprivation) (Lima et al., 2005), impairing their cognitive abilities (Cirelli and Tononi, 2008) and therefore increasing their vulnerability to predation (Lima et al., 2005) and ultimately affecting their vital rates (Bejder and Lusseau, 2008; Tyne et al., 2014), although such direct evidence is not always emerging in short-term studies (Weinrich and Corbelli, 2009; Christiansen and Lusseau, 2015; Christiansen et al., 2015).

The current level of protection employed in Samadai reef seems adequate as the population vital rates are not alarming, nevertheless long-term detrimental effects on the viability and fitness of individuals and their

populations could take some time to emerge (Lusseau, 2004; Bejder et al., 2006; Lusseau and Bejder, 2007; Higham et al., 2009) and could have been gone undetected given the relatively short duration of this study. Therefore, long-term consistent monitoring of the dolphins and of the tourist activities is strongly advised. Moreover, the implementation of site-specific management measures (e.g. further restricting tourists access, both spatially and temporally, to resting dolphins when newborns and calves are present in the group) during the most sensitive months (June, July and August), when newborns have the highest mortality rate and females are more susceptible to natural (*i.e.* predation) and anthropogenic (*i.e.* tourism) pressures, are also recommended.

The success story for Samadai reef should be used as an example in the region to prove that conservation efforts cohabit with stakeholder needs to ultimately boost conservation efforts in other reefs. The findings of this thesis, combined with those obtained for the region at large (Fumagalli, 2016; Costa, 2015), highlight the need to develop a strategy for the conservation of the adjacent resting areas (Figure 1.1, Chapter 1) that do not yet have a management plan in place and offer virtually no level of protection despite being within the boundaries of national parks or conservation areas (Figure 1.2, Chapter 1; Fumagalli, 2016). Although all resting areas should ideally receive attention, as studies conducted in Hawaii indicate that they represent critical areas for spinner dolphins (Tyne et al., 2015), this is particularly urgent for Satayah reef, where tourist activities are increasing and first results showed that they are having a negative effect (Fumagalli, 2016) potentially unsustainable for the dolphins.

This study also pointed out how natural history studies, such as studies of growth and morphometrics, represent an integral component in acquiring a better understanding of the age-structure and sex ratio of a population, which, in turn, is crucial for modelling population parameters, understanding socio-behavioural ecology and assessing population viability. Therefore the continuation and expansion of the photogrammetric

technique to other individuals of Samadai reef as well as of other populations in the region is advised. More importantly, morphology and morphometrics measurements revealed some intraspecific differences that would need further investigation. Given the steadily increasing tourism development in the region, resolution of taxonomic uncertainties of spinner dolphins is evidently needed, as it is critical to address conservation issues at an appropriate geographic scale. In the meanwhile, the Red Sea spinner dolphin, inclusive of the animals inhabiting the adjacent Gulf of Aden (Robineau and Rose, 1983), should be recognised an Evolutionary Significant Unit (Cat. III) for management purposes and likely a new ecotype. As new studies take place and further data is gathered, the morphometric data presented here may contribute to a more thorough evaluation of the taxonomic status of the Red Sea spinner dolphin.

#### **7.4 Future research**

In cetaceans, various aspects of population ecology, such as population size, survival, reproductive success and the response of populations to environmental change and constraints are influenced by the behavioural ecology and by the quantity and quality of social interactions between individuals (Sutherland, 1996; Frère et al., 2010; Stanton and Mann, 2012; Krützen et al., 2004; Hinde, 1976; Wilson, 1975; Wells, 2014). How an individual interacts with a particular conspecific depends on numerous factors, including age, sex and kinship. Moreover, environmental factors, such as habitat features and ecological variables, greatly influence animal interaction patterning, resulting in a intraspecific differentiation of social structures (Gowans et al., 2008). The divergence of the socio-behavioural ecology of spinner dolphins in Hawaiian waters is a good example: dolphins living off the main islands, where large and abundant resting habitats are available, exhibit fission-fusion group dynamics as a consequence of diurnal resting and socializing activities and nocturnal cooperative forays (Norris and Dohl, 1980; Norris et al., 1994); by contrast, dolphins inhabiting the waters of the isolated far-western Hawaiian islands, form long-term bisexually bonded stable groups (Karczmarski et al., 2005).

Samadai reef community seems to be relatively isolated from other reef-associated communities and the preliminary socio-ecological investigations indicated a structured population (Appendix VI) with strong preferred association of males who could possibly cooperate with (and perhaps against) conspecifics over access to females (Cesario et al., 2013). A further investigation of the social structure of the Red Sea spinner dolphin will provide the knowledge needed to assess whether the intermediacy of resources in terms of abundance and predictability of resting sites (mosaic of primary, secondary and occasional resting areas relatively closely located, Chapter 1), leads to an intermediate social system between the fission-fusion scenario and the stable social structure. This intermediate social system characterized by resident and stable reef-associated communities, would be close to the metapopulation structure proposed by Oremus et al. (2007) with the additional offshore component that possibly contribute to maintain a diverse genetic pool.

Genetic analyses performed on Hawaiian spinner dolphins found that dispersal is not male-biased, as for the majority of mammalian species (Greenwood, 1980), but equally dependent on both sexes (Andrews et al., 2010). Oremus and colleagues (2007) suggested instead greater female philopatry and some male-biased dispersal for the South Pacific dolphin communities. A genetic investigation of the Red Sea spinner dolphin is therefore also recommended as it will shed light on the apparent, as suggested by this study, male-biased dispersal. Furthermore, genetic study would greatly benefit the general understanding of the species taxonomic status in the region. The findings of the current study revealed some intraspecific differences. Recognizing intraspecific taxonomic groups is key to conservation efforts as it provides a foundation for protecting these unique biological entities by: (1) including them in national and international lists that have important legal and financial ramifications, (2) appropriately managing resources allocation, and (3) increasing the sense of ownership and conservation responsibility of locals towards wildlife (Haig et al., 2006). Taxonomic information and social dynamics

(Sutherland, 1998; Smith et al., 2016), are essential elements in species conservation management, and incorporating this knowledge will likely further ameliorate the current management that is in place at Samadai reef and more broadly in the region.

## 8. Appendices

### Appendix I. Photographic quality and dolphin distinctiveness scores for underwater photo-identification

#### Overall Photographic Quality

Overall Photographic Quality (OPQ) is based on the quality of the photograph independent of the distinctiveness of the fin.

The OPQ score is based on the evaluation of the following characteristics and sum of their scores (Table A I.1 and Table A I.2):

- Focus/Clarity: crispness or sharpness of the image. Lack of clarity may be caused by poor focus, poor resolution resulting in large pixels. This characteristic accounts for water visibility.
- Contrast: range of tones in the image. Images may display too much contrast or too little. Photographs with too much contrast lose detail as small features wash out to white. Images with too little contrast lose the fin into the background and features lack definition. This characteristic accounts for water surface reflection.
- Angle: angle of the fin/body to the camera.
- Dorsal fin visibility: the score is assigned only when the fin is partially covered e.g. by another dolphin, fish etc.. Otherwise its value is zero.

*NB: Digital manipulation of pictures is performed in Adobe Photoshop CS6 and Camera Raw 9.1 plug-in prior to quality assignment and may include cropping, enhancement in terms of white balance, sharpness, and/or contrast. Photographs collected from 2013 are in RAW image file format; JPEG format was used before.*

Table A I.1. Scores and descriptions of the photographic quality characteristics. Scores for Focus, Angle and Dorsal Fin visibility categories are weighted in a way that inadequate quality in one category alone pushes the photograph over the poor quality (Q5) threshold (see Table A I.2).

| Characteristic               | Score | Description  |
|------------------------------|-------|--|
| <b>Focus/Clarity</b>         | 1     | Excellent: perfect focus - outline and all details are visible   |
|                              | 3     | Good: good focus - all details visible but small nicks not perfectly focused   |
|                              | 5     | Moderate: no blur - general outline visible, small nicks not visible   |
|                              | 9     | Poor: very blurry - details are not visible  |
| <b>Contrast</b>              | 1     | Ideal: perfect exposure  |
|                              | 2     | Good: slight light or dark   |
|                              | 3     | Excessive or minimal: too light or dark, marks on the edges may still be seen but not the scratches; presence of water surface reflection on the fin |
| <b>Angle</b>                 | 1     | Perpendicular or nearly perpendicular: <10°  |
|                              | 2     | Slight to moderate: between 10° and 45°  |
|                              | 8     | Oblique: >45°  |
| <b>Dorsal Fin Visibility</b> | 0     | Fin entirely visible   |
|                              | 2     | Trailing edge is fully visible   |
|                              | 8     | Fin is mostly obscured   |

Table A I.2. Overall Photographic Quality categories. High quality pictures (Q1 and Q2) are retained for analyses.

| Quality category | ΣScore |
|------------------|--------|
| Q1 (Excellent)   | 3-4    |
| Q2 (Very good)   | 5-6    |
| Q3 (Good)        | 7-8    |
| Q4 (Fair)        | 9-10   |
| Q5 (Poor)        | 11+    |

### Individual distinctiveness

Individual distinctiveness is based on the amount of information contained on the dorsal fin and on the body; information content is drawn from features visible from both sides on the dorsal fin leading and trailing edges (Figure A I.1) and on the body profile (Figure A I.2) and are described in Table A I.3.

Table A I.3. Individual distinctiveness categories and descriptions.

| Category for analyses                              | Distinctiveness Category | Description  | E.g.   |
|--|--------------------------|--|--|
| <b>HMI</b><br><b>(Highly Marked Individuals)</b>   | <b>D1</b>                | Very distinctive; features evident even in distant or poor quality photographs | <b>Dorsal fin</b> <ul style="list-style-type: none"> <li>• Deformed</li> <li>• Mutilated</li> <li>• Big chunk missing</li> <li>• Tip missing</li> <li>• 1+ notch</li> <li>• 2+ nicks</li> </ul> <b>Body mark (usually on the back/peduncle)</b> <ul style="list-style-type: none"> <li>• Large notch on the body profile</li> <li>• Scar (which deforms the body profile)</li> </ul> |
|  | <b>D2</b>                | Distinctive, average amount of information content                             | <b>Dorsal fin only</b> <ul style="list-style-type: none"> <li>• 1 nick AND 1+ small nicks</li> <li>• 4+ small nicks</li> <li>• Peculiar shape</li> </ul>   |
| <b>MI</b><br><b>(Marked Individuals)</b>           | <b>D3</b>                | Distinctive, little amount of information content                              | <b>Dorsal fin</b> <ul style="list-style-type: none"> <li>• 1 nick ONLY</li> <li>• 3 small nicks</li> </ul> <b>Body mark (usually on the back/peduncle)</b> <ul style="list-style-type: none"> <li>• 1+ small mark(s) on the body profile</li> </ul>  |
| <b>NDI</b><br><b>(Non-Distinctive Individuals)</b> | <b>D4</b>                | Very little information in content   | <b>Dorsal fin only</b> <ul style="list-style-type: none"> <li>• 1-2 small nicks</li> </ul>   |
|  | <b>D5</b>                | No information content   | <b>Dorsal fin only</b> <ul style="list-style-type: none"> <li>• Clean fin</li> </ul>   |

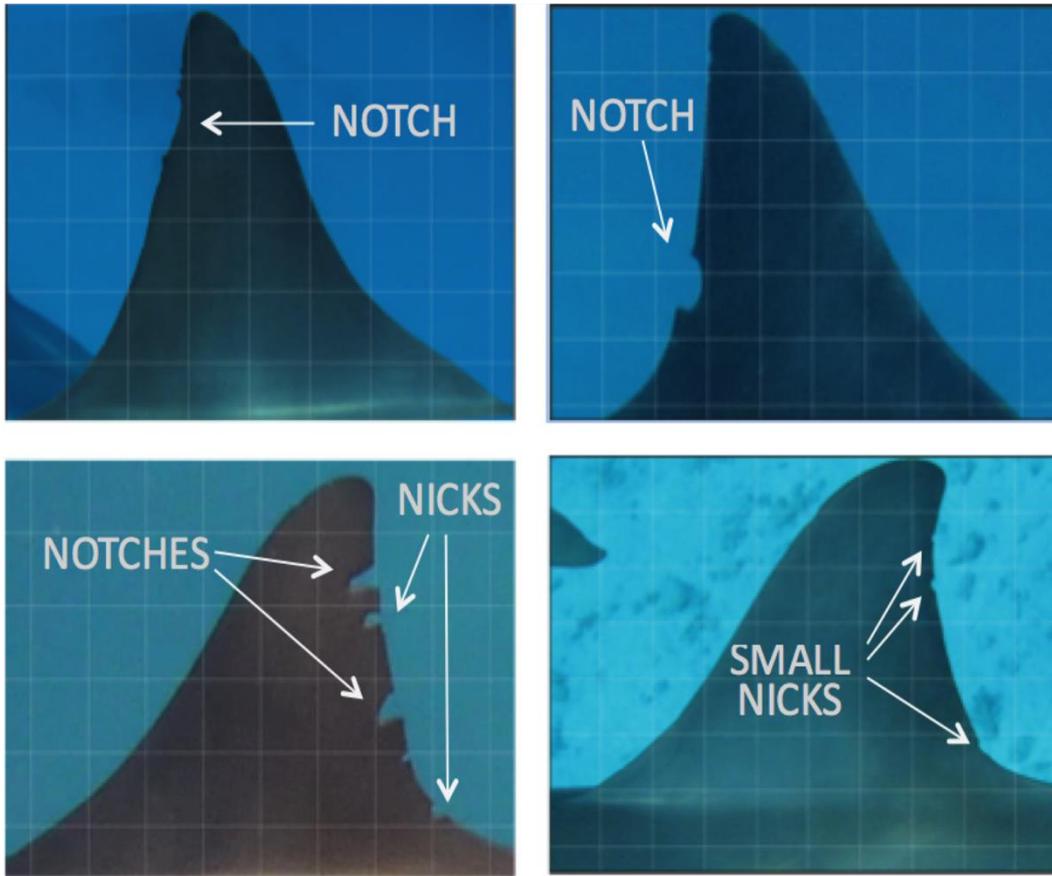


Figure A I.1. Natural markings on dorsal fin. The definition of the mark relates to the proportional size rather than the absolute size (tentative absolute sizes for adults are indicated in brackets). Notch: indentation  $1/6$  ca. of the total height of the dorsal fin, including jagged indentation (3 cm ca.); Nick: (smaller notch) indentation  $1/18$  ca. of the height of the dorsal fin (1-2 cm ca.); Small nick: indentation smaller than nick (<1 cm ca.). A gridded background is provided for clearer representation.

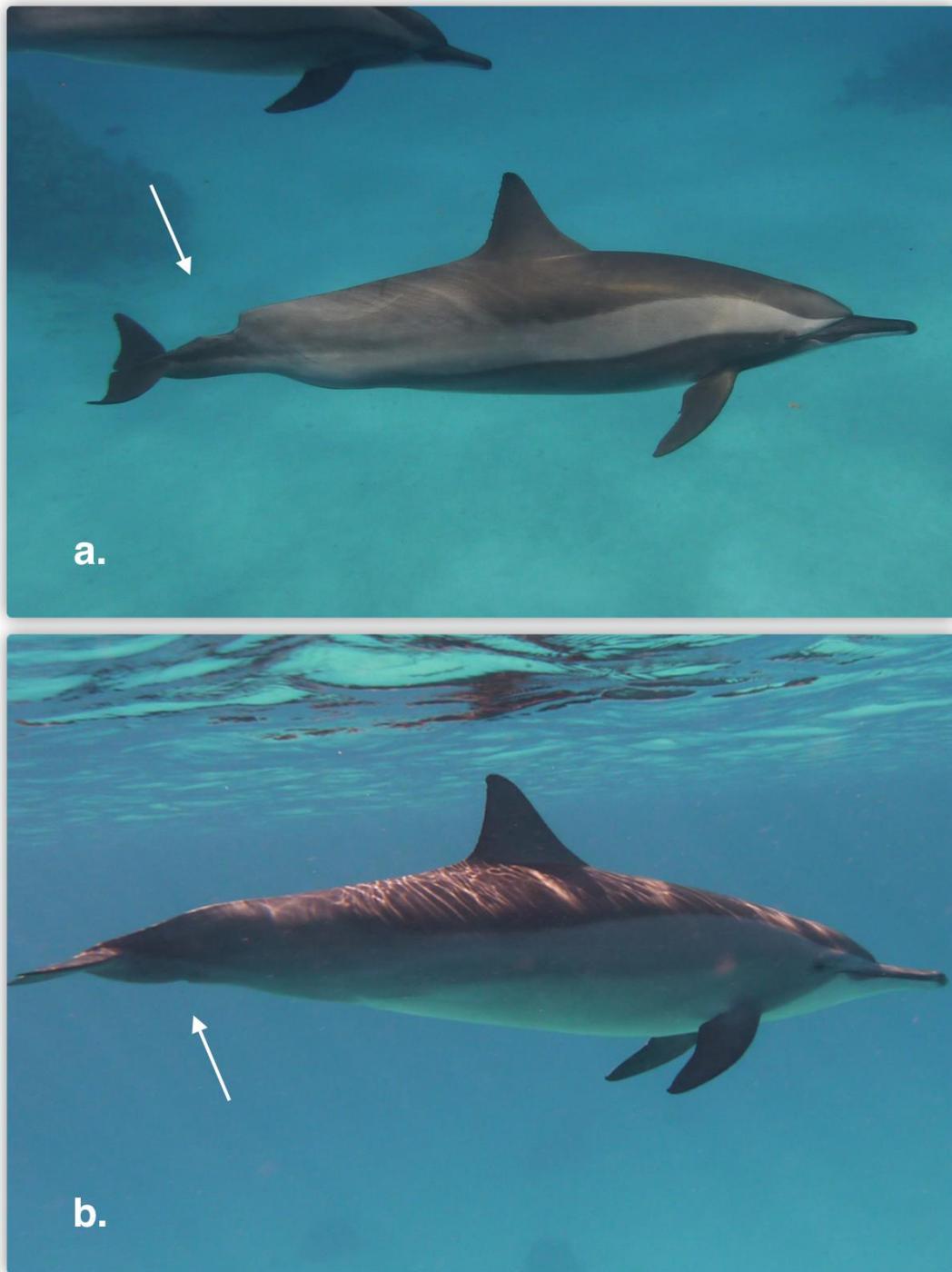


Figure A I.2. Natural markings on body profile. Marks on the body are considered large (a) when visible even in poor quality pictures and considered small (b) when at least a very good quality picture is needed.

### **Scores and categories**

Scores and categories are based on the system developed by Urian et al. (1999), modified by Read et al. (2003) and the SDRP (2006), accounting for Friday et al. (2000) and Gowans and Whitehead (2001) considerations,

following the recommendations by Urian and colleagues (2015) and finally adapted to better fit underwater data collection.

## Appendix II. Ontogeny of pigmentation

Female individual SL0187 from 2005 to 2014. Colouration: from faint to moderate. Age class: from juvenile (4 years *ca.*) to adult (13 years *ca.*). Seen the first time with a calf in 2014. Unseen calves or perinatal deaths in late stage pregnancy cannot be excluded between 2007 and 2010, but certainly did not occur between 2011 and 2013.



Male individual SL0009 from 2006 to 2014. Colouration: from three tone to dark. Age class: from juvenile (4 years *ca.*) to adult (12 years *ca.*). Dorsal fin shape became slightly more erect but is yet far from being canted forward.



## Appendix III. Morphometric data

Table A III.1. Average of morphometric measurements, number of photographs (n), and CVs (%) for 33 adult females. CVs were calculated for  $n \geq 3$ . Not all morphometrics were measurable in all photographs.

| ID     | n | Mean TL | CV TL | Mean DFW | CV DFW | Mean DFH | CV DFH |
|--------|---|---------|-------|----------|--------|----------|--------|
| SL0008 | 2 | 164.5   | -     | 24.2     | -      | 14.3     | -      |
| SL0041 | 1 | 164.6   | -     | 23.6     | -      | 18.1     | -      |
| SL0062 | 1 | 177.5   | -     | -        | -      | -        | -      |
| SL0108 | 2 | 157.1   | -     | 20.4     | -      | 15.7     | -      |
| SL0130 | 1 | 182.4   | -     | 24.8     | -      | 17.6     | -      |
| SL0138 | 1 | 165.8   | -     | 23.7     | -      | 17.8     | -      |
| SL0181 | 1 | 171.4   | -     | 24.3     | -      | 17.0     | -      |
| SL0187 | 4 | 164.2   | 6.5%  | 23.7     | -      | 16.6     | -      |
| SL0199 | 1 | 161.6   | -     | -        | -      | -        | -      |
| SL0218 | 2 | 167.2   | -     | 22.2     | -      | 13.8     | -      |
| SL0224 | 1 | 175.0   | -     | 23.4     | -      | 16.0     | -      |
| SL0239 | 1 | 155.9   | -     | 22.4     | -      | 15.0     | -      |
| SL0269 | 5 | 159.6   | 2.8%  | 22.9     | 4.5%   | 16.1     | 8.8%   |
| SL0272 | 1 | 168.0   | -     | 24.6     | -      | 18.1     | -      |
| SL0278 | 1 | 152.3   | -     | 21.7     | -      | 15.9     | -      |
| SL0282 | 2 | 167.7   | -     | 22.5     | -      | 16.3     | -      |
| SL0292 | 1 | 166.8   | -     | -        | -      | -        | -      |
| SL0303 | 4 | 170.4   | 2.1%  | 22.9     | 5.9%   | 17.4     | 3.3%   |
| SL0377 | 1 | 166.2   | -     | -        | -      | -        | -      |
| SL0379 | 1 | 176.8   | -     | 23.4     | -      | 17.3     | -      |
| NDI01  | 1 | 174.3   | -     | 23.2     | -      | 16.1     | -      |
| NDI02  | 5 | 169.3   | 2.9%  | 23.6     | 5.8%   | 16.0     | 6.2%   |
| NDI03  | 1 | 164.0   | -     | 21.4     | -      | 15.3     | -      |
| NDI05  | 1 | 162.4   | -     | -        | -      | -        | -      |
| NDI06  | 1 | 171.8   | -     | -        | -      | -        | -      |
| NDI07  | 1 | 156.2   | -     | 23.6     | -      | 16.3     | -      |
| NDI08  | 1 | -       | -     | 24.3     | -      | 18.6     | -      |
| NDI09  | 1 | 164.7   | -     | 22.9     | -      | 16.7     | -      |
| NDI11  | 1 | 179.7   | -     | -        | -      | -        | -      |
| NDI12  | 1 | 177.1   | -     | -        | -      | -        | -      |
| NDI13  | 1 | 156.0   | -     | 21.8     | -      | 16.7     | -      |
| NDI35  | 1 | 174.0   | -     | -        | -      | -        | -      |
| NDI73  | 1 | 158.1   | -     | -        | -      | -        | -      |

Table A III.2. Average of morphometric measurements, number of photographs (n), and CVs (%) for 28 adult males. CVs were calculated for n≥3. Not all morphometrics were measurable in all photographs.

| ID     | n | Mean TL | CV TL | Mean DFW | CV DFW | Mean DFH | CV DFH |
|--------|---|---------|-------|----------|--------|----------|--------|
| SL0005 | 1 | 199.1   | -     | 26.3     | -      | 19.3     | -      |
| SL0009 | 1 | 174.0   | -     | 24.9     | -      | 18.8     | -      |
| SL0037 | 1 | -       | -     | 24.9     | -      | 18.3     | -      |
| SL0053 | 1 | 194.1   | -     | 27.3     | -      | 18.8     | -      |
| SL0054 | 3 | 186.5   | -     | 26.1     | 5.8%   | 20.8     | 1.5%   |
| SL0055 | 1 | 184.3   | -     | 25.6     | -      | 21.0     | -      |
| SL0057 | 2 | 177.0   | -     | 26.8     | -      | 20.9     | -      |
| SL0059 | 3 | 182.7   | 1.6%  | 26.0     | 8.2%   | 21.8     | 7.5%   |
| SL0060 | 1 | -       | -     | 24.4     | -      | 21.2     | -      |
| SL0061 | 3 | 184.2   | 1.3%  | 26.0     | 2.1%   | 20.9     | 2.9%   |
| SL0063 | 1 | 177.5   | -     | 29.7     | -      | 21.2     | -      |
| SL0065 | 2 | 189.3   | -     | 26.7     | -      | 20.2     | -      |
| SL0072 | 1 | 181.3   | -     | 27.2     | -      | 20.6     | -      |
| SL0077 | 3 | 191.1   | 3.2%  | 29.5     | 5.8%   | 21.6     | 3.0%   |
| SL0078 | 1 | 196.7   | -     | 28.8     | -      | 21.7     | -      |
| SL0079 | 3 | 182.7   | 3.5%  | 27.8     | 4.0%   | 21.0     | 7.7%   |
| SL0094 | 3 | 182.7   | 1.5%  | 26.6     | 2.8%   | 22.4     | 3.1%   |
| SL0174 | 1 | 189.0   | -     | 25.9     | -      | 21.5     | -      |
| SL0211 | 1 | 187.8   | -     | 27.5     | -      | 20.4     | -      |
| SL0213 | 2 | 172.6   | -     | 23.6     | -      | 19.2     | -      |
| SL0231 | 1 | 175.5   | -     | 27.1     | -      | 15.5     | -      |
| SL0255 | 1 | 171.9   | -     | 23.5     | -      | 19.1     | -      |
| SL0258 | 1 | 185.9   | -     | 24.3     | -      | 19.7     | -      |
| SL0261 | 1 | 185.0   | -     | 25.7     | -      | 18.7     | -      |
| SL0286 | 1 | 176.0   | -     | 24.3     | -      | 18.0     | -      |
| SL0291 | 2 | 172.7   | -     | 23.5     | -      | 20.4     | -      |
| SL0371 | 1 | -       | -     | 26.6     | -      | 19.6     | -      |
| SL0384 | 1 | 185.5   | -     | -        | -      | -        | -      |

Table A III.3. Average of morphometric measurements, number of photographs (n), and CVs (%) for 52 immature dolphins. Sex (when available) and Age Class are reported (NB: <2months; C1: 1 year old; C2: 2 years old; C3:3 years old; J: >4 years old). CVs were calculated for n≥3. Not all morphometrics were measurable in all photographs.

| ID          | Sex | Age Class | n  | Mean TL | CV TL | Mean DFW | CV DFW | Mean DFH | CV DFH |
|-------------|-----|-----------|----|---------|-------|----------|--------|----------|--------|
| SL0187-SON1 | n/a | NB        | 7  | 84.2    | 4.3%  | 11.8     | 1.8%   | 7.9      | 5.4%   |
| SL0224-SON3 | n/a | NB        | 2  | 85.0    | -     | 13.9     | -      | 7.6      | -      |
| NDI04       | n/a | NB        | 1  | 85.9    | -     | -        | -      | -        | -      |
| NDI16       | n/a | NB        | 1  | 84.2    | -     | 12.2     | -      | 8.8      | -      |
| NDI26       | n/a | NB        | 1  | 78.9    | -     | -        | -      | -        | -      |
| NDI27       | n/a | NB        | 1  | 83.3    | -     | -        | -      | -        | -      |
| NDI28       | n/a | NB        | 1  | 80.8    | -     | -        | -      | -        | -      |
| NDI29       | n/a | NB        | 1  | 81.7    | -     | -        | -      | -        | -      |
| NDI56       | n/a | NB        | 1  | 85.2    | -     | -        | -      | -        | -      |
| NDI57       | n/a | NB        | 1  | 79.5    | -     | -        | -      | -        | -      |
| NDI58       | n/a | NB        | 1  | 76.1    | -     | -        | -      | -        | -      |
| NDI59       | n/a | NB        | 1  | 78.6    | -     | -        | -      | -        | -      |
| NDI60       | n/a | NB        | 1  | 86.2    | -     | -        | -      | -        | -      |
| NDI61       | n/a | NB        | 1  | 97.1    | -     | -        | -      | -        | -      |
| NDI62       | n/a | NB        | 1  | 93.9    | -     | -        | -      | -        | -      |
| NDI63       | n/a | NB        | 1  | 94.4    | -     | -        | -      | -        | -      |
| NDI64       | n/a | NB        | 1  | 98.1    | -     | -        | -      | -        | -      |
| NDI65       | n/a | NB        | 1  | 89.9    | -     | -        | -      | -        | -      |
| NDI66       | n/a | NB        | 1  | 83.2    | -     | -        | -      | -        | -      |
| NDI67       | n/a | NB        | 1  | 88.7    | -     | -        | -      | -        | -      |
| NDI68       | n/a | NB        | 1  | 90.1    | -     | -        | -      | -        | -      |
| NDI74       | n/a | NB        | 3  | 80.5    | 2.7%  | -        | -      | -        | -      |
| NDI76       | n/a | NB        | 3  | 84.5    | 0.9%  | -        | -      | -        | -      |
| SL0210-SON2 | M   | C1        | 3  | 109.4   | 1.1%  | 19.6     | 4.3%   | 12.4     | 1.1%   |
| SL0327-SON2 | M   | C1        | 4  | 121.3   | 6.8%  | 18.2     | -      | 12.2     | -      |
| SL0048-SON4 | n/a | C1        | 4  | 123.8   | 5.6%  | 22.2     | 5.1%   | 13.3     | 1.6%   |
| SL0104-SON3 | n/a | C1        | 10 | 121.4   | 3.2%  | 18.6     | -      | 13.2     | -      |
| SL0282-SON3 | n/a | C1        | 7  | 115.5   | 5.3%  | 17.3     | 0.8%   | 12.8     | 1.1%   |
| SL0289-SON4 | n/a | C1        | 1  | 137.3   | -     | -        | -      | -        | -      |
| SL0379-SON2 | n/a | C1        | 2  | 125.7   | -     | 19.1     | -      | 12.9     | -      |
| SL0274-SON2 | M   | C2        | 1  | 146.4   | -     | -        | -      | -        | -      |
| SL0062-SON2 | F   | C2        | 2  | 135.6   | -     | -        | -      | -        | -      |
| SL0269-SON1 | F   | C2        | 7  | 129.9   | 3.5%  | 18.2     | 6.1%   | 12.5     | 7.9%   |
| SL0292-SON1 | F   | C2        | 2  | 133.7   | -     | 18.4     | -      | 13.1     | -      |
| SL0370      | F   | C2        | 5  | 137.9   | 5.7%  | 20.0     | 4.6%   | 14.7     | 3.8%   |
| SL0010-SON2 | n/a | C2        | 3  | 139.3   | 0.2%  | 20.2     | -      | 15.4     | -      |
| SL0044-SON2 | n/a | C2        | 2  | 133.8   | -     | 21.0     | -      | 15.1     | -      |
| SL0068-SON1 | n/a | C2        | 1  | 134.6   | -     | 19.5     | -      | 12.7     | -      |
| SL0130-SON1 | n/a | C2        | 2  | 145.8   | -     | -        | -      | -        | -      |
| SL0181-SON2 | n/a | C2        | 5  | 144.8   | 2.9%  | 21.1     | 3.8%   | 15.7     | 1.1%   |
| SL0205-SON1 | n/a | C2        | 5  | 131.3   | 3.6%  | -        | -      | -        | -      |
| SL0303-SON2 | n/a | C2        | 3  | 142.8   | 3.4%  | -        | -      | -        | -      |
| SL0378-SON2 | n/a | C2        | 3  | 136.4   | 5.3%  | 19.5     | -      | 14.1     | -      |
| SL0364      | M   | C3        | 3  | 155.9   | 3.2%  | 20.5     | 0.3%   | 16.1     | -      |
| SL0228-SON1 | n/a | C3        | 3  | 148.1   | 3.9%  | 19.7     | 5.7%   | 15.5     | 0.0%   |
| SL0142      | M   | J         | 1  | 173.9   | -     | 23.5     | -      | 17.6     | -      |
| SL0204      | M   | J         | 2  | 161.2   | -     | 21.9     | -      | 16.9     | -      |
| SL0365      | M   | J         | 2  | 164.2   | -     | 20.5     | -      | 16.3     | -      |
| SL0397      | M   | J         | 5  | 153.9   | 5.1%  | 22.4     | 6.5%   | 18.1     | 2.0%   |
| SL0413      | M   | J         | 1  | 136.8   | -     | 22.9     | -      | 14.7     | -      |
| SL0368      | n/a | J         | 1  | 173.2   | -     | 22.3     | -      | 16.9     | -      |
| NDI15       | M   | J         | 1  | 147.9   | -     | -        | -      | -        | -      |

Table A III.4. Mean Total body Length (TL), Age, Date Of Birth (DOB) and DOB accuracy for 96 dolphins. DOB accuracy was classified as "Exact":  $\pm 3$ days; "Best":  $\pm 1$  week; "Good":  $\pm 2$  weeks; "Fair":  $\pm 1.5$  month; "Year":  $\pm 3-6$  months and "Tyear", a tentative DOB year assigned referentially. Sex (when available) and Age Class are also reported (NB: <2months; C1: 1 year old; C2: 2 years old; C3:3 years old; J: >4 years old; A: mature individual).

| ID          | Sex | Age Class | TL    | Age (years) | DOB       | DOB Accuracy |
|-------------|-----|-----------|-------|-------------|-----------|--------------|
| NDI04       | n/a | NB        | 85.9  | 0.1         | 22-Jun-14 | Fair         |
| NDI16       | n/a | NB        | 84.2  | 0.1         | 11-May-14 | Fair         |
| NDI26       | n/a | NB        | 78.9  | 0.1         | 15-Jun-14 | Fair         |
| NDI27       | n/a | NB        | 83.3  | 0.1         | 15-Jun-14 | Fair         |
| NDI28       | n/a | NB        | 80.8  | 0.1         | 15-Jun-14 | Fair         |
| NDI29       | n/a | NB        | 81.7  | 0.1         | 15-Jun-14 | Fair         |
| NDI56       | n/a | NB        | 85.2  | 0.1         | 15-Jun-14 | Fair         |
| NDI57       | n/a | NB        | 79.5  | 0.1         | 15-Jun-14 | Fair         |
| NDI58       | n/a | NB        | 76.1  | 0.1         | 15-Jun-14 | Fair         |
| NDI59       | n/a | NB        | 78.6  | 0.1         | 16-Jun-14 | Fair         |
| NDI60       | n/a | NB        | 86.2  | 0.1         | 22-Jun-14 | Fair         |
| NDI61       | n/a | NB        | 97.1  | 0.1         | 06-Jul-14 | Fair         |
| NDI62       | n/a | NB        | 93.9  | 0.1         | 06-Jul-14 | Fair         |
| NDI63       | n/a | NB        | 94.4  | 0.1         | 06-Jul-14 | Fair         |
| NDI64       | n/a | NB        | 98.1  | 0.1         | 06-Jul-14 | Fair         |
| NDI65       | n/a | NB        | 89.9  | 0.1         | 14-Jul-14 | Fair         |
| NDI66       | n/a | NB        | 83.2  | 0.1         | 14-Jul-14 | Fair         |
| NDI67       | n/a | NB        | 88.7  | 0.1         | 16-Jul-14 | Fair         |
| NDI68       | n/a | NB        | 90.1  | 0.1         | 16-Jul-14 | Fair         |
| NDI74       | n/a | NB        | 80.5  | 0.1         | 15-Jun-14 | Fair         |
| NDI76       | n/a | NB        | 84.5  | 0.1         | 15-Jun-14 | Fair         |
| SL0187-SON1 | n/a | NB        | 84.2  | 0.1         | 14-Jun-14 | Exact        |
| SL0224-SON3 | n/a | NB        | 85    | 0.0         | 01-Jun-14 | Good         |
| SL0048-SON4 | n/a | C1        | 123.8 | 1.0         | 01-Aug-13 | Best         |
| SL0104-SON3 | n/a | C1        | 121.4 | 1.0         | 07-Jul-13 | Best         |
| SL0210-SON2 | M   | C1        | 109.4 | 1.0         | 05-Aug-13 | Best         |
| SL0282-SON3 | n/a | C1        | 115.5 | 0.9         | 21-Aug-13 | Good         |
| SL0289-SON4 | n/a | C1        | 137.3 | 1.1         | 15-May-13 | Good         |
| SL0327-SON2 | M   | C1        | 121.3 | 1.0         | 30-Jul-13 | Best         |
| SL0379-SON2 | n/a | C1        | 125.7 | 1.1         | 01-Jul-13 | Best         |
| SL0010-SON2 | n/a | C2        | 139.3 | 1.8         | 15-Aug-12 | Best         |
| SL0044-SON2 | n/a | C2        | 133.8 | 2.0         | 01-Jul-12 | Year         |
| SL0062-SON2 | F   | C2        | 135.6 | 2.0         | 01-Jul-12 | Fair         |
| SL0068-SON1 | n/a | C2        | 134.6 | 2.1         | 01-Jul-12 | Fair         |
| SL0130-SON1 | n/a | C2        | 145.8 | 2.0         | 01-Jul-12 | Year         |
| SL0181-SON2 | n/a | C2        | 144.8 | 2.0         | 01-Jul-12 | Fair         |
| SL0205-SON1 | n/a | C2        | 131.3 | 2.0         | 01-Jul-12 | Fair         |
| SL0269-SON1 | F   | C2        | 129.9 | 2.0         | 01-Jul-12 | Year         |
| SL0274-SON2 | M   | C2        | 146.4 | 1.9         | 01-Jul-12 | Year         |
| SL0292-SON1 | F   | C2        | 133.7 | 1.9         | 01-Jul-12 | Fair         |
| SL0303-SON2 | n/a | C2        | 142.8 | 2.0         | 01-Jul-12 | Good         |
| SL0370      | F   | C2        | 137.9 | 2.0         | 01-Jul-12 | Fair         |
| SL0378-SON2 | n/a | C2        | 136.4 | 2.1         | 01-Jul-12 | Year         |
| SL0228-SON1 | n/a | C3        | 148.1 | 3.0         | 01-Jul-11 | Year         |
| SL0364      | M   | C3        | 155.9 | 2.8         | 15-Aug-11 | Best         |
| SL0142      | M   | J         | 173.9 | 10.1        | 01-Jul-04 | Year         |
| SL0204      | M   | J         | 161.2 | 8.3         | 12-Apr-06 | Tyear        |
| SL0365      | M   | J         | 164.2 | 5.8         | 03-Sep-08 | Tyear        |
| SL0368      | n/a | J         | 173.2 | 5.7         | 16-Nov-08 | Tyear        |

Table A III.4 continue. Mean Total body Length (TL), Age, Date Of Birth (DOB) and DOB accuracy for 96 dolphins. DOB accuracy was classified as "Exact":  $\pm 3$ days; "Best":  $\pm 1$  week; "Good":  $\pm 2$  weeks; "Fair":  $\pm 1.5$  month; "Year":  $\pm 3-6$  months and "Tyear", a tentative DOB year assigned referentially. Sex (when available) and Age Class are also reported (NB: <2months; C1: 1 year old; C2: 2 years old; C3:3 years old; J: >4 years old; A: mature individual).

| ID     | Sex | Age Class | TL    | Age (years) | DOB       | DOB Accuracy |
|--------|-----|-----------|-------|-------------|-----------|--------------|
| SL0397 | M   | J         | 153.9 | 4.0         | 12-Jun-10 | Tyear        |
| SL0413 | M   | J         | 136.8 | 4.0         | 01-Jul-10 | Year         |
| SL0005 | M   | A         | 199.1 | 17.1        | 03-May-97 | Tyear        |
| SL0008 | F   | A         | 164.5 | 15.0        | 17-Jul-99 | Tyear        |
| SL0009 | M   | A         | 174   | 12.4        | 15-Jan-02 | Tyear        |
| SL0041 | F   | A         | 164.6 | 15.2        | 14-May-99 | Tyear        |
| SL0053 | M   | A         | 194.1 | 17.1        | 27-Apr-97 | Tyear        |
| SL0054 | M   | A         | 186.5 | 17.2        | 27-Apr-97 | Tyear        |
| SL0055 | M   | A         | 184.3 | 17.2        | 27-Apr-97 | Tyear        |
| SL0057 | M   | A         | 177   | 17.2        | 27-Apr-97 | Tyear        |
| SL0059 | M   | A         | 182.7 | 17.2        | 27-Apr-97 | Tyear        |
| SL0061 | M   | A         | 184.2 | 17.1        | 27-Apr-97 | Tyear        |
| SL0062 | F   | A         | 177.5 | 12.7        | 26-Oct-01 | Tyear        |
| SL0063 | M   | A         | 177.5 | 12.6        | 26-Oct-01 | Tyear        |
| SL0065 | M   | A         | 189.3 | 17.2        | 27-Apr-97 | Tyear        |
| SL0072 | M   | A         | 181.3 | 17.1        | 03-May-97 | Tyear        |
| SL0077 | M   | A         | 191.1 | 17.2        | 27-Apr-97 | Tyear        |
| SL0078 | M   | A         | 196.7 | 17.1        | 30-Apr-97 | Tyear        |
| SL0079 | M   | A         | 182.7 | 17.1        | 30-Apr-97 | Tyear        |
| SL0094 | M   | A         | 182.7 | 17.2        | 08-May-97 | Tyear        |
| SL0108 | F   | A         | 157.1 | 12.8        | 15-Nov-01 | TYear        |
| SL0130 | F   | A         | 182.4 | 14.6        | 09-Nov-99 | Tyear        |
| SL0138 | F   | A         | 165.8 | 14.7        | 11-Nov-99 | Tyear        |
| SL0174 | M   | A         | 189   | 16.4        | 02-Jan-98 | Tyear        |
| SL0181 | F   | A         | 171.4 | 15.0        | 17-Jul-99 | Tyear        |
| SL0187 | F   | A         | 164.2 | 10.6        | 17-Nov-03 | TYear        |
| SL0199 | F   | A         | 161.6 | 15.1        | 04-May-99 | Tyear        |
| SL0211 | M   | A         | 187.8 | 11.6        | 10-Nov-02 | Tyear        |
| SL0213 | M   | A         | 172.6 | 11.6        | 09-Nov-02 | Tyear        |
| SL0218 | F   | A         | 167.2 | 9.6         | 08-Nov-04 | Tyear        |
| SL0224 | F   | A         | 175   | 12.0        | 05-Jul-02 | Tyear        |
| SL0231 | M   | A         | 175.5 | 8.2         | 14-Apr-06 | Tyear        |
| SL0239 | F   | A         | 155.9 | 9.1         | 09-May-05 | Tyear        |
| SL0255 | M   | A         | 171.9 | 12.7        | 12-Oct-01 | Tyear        |
| SL0258 | M   | A         | 185.9 | 11.6        | 08-Nov-02 | Tyear        |
| SL0261 | M   | A         | 185   | 12.4        | 20-Jan-02 | Tyear        |
| SL0269 | F   | A         | 159.6 | 12.6        | 06-Nov-01 | Tyear        |
| SL0272 | F   | A         | 168   | 15.0        | 15-Jun-99 | Tyear        |
| SL0278 | F   | A         | 152.3 | 9.3         | 11-Mar-05 | Tyear        |
| SL0282 | F   | A         | 167.7 | 15.1        | 08-May-99 | Tyear        |
| SL0286 | M   | A         | 176   | 12.6        | 06-Nov-01 | Tyear        |
| SL0291 | M   | A         | 172.7 | 12.7        | 13-Oct-01 | Tyear        |
| SL0292 | F   | A         | 166.8 | 8.2         | 13-Apr-06 | Tyear        |
| SL0303 | F   | A         | 170.4 | 14.6        | 18-Dec-99 | Tyear        |
| SL0377 | F   | A         | 166.2 | 4.9         | 09-Jul-09 | Tyear        |
| SL0379 | F   | A         | 176.8 | 15.1        | 18-May-99 | Tyear        |
| SL0384 | M   | A         | 185.5 | 16.9        | 17-Jul-97 | Tyear        |

## Appendix IV. Lagged identification rates (2011-2014)

The best fitting models for the lagged identification rate calculated using data collected from May 2011 to August 2014 differed between sexes. The emigration and reimmigration and mortality model fitted the male data best, whereas the best fit for females was the emigration and reimmigration model (Table A IV.1 and Figure A IV.1). This suggests that females and males use the resting area in different fashions: 1) males visit the lagoon more frequently but for shorter time than females; 2) permanent emigration remains a prerogative of males only. Nonetheless it corroborates that Samadai reef represents a vital part of the habitat for both sexes.

Table A IV.1. Residency parameters ( $\pm$ SE) for adult male and female spinner dolphins seen from May 2011 to August 2014. Best fitting models and supported models based on Quasi Akaike Criterion (QAIC) are listed. Bootstrapped 95% CI are reported in parentheses.

| Dataset                | Model                                  | No. of individuals at any given time | Mean residence time in         | Mean residence time out       | Mortality                                     | QAIC    | $\Delta$ QAIC* |
|------------------------|--|--------------------------------------|--------------------------------|-------------------------------|---|---------|----------------|
| <b>Males (N=143)</b>   |  |                                      |                                |                               |   |         |                |
| <i>best model</i>      | Emigration + reimmigration + mortality | 39 $\pm$ 5.2<br>(36.4 - 54.7)        | 12 $\pm$ 67.3<br>(8.3 - 178.9) | 9 $\pm$ 511.4<br>(5.6 - 95.0) | 0.0003 $\pm$ 0.0003<br>(3.87e-05 - 0.0005)    | 14117.8 | 0              |
| <b>Females (N=47)</b>  |  |                                      |                                |                               |   |         |                |
| <i>best model</i>      | Emigration + reimmigration             | 17 $\pm$ 2.0<br>(11.8 - 20.6)        | 46 $\pm$ 22.8<br>(5.9 - 95.6)  | 36 $\pm$ 15.1<br>(7.0 - 62.7) |   | 28438.3 | 0              |
| <i>supported model</i> | Emigration + reimmigration + mortality | 17 $\pm$ 1.9<br>(12.0 - 19.8)        | 49 $\pm$ 17.6<br>(5.6 - 84.3)  | 40 $\pm$ 14.6<br>(7.3 - 62.4) | -3.78e-05 $\pm$ 7.5e-05<br>(-0.0001 - 0.0001) | 28440.0 | 1.7            |

\*QAIC values for other fitted models not shown here.

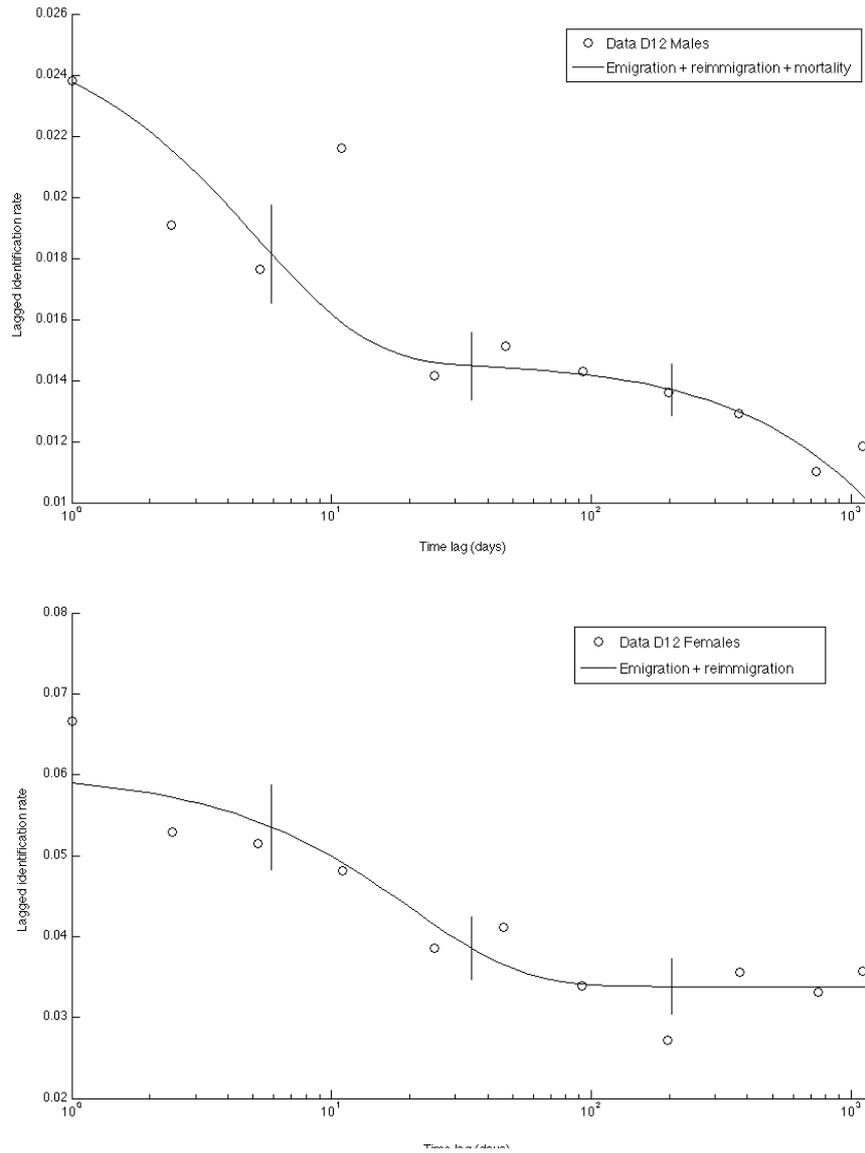


Figure A IV.1. Lagged identification rate against time lag (days) of highly marked male (top) and female (bottom) spinner dolphins seen at Samadai reef from May 2011 to August 2014. The best-fitting models are shown with vertical lines indicating bootstrapped error bars.

## Appendix V. Photographic Coverage

Photographic coverage was estimated as follow:

1- Firstly, it was calculated for 114 sightings as the total number of pictures per sighting / group size. When this ratio was  $> 3$ , photographic coverage was considered complete or quasi complete and sightings included in the analyses (following Ottensmeyer and Whitehead, 2003).

2- Secondly, it was estimated as the total number of “distinct individuals” (D1-D5) per sighting / group size. Where “distinct individuals” included also individuals assigned to D5 category (*i.e.* with no distinctive fins or body profiles) that displayed secondary markings on either side of their body (*e.g.* tooth rakes, scrapes, scars) and were therefore considered distinctive enough for individual identification within the sighting and were assigned a temporary identification code. Given the intrinsic impossibility of matching the left side with the right side of D5 individuals, the higher number of D5 individuals between the left and the right side was included in the final total number of “distinct individuals”, to avoid the inclusion of the same individual twice. The photographic coverage calculated using this method had mean=83% (SD=15%; n=105), *i.e.*, on average 83% of the individuals seen in the lagoon of Samadai reef were also photographically captured.

Using the first method, 12 sightings out of 114 returned a photographic coverage  $< 3$ , however only 9 were excluded as in three cases the matching procedure (method 2) showed that most of the individuals had been photographed (Table A V.1). The final total number of sightings suitable for mark-recapture analysis was 105.

Table A V.1. Photographic coverage of the groups of dolphins (2011-2014).

| Year     | Date     | Group size | Total No. of pictures | Photographic Coverage <sup>a</sup> | Mark-recapture analysis idoneity |
|----------|----------|------------|-----------------------|------------------------------------|----------------------------------|
| 2011     | 5/8/11   | 62         | 444                   | 7.2                                | Included (79%) <sup>b</sup>      |
|          | 5/9/11   | 68         | 178                   | 2.6                                |                                  |
|          | 5/10/11  | 130        | 524                   | 4.0                                |                                  |
|          | 5/11/11  | 75         | 281                   | 3.7                                |                                  |
|          | 5/12/11  | 80         | 412                   | 5.2                                |                                  |
|          | 7/12/11  | 108        | 536                   | 5.0                                |                                  |
|          | 7/13/11  | 94         | 409                   | 4.4                                |                                  |
|          | 7/16/11  | 101        | 788                   | 7.8                                |                                  |
|          | 8/4/11   | 6          | 29                    | 4.8                                |                                  |
|          | 8/7/11   | 59         | 423                   | 7.2                                |                                  |
|          | 8/8/11   | 102        | 415                   | 4.1                                |                                  |
|          | 9/24/11  | 46         | 428                   | 9.3                                |                                  |
|          | 9/26/11  | 13         | 112                   | 8.6                                |                                  |
|          | 9/27/11  | 65         | 352                   | 5.4                                |                                  |
|          | 9/28/11  | 44         | 360                   | 8.2                                |                                  |
|          | 10/28/11 | 10         | 123                   | 12.3                               |                                  |
|          | 10/29/11 | 22         | 116                   | 5.3                                |                                  |
|          | 10/30/11 | 14         | 204                   | 14.6                               |                                  |
|          | 10/31/11 | 31         | 440                   | 14.2                               |                                  |
|          | 12/3/11  | 6          | 60                    | 10.0                               |                                  |
| 12/4/11  | 5        | 31         | 6.2                   |                                    |                                  |
| 12/5/11  | 48       | 411        | 8.6                   |                                    |                                  |
| 12/7/11  | 32       | 42         | 1.3                   | Excluded                           |                                  |
| 2012     | 1/18/12  | 113        | 560                   | 5.0                                |                                  |
|          | 1/19/12  | 29         | 283                   | 9.8                                |                                  |
|          | 1/22/12  | 6          | 80                    | 13.3                               |                                  |
|          | 1/23/12  | 22         | 260                   | 11.8                               |                                  |
|          | 2/20/12  | 43         | 427                   | 9.9                                |                                  |
|          | 2/21/12  | 140        | 830                   | 5.9                                |                                  |
|          | 2/22/12  | 107        | 500                   | 4.7                                |                                  |
|          | 3/19/12  | 49         | 360                   | 7.3                                |                                  |
|          | 3/20/12  | 106        | 596                   | 5.6                                |                                  |
|          | 3/21/12  | 8          | 141                   | 17.6                               |                                  |
|          | 3/22/12  | 38         | 246                   | 6.5                                |                                  |
|          | 4/15/12  | 27         | 374                   | 13.9                               |                                  |
|          | 4/16/12  | 25         | 190                   | 7.6                                |                                  |
|          | 4/17/12  | 15         | 257                   | 17.1                               |                                  |
|          | 5/15/12  | 82         | 1014                  | 12.4                               |                                  |
|          | 5/16/12  | 73         | 547                   | 7.5                                |                                  |
|          | 5/17/12  | 36         | 317                   | 8.8                                |                                  |
|          | 5/19/12  | 133        | 1018                  | 7.7                                |                                  |
|          | 7/22/12  | 39         | 574                   | 14.7                               |                                  |
|          | 7/24/12  | 40         | 574                   | 14.4                               |                                  |
|          | 7/26/12  | 3          | 39                    | 13.0                               |                                  |
|          | 7/27/12  | 28         | 230                   | 8.2                                |                                  |
|          | 8/20/12  | 5          | 77                    | 15.4                               |                                  |
|          | 8/21/12  | 8          | 32                    | 4.0                                |                                  |
|          | 8/22/12  | 8          | 99                    | 12.4                               |                                  |
|          | 9/1/12   | 68         | 507                   | 7.5                                |                                  |
|          | 9/2/12   | 39         | 421                   | 10.8                               |                                  |
|          | 10/21/12 | 11         | 66                    | 6.0                                |                                  |
|          | 10/22/12 | 17         | 288                   | 16.9                               |                                  |
|          | 11/15/12 | 125        | 1540                  | 12.3                               |                                  |
| 11/16/12 | 43       | 392        | 9.1                   |                                    |                                  |
| 11/17/12 | 61       | 874        | 14.3                  |                                    |                                  |
| 11/19/12 | 41       | 451        | 11.0                  |                                    |                                  |

<sup>a</sup> Photographic coverage: Tot. No. of pictures/Group Size

<sup>b</sup> Number of dolphins (all distinctiveness D1-D5) over the group size, expressed in percentage. If this percentage was above 75%, the group coverage assumption was considered satisfied and the sighting included in the analyses.

Table A V.1. Continue. Photographic coverage of the groups of dolphins (2011-2014).

| Year    | Date    | Group size | Total No. of pictures | Photographic Coverage <sup>a</sup> | Mark-recapture analysis idoneity |
|---------|---------|------------|-----------------------|------------------------------------|----------------------------------|
| 2013    | 6/17/13 | 66         | 212                   | 3.2                                |                                  |
|         | 6/18/13 | 34         | 275                   | 8.1                                |                                  |
|         | 6/20/13 | 24         | 266                   | 11.1                               |                                  |
|         | 6/21/13 | 13         | 14                    | 1.1                                | Excluded                         |
|         | 6/23/13 | 25         | 228                   | 9.1                                |                                  |
|         | 6/24/13 | 78         | 166                   | 2.1                                | Excluded                         |
|         | 6/25/13 | 45         | 175                   | 3.9                                |                                  |
|         | 6/26/13 | 42         | 253                   | 6.0                                |                                  |
|         | 6/27/13 | 65         | 191                   | 2.9                                | Included (95%) <sup>b</sup>      |
|         | 6/29/13 | 17         | 127                   | 7.5                                |                                  |
|         | 6/30/13 | 12         | 82                    | 6.8                                |                                  |
|         | 7/1/13  | 26         | 145                   | 5.6                                |                                  |
|         | 7/8/13  | 75         | 402                   | 5.4                                |                                  |
|         | 7/11/13 | 75         | 441                   | 5.9                                |                                  |
|         | 7/15/13 | 30         | 354                   | 11.8                               |                                  |
|         | 7/16/13 | 36         | 438                   | 12.2                               |                                  |
|         | 7/17/13 | 6          | 61                    | 10.2                               |                                  |
|         | 7/18/13 | 65         | 370                   | 5.7                                |                                  |
|         | 7/19/13 | 57         | 281                   | 4.9                                |                                  |
|         | 7/21/13 | 105        | 425                   | 4.0                                |                                  |
|         | 7/25/13 | 15         | 111                   | 7.4                                |                                  |
|         | 8/5/13  | 9          | 87                    | 9.7                                |                                  |
|         | 8/6/13  | 75         | 169                   | 2.3                                | Excluded                         |
|         | 8/7/13  | 95         | 45                    | 0.5                                | Excluded                         |
|         | 8/12/13 | 54         | 301                   | 5.6                                |                                  |
|         | 8/13/13 | 35         | 120                   | 3.4                                |                                  |
| 8/15/13 | 38      | 217        | 5.7                   |                                    |                                  |
| 8/16/13 | 15      | 85         | 5.7                   |                                    |                                  |
| 8/18/13 | 72      | 314        | 4.4                   |                                    |                                  |
| 8/20/13 | 58      | 186        | 3.2                   |                                    |                                  |
| 8/23/13 | 78      | 720        | 9.2                   |                                    |                                  |
| 8/25/13 | 7       | 74         | 10.6                  |                                    |                                  |
| 8/26/13 | 73      | 731        | 10.0                  |                                    |                                  |
| 2014    | 6/10/14 | 59         | 386                   | 6.5                                |                                  |
|         | 6/11/14 | 45         | 343                   | 7.6                                |                                  |
|         | 6/12/14 | 45         | 480                   | 10.7                               |                                  |
|         | 6/13/14 | 29         | 294                   | 10.1                               |                                  |
|         | 6/14/14 | 120        | 720                   | 6.0                                |                                  |
|         | 6/17/14 | 130        | 219                   | 1.7                                | Excluded                         |
|         | 6/18/14 | 120        | 814                   | 6.8                                |                                  |
|         | 6/20/14 | 29         | 217                   | 7.5                                |                                  |
|         | 7/5/14  | 9          | 36                    | 4.0                                |                                  |
|         | 7/9/14  | 75         | 256                   | 3.4                                |                                  |
|         | 7/14/14 | 51         | 273                   | 5.4                                |                                  |
|         | 7/15/14 | 76         | 449                   | 5.9                                |                                  |
|         | 7/16/14 | 68         | 228                   | 3.4                                |                                  |
|         | 7/22/14 | 18         | 175                   | 9.7                                |                                  |
|         | 7/23/14 | 8          | 18                    | 2.3                                | Excluded                         |
|         | 7/24/14 | 86         | 333                   | 3.9                                |                                  |
|         | 7/26/14 | 46         | 92                    | 2.0                                | Included (80%) <sup>b</sup>      |
|         | 7/27/14 | 12         | 76                    | 6.3                                |                                  |
|         | 7/28/14 | 53         | 332                   | 6.3                                |                                  |
|         | 8/5/14  | 81         | 346                   | 4.3                                |                                  |
| 8/7/14  | 74      | 195        | 2.6                   | Excluded                           |                                  |
| 8/9/14  | 51      | 95         | 1.9                   | Excluded                           |                                  |
| 8/11/14 | 69      | 211        | 3.1                   |                                    |                                  |
| 8/13/14 | 20      | 201        | 10.1                  |                                    |                                  |
| 8/15/14 | 42      | 445        | 10.6                  |                                    |                                  |

<sup>a</sup> Photographic coverage: Tot. No. of pictures/Group Size

<sup>b</sup> Number of dolphins (all distinctiveness D1-D5) over the group size, expressed in percentage. If this percentage was above 75%, the group coverage assumption was considered satisfied and the sighting included in the analyses.

## Appendix VI. Social structure

Social structure can influence the ecology, genetics, and population biology of a species (Wilson, 1975; Whitehead, 2008a). Understanding social organization in cetaceans therefore has important implications for management and conservation.

A sampling period of a day was used as in the present study one sighting equals one day (Chapter 2); all non-calf highly marked individuals (Appendix I) photographed at Samadai reef in the same group on the same day were considered associated.

The rate of association of any two individuals, *i.e.* the frequency of co-occurrence, was measured with the half-weight index (HWI) (Cairns and Schwager, 1987), which is suggested when not all individuals within a sampling period are identified or when individuals are more likely to be identified when they are not in association (Cairns and Schwager, 1987; Whitehead, 2008a). HWI values range between zero, for two individuals never seen in the same group, and one, for individuals always seen in the same group. Individuals seen more than four times were included in calculating association indices (Whitehead, 2008a).

To test the null hypothesis that associations rates between and within sex classes are similar (Schnell et al., 1985b) a Mantel test with 1000 permutations was conducted. Results are expressed as the t-value, p-value, and matrix correlation coefficient. If within class associations/interactions are higher, t is positive, p large (for a two-tailed 0.05 test, reject the null hypothesis if  $p < 0.025$  or  $p > 0.975$ .), and the matrix correlation is positive. Mean and maximum association indices between and within sex classes were also calculated.

A useful attribute of the social structure of a community is its social differentiation, *i.e.* a measure of how varied the social system is. To

assess the social differentiation in Samadai reef spinner dolphins, the coefficient of variation of true association indices was estimated (Whitehead, 2008a). A coefficient of variation  $\leq 0.3$  indicates a homogeneous society, a value  $\geq 0.5$  indicates a well-differentiated society and a value  $\geq 2$  indicates a population with extreme social differentiation (Whitehead, 2008b; a). The correlation between true and estimated association indices (Pearson's correlation coefficient) was calculated to measure accuracy in data representation, with a value of  $\sim 1$  indicating an excellent representation,  $\sim 0.8$  a good reliable representation, whereas  $\sim 0.4$  being somewhat representative (Whitehead, 2008b; a).

In order to assess whether realistic divisions existed within the study group, hierarchical cluster analyses were performed, with the use of a cophenetic correlation coefficient (CCC) to indicate if the dendrogram was truly representative of the social structure. The CCC indicates the effectiveness of a hierarchical cluster analysis, with values above 0.8 being considered indicative of a well-represented population (Bridge 1993; Whitehead, 2008b; a; 2009).

Social structure analyses were undertaken in SOCPROG 2.6 (Whitehead, 2009).

### **Results**

Results indicate a well-differentiated social organization (0.758) and a good representation of the data (0.823). Association indices within sex classes were higher than those between sex classes (Mantel test,  $t=3.097$ ;  $p=0.99$ ; Matrix correlation=0.087). Males and females formed associations approximately equally strong within sex, with mean association index of 0.23 and 0.24, respectively. However, males had an observed mean of maximum association index (0.81) higher than females (0.57) (Table A VI.1 and Figure A VI.1). Hierarchical cluster analysis indicated the division of the community into representative (CCC=0.80) clusters of variable size and association strength (Figure A VI.2).

Table A VI.1. Mean and maximum half-weight association indices (HWI) and number of associates within and between sexes, calculated for spinner dolphins seen at Samadai reef between May 2011 and August 2014. SDs are in parentheses.

| <b>Sex class</b> | <b>Mean<br/>(SD)</b> | <b>Mean number of<br/>associates<br/>(SD)</b> | <b>Mean of maximum<br/>(SD)</b> |
|------------------|----------------------|---|---------------------------------|
| F                | 0.21 (0.05)          | 22.41 (4.84)                                  | 0.59 (0.08)                     |
| M                | 0.22 (0.06)          | 23.29 (6.43)                                  | 0.81 (0.20)                     |
| F-F              | 0.24 (0.06)          | 8.13 (1.72)                                   | 0.57 (0.10)                     |
| F-M              | 0.20 (0.05)          | 14.29 (3.38)                                  | 0.47 (0.08)                     |
| M-F              | 0.20 (0.06)          | 6.24 (1.81)                                   | 0.43 (0.06)                     |
| M-M              | 0.23 (0.07)          | 17.05 (4.90)                                  | 0.81 (0.20)                     |
| Within           | 0.23 (0.07)          | 14.34 (5.88)                                  | 0.74 (0.21)                     |
| Between          | 0.20 (0.06)          | 8.68 (4.42)                                   | 0.44 (0.07)                     |
| Overall          | 0.22 (0.06)          | 23.02 (5.98)                                  | 0.74 (0.20)                     |

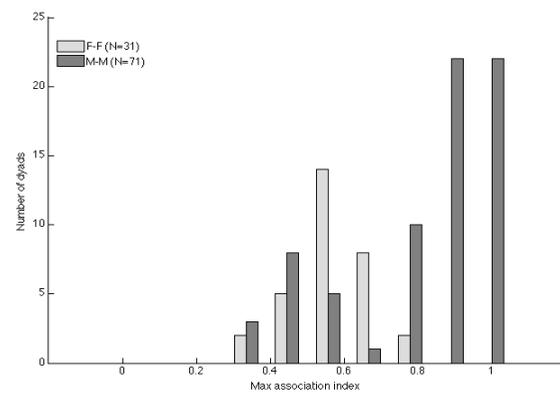
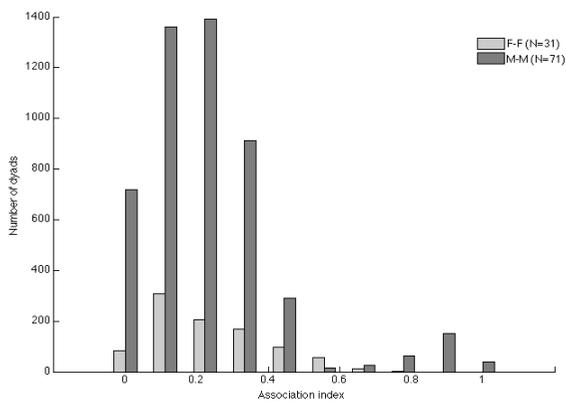
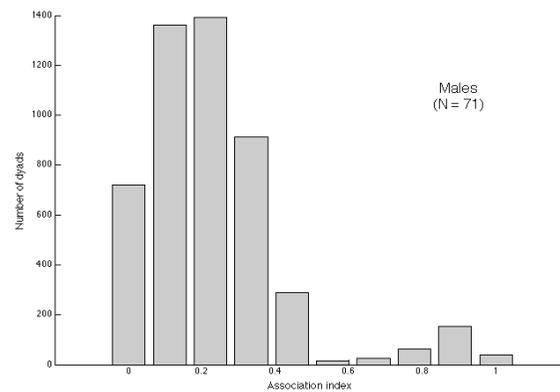
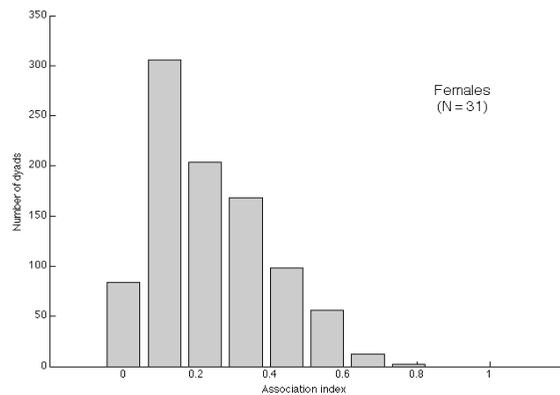


Figure A VI.1. Distribution of values of the half-weight association indices and maximum association indices for highly marked males and females spinner dolphins seen >4 times at Samadai reef between 2011 and 2014.



## Appendix VII. Feeding habits

From April to September 2006, 81 samples of regurgitated material were collected from spinner dolphins in Samadai reef from males and females of different age classes (excluding non-weaned calves). Cephalopods remains (*i.e.* beaks, hooks and eye lens) were found in most of the samples collected (93%) throughout the sampling period, whereas remains of unidentified mesopelagic fish (*i.e.* vertebrae, spines and rarely otoliths) were identified less frequently (28%).

A total of 2163 lower beaks and 1778 upper beaks of cephalopods were sorted and identified. 94% of the specimens resulted belonging to juveniles stages of the family Enoplotheutidae, suggesting they represent the primary source of food for spinner dolphins frequenting Samadai reef, at least during the months sampled. Two cephalopod experts were consulted to confirm the identification first assigned by Cesario (2008) according to Clarke (1986) (Table A VII.1).

Table A VII.1. Identification of lower and upper beaks of cephalopods found in regurgitated material from spinner dolphins in Samadai reef. Identification performed by 3 different researchers.

| Cephalopod beak ID - <i>Stenella longirostris</i> regurgitation, Egyptian Red Sea. |        |                 |                 |                        |                 |                 |
|--|--------|-----------------|-----------------|------------------------|-----------------|-----------------|
| Beak   | Figure | Amina Cesario   | Carmen Blanco   |                        | Yves Cherel     |                 |
|  |        | Fam.            | Fam.            | Gen.                   | Fam.            | Notes           |
|  | 1      | Enoplotheutidae | Enoplotheutidae | Abraliopsis            | Enoplotheutidae |                 |
|  | 2      | Enoplotheutidae | Enoplotheutidae | Abraliopsis            | Enoplotheutidae | several species |
| Lower  | 3      | Ommastrephidae  | Ommastrephidae  | Illex (or Todaropsis?) | Ommastrephidae  | juvenile        |
|  | 4      | Unknown         | Ommastrephidae  | Illex (or Todaropsis?) | Ommastrephidae  | large juvenile  |
|  | 5      | Unknown         | Ommastrephidae  | Illex (or Todaropsis?) | Ommastrephidae  | large juvenile  |
| Upper  | 6      | Unknown         | Unknown         | Unknown                | Ommastrephidae  | large juvenile  |
|  | 7      | Unknown         | Unknown         | Unknown                | Ommastrephidae  | juvenile        |

Figures of identified lower and upper beaks follow, beak measurements are reported in the captions (LRL: lower rostrum length; LHL: lower hood length; URL: upper rostrum length; UHL: upper hood length).

### LOWER BEAKS



Figure A VII.1. LRL=2.30 mm; LHL=2.45 mm



Figure A VII.2. Beaks Series. LRL = min. 0.5 mm; max. 2.0 mm.



Figure A VII.3. LRL =2.40 mm; LHL = 6.95 mm.



Figure A VII.4. LRL=3.55 mm; LHL = 3.80 mm.

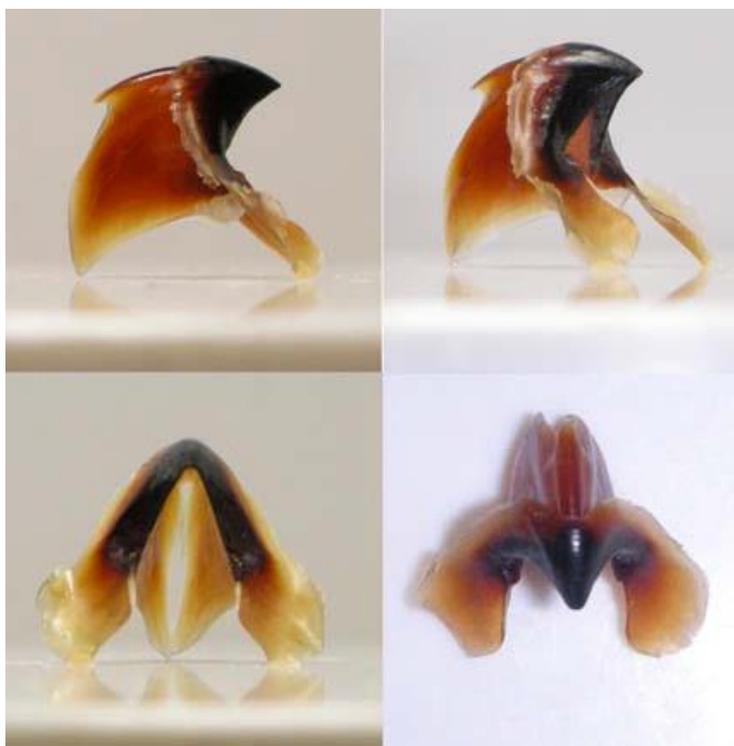


Figure A VII.5. LRL = 3.75 mm; LHL = 3.40 mm.

**UPPER BEAKS**



Figure A VII.6. URL=5.80 mm; UHL=15.05 mm.



Figure A VII.7. URL=4.60 mm; UHL=13.0 mm.

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