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Ecology of bottlenose dolphins (*Tursiops truncatus*) in the seaside resort of Panama City, Florida

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Thesis presented for the degree of Doctor of Philosophy

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Abstract

Between 2004 and 2007, field surveys were conducted to study bottlenose dolphins (*Tursiops truncatus*) in the seaside resort of Panama City, Northwest Florida. Using boat-based photo-identification surveys, mark-recapture surveys were performed to estimate the abundance of bottlenose dolphins. According to months, the estimate population size varied between 57 to 178 individuals, with the lowest abundance occurring during the spring. A total of 263 different dolphins were photo-identified. The spatio-temporal distribution of dolphins revealed that animals showed preferred habitat, mainly concentrated in and around the Channel Entrance. Mean group size composed of 5 dolphins, showed significant variations according to the observed zone, the time of the day, and the behaviours of dolphins. Social behaviours were dominant throughout the day Evidence of a feeding peak in the evening was recorded, while playing, sexual and begging were more frequently observed in the afternoon. Using a Geographic Information System (GIS), a foraging hotspot was detected within the study area. Human activities, especially tourism and recreational fishing revealed significant impacts on dolphins behaviours, with several individuals seen to beg regularly close to boats. This unnatural behaviour of begging, were more often observed during the tourism season (between April to August), and occurred mainly near shore the East jetties. Social structure is an important component of the bottlenose dolphin populations. Highly significant differences were found in associations between and within sex classes. Indeed, males associations were stronger than between inter-sexual associations or between females only. Sociogram of males revealed a complex network with strong associations between pairs or trios. The population structure seems to be temporally stable over the study with constant companionship observed in the dolphin population in Panama City.

« Quoi qu'il arrive, cultive toujours ton chemin, c'est le tien »

DidiL

ACKNOWLEDGEMENTS

Safe towed return to the marina. Photo by Th. Bouveroux. Grand Lagoon, 8 October, 2005

I am particularly happy to write this section of my thesis. Indeed, it is obvious that this project would not have been realised without the help and support of several persons. Therefore, it is with emotion that I will thank all people that contributed to make this research possible.

I must first thank my promoter, Pr Jérôme Mallefet, for giving me confidence to develop this new research program on dolphin ecology, as well as for your continued support and encouragement. Thank you so much!

The second person that I have to thank deeply is Dr Douglas Nowacek, from Duke University, North Carolina. Your guidance, your great experience in field work and your knowledge about dolphin ecology were essential for me during my research. Thanks to you, this research was carried out under your General Application No. 1055-1732, delivery by NOAA Fisheries, as a Co-Investigator. Many thanks also for your confidence! Also, I would like to thank your colleagues Reny Tyson, Dr David Johnston and Stephanie Nowacek, who gave plenteous advice.

To my committee, Pr Thierry Hance, Pr Eric Le Boulengé, Pr Hans Van Dyck and Dr Thierry Jauniaux, go to my heartfelt thanks.

During fieldwork in Panama City, cars, rooms and boats were provided by Denis (alias Big Chief!) and Nathalie Richard. Thank you very very much for all your help that made this research possible!! I will never forget your generosity, your passion and your values. During my stays in Panama City, we also spent a lot of time together, eating some delicious grilled fish (groupers, cobias or pompanos) and sharing your knowledge about dolphins. So, one more time thank you to you my friends!!

Several other people have given invaluable aid during the course of my work. Dr Jérôme Vrancken (catholic University of Louvain) for statistical consulting, badminton matches, and, most important your friendship! Pr Philip Hammond and Dr Sanna Kuningas (University of St Andrews, UK - Sea Mammal Research Unit) for assistance and guidance in mark-recapture analysis and the program MARK. Pr Hal Whitehead (University of Dalhousia, Canada) and Dr David Lusseau (University of Aberdeen, UK) for valuable advice during the social structure analysis with the program SocProg, Sabrina Bowen, *Jonathan Jaeger (Institut de Statisique, catholic University of Louvain), also gave some important help with statistics on log-linear models. Mister Goupyl provided excellent IT assistance to facilitate my work. Finally, thank you to those people that have contributed to in data collection in the field: Audrey Binet, Kim Verbeke, Thomas Maes, Stéphane Jansegers, Laurent Duponchelle and Sarah Lessire.*

On the private side, my family, especially my parents, provided a powerful and essential support and comprehension during all my studies. Without you, I would not have been able to complete the work presented in this document. Thank You to the Lessire family and all friends, deep thanks to you.

Finally, I would like to thank to everyone who contributed to my safe return to the marina after engine failure.

This research would not have been possible without funding and donations. Therefore, it is important for me to send all my gratitude to:
La Fondation Delphus, la Fondation Léopold III pour l'Exploration et la Conservation de la Nature, la Communauté Française de Belgique. Canon Belgium provided some photographic materials necessary during field trips.

This research is a contribution to Biodiversity Research Centre (BDIV) of Louvain-La-Neuve.

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Figure 1.1. Illustration of tourism activities towards bottlenose dolphins.

I. Introduction

1. Context

The bottlenose dolphin (*Tursiops truncatus*) is a cosmopolitan species that lives in almost all oceans, seas and inhabits in a wide range of habitats, such as coastal shallow waters, pelagic waters, estuaries, bays, fjords, lagoons and even in large rivers (Scott et al., 1990b; Bräger et al., 1994; Wilson et al., 1997; Defran and Weller, 1999; Ingram and Rogan, 2002; Zolman, 2002; Lusseau et al., 2003; Nowacek, 2005). Just like all toothed whales, bottlenose dolphins are protected by *The Convention of International Trade in Endangered Species* (CITES); Appendix II, that includes species identified as threatened, or likely to become endangered if trade is not regulated. Moreover, in and around U.S. waters, all marine mammals are protected by the *Marine Mammal Protection Act* of 1972 (MMPA). Under the MMPA, it is illegal to harm, to harass, to touch and to feed marine mammals in the wild (NMFS, 2007).

Despite this protection, prohibited practices continue, in particular on bottlenose dolphins in Panama City, Florida. Indeed, the presence of this dolphin population is well known by tourists who have come to Panama City to interact, to swim and to feed dolphins, for long time (Samuels and Spradlin, 1995; Colborn, 1999; Samuels and Bejder, 2004) (Figure 1.1). In addition, this bottlenose dolphin population is constantly subject to other significant human activities such as yachting, fisheries, military activities, and harbour activities. Several studies on cetaceans report that human activities can generate some disturbances on populations (Nowacek et al., 2001; Constantine et al., 2003; Glen, 2003; Read et al., 2003a; Finn, 2005).

Between 1999 and 2006, along the Northwest coast of Florida Panhandle, several «Unusual Mortality Events» (UMEs) on dolphins

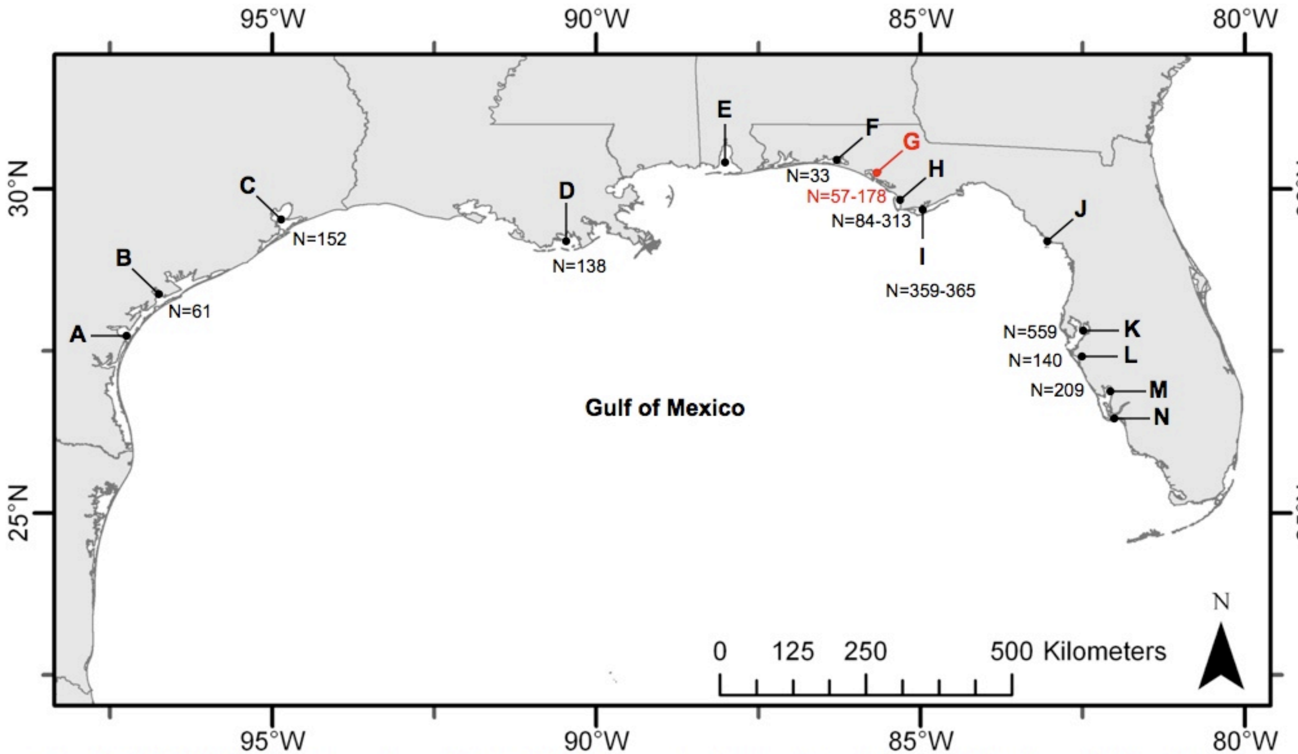


Figure 1.2. USA Gulf of Mexico bays and sounds. Each of the alpha-numerically designated a study area with bottlenose dolphins. When known, the population size is given (N).

A) Port Aransas; B) Matagorda Bay ([1]N=61); C) Galveston Bay ([1]N=152); D) Barataria Bay ([2]N=138); E) Mississippi Sound; F) Pensacola Bay ([1]N=33); **G) Panama City ([6]N=57-178)**; H) St Joseph Bay ([4]N=84-313); I) Apalachicola Bay ([5]N=359-365); J) Cedar Key; K) Tampa Bay ([1]N=559); L) Sarasota Bay ([3]N=140); M) Pine Sound, Charlotte Harbor ([1]N=209); N) Sanibel Island.

[1]Baylock and Hoggard, 1994; [2]Miller, 2003; [3]Wells, 2004 (pers. com.); [4]Balmer, et al., 2008; [5]Tyson, 2008; [6]Bouveroux et al., submitted.

have been reported by the *National Marine Fisheries Service* (NMFS), with more than 300 dead animals. All these events appear to have been correlated spatially and temporally with blooms of *Karenia brevis*, a dinoflagellate known to cause red tide in Florida (NMFS, 2004; Tyson, 2008).

Until 2004 no systematic surveys of these animals had been carried out in the area. Therefore, very little information is available in the scientific literature on bottlenose dolphins in Panama City. Information available that confirms a bottlenose dolphins population in this region comes from aerial surveys conducted in 1993 (Blaylock and Hoggard 1994), and from some quantitative studies on human-dolphin interactions (Samuels and Spradlin, 1995; Colborn, 1999; Samuels and Bejder, 2004).

Concerns about increasing human activities and recent observation of UMEs raise question about the status of this dolphins population: should we consider it as threatened?

An integral part of any management strategy is the assessment of the number of individuals in a population and trends in abundance (Wilson et al., 1999). Because the most recent estimates of abundance of dolphins in this region are based on 1993 aerial surveys (Blaylock and Hoggard, 1994), we have no way to assess how this population was affected by these UMEs and how it could be affected if other UMEs occur in the future. To date, efforts are made to allow a better identification of biologically-meaningful stocks[1] of bottlenose dolphins in the northern part of the Gulf of Mexico (Figure 1.2). Therefore, the first goal of this research will be to estimate the population size of bottlenose dolphins and to provide the first seasonal trends of its abundance.

[1] The term stock was established for wildlife management purposes and is basically the same as a population (Reynolds et al., 2000).

Another very important part of the ecology of an animal population, is to characterise the diurnal and the seasonal distribution of animals as well as their site fidelity. Thus, in this study we will try to answer several of the following questions: do we see the same individuals throughout the months? What is the proportion of resident dolphins in the study area? Can we detect out the presence of hotspots with higher density of dolphins or higher probabilities of dolphin sightings through the study area?

Once the distribution of animals is known, we will establish the behavioural patterns of bottlenose dolphins in Panama City. Indeed, to strategically target areas where conservation strategies must be applied, an accurate knowledge of the spatial arrangement of the dolphins behaviours is required, to determine how animals use their habitat for vital activities such as foraging, mating or socialising. Face to human activities, do we observe any influence of anthropic activities on the behavioural patterns of dolphins?

Finally, this study is probably the first to investigate the social organisation of bottlenose dolphins living in a popular seaside resort where intensive human activities are reported. Therefore, we will evaluate association patterns between individuals, as well as the difference in dolphins relationships depending on sex, and results will be compare to other coastal populations submitted to less disturbance.

This research have been approved by The Office of Protected Resources' Permits, Conservation and Education Division (*National Marine Fisheries Service, NMFS*), and the status of Co-Investigator to the General Authorization (GA) of Dr. Doug Nowacek was delivery (Appendix A).

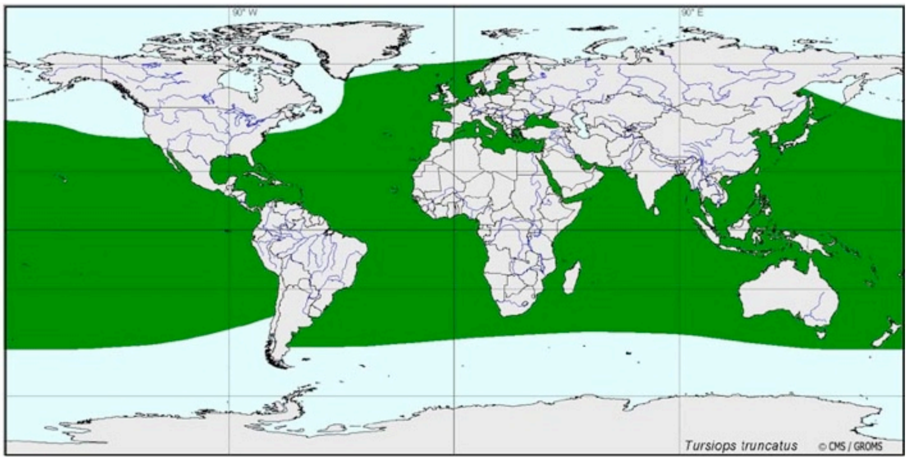


Figure 1.3. World wide distribution (in green) of bottlenose dolphins, *Tursiops sp.* This species is observed in cold temperate to tropical seas. *Copyright: CMS / GROMS.*

2. Generalities on bottlenose dolphins, *Tursiops truncatus* (*Montagu, 1821*)

The bottlenose dolphin (*Tursiops truncatus*) is a marine mammal that belongs to the Order Cetacea, Suborder Odontoceti, Family Delphinidae and Genus *Tursiops*. As all toothed whales, bottlenose dolphins are protected by the CITES; Appendix II, that includes species identified as threatened, or likely to become endangered if trade is not regulated. Moreover, in and around U.S. waters, all marine mammals are protected by the *Marine Mammal Protection Act* of 1972 (MMPA). According to the MMPA, it is illegal to harm, to harass, to touch or to feed marine mammals in the wild (NMFS, 2007).

The bottlenose dolphin is a cosmopolitan species (Figure 1.3) that can be found in almost all oceans, seas and that lives in a wide range of habitats, such as coastal shallow waters, pelagic waters, estuaries, bays, fjords, lagoons and sometimes large rivers (Scott et al., 1990b; Bräger et al., 1994; Wilson et al., 1997; Defran and Weller, 1999; Ingram and Rogan, 2002; Zolman, 2002; Lusseau et al., 2003; Nowacek, 2005). The life history of *Tursiops* is well documented from both captive and wild animals. Analyses of dentinal and cemental growth layer groups in teeth have shown that males of the species can live for 40 years or more whilst females can typically surpass 50 years (Connor et al., 2000; Mann et al., 2000; Reynolds et al., 2000; Perrin et al., 2002). The age at sexual maturity varies by region and differs between males and females, with estimates from 8 to 14 years and 5 to 13 years, respectively (Mann et al., 2000; Reynolds et al., 2000; Perrin et al., 2002). In temperate environments, the peak time for births appears to be in the warmer summer months (Wilson, 1995), but in tropical and sub-tropical habitats births have been reported throughout the year (Wells and Scott, 2002). Gestation is estimated at 12 months but variation in the suckling duration can differ between 1,5 to 4 years, and calving intervals may vary from 3 to 6 years (Mann et al., 2000; Reynolds et al., 2000; Dierauf and Gulland, 2001; Perrin et al., 2002; Wells and Scott, 2002; Grellier et al., 2003; Kogi et al., 2004).

Bottlenose dolphins from different locations can appear quite different morphologically, and these variations are primarily attributed to environmental differences from one habitat to the next (Reynolds et al., 2000). Depending on their geographic location, adult bottlenose dolphins range in size from 2 meters to nearly 4 meters for a weight close to 300 Kg. Bottlenose dolphins often exhibit offshore-inshore separation. Indeed, two morphological types, often referred to as ecotypes, are found among adult bottlenose dolphins, with haematological, morphological, and genetic differences between these two ecotypes (Duffield et al., 1983; Perrin, 1984; Hersh and Duffield, 1990; Van Waerebeek et al., 1990). However, two species of *Tursiops* have been recognised and recently confirmed from genetic information; the «common bottlenose dolphin», *T. truncatus*, and the «Indian Ocean bottlenose dolphin», *T. aduncus (Ehrenberg, 1833*) (Reynolds et al., 2000; Perrin et al., 2002; Shirakihara et al., 2003; Natoli et al., 2004).

Bottlenose dolphins swim with a speed around 5-10 km/h, and can reach speeds of 30 to 35 km/h (Reynolds et al., 2000). They are often described as opportunistic foragers, feeding on a wide variety of benthic and surface preys such as fish, cephalopod and invertebrate species, and using a great variety of foraging techniques to catch their prey (Barros and Odell, 1990; Shane, 1990a; Perrin et al., 2002). Main prey items of bottlenose dolphins differ among locations, reflecting the abundance of local prey species (Barros et Odell, 1990).

According to the level of social associations, the genetic relationships and home range of individuals, we can make distinction between a population and a community:

A *population* is define as a group of organisms that occupies the same region and interbreeds as a closed reproductive group, while a *community* is a regional society of individuals that share ranges, socials associates, and gene pools (Reynolds et al., 2000).

3. Dolphins abundance and site fidelity

In some situations, population size is unknown. In term of conservation and management, temporal changes in the population such as growth, stationary state, decline or even extinction are of primary interest. Similarly, the composition of the population is essential: year-round residents, seasonal resident individuals or transient animals. In other terms, is the population prone to movements of individuals in and out the study area (immigration and emigration)?

As generally, it is impossible to enumerate all individuals in a population or a community, estimating methods have to be developed. This is certainly true for marine mammals, which spend most of their time underwater and are thus not visible. Therefore, to estimate the size of a population, a sample of data is collected and extrapolation is done from this sample to the whole population or area (Hammond, 2001). Two methods for estimating the size of marine mammals populations are mainly used by scientists: the line transect methods and the mark-recapture methods.

3.1. Line Transect Methods

Line transect methods were first developed for terrestrial animals, but are now also often used to estimate the abundance of cetacean populations using shipboard or aerial surveys (Blaylock and Hoggard, 1994; Hammond, 2002; Perrin et al., 2002). In this method, the study area is sampled by a survey platform searching along predefined transects, placed so that the whole area is representatively sampled. The distance and angle to sighted animals are measured or estimated, allowing the calculation of perpendicular distance from sighting to the transect line. Sighting surveys thus provide an estimate of the number of animals in a given area at a given time but not an estimate of the size of a biological population (Hammond, 2002). However, number of practical difficulties are met with the line transect sampling of cetacean populations such as accurate angle and distance measurements, and estimating school size. In some situations, this method is unfeasible or even inappropriate. For example, in the North Atlantic Ocean, two types of bottlenose dolphins exist: offshore and inshore ecotypes, that are indistinguishable from the distance. In other cases, line transects using aerial surveys over waters such as bays, sounds, and estuaries are often inappropriate because visibility of these waters is limited, while shipboard line-transect surveys are unfeasible because these waters are shallow and only small boats can enter these waters.

3.2. Mark-Recapture Methods

Mark-recapture methods use data on the number of animals marked in a first sample and the proportion of marked animal present in a second sample of recaptured animals to estimate population parameters, including abundance (Hammond, 2001). This method is most valuable when a researcher fails to detect all individuals present within a population every time that the researcher visits the study area. In this procedure, biologists use traps to capture the animals alive and mark them in some way (Hammond, 1986; Wells and Scott, 1990; Allaby, 1999; Schtickzelle et al., 2003). Indeed, mark-recapture is usually conducted by altering in some way the physical appearance of the captured animals. This can be done by attaching artificial tags, applying an indelible substance (e.g. painting insects), or by removal or alteration of part of the animal itself (Hammond, 1986). However, in some cases, capture events may cause stress in animals that can therefore manifest by behavioural disturbances («trap shy» or «trap happy») or may sometimes lead to death of the animal (Cooch and White, 2007). Therefore, in the late 70's, scientists have developed a non-invasive method to identified animals in a population using natural marks present on their body (Würsig and Würsig, 1977; Würsig and Jefferson, 1990). This method, called photo-identification, uses photography techniques as a means of capturing and then identifies the individuals. This method is currently the most commonly used to study cetacean populations and will be discussed in the next section (Berrow et al., 1996; Chaloupka et al., 1999; Campbell et al., 2002; Eisfeld, 2003; Calambokidis and Barlow, 2004; Culloch, 2004; Kerr et al., 2005; Parra et al., 2006; Posada, 2006; Balmer et al., 2008; Tyson, 2008).

Several models can be used to calculate the number of animals present in a population. Based on characteristics of the studied population, an animal population can be defined as a closed or an open population, depending if changes in population size occur through time due to births, deaths, immigration and emigration (Cooch and White, 2007). In closed population it is assumed that no births, deaths or migrations (emigration and immigration) occur during the sampling period, whereas open population allows for these assumptions (Wilson et al., 1999; Culloch, 2004).

3.2.1. Closed population models

Four assumptions have to be met to provide good estimation of the abundance with closed population models (Hammond, 1986; Chilvers and Corkeron, 2003; Eguchi, 2003; Cooch and White, 2007):

(i) Population has to be demographically and geographically closed

Bottlenose dolphins are long living animals, with low reproductive rate, high survival rate and low natality and mortality during a short sampling interval (Wells and Scott, 1999; Connor et al., 2000; Reynolds et al., 2000; Read et al., 2003b). Coastal bottlenose dolphin populations can display seasonal movements patterns. However, when they are studied on a short sampling period (few days), the populations can be considered as being closed (Wells, 1991; Read et al., 2003b; Torres et al., 2003). Immigration and emigration have been also reported, but during a short sampling period they are likely to remain at a relative low level (Read et al., 2003b).

(ii) Homogeneity of capture probabilities

Homogeneity assumes that every marked animal present in the population at a given time (***i***) has the same probability of recapture (***pi***) (Eguchi, 2003; Cooch and White, 2007). This assumption is met for coastal dolphins that encounter boats on a regular basis. When photo-identification methods are used, it is unlikely to change the dolphins' behaviours, allowing homogeneity in capture probabilities (Hammond, 1990; Read et al., 2003b).

(iii) Marks are recognised on recapture

This assumption requires that the distinctive nicks and notches that identify an individual will be recognised upon resighting. Read et al., (2003b) suggest that, with good quality pictures and great distinctiveness of marks in dorsal fins, individuals can be correctly identified during resighting of individuals with a 95% confidence.

(iv) Marks are not lost or missed during the study period

Although dorsal fins can change in appearance over time (Würsig and Jefferson, 1990; Wilson et al., 2000), marks along leading and trailing edges of dorsal fins are considered long lasting, and sometimes even permanent marks (Wilson et al., 1999).

Several closed population estimators have been developed to calculate with confidence the abundance of an animal population. Although capture homogeneity may be possible, numerous estimators have been developed to allow for heterogeneity in capture probabilities between individual (**Mh**), behavioural capture response (**Mb**), and capture/recapture time (**Mt**). In total, 11 available models exist that test combinations of the three sources of variation in sighting probabilities, and that incorporate more than one departure from the assumptions of closed models (e.g. heterogeneity in capture probabilities with behavioural response, **Mbh; Mth**; **Mtb; ...**) (Thompson et al., 1998).

Model **Mh** assumes that each individual has its own capture probability and capture probabilities do not change over time (Thompson et al., 1998); model **Mt** assumes that capture probabilities vary by sample period, but all individuals have the same capture probability within the sampling period (Otis et al., 1978).

A. Single recaptures - The Petersen estimator

The Petersen estimator is the simplest mark-recapture method and is based on the simple argument that proportion of marked animals recaptured in a sample of the population is equivalent to the proportion of marked animals in the total population, N (Schwarz and Seber, 1999; Cooch and White, 2007). In the capture-recapture experiment, a known number of individuals n_1 from the population are marked or identified in some way. At a later time, a second sample of individuals n_2 is taken from the population. These individuals are examined for marks and the number of marked m_2 individuals in the second sample are recorded. Thus, we can consider the equation:

$$m_2/n_2 = n_1/N$$

and the estimator for population size is,

$$\tilde{N} = n_1 n_2/m_2$$

B. Multiple recaptures - The Schnabel estimator

This estimator is an extension of the Petersen method to a series of samples (2, 3, 4…, n), with the same assumptions as for the Petersen estimator (Hammond, 1986). In this model, individuals caught at each sample are first examined for marks, then marked and released. Only a single type of mark needs to be used because we just have to distinguish 2 types of individuals: *marked*, caught in one or more prior samples; and *unmarked*, never caught before. Thus, for each sample *t*, the following is determined:

C_t = Total number of individuals caught in sample t
R_t = Number of individuals already marked (Recaptures) when caught in sample *t*
M_t = Number of marked animals in the population, before the *t* th sample.

Schnabel estimator treats the multiple samples as a series of Lincoln-Peterson (L-P) samples and obtains a population estimate as a weighted average of the L-P estimates which is an approximation to the maximum likelihood estimate of *N*:

$$N = SUM\ (M_t\ C_t) / ((SUM\ R_t) + 1)$$

Various types of multiple-recapture closed models have been developed including different assumptions regarding capture and recapture probabilities (**M0, Mt, Mh, Mb**).

3.2.2. Open population models

These models are an application of the Schnabel method to an open population in which there is possibly death, recruitment, immigration, and permanent emigration (Schwarz and Seber, 1999; Cooch and White, 2007). One important biological issue is that only apparent survival can be estimated in the open mark-recapture studies, because it is not possible to distinguish between losses due to death and emigration (Pledger et al., 2003). Two mains models have been developed based on parameters of the apparent survival and recapture probabilities (**ϕ, p**) (Schwarz and Seber, 1999).

A. Jolly-Seber model

While population size can be estimated, it is often very difficult to avoid substantial bias for the estimation of this parameter set because of individual heterogeneity. However, the fully open population models of Jolly-Seber (JS) allows the estimation of apparent survival (**ϕ**), capture probability (**p**), population size (**N**), and number of new individuals entering in the population (**B**). The estimates for survival and capture probabilities use only information on recaptures of marked animals (Pledger et al., 2003). However, this often requires that the number of unmarked animals is also recorded at each sampling occasion and that these are marked and returned to the population.

B. The Cormack-Jolly-Seber model

The Cormack-Jolly-Seber (CJS) model is a restricted model of Jolly-Seber that focuses on estimates of apparent survival (**ϕ**) and capture probability (**p**) of marked animals (Pledger et al., 2003). This model assume that all animals have equal catchabilities in each sample and that all animals alive at the beginning of a period have the same chance of surviving the interval (Schwarz and Seber, 1999; Pledger et al., 2003). Therefore, assumptions that must be encountered during a sampling are:

1. Every animal present (marked or unmarked) in the population at the time of the *i*-th sample (***i*** = 1, 2, …, k) has the same probability of being caught (i.e., constant **pi** for all animals in the population).
2. Every marked animal present in the population immediately after the *i*-th sample has the same probability of survival (**ϕ*i***) until the (*i*+1)th sampling time (***i*** = 1, 2, …, k-1).
3. Marks are not lost or overlooked.
4. All samples are instantaneous and each release is made immediately after the sample.
5. Immigration cannot be separated from the birth and death from emigration without additional information.
6. All emigration from the sampling population is permanent.

3.2.3. The Robust Design

A method which combines closed-populations and open-populations have also been developed (Pollock, 1982). In the Pollock's robust design, the abundance is determined during multiple short-term periods with closed population models combined to the Jolly-Seber open population model to estimate survivorship and migration rates. This approach allows for abundance estimates to be determined during multiple, short term periods with closed population models (**Petersen**, **Mh, Mt, Mb**) and uses the Jolly-Seber open population model to estimate survivorship, emigration rates and capture-recapture probabilities between the short term survey periods (Pollock, 1982; Pine et al., 2003). This is made possible by structuring capture-recapture sessions into primary and secondary periods. The basic structure of the standard Pollock's robust design can be represented schematically by the following figure (Figure 1.4):

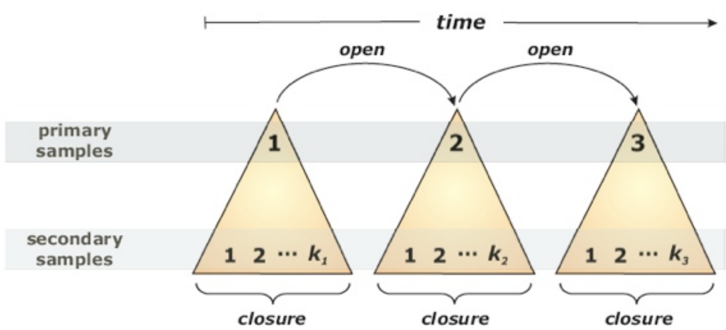


Figure 1.4 Basic structure of 'classical' form of the Pollock's robust design (from Cooch and White, 2007)

The population size can therefore be obtained for each of the primary sampling periods (N_1, N_2… N_i) (Pollock et al., 1990). During the intervals between trapping sessions (*primary sampling periods),* gains (birth and immigration) and losses (death and emigration) in the population can occur. *Secondary sampling periods* are the intervals where the population is closed for gains and losses, and where each trapping session can be viewed as a closed capture survey. For each secondary trapping session, the probability of first capture (***p***) and the probability of recapture (***c***) are estimated along with the number of animals in the population that are found within the trapping area (***N***).

3.3. Photo-Identification Technique

When population estimates are required, a researcher needs to be able to distinguish between individual animals. In early studies of coastal cetaceans, artificial tagging methods, such as freeze-branding, tattooing, flag tags, button tags, and spaghetti tags were all used to identify individuals within a population (Evans et al., 1972; Irvine et al., 1982; Wells and Scott, 1990). Whilst some of these methods are still being used today (for example, Scott et al., 1990a; da Silva and Martin, 2000), artificial tagging has been largely superseded by the more recent application of photo-identification.

Photo-Identification (photo-ID) is a method of individual recognition by photography that uses natural marks present on the animals to identify them. This non-invasive technique is frequently used in studies on cetaceans throughout the world (Würsig and Würsig, 1977; Wells et al., 1980; Hansen and Defran, 1990; Würsig and Jefferson, 1990; Hammond and Thompson, 1991; Urian et al., 1999; Reynolds et al., 2000; Rogan et al., 2000; Baird et al., 2001; Tyson, 2008). The technique has been principally developed in the 1970s and was improved in the 1980s (Würsig and Würsig, 1977; Würsig and Jefferson, 1990; Whitehead et al., 2000).

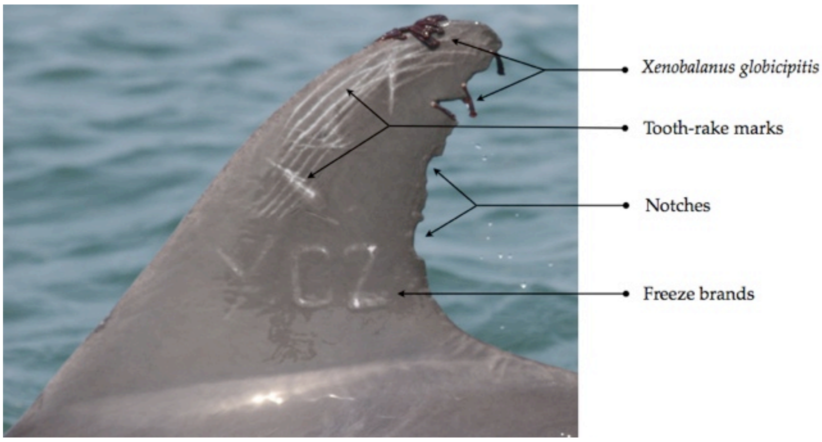


Figure 1.5. Example of a good quality picture (perpendicular, in focus, not fuzzy, un-obscured and without spray). The fin of the individual «AM68» shows clear distinctive features as notches and tooth-rake marks. This animal was tagged by Balmer in 2005 around St Joseph Bay, Florida, and displays freeze brands (X02) (Balmer, 2007). On this picture, we can also observed commensal barnacles, *Xenobalanus globicipitis,* present on the leading and trailing edges of the dorsal fin. (Photo by Th. Bouveroux)

The photo-ID technique consists of taking good quality[1] photographs of dorsal fins or the fluke of animals, depending on species studied, to identify individuals. For most dolphins and porpoises, the trailing edge of the dorsal fin is very thin and is easily damaged, resulting in a unique dorsal fin profile (Würsig and Würsig, 1977; Ingram and Rogan, 2002). The number of marks increase over time as a result of interactions with other dolphins, other animals (predators or not) and human activities (injuries often caused by boat propellers or fishing lines) leading to well marked individuals that can easily be identified. The occurrence and localisation of missing pieces of tissues from the dorsal fin of dolphins (nicks and notches) as well as the fin shape are the most distinguishable features that provide a permanent «print» from which the individual can be identified. Other identification marks are used in photo-ID, which may be considered permanent or semi-permanent, including tooth-rake marks, scars, blemishes, coloration patterns and scratches, that can be found on the dorsal fin or other parts of the body (Figure 1.5).

[1] A good quality picture is defined as to be perpendicular to the plane of the photograph, in focus, not fuzzy, un-obscured and without spray (Urian et al., 1999)

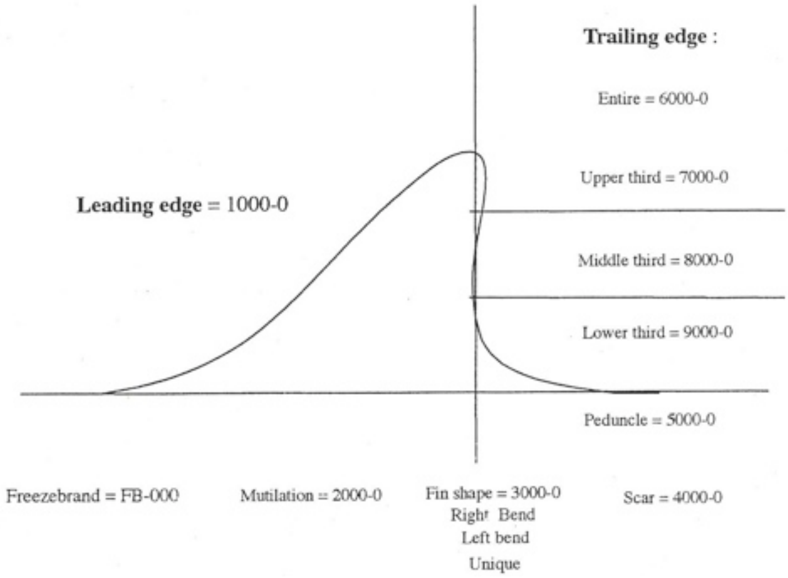


Figure 1.6. Dorsal fin categories based on the location of the most prominent feature on the dorsal fin, (from Urian et al., 1999).

3.3.1. The Photo-ID catalogue

All identified dolphins were entered in a photo-ID catalogue. For comparison and standardization of catalogues, the classification system of dorsal fins designed by Urian et al., (1999) was used. In this system, photographs of dorsal fins are sorted by ten categories based on the locations of the most prominent distinctive markings along the fins and then received an identification numbers (Urian et al., 1999) (Figure 1.6; Appendix B). Thus, we will assign the Urian's code «8001-0» for the first dolphin identified that has a major characteristic located in the middle third of the trailing edge. If this animal, is a female with a calf having a clean dorsal fins, the calf will be identified by the Urian code of its mother and the last digit indicates the serial position of the calf in its mother's offspring history (e.g. 8001-1). This classification method offers two advantages:

(i) facilitating the comparison of new dorsal fins with those already in the catalogue, and,

(ii) faster comparison with other photo-ID catalogues developed in other study areas close to the studied area.

We also used the system developed by Urian et al., (1999) to measure the distinctiveness of dolphins and photographic quality. Dorsal fin images were cropped, graded on both the distinctiveness of the dorsal fin (D) and the quality of the photograph (Q) (Appendix B).

Distinctiveness grades (D) were based on the patterns of predominant marks located along the trailing-edge of the dorsal fin and ranged from 1-3. Dolphins with the most distinctive features (evident in even a poor-quality photograph) were scored D1; those with intermediate features (at least two distinguishing features or one major feature) were scored D2; and animals with few or no distinctive characteristics were scored D3 (From Urian et al., 1999 and Tyson, 2008).

Photographic quality grades (Q) were based on clarity and contrast of the image, angle between the fin and the photographer, and proportion of the frame filled by the fin. A photograph that was perfectly focused, had ideal contrast, had the dorsal-fin angled perpendicular to the frame of the camera, and filled the majority of the frame was graded Q1; one that was still sharply focused, had minimal contrast, had the fin occupying a smaller portion of the image, and/or had the fin photographed slightly off angle was graded Q2; and a photograph that was out of focus, had excessive contrast, had the fin occupying only part of the frame, and/or was off angle was graded Q3 (From Urian et al., 1999 and Tyson, 2008).

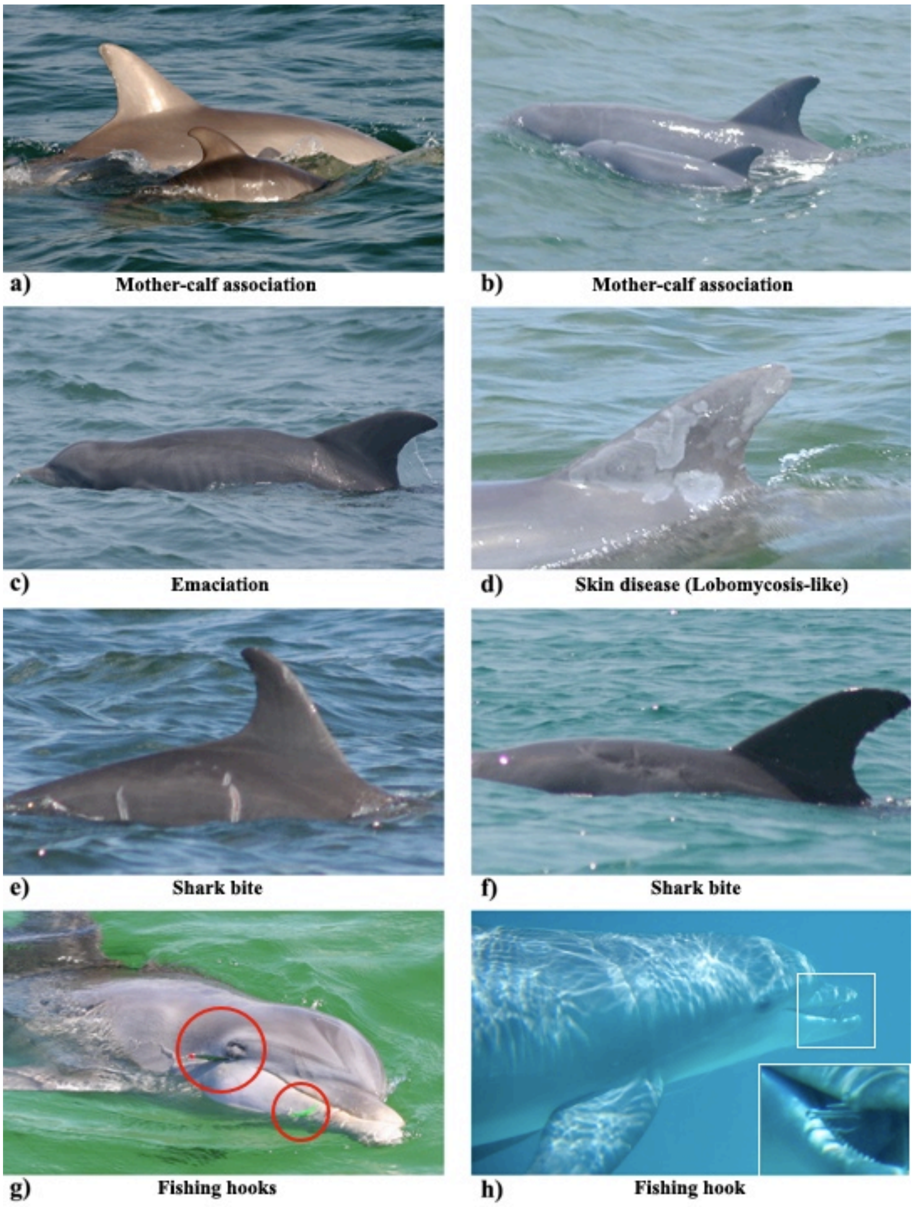


Figure 1.7. Illustration of the importance of the photo-ID technique in dolphins research. (a) & (b) approximate date of a birth, mother-calf associations; (c) & (d) health statement; (e) & (f) evidence of interactions with predators; (g) & (f) evidence of injuries from human interactions.

3.3.2. The importance of the Photo-ID technique in Cetaceans' studies

The recognition of individuals enhances research on animal behaviour and ecology, especially for abundance and social structure of cetaceans (Würsig and Jefferson, 1990). Indeed, to estimate population size of marine mammals, the photo-identification technique is now used in mark-recapture studies (Würsig and Jefferson, 1990; Wilson et al., 1999; Rogan et al., 2000; Balmer et al., 2008; Bearzi et al., 2008; Tyson, 2008). Traditionally, such studies relied on manual tagging of captured animals and studying recapture frequencies of these marked animals to derive population parameters (Wells and Scott, 1990), but this method is not without consequences for captured animals. So, it is well established that with good pictures, a reasonable portion of the population of almost any cetacean species can be easily identified (Würsig and Jefferson, 1990). Therefore, photo-identification is now applied to several cetacean species such as humpback whales, southern right whales, blue whales, fin whales, sperm whales, grey whales, killer whales, Hector's dolphins, and bottlenose dolphins (Würsig and Würsig, 1977; Hansen and Defran, 1990; Würsig and Jefferson, 1990; Wilson et al., 1997; Urian et al., 1999; Tyson, 2008).

The photo-ID technique also allows to study space-use and residency patterns: short-term movement and migration can be ascertained when photographs of animals are obtained at more than one locality (Urian et al., 1999). Life history information can also be recorded from photographs (Figure 1.7), e.g. approximate date of a birth, mother-calf associations (Pictures a & b), calving intervals, length of nursing, information on disease or health statement (Pictures c & d), evidence of interactions with predators (Pictures e & f), presence of injuries from human interactions (Pictures g & h), and sometimes to determine the sex of individuals. So it is an essential tool for studying marine mammals.

4. The distribution, habitat preference, home range and movements of bottlenose dolphins

Studies on distribution and habitat use may provide relevant data for conservation and management of a species in a given area. Indeed, a very important part of the ecology of an animal population is to know where animals live in a given area and how animals are distributed both daily and seasonally. Because of the high variability in the distribution and habitat preference of coastal bottlenose dolphins, it is difficult to predict the distribution patterns of a *Tursiops* population. It is not possible to develop consistent management strategies without information on the spatial arrangement of dolphins, such as presence of hots spots with higher density of animals or higher probabilities of dolphins' sight in an area.

Bottlenose dolphins are found in offshore waters as well as in coastal waters of all continents and occupy a wide variety of habitats. The environmental heterogeneity has been shown to influence distribution and habitat use, such as water temperature, bathymetry, topography, seabed gradient, sediment type, presence of predators, food availability or tidal cycles (Heithaus and Dill, 2002; Ingram and Rogan, 2002; Mendes et al., 2002; Griffin and Griffin, 2004). The coastal bottlenose dolphins are also found throughout the year in some estuaries, inlets, and rivers (Scott et al., 1988; Hohn, 1997; Caldwell et al., 2001; Gubbins, 2002a; Zolman, 2002). Results of photographic identification studies indicate that there is a difference in residency among dolphins: some populations are resident within confined areas (Wells et al., 1987), whereas others are migratory or sometimes even nomadic (Wilson et al., 1999). In Sarasota Bay, Florida, some marked bottlenose dolphins have maintained fidelity to the area for over 17 years (Scott et al., 1990b).

The concept of home range can be define as the area crossed by the individual during its normal activities of food gathering, mating and caring for young (Ingram and Rogan, 2002). Home ranges of coastal bottlenose dolphins may vary between 15 to 99 km^2 (Gubbins, 2002a). Home range can shift from one year to the other as conditions change (Reynolds et al., 2000). The best illustrated phenomenon is found in southern California where dolphins did shift their range over 500 km north during an El Nino event. Home ranges of males are known to be larger than females (Quintana-Rizzo and Wells, 2001). Transitory movements between populations are common especially by males, presumably allowing for genetic exchange between resident communities (Scott et al., 1990b; Wells, 1991; Wells and Scott, 1999). Continuous movements of bottlenose dolphins have been estimated using satellite telemetry. Mate et al. (1995), in Tampa Bay, Florida, found that dolphin did travel at least 581 km during 25 days, and the longest distance covered in a day was 50,2 km. Similar results have been reported for resident bottlenose dolphins in Sarasota Bay, Florida (Irvine et al., 1981). However, a satellite-tagged bottlenose dolphin off Japan covered approximately 604 km in 18 days (Tanaka, 1987). Two rehabilitated adult bottlenose dolphins, were tagged and tracked using satellite transmitters. One was released in the Gulf of Mexico but moved around Florida peninsula and northward to off Cape Hatteras, NC, covering 2050 km in 43 days; the other one was released off Cape Canaveral, Florida, and moved offshore covering 4200 km in 47 days (Wells et al., 1999).

Throughout the range of the species, two morphological types are found among adult bottlenose dolphins, which often are referred to as ecotypes (Perrin, 1984; Van Waerebeek et al., 1990). Bottlenose dolphins often exhibit offshore-inshore separation, and there are haematological, morphological, and genetic differences between those two ecotypes (Duffield et al., 1983; Hersh and Duffield, 1990). Several studies have indicated that coastal bottlenose dolphins have limited home ranges (Connor and Smolker, 1985; Scott et al., 1990b; Hammond and Thompson, 1991; Caldwell et al., 2001; Gubbins, 2002b; Zolman, 2002), while the offshore ecotype is less restricted in its range and movements (Leatherwood and Reeves, 1983; Leatherwood et al., 1988; Scott and Chivers, 1990).

Dolphin movements and distribution often have a seasonal component, which is likely to be related to the movement of prey and environmental conditions, such as water temperature. Seasonal north-south migration of coastal bottlenose dolphins have been reported in Cape Hatteras, North Carolina, and researchers have hypothesised that coastal bottlenose dolphins migrate latitudinally in response to the seasonal change in the water temperature (Mead and Potter, 1990).

5. Behavioural studies of coastal bottlenose dolphins

Another very important part in the ecology of an animal population, also for conservation, is the study of behaviours. Indeed, an accurate knowledge of the spatial arrangement of the daily and seasonal behaviours is required to determine how animal populations use their habitat for their vital activities such as feeding, mating or resting. Therefore, it is of high importance to characterise the habitat use of the population, in order to strategically target areas where conservation strategies must be applied.

In cetacean studies, «Sampling method» is a frequent procedure used to sample behaviours of individuals or groups. This procedure contains several methods that include *ad libitum, continuous, focal-group, one-zero, point, scan, predominant activity, sequence, and all-event/incident sampling.* The success of each method depends on whether a researcher is focusing on events (brief behaviours, measured in frequency) or states (long behaviours of measurable duration) (Mann, 1999). The focal-group sampling method used in our study can be defined as a continuous assessment of group activity and where the dolphins activity is scored at regular intervals (predominant group activity every 5 minutes). This methods is widely used in cetacean research when observers follow groups and are focusing on states (Mann, 1999).

In ethology, the «behavioural unit» is defined as is a single recognisable pattern of movement that can be characteristic, such as bow riding or rolling 360°. The «behavioural mode» can also be defined; it is a broad category of activities such as sexual, social or feeding behaviours and it integrates a number of «behaviour unit» (bow riding, rolling 360°,…). In our study, we use definitions of the «behavioural units» applied for Atlantic spotted dolphins, *Stenella frontalis*, and developed by Dudzinski, in 1996 (Dudzinski, 1996), since no specific and accurate ethogram for *Tursiops* was available in the literature when we started our study. Behavioural units were thus selected in this ethogram to characterise wild «behavioural modes» studied, such as sexual, social, playing, traveling or foraging. A list of all behavioural units and modes studied are presented in Appendix C. In addition to natural activities, some particular behaviours engendered by humans activities were defined and recorded. Therefore, the behavioural mode of «Begging» was added into the ethogram of this wild dolphins population, since some individuals are fed by humans since a long time.

Bottlenose dolphins are opportunistic and have a complex pattern in their behaviours, therefore it is very difficult to make generalities on behaviours. Indeed, behaviours can change during lifetime of an individual or even during a single day in response to changing conditions and needs of the animal (Reynolds et al., 2000). The behavioural flexibility has thus contributed to the dolphin's success in diverse habitats such as its wide variety of feeding behaviours (Shane, 1990a). However, several studies have shown that dolphins' activities vary on a daily period, but vary in a manner somewhat different from one study area to another (Shane, 1990b; Reynolds et al., 2000). Activity budgets have been described for bottlenose dolphin communities throughout the world such as in Sarasota Bay, (Florida), Sanibel (Florida), Indian River Lagoon (Florida), or Port Arasans (Texas). Traveling was determined as the dominant activity each day and ranges between 45 to 67% of time. Feeding behaviours usually range between 13 to 40% of the daily budget of bottlenose dolphins (Shane, 1990b; Reynolds et al., 2000). Thus, activity budget appears to be dependent upon seasonal, ecological and spatial consideration. Seasonal patterns in the behaviours of *Tursiops* have been also reported in different locations (Reynolds et al., 2000). Seasonality in traveling, feeding and mating patterns occur for dolphins in Matagorda Bay (Texas). Seasonal variation in the percent occurrence of traveling, feeding and socialising have been also reported by Shane (1990b) for bottlenose dolphins in Port Aransas (Texas) and in Sanibel (Florida). Reynolds et al., (2000) suggest that feeding peaks were associated with a shift in the distribution of fish and invertebrates. Thus, changes in activity patterns between seasons could be attributed to the need for the dolphins to vary the thickness of their blubber layer throughout the year. Indeed, studies have determined that blubber[1] layers were ticker in the winter than the summer in Sarasota, Florida (Reynolds et al., 2000).

6. The social structure of coastal bottlenose dolphins

Bottlenose dolphins are herding animals that live within structurally coordinated social groups. They are long lived social marine mammals interacting with other individuals inside the population or sometimes between populations or communities (Wells et al., 1987; Connor et al., 2000; Reynolds et al., 2000). Several long-term studies were conducted by Connor et al., in Shark Bay (Western Australia), and by Wells et al., in Sarasota Bay (Florida). These researches were conducted to understand and characterise the social network of bottlenose dolphins.

The social organisation of all populations of *Tursiops* is defined as a fission-fusion grouping pattern in which individuals associate in small groups that can change in size and composition, often on a daily or hourly basis (Wells et al., 1987; Smolker et al., 1992; Lusseau et al., 2003; Gibson and Mann, 2008). At a given time, an individual may have the opportunity to associates with a number of small groups or to be alone.

Studies on association patterns are typically realised using the survey method, in which researchers travel across the study area and record the composition of groups observed, and photo-identify them. Repeated over a number of days, months or years, surveys can provide an accurate short-term or long-term representation of

[1] Blubber is a specialised layer of fat that functions as an insulator, found between the skin and underlying muscle of most marine mammals. (Perrin et al., 2002).

individual association patterns. These associations are presented as coefficients of association estimating the percentage of time that two individuals are found together (Cairns and Schwager, 1987; Smolker et al., 1992; Bejder et al., 1998; Connor et al., 1999; Connor et al., 2000; Connor et al., 2001; Lusseau et al., 2003; Rogers et al., 2004; Gero et al., 2005; Lusseau et al., 2005; Lusseau, 2007; Whitehead, 2008b). The most common coefficients of association used to quantify relationships between individuals is the Half-Weight-Index (HWI), in which the association between two dolphins A and B,

$$\mathbf{X_{ab} / (X_{ab} + 0.5(Y_a + Y_b))}$$

where $\mathbf{X_{ab}}$, is the number of times both individual A and B were seen together in the same group; $\mathbf{Y_a}$, is the number of times individual A was seen but not individual B and $\mathbf{Y_b}$, is the number of times individual B was seen but not individual A. Association patterns can be represented by a hierarchical cluster. Bottlenose dolphins may form relatively permanent social groups based on sex and age (Shane et al., 1986). However, in many habitats, sex determination of individuals is difficult to investigate.

6.1. Female-Female relationships

Connor et al., (2000), did show that females seem to have a large network of associates than males and are linked to most other females in an area. Most females associate most strongly with a subset of other females in «bands», while a minority of females do not belong to any particular band (Connor et al., 2000). Bands may maintain their basic structure for many years, but can change over time as the female composition of the community changes. Within bands, females with calves of similar age tend to associate with each other, as do females without calves (Wells et al., 1987). It was observed in both Sarasota and Shark Bay, that female-female relationships vary in «sociability»: some females usually tend to be associates while others are found rather solitary (Wells et al., 1987; Smolker et al., 1992; Connor et al., 2000). Not surprisingly, mothers with calves associate strongly for their first few years. Adult females can create several relatively discrete spatial groups, with each group occupying different and relatively limited core areas that broadly overlap. Adult males travel from one female group to another (Scott et al., 1990b).

6.2. Male-Male relationships

Male bottlenose dolphins exhibit two levels of alliance formation. First, males in pairs or trios form a «first-order» alliance. In these alliances, males cooperate to form coercively maintained consortships with females (Connor et al., 1999; Connor et al., 2000). «First-order» of alliances are strong and stable over long periods, lasting up to 12 years in Shark Bay and up to 20 years in Sarasota Bay. Second, teams of two or more stable alliances are sometimes observed to cooperate and to form «second-order» alliances to attack other alliances in attempts to take female consorts from other alliances or to defend against such attacks (Connor et al., 1999). Second-order alliance relationship, also called «super-alliance» do not generally endure for more than a few years. Alliances that normally cooperate may oppose each other in some social contexts. However, cooperative association between alliances have not been identified to date in all population as for instance in Sarasota Bay, Florida (Connor et al., 2000).

6.3. Male-Female relationships

Association between males and females are strongly tied to female reproduction status, in Sarasota and Shark Bay. Smolker et al., (1992), did show that associations between particular females and males were much strongerer during years when a female was cycling than during years when she was pregnant. In Shark Bay, males in pairs and trios form consortships with single females that may last anywhere from a few minutes to over a month. Males may either capture a female when she is alone or isolate her from a group of females.

6.4. Mother-Calf associations

For many social marine mammals, mother-calf relationships are long-lasting and extend beyond the nursing period. In the first few months, calves energetically depend on their mothers, after the mother-calf relationship has other functions such as social development, acquisition of cultural knowledge (Grellier et al., 2003; Krützen et al., 2005), learning of feeding techniques, and vigilance against predators. These prolonged relations between mothers and calves aim to ensure the enhancement of calves' survival. The proportion of time that calves spend in proximity to their mother decreases as infant age increases over the first few weeks or months of life. The length of time a calf remains with its mother may vary according to the locations and can reach up to 10 years, in Sarasota Bay, Florida, for instance (Wells et al., 1987; Smolker et al., 1992; Grellier et al., 2003).

7. Methodology

7.1. Data collection

This research project was conducted between March 2004 and July 2007. During this period, fieldwork was performed over four periods: (1) 20 March to 31 May 2004, (2) 28 September to 31 November 2005, (3) 20 July to 21 August 2006, and (4) 1 June to 25 July 2007. Using boat-based surveys, a total of 162 days were carried out in a Beaufort Sea State of three or less to optimise sightability and along predetermined transect lines to ensure that the entire region was surveyed uniformly (Otis et al., 1978; Pollock et al., 1990). When a group of dolphins was sighted, the boat left the transect line and slowly approached the group. After data have been collected, the boat returned to the location where it left the transect line and continued to follow the predetermined route.

For logistic reasons and accuracy in data recording, we did not collect all data in the same time. Indeed, data on mark-recapture, on dolphin behaviours and on the social structure were not collected simultaneously, and two kind of surveys design were thus assigned: (i) surveys with special attention to collect data on mark-recapture and on the social structure by photo-ID, and (ii) surveys devoted to dolphins behaviours recording. However, For every observation, the position of the animals was recorded (with a hand-held GPS); the number of individuals (adults, juveniles, calves and neonates) in the group, the zone and the time of observation were noted, in order to document the distribution of dolphins in the study area. At the end of the day, information concerning the tidal current (flood tide or ebb tide) were add to the data set from the website,
http://www.saltwatertides.com.

(i) Data collection: mark-recapture and social structure

To allow for the assumption of a closed population from births, deaths, and movements in and out of the population (Otis et al. 1978, Read et al., 2003b), mark-recapture data by photo-ID have been recorded during several short periods of time (called secondary samples) spaced in time by several days. Thus, within the 2004 study period, 12 days were devoted to photo-ID. Those 12 days were clumped together into four secondary samples of three days evenly distributed over the whole stay. In 2005, six secondary samples of five days, were created; in 2006, three secondary samples of five days were made. Finally, in 2007, four secondary samples of five days were made. During the mark-recapture surveys, photographs of dorsal fins and other distinguishing features (e.g., peduncle) of each individual in the group were taken. At the end of each encounter, one picture of a small whiteboard indicating some information on the followed group (zone, time of the day, group size and composition) were taken to well separate each groups from each other.

(ii) Data collection: dolphins behaviour

Between secondary samples, survey days were devoted to record data on dolphins behaviours using focal-group sampling method. In this method, data on group activity were recorded every five minutes, with a sampling duration of five minutes that allowed adequate time for both observations and recording of dolphins' activity and then upon a change in group (modified from Shane, 1990a; Samuels and Bejder, 2004). Six behavioural modes have been recorded (playing, social, sexual, foraging, traveling and begging).

7.2. Statistics

(i) Statistical analysis

To study how average groups size of dolphins vary according to variables, such as zones of observation, times of the day and months, data were analysed using analysis of variance (one-way ANOVA).

Influence of the zones, time of the day and the tidal currents (flood tide or ebb tide) on the frequency of sightings were analysed using chi-square contingency table. A Generalised linear model (GLM) was also used to describe the influence of zones and time of the day on the frequency of dolphin sightings, including seven contrasts test using the estimate statement in the software SAS (SAS Institute) have been performed to investigate differences in the frequency of sightings according zones and time of the day.

The behavioural data were analyzed according to zones for every time of the day (AM, PM1 and PM2). Because zones were not surveyed with the same time effort, given their surfaces, the number of observations of each behaviours was weighted by the number of hours spent in each zones, and then reported to 24 hours.

Generalised linear models were also used to investigate how the mean group size of dolphins varies according the three following variables: zones, time of the day and behaviours. Three different models have been tested:

(i) $\mathbf{Log(}\boldsymbol{Gs_i}\mathbf{) = \mu + B_{1i} + B_{2i} + B_{3i} + B_{4i} + B_{5i} + B_{6i} + \varepsilon_i;}$

(ii) $\mathbf{Log(}\boldsymbol{Gs_i}\mathbf{) = \mu + B_{1i} + B_{2i} + B_{3i} + B_{4i} + B_{5i} + B_{6i} + Z_i + \varepsilon_i;}$

(iii) $\mathbf{Log(}\boldsymbol{Gs_i}\mathbf{) = \mu + B_{1i} + B_{2i} + B_{3i} + B_{4i} + B_{5i} + B_{6i} + Z_i + Ti + \varepsilon_i;}$

Model suitability was determined by having the lowest Akaike's Information Criteron (AIC).

The GLM predicts one variable (*Y; here Log*(Gs_i) *)* from variables (X_i) (usually called *explanatory* variables; *here variable Behaviours,* B_i*; Zones,* Z_i*; and time of the day,* T_i), with the null hypothesis that there is no interactions of two or more variables (Zar, 1999). In fitting a linear model to a set of data, one finds at a series of *weights* (also called *coefficients*)—one weight for each independent variable—that satisfies some statistical criterion. The two additional features of a linear model are an *intercept (*μ) and *prediction error (*ε*)*. The intercept is simply a mathematical constant that depends on the scale of the dependent and independent variables. A prediction error (also called a *residual* or *error*) is the difference between the observed value of the dependent variable for a given observation and the value of the dependent variable predicted for that observation from the linear model. The term "linear" in linear model comes from the mathematical form of the equation, not from any constraint on the model that it must fit only a straight line. That mathematical form expresses the dependent variable for any given observation as the sum of three components: (1) the intercept; (2) the sum of the weighted independent variables; and (3) error. Therefore, for *k* independent variables, the fundamental equation for the GLM is:

$$Y = \mu + \beta_1 X_1 + \beta_2 X_2 + K\beta_k X_k + \varepsilon$$

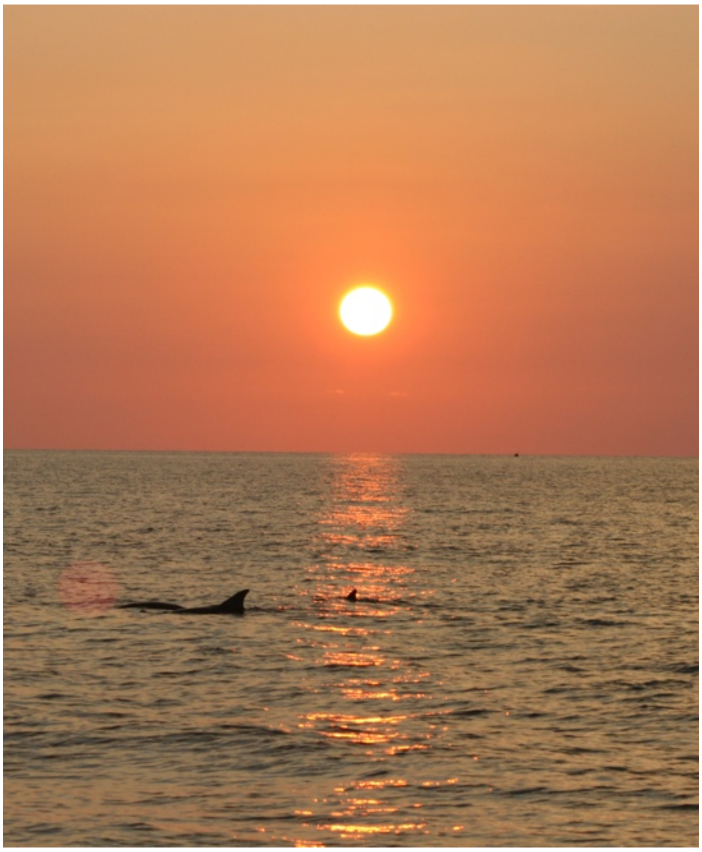
The equation for the predicted value ($\hat{Y}$) of the dependent variable is:

$$\hat{Y} = \mu + \beta_1 X_1 + \beta_2 X_2 + K\beta_k X_k$$

All statistical methods were implemented with the software SAS v. 8.0 (SAS Institute).

(ii) Spatial analysis

In order to document the density of observations and dolphin behaviours in the study area, we divided the survey area into cells of 250mx250m. To investigate whether the spatial distribution of dolphins groups, and the behaviours showed a consistent pattern, the number of observations recorded inside each cells were calculated using the application *count point in polygone*, (Arcview version 3.3 - ESRI Inc.) and then plotted on a chart.



Bottlenose dolphins at sunset. Photo by Th. Bouveroux.
Panama City, Octobre, 2005.

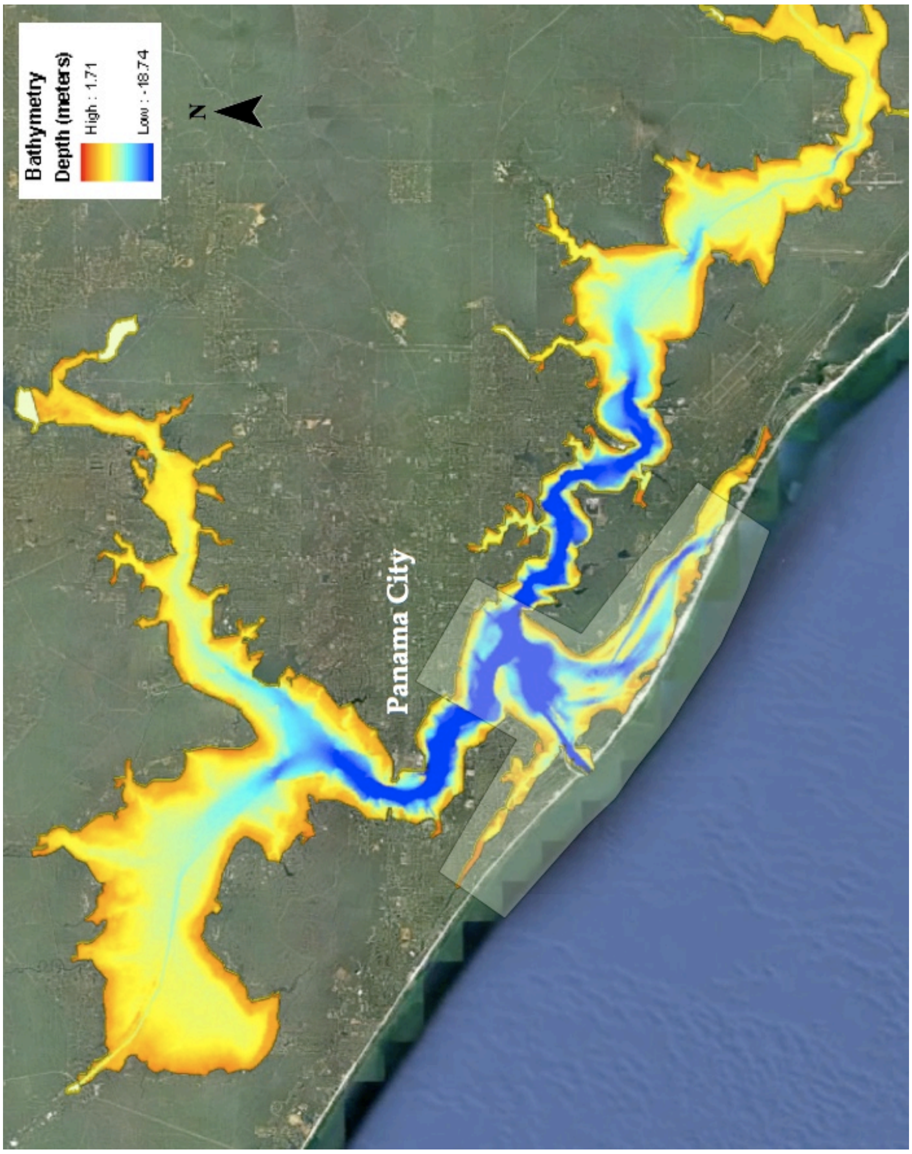


Figure 2.1. Map of Panama City (Florida), showing the bathymetry features. The white box represents the selected study area where surveys were performed between 2004 and 2007.

II. Aims of the study

This research project is the first ecological study addressing in the abundance, the distribution, the behaviours and the social structure of bottlenose dolphins in Panama City, Northwest Florida (Figure 2.1). As such, the first step to understand an unknown population of marine mammals required a comprehensive descriptive work to encompass globally the ecology of this population.

The lack of scientific knowledge on this dolphin population, the potentially disturbed area by intensive human activities (tourism, whale watching, recreational boating, fisheries, harbour activities and military activities), and the Unusual Mortality Events (UME's) that were observed in this region, make it a potentially vulnerable population.

Therefore, we conduct an ecological study to provide information and baseline that could be used for an effective conservation and management of the *Tursiops* population in Panama City.

First, we investigate the abundance of dolphins using mark-recapture by the photo-identification technique. This first step will allow us to estimate how many individuals live in the selected study area and to characterise site fidelity patterns of dolphins in Panama City (i.e. do we see the same individuals throughout the year?). With the photo-ID technique, a catalogue indexing all identified dorsal fins will be created and will provide an essential tool to investigate the social structure of this dolphins population.

The second objective of this study, aims to document the spatio-temporal distribution and the variation in group size of dolphins. Questions addressed here are: do dolphins show habitat preference through the study area? Do we observe any variations in daily and monthly distribution? Does the tidal current influence the distribution of dolphins? Is there variability in group size?

The third objective is to document the behavioural patterns of dolphins in an area exposed to significant human activities. This part of the study aims to document how dolphins use their habitat with regard to their behavioural activities. Do we observe, through the study area, some preferential places for dolphins activities? Do dolphins show variations in group size according to the behaviours observed?

Finally, the study on the social structure of dolphins aims to broaden our knowledge of the social organisation in an area highly disturbed by human activity. With this study we will try to assess the relationships among individuals, and answer the following questions: do we observe strong preferred associations among individuals? Can the social structure of bottlenose dolphins be compared with that observed in other places, with the presence of «*first-order*» and «*second-order*» of alliances as well as the presence of superalliance within the population? Do dolphins reveal variations in their association patterns depending on sex?

Structure of the thesis

This thesis is a compilation of published, submitted and unpublished papers; it is designed according to four main axes: (i) the abundance and residence patterns, (ii) the distribution and groups size assessment, (iii) the behavioural patterns and finally (iv) the social structure of the bottlenose dolphin population in Panama City, Florida.

Chapter 1: Abundance and site fidelity of dolphins

The first publication of this thesis gives the results on the estimate size of the dolphins population in Panama City, Florida, as well as the first trends of a seasonal variation in the dolphins abundance. This paper evaluates also the site fidelity patterns of the dolphin population, in order to evaluate the proportion of resident individuals that use regularly the study area throughout the years. Using the powerful tool of photo-identification to identify individuals constituting a population from dorsal fins, the photo-ID catalogue of bottlenose dolphins in Panama City has been created. The photo-ID catalogue is presented and summary after the publication and can be view from the CD-ROOM, p79.

Chapter 2: Distribution and group size of dolphins

In this chapter, we present data on the spatio-temporal distribution of bottlenose dolphins in Panama City. The distribution study allows us to highlight the daily and monthly variations in the distribution of dolphins and thus to characterise possible hotspots in the dolphins' habitat. In this research, the presence of dolphins is evaluated through the frequency of observations and the mean group size of dolphins. The presence of dolphins inside and outside the bay is also evaluated according to the type of tidal current. A Geographic

Information System (GIS) is used to visualise the spatial distribution of dolphin sightings within the study area.

Chapter 3: Behavioural activity of dolphins

The behavioural study aims to understand the strategy of habitat use by dolphins within the study area. Behavioural patterns of dolphins are characterised in relation to the number of dolphins present in a group, the zone of observation and the time of the day. The analysis of the behavioural activities among bottlenose dolphins also highlights the influence of human activities in wild dolphins behaviours. A Geographic Information System (GIS) is also used to characterise the spatial distribution of dolphin behaviours within the study area.

Chapter 4: Social structure of bottlenose dolphins

This part of the study aims to characterise association patterns between individuals within the population. Coefficient of associations (CoAs) were calculate using the Half-Weight-Index. Preferred associations between and within sex are documented as well the temporal stability and constant companionships among the dolphin population in Panama City. Using Socprog 2.3, coefficient associations among individuals were calculated and represented on a cluster, while sociograms represent CoAs within sex.

RESULTS

Photography of a bottlenose dolphin illustrating the begging behaviour, with the head out of the water and open-mouthed. Photo by Th. Bouveroux, St Andrew Bay, June 2007.

Article 1:

Abundance and site fidelity of bottlenose dolphins, *Tursiops truncatus*, in Panama City, Florida.

Bouveroux, Th., Le Boulengé, E., Nowacek, D.P., and Mallefet, J.

Submitted to the *J. Mar. Biol. Assoc. of UK***.**

Photography of a group of dolphins. Panama City, July, 2007.Photo by Donald Tipton.

1.1. Context

This first article was submitted to the *Journal of the Marine Biology Association of the United Kingdom* and is the first attempt to estimate the population size of bottlenose dolphins in Panama City, using mark-recapture method. In cetacean studies, animals are captured by the photo-identification technique. Thus, animals are photographed and identified mainly from the shape and nicks patterns present on the dorsal fins of each individual. Based on the characteristics of the studied population, we selected the method of the Robust Design to estimate the population size, because this method combines models for closed and open population. Estimates were calculated according to months surveyed during the study period. However, the lack of repeated data for each month through the years, as well as the lack of data during the winter, do not allow us to provide accurate information on the seasonal abundance of bottlenose dolphins in Panama City. Nevertheless, it can be view as first trends in the variation of dolphins abundance by months. This paper evaluates also the site fidelity of dolphins in order to estimate the proportion of resident and transient dolphins that frequently use the study area.

Population sizes vary according to months, with the highest abundance observed in June 2007 and the lowest abundance recorded in May 2004. A total of 263 dolphins have been identified and indexed in a photo-ID catalogue. Residency patterns of this dolphin population reveal that only twelve percent of the population are considered as resident dolphins.

1.2. Manuscript:

Abundance and site fidelity of bottlenose dolphins, *Tursiops truncatus,* in St Andrew Bay, Panama City, Florida.

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ABSTRACT

The seaside resort of Panama City Beach, Florida, in the Gulf of Mexico, is famous for its population of bottlenose dolphins, Tursiops truncatus, living in the waters of St. Andrew Bay. Although little is known about this dolphin population, it has become a major tourist attraction. Field surveys were conducted between March 2004 and July 2007. During this period, 77 survey days, distributed in 17 captures sessions were performed to document the abundance and site fidelity of bottlenose dolphins in this area. Photographic-identification and mark-recapture techniques were used to conduct this study. A Robust Design model was used to obtain an abundance estimation ranging between 57 and 178 individuals, depending on months, with the lowest abundance occurring during the spring. During the study period, 263 dolphins were photo-identified and a photo-identification catalogue has been created, indexing all identified animals. Site fidelity of bottlenose dolphins reveal that only seven percent (n=18) of individuals are considered as "common" in the study area. Twelve percent of dolphins are considered as resident animals, since they were seen in all four years while 58% are observed only in one year and are thus defined as transient dolphins. This first study on dolphins abundance in Panama City, represent basic information that could be used for conservation and management of the dolphin population, and a repeated long term study will give us information about variations in the dolphins abundance throughout years.

KEYWORDS: Dolphins, *Tursiops truncatus*, abundance, photo-identification, site fidelity, robust design.

INTRODUCTION

The bottlenose dolphin, *Tursiops truncatus*, is distributed continuously along shoreline of the Gulf of Mexico coast of the United States. Some regions of this shoreline are intensively developed with significant human activities. However, studies throughout the world have indicated that human activities, such as military activities, fisheries, boat traffic, and recreational beach activities, may unintentionally increase the mortality of wildlife cetaceans‘ populations (Kraus, 1990; Wells & Scott, 1997; Nowacek, 1999; Nowacek et al., 2001; Constantine et al., 2003; Glen, 2003; Read et al., 2003a; Finn, 2005; Bejder et al., 2006). In the Atlantic coast of the United State, Palka and Rossman (2001) reported that 146 bottlenose dolphins were killed by interactions with fishing operations off North Carolina and Virginia during winter 2000. After, Waring et al., (2002) more than 50% of stranded carcasses of bottlenose dolphins in the coastal water of North Carolina exhibited signs of human interactions.

In Panama City, Florida, the presence of a bottlenose dolphins population is well known by tourists who are coming to interact, to swim and to feed dolphins, since along time (Samuels & Spradlin, 1995; Colborn, 1999; Samuels & Bejder, 2004), while these activities are prohibited by the *Marine Mammal Protection Act* (NMFS, 2007). This bottlenose dolphin population is also constantly submissive to other significant human activities such as boating, fisheries, military activities, and harbour activities. In addition, between 1999 and 2006, along the Northwest coast of Florida Panhandle, several «unusual mortality events» (UMEs) on dolphins have been reported by the *National Marine Fisheries Service* (NMFS), with more than 300 dead animals (NMFS, 2004). All these events appear to have been correlated spatially and temporally with blooms of *Karenia brevis*, a dinoflagellate known to cause red tide in Florida (NMFS, 2004; Tyson, 2008). However, very few information are available in the scientific literature on bottlenose dolphins in Panama City. Indeed, the only information that confirms a bottlenose dolphins population in this region, comes from aerial surveys conducted in 1993 using standard line-transect techniques to estimate population size of dolphins (Blaylock & Hoggard 1994), and from some quantitative studies on human-dolphin interactions (Samuels & Spradlin, 1995; Colborn, 1999; Samuels & Bejder, 2004). Aerial surveys were conducted only over coastal waters and excluded bays, sounds, and estuaries (Eguchi, 2003). Consequently, there are no recent and reliable estimates of abundance for this population of *Tursiops*. Therefore, this lack of knowledge hampers our ability to assess the impact of human activities on this bottlenose dolphins' abundance.

The objectives of this study are (i) to estimate population size of bottlenose dolphins, using the mark-recapture by photo-identification (photo-ID) method, (ii) to create a photo-identification catalogue, indexing all identified dolphins in Panama City, and (iii) to characterise their site fidelity. Because, in many other areas, scientists have observed that populations size of bottlenose dolphins may vary with seasons (Forney & Barlow, 1998; Hubard et al., 2004; Torres et al., 2005; Balmer, et al., 2008; Tyson, 2008), we analysed our data in order to provide also a first estimate of the abundance for a period of seven months.

MATERIALS AND METHODS

Study area

Panama City (30°07’N, 85°43’O) is located on the northwest coast of Florida (Figure 1).

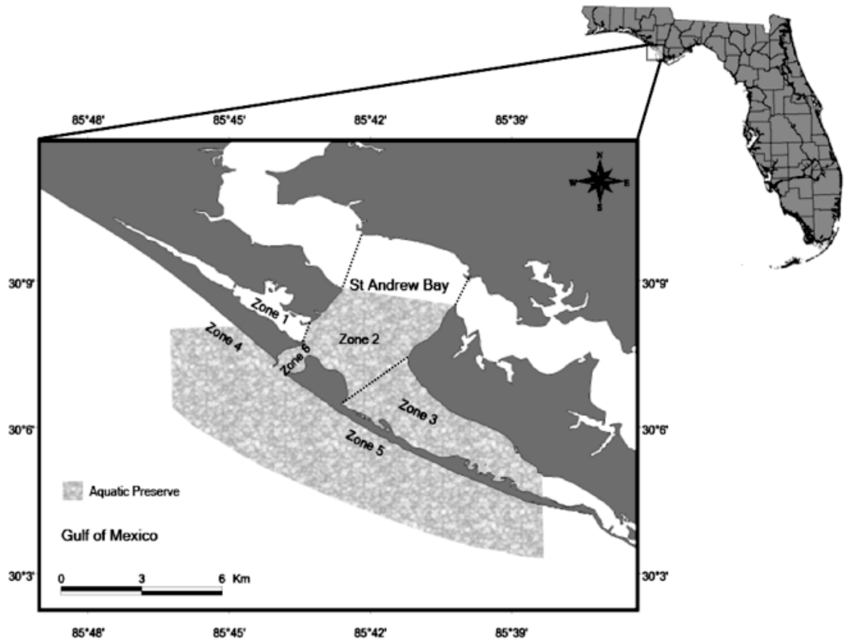

Figure 1. Map of the study area showing the study area divided into six different zones delimited based on easily recognizable landmarks. The Aquatic Preserve is represented in light grey.

A sand barrier created 5000 years ago by the action of currents, tide, and waves formed St. Andrew Bay (Spinner, 1994). St Andrew Bay is linked to the Gulf of Mexico by a single narrow channel. The bay is also connected to the north by the West and East Bays.

St Andrew Bay is connected to several small and shallow inlets that exhibit different characteristics. On the southwest, St Andrew Bay forms a lagoon, called Grand Lagoon with shallow waters of seagrass beds and oyster reefs. St Andrew Bay also spreads to the southeast between Shell Island and the Tyndall Air Force Base, forming another small lagoon with shallow waters consisting of seagrass beds and oyster reefs.

The study area was focused only in and around the Aquatic Preserve that encompasses a surface area of approximately 323 Km^2 (Figure 1). Thus, the West Bay and the East Bay were not investigated in order to limit the surface of the study area.

Data collection

We conduct photo-identification (photo-ID) surveys from small boats (5-7m) powered by 55 to 85 HP outboard engines between March 2004 and July 2007. During this period, 77 photo-ID surveys were performed for a total of 366 hours spent searching for and photographing dolphins in the waters of St. Andrew Bay (Table 1).

Months	N Days	N sessions	N Hours	N sightings
March-April 2004	6	2	37	63
May 2004	6	2	34	76
Sept-October 2005	15	3	69	129
November 2005	15	3	56	156
July-August 2006	15	3	68	186
June 2007	10	2	52	89
July 2007	10	2	50	103
Total	**77**	**17**	**366**	**802**

Table 1. Summary of mark-recapture photo-identification surveys of bottlenose dolphins in Panama City, Florida, between 2004 and 2007.

To avoid problems associated with pseudo-replication, photo-ID surveys were not carried out all days (Wilson et al., 1999). Within the 2004 study period, 12 days were devoted to photo-ID. Those 12 days were clumped together into four sessions of three days evenly distributed over the whole stay. In 2005, six photo-ID sessions of five days, were created; in 2006, three sessions of five days were made. Finally, in 2007, four sessions of five days were made.

Surveys were carried out in a Beaufort sea state of three or less and followed predetermined routes (Figure 2) until a school of dolphins was encountered, whereupon the survey vessel slowly approached the group of dolphins and ran parallel to its course.

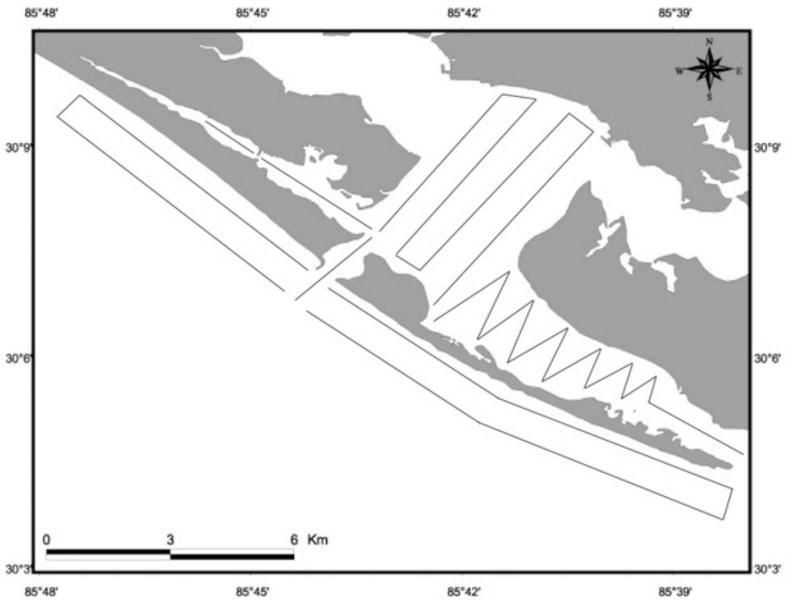

Figure 2. Typical transects used for surveys of bottlenose dolphins during fieldworks between 2004 and 2007.

During each encounter, geographical position were recorded using a GPS (Garmin GPSMAP 76S), and photo-ID pictures were taken using a Canon EOS 350D camera equipped with 18-55 mm (f 3.5-5.6), 35-80 mm (f4.5-6) or 90–300 mm (f4.5-5.6) zoom lenses. Individuals were identified from photographs using unique natural markings such as nicks and notches in the dorsal fin and tooth rakes marks, scratches, scars, and skin lesions on the dorsal fin and back (Würsig & Würsig, 1977; Wells & Scott, 1990; Wilson et al., 1999; Würsig & Jefferson, 1999). Neonates were distinguished from other age classes by their small size, darker skin, and the presence of foetal bands (vertical light lines on the sides of the body) (Wells et al., 1987; Perrin et al., 2000). Calves differed from neonates because foetal bands were no longer present nor were they observed to swim constantly in echelon position with their mothers (Reynolds et al., 2000; Grellier et al., 2003); juveniles were characterized by a body size up to 2/3 the size of an adult (Wells et al., 1987). Photo-ID remains one of the best non-invasive methods used for gathering information about cetacean societies in the wild (Culloch, 2004).

Dolphins with clear markings were identified from a high-quality picture, and only good quality photographs (in focus, not fuzzy, un-obscured, with the dorsal fin relatively perpendicular to the plane of the photograph and without spray) were used in the analyses (Baird et al., 2001). A photo-ID catalogue was created, indexing all recognized individuals. When possible, dolphin sex was determined by direct observations of the genital area and sometimes during mating behaviours with male erection. Females were indicated by the constant presence of a small animal presumed to be their calf.

For a faster identification of individuals, we used a codification system. We have indeed assigned a code **XYZ** to each identified dolphins, where:

X, is the age class (*A= adult, J= juvenile or C= calf);*

Y, represents the sex (*M= male, F= female or X= unknown*);

Z, the individual number.

For instance, AM01 is the first identified dolphin, and it is a male adult. Finally, in order to facilitate the comparison of dorsal fins in the photo-ID catalogue, we used the classification system of dorsal fins designed by Urian et al. (1999). This method of fins' classification allow also to facilitate the comparison of dorsal fins in photo-ID catalogues created in different places, in order to document the possible movements of dolphins between different populations.

Estimation of population size

Population size was estimated from mark-recapture methods using a robust design model (Pollock, 1982; Pollock et al., 1990). This model combines characteristics of both closed and open population abundance estimates. The abundance was determined during multiple short-term periods with closed population models combined with a Jolly-Seber open population model to estimate survivorship and emigration rates.

The robust design model was preferred to close population models for two reasons:

(i) Evidence of dolphin movements outside the study area in Panama City. Indeed, another bottlenose dolphins population lives 30nm from St Andrew Bay, in St Joseph Bay. Researches, such as tagging and photo-ID are currently underway there. Among those tagged in St Joseph Bay, six tagged dolphins were also observed in Panama City.

(ii) Evidence of mortality and birth: during fieldwork, newborns and dead dolphins were observed.

Therefore, our model is based on the assumption that the population is open during the course of the study, and closed during photo-ID sessions of because the sampling periods were short (3 or 5 days). During the intervals between photo-ID sessions (*primary sampling periods)* gains (birth and immigration) and losses (death and emigration) in the population can occur. *Secondary sampling periods* are the intervals where the population is closed to gains and losses, and where each photo-ID sessions can be viewed as a closed capture survey. For each photo-ID session, the probability of first capture (p) and the probability of recapture (c) are estimated along with the number of animals in the population that are found within the trapping area (N).

It is not necessary that the number of secondary sampling periods is equal to all the primary sampling periods (Pollock et al., 1990). In our study, seven primary sampling periods were defined and composed by several consecutive days. Thus, we are able to obtain the population size estimate for each of the primary sampling periods (N_1, N_2… N_7) (Pollock et al., 1990). To analyze data, the encounter histories for the identified animals were first transformed into a binary: the number ‘1’ indicating that an animal has been sighted, and ‘0’ indicating that the animal has not been sighted during mark-recapture periods. Those mark-recapture histories were subsequently analyzed by the program MARK.

In the robust design, the heterogeneity model - M_h - (capture probability can vary for individuals) for closed population was selected because humans have interacted with this dolphin population in Panama City (feeding and swimming with the animals), for several years. Despite of their prohibition by the *Marine Mammal Protection Act*, these practices are still observed in Panama City, which create an heterogeneity in the capture probability of some individuals often seen begging close to boats (Samuels & Bejder, 2004; Bouveroux & Mallefet, 2008).

Site fidelity

We examined resighting patterns using the temporal distribution of individual dolphin sightings during 17 capture sessions and 77 sightings. Dolphins were classified into one of four arbitrary categories based on the number of capture sessions, an individual was observed (modified from Wilson et al., 1997): (1) “common”: dolphins sighted during more than 13 captures occasions, (2) “frequent”: dolphins sighted during 9-12 occasions, (3) “occasional”: dolphins sighted during 5-8 occasions, and (4) “rare”: dolphins sighted during 1–4 capture occasions.

RESULTS

Photo-identification

Between 2004 and 2007, 16,766 pictures were taken and 263 bottlenose dolphins were identified and indexed in a photo-ID catalogue. As newborns and calves did not have enough distinctive features on their dorsal fins, they were not included in the analysis of population size. The catalogue contains the following information: right side and/or left side of each identified dorsal fin, notes such as "begging" (a "particular behaviour") or life history (presence of embedded hooks in the jaw, eye or other parts of the body, shark bites or female with a new-born or calf), the Urian's Code and months where each individual was observed.

Population size estimation

The abundance of bottlenose dolphins in Panama City appears to be quite stable during summer and fall. However, in June 2007 the abundance was estimated at 178 dolphins, while the lowest abundance was observed during spring 2004 with only 57 dolphins in the population (Table 2).

Months	Season	N	Standard Error	95% CI LOWER	95% CI UPPER
March-April 2004	Spring	86	19,8	62	146
May 2004	Spring	57	6,3	51	82
Sept-October 2005	Fall	135	9,5	121	160
November 2005	Fall	128	7,8	117	149
July-August 2006	Summer	129	10	115	156
June 2007	Summer	177	16,6	153	220
July 2007	Summer	117	9,7	104	144

Table 2. Mean population size according to months, with standard error and the 95% confidence interval lower and upper.

Site fidelity

Dolphins were observed on each of the 77 surveys realised. On 77 capture occasions, 42% of the dolphins were only captured once and 7% were captured more than 21 times (Figure 3).

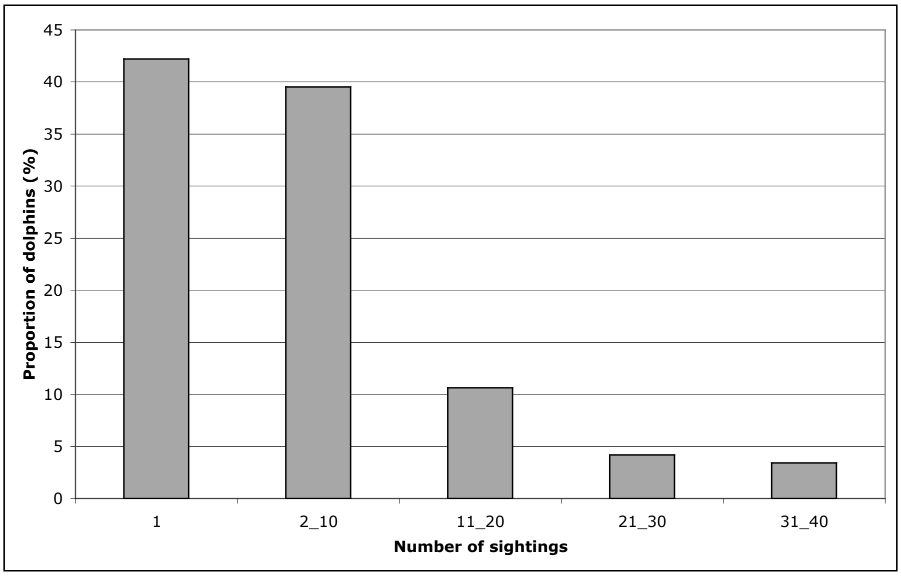

Figure 3. Proportion of individuals seen according to the number of sightings.

Among the 17 sessions of photo-ID, 75% of dolphins (n=197) were considered as «rare»; 11% (n=29) were «occasional», while 7% were considered to «frequent» (n=19) and 7% as «common» (n=18). 12% of dolphins were seen in all four years and are thus considered as resident animals, while 58% of the population was observed only during one year and are therefore referred to transient dolphins (Table 3).

	One Season	Two Seasons	Three Seasons	Four Seasons
# of dolphins sights	154	47	29	33
% of dolphins seen a least once	58,5	17,9	11,1	12,5

Table 3. Number and the percentage of dolphins sightings in function of the seasons.

We evaluated also the seasonal variation in the re-sighting probabilities (Figure 4).

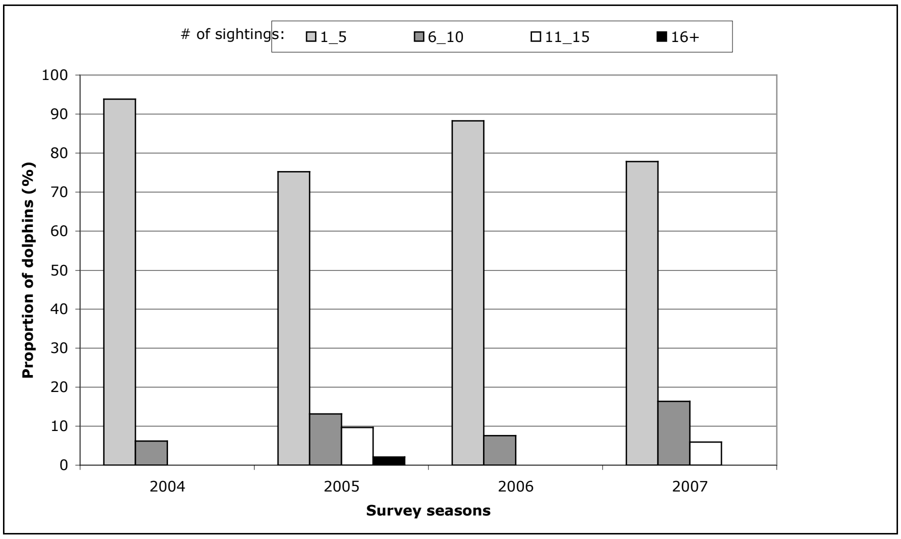

Figure 4. Resighting frequency distribution per year.

For a single season more than 75% of dolphins were seen between one to five times. A greater number of dolphins were re-sighted during the fall of 2005 and summer of 2007 than all other seasons.

DISCUSSION

This study has shown that the abundance of animals is quite stable throughout the fall and summer. However, we recorded a strong abundance in June and a weak abundance in April and May. Similar influxes have been reported from several studies (Shane, 1980; Ballance, 1990; Wilson et al., 1997; Rogan et al., 2000; Culloch, 2004; Hubard et al., 2004). Such changes have been attributed to spatial variations in local conditions, resulting in certain area being more suitable for mating, prey availability or predator avoidance (Wells et al., 1980; Rogan et al., 2000; Culloch, 2004). In the closest bay of Panama City, Balmer et al., (2008) found that, bottlenose dolphins in St Joseph Bay show also a seasonal fluctuation in their abundance, with the highest abundance recorded in May 2005 and the lowest in July 2005.

In our study, each season were investigated only once during the study period, thus we cannot make clear assumptions on a possible seasonal variation in the dolphins' abundance in Panama City. However, data recording, the method and the model used seem to be suit. Indeed, (i) this population follows the same trends in the variation of the population size that found in other areas (Shane, 1980; Ballance, 1990; Wilson et al., 1997; Rogan et al., 2000; Culloch, 2004; Hubard et al., 2004). Moreover, (ii) our results are exactly the opposite of those found by Balmer in St Joseph Bay (2008), and could be compatible if we consider that dolphin's movements occur between

St Joseph Bay and Panama City. Indeed, over 263 identified dolphins we observed six dolphins that were tagged by researchers working in St Joseph Bay (Balmer et al., 2008). These observations provide direct evidence of short movements of dolphins between the two study areas. In addition, tagged dolphins observed in Panama City confirm also the model used to estimate the abundance: a closed population during short photo-ID sessions (3 or 5 days) with an open population, where gains and losses are allowed across longer periods.

Previous works have shown that coastal bottlenose dolphins can reside year-round, such as in the Moray Firth, Scotland with 73 resident dolphins and at least 13 resident bottlenose dolphins in Monterey Bay, California (Zolman, 2002). Resighting data defined a small community of resident dolphins in Panama City, Florida, with high rate of transient dolphins. This high proportion of transient dolphins reveals also important movements in and out of the study area. These transient dolphins may come either from St Joseph Bay, West Bay or East Bay.

However, it is possible that, results have been biased by large individual home ranges, extending beyond the limits of the study area. As we have never prospected West Bay and East Bay, it is unlike that an individual's home range would coincide exactly with the selected boundaries of the study area. Therefore, such biases can provide an underestimation in the proportion of residents and seasonal residents dolphins in Panama City.

Photo-ID catalogues have been created by the researchers working in St Joseph Bay (Balmer et al., 2008) and Apalachicola Bay (Tyson, 2008). In the future, it would be very interesting to match all photo-ID catalogues to give insights into dolphins' movements in the

Florida panhandle and would allow us to estimate the importance of dolphins' movements between those studies areas.

In terms of conservation, the results have shown that dolphins use the study area on a daily basis, with resident animals but also an important proportion of transient dolphins. Trends on seasonal variation are probably observed in Panama City, with the highest abundance recorded in June, when tourism activities are important. It is important to continue and to extend this study on dolphins' abundance and site fidelity to the West Bay and East Bay in order to improve our knowledge about seasonal effect on the population size of *Tursiops* in Panama City. With further information on the population size, we could assess whether this marine mammal population, submitted to significant human activities, is declining or not.

ACKNOWLEDGEMENTS

Special thanks to Thierry Jauniaux, Thierry Hance and Hans Van Dyck for providing encouragement, guidance, and support that made this project possible. I would like to thanks Mr. and Mrs. Richard for all their logistic support during fields work. I thank also Sarah Lessire, Audrey Binet and Kim Verbeke for their help in data collecting. Reny Tyson, Stephanie Nowacek, Dave Johnston from Duke University, in Beaufort, North Carolina and Bryan Balmer from the University of North Carolina Wilmington. Jérôme Vrancken from Université catholic de Louvain for his statistical consulting. Master Goupyl provided informatics assistance. Finally, thanks to Sanna Kuningas, from the *Sea Mammal Research Unit*, for her assistance in program MARK.

This research was carried out under the General Authorization GA LOC # 1055-1732 delivery by NOAA Fisheries, and is a contribution to Biodiversity Research Centre (BDIV) of Louvain-La-Neuve.

FINANCIAL SUPPORT

Research funding was obtained through donations from *Delphus Foundation, the Foundation Léopold III pour l'Exploration et la Conservation de la Nature and Communauté Française de Belgique*. *Canon Belgium* provided the photographic material.

1.3. The Photo-ID catalogue

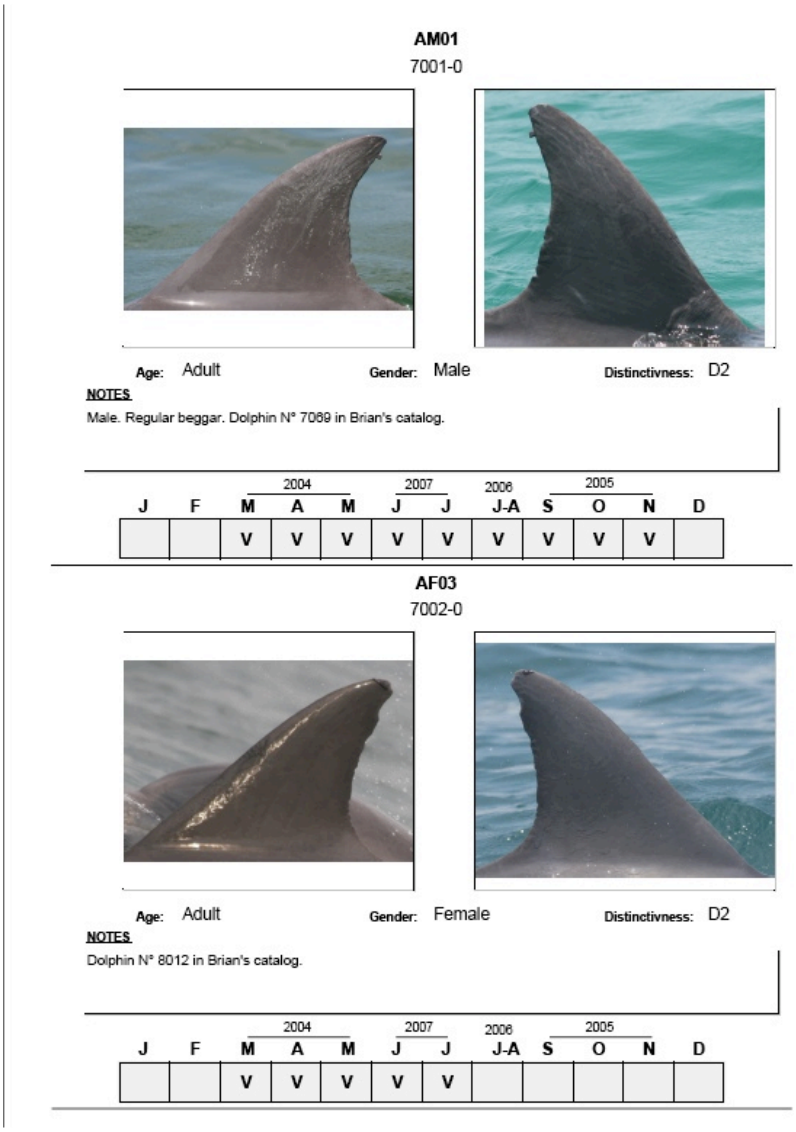

Figure 4.1. An sample of an identification sheet from the photo-ID catalogue, given all information on the identified animal, including ID-codes, the age class, the gender, the distinctiveness and months where the dolphin has been observed.

From the 16,766 pictures that were taken between 2004 and 2007, 263 bottlenose dolphins were identified from the characteristics present on dorsal fins. Dorsal fin image were cropped using Adobe Photoshop CS2©. A photo-ID catalogue has been established in which each individual received two unique identification codes (ID-code):

(i) The first ID-code, **XYZ**, is based on the age class and the gender of identified animals.

(ii) The second ID-code, correspond to the classification system developed by Urian et al. (1999), based on the location of the prominent distinctive markings along trailing edges of dorsal fins.

The catalogue consists of an identification sheet indexing two identified bottlenose dolphins and that contains for each individual, the following information (Figure 4.1):

- the identification code XYZ *(AM01 or AF03)*
- the Urian's ID code *(7001-0, 7002-0,…)*
- the best right side and/or left side of each individual
- the age class *(adult, juvenile or calf)*
- the gender *(male, female or unknown)*
- the distinctiveness *(D1, D2 or D3)*
- notes such as particular behaviours (regular beggar) or life history (presence of hooks in the jaw, eye or other parts of the body, shark bites or female with a new-born or calf)
- and finally, months where each individual have been observed.

The number of individuals present in each categories of the catalogue is resume in the following tables (Tables 4.1).

Using the photo-ID catalogue presented here, researchers will now be able to track all identifiable dolphins for years to come. With this tool, future sightings will reveal the presence or absence of long-term associations between individuals, life history such as future mother-calf pairs and possibly also will provide information on the animals' longevity.

Categories	# individuals
FB-000	6
1000-0	7
2000-0	12
3000-0	7
4000-0	7
5000-0	2
6000-0	74
7000-0	78
8000-0	35
9000-0	35
Total	**263**

Gender	# individuals
Males	15
Females	22
Unknowns	226
Total	**263**
Age Classes	**# individuals**
Adults	238
Juveniles	22
Calves	3
Total	**263**

Tables 4.1. Summary of the number of animals present in the different classes of the photo-ID catalogue as well, the number of dolphins in the three age classes and gender.

Photo-ID catalogue of Panama City

Article 2:

Distribution and group size of bottlenose dolphins, *Tursiops truncatus*, in St Andrew Bay, Panama City, Florida

Bouveroux, Th., and Mallefet, J.

Submitted to the *J. Mar. Biol. Assoc. of UK*.

Inside a group of *Tursiops*. Panama City, July 2007. Photo by Donald Tipton.

2.1. Context

Once we estimated the number of dolphins in Panama City and then the site fidelity of the population, it is essential to determine how animals are distributed in the study area. Moreover, to help consistent conservation and management of this dolphin population, we have to determine the habitat use of animals to determine whether hotspots are present in the study area. Therefore, the second paper, submitted to the *Journal of the Marine Biology Association of the United Kingdom*, investigates the habitat preference and groups size of *T. truncatus.* To characterise their spatio-temporal distribution, we analysed the number of sightings according to zones, the time of the day and months as well as the variation in groups size. GPS data have been analysed by months and plotted on a chart of the study area in order to better delimitate hotspots frequently used by dolphins in Panama City. Tidal influence on dolphin distribution was also evaluated.

Our results show that on average, five dolphins are observed in a group, with significant variation according to zones, time of the day and months. While dolphins are spread throughout the whole of the study area, GPS data reveal a hotspot in and around the mouth of the Channel Entrance, which represents the single connection between the St Andrew Bay and the Gulf of Mexico.

2.2. Manuscript

Distribution and group size of bottlenose dolphins, *Tursiops truncatus,* in St Andrew Bay, Panama City, Florida.

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ABSTRACT

Distribution and group size of bottlenose dolphins in the coastal waters of Panama City, Florida, were assessed between March 2004 and July 2007. 162 surveys, totalling over 1,000 hours spent searching and observing dolphins in a Beaufort Sea State of three or less. During the study period, a total of 1330 groups and 5193 dolphins have been encountered. Dolphins were observed during all surveys. More dolphins were observed during the month of October. The average group size was five dolphins, but varied depending on location, time of the day and months. Habitat preferred by bottlenose dolphins is located in and around the Channel Entrance of Panama City. Tidal modified also the distribution of bottlenose dolphins in the study area. It is suggested that dolphins distribution fluctuates according to prey availability. Data provided by this study might be considered in order to enhance management and conservation of this dolphins population.

KEYWORDS: Bottlenose dolphin, *Tursiops truncatus*, Panama City, distribution, tidal influence, group size, habitat preference.

INTRODUCTION

Common bottlenose dolphins (*Tursiops truncatus*) have an extensive distribution and they are commonly found in shallow coastal habitats, including bays, sounds, estuaries and sometimes in large rivers (Shane, 1980, 1990; Berrow et al., 1996; Reynolds et al., 2000; Quintana-Rizzo & Wells, 2001; Zolman et al., 2002; Read et al., 2003b; Balmer et al., 2008; Cribb et al., 2008). In recent years, many studies aimed to identify critical habitats for bottlenose dolphins. Their spatio-temporal distributions have been related to tidal cycle, bathymetry, prey distribution, risk of shark predation, human presence and/or oceanographic fronts (Hastie et al., 2003b; Ingram & Rogan, 2002; Heithaus & Dill, 2002; Mendes et al., 2002; Cribb et al., 2008).

In the seaside resort of Panama City, a resident bottlenose dolphin population is well known by local people over a long period. Hence, this bottlenose dolphin population became a popular attraction for tourists, who are coming to interact, swim and feed dolphins (Samuels & Spradlin, 1995; Colborn, 1999; Samuels & Bejder, 2004). Moreover, this population is also constantly exposed to other important human activities such as fisheries, military exercises and harbour activities. Therefore, bottlenose dolphins are at risk from anthropogenic disturbance and potential degradation of their habitat.

Management and conservation decisions regarding coastal bottlenose dolphin require basic information on population parameters such as population size, stability, distribution, habitat use, behaviours as well as social organization. Although, the presence of bottlenose dolphin in Panama City has been known for a long time, and occur throughout the year, however group size, and spatio-temporal distribution have not been documented. Data collected at different months will provided also a baseline on the monthly patterns of bottlenose dolphin distribution in Panama City, Florida. These data might be useful for better management and conservation of the Panama City bottlenose dolphin population.

MATERIALS AND METHODS

Study area

The study was conducted in the seaside resort of Panama City (30°07'N, 85°43'W), along the Northwest coast of Florida, where a sand barrier created 5000 years ago by the action of currents, tide, and waves formed St Andrew Bay (Spinner, 1994). St Andrew Bay is linked to the Gulf of Mexico by a single narrow passage, the Channel Entrance. This single passage between the Gulf and the bay may represent an important area for this dolphin population, reason why, we limited the survey area of waters in and around the aquatic preserve, which represent a surface area of approximately 323 Km^2 encompassing the Channel Entrance (Figure 1).

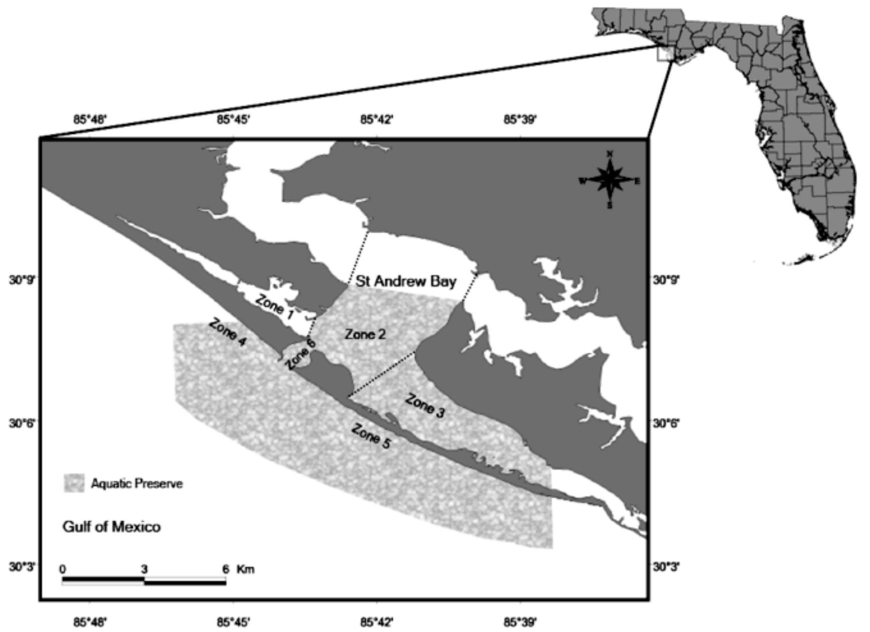


Figure. 1. Map of the study area divided into six different zones delimited based on easily recognisable landmarks. The Aquatic Preserve is represented in light grey.

In order to analyse the spatial distribution of dolphins, we divided the study area in six geographical zones; these zones were delimited based on the topography of the bay: Zone 1: Grand Lagoon (13.8 km^2); Zone 2: St Andrew Bay (109.3 km^2); Zone 3: St Andrew Bay Southeast (76 km^2); Zone 4: West Jetties (52.8 km^2); Zone 5: East Jetties (71 km^2) and Zone 6: Channel Entrance (5.7 km^2). To highlight tidal effects on dolphin distribution, we defined two major sectors in gathering together data collected in zones: the Interior Sector (INT) corresponds to St Andrew Bay waters, including zones 1, 2 and 3; and the Exterior Sector (EXT) i.e. Mexico Gulf waters, that encompasses zones 4 and 5. Finally, to study temporal variations, sampling time was divided into three times periods: AM: 08:00-11:59 hours; PM1: 12:00-15:59 hours and PM2: 16:00-20:00 hours (following Bearzi et al., 1999).

Data collecting

Fieldwork was conducted over four periods: (1) 20 March to 31 May 2004, (2) 28 September to 31 November 2005, (3) 20 July to 21 August 2006, and (4) 1 June to 25 July 2007. Surveys were conducted using small boats powered by 55 to 85 HP outboard engines at a speed around 10 knots, and in a Beaufort Sea State of three or less to optimise sightability. Surveys followed predetermined routes (Figure 2) until a group of dolphins was located, whereupon the survey vessel slowly approached the group and ran parallel to its course, avoiding sudden directional changes.

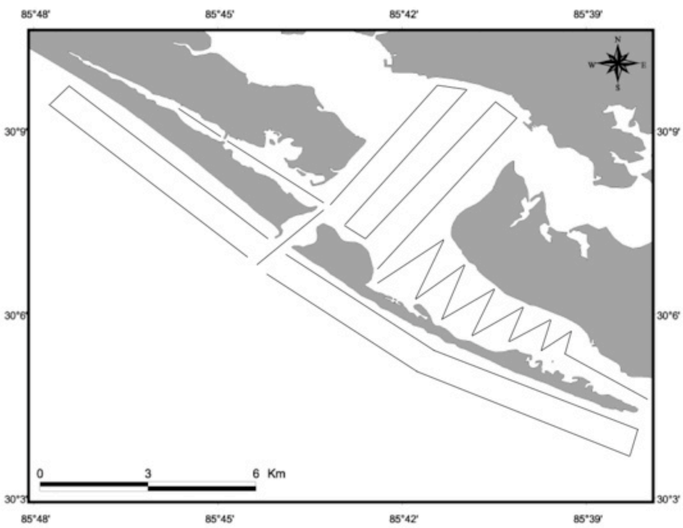


Figure. 2. Typical transects followed for surveys of bottlenose dolphins during the 3-years study (2004-2007).

These predetermined routes ensure an equal effort of observation since the entire region was surveyed uniformly (Table 1). Along these predetermined routes, the total number of dolphins observed was recorded during a complete scan of the studied zone. When dolphins were sighted, the time, the zone of observation, the geographical position using a GPS (Garmin GPSMAP 76S), the tidal current, group size and its composition (number of adults, juveniles, calves and neonates) were recorded. GPS positions of each sighting were plotted on a chart using ArcView 3.3, to observe the repartition and the density of dolphin sightings throughout the study area.

RESULTS

During field periods, 162 survey days were carried out and a total of 1,062 hours were spent searching and observing dolphins in the waters of Panama City (Table 1). During the study period, 1330 groups and 5193 dolphins were encountered (Table 2). Dolphin groups were seen during every survey, but the number of dolphins and groups were highest during the month of October while approximately three times less dolphins were observed in July 2007. The lowest number of dolphin groups was encountered in March-April 2004, with only 95 groups (Table 2).

Months	Days	Zones						
		1	*2*	*3*	*4*	*5*	*6*	**Total**
March-April 2004	26	0,94	0,57	0,37	0,28	0,47	1,71	4,34
May 2004	23	0,8	0,61	0,3	0,28	0,53	1,45	3,97
Sept-October 2005	29	0,9	0,65	0,35	0,42	0,62	1,63	4,57
November 2005	24	0,67	0,54	0,33	0,21	0,42	1,96	4,13
July-August 2006	25	0,87	0,59	0,26	0,26	0,46	1,62	4,06
June 2007	18	0,72	0,53	0,25	0,21	0,35	1,96	4,02
July 2007	17	0,65	0,5	0,23	0,17	0,31	1,22	3,08
Total	**162**	**5,55**	**3,99**	**2,09**	**1,83**	**3,16**	**11,55**	

Table 1. Summary of the amount of time effort (hour/km^2) in each zones and for each months.

Months	Days	N groups	N dolphins
March-April 2004	26	95	589
May 2004	23	196	889
Sept-October 2005	29	270	1159
November 2005	24	224	858
July-August 2006	25	233	575
June 2007	18	172	659
July 2007	17	140	464
Total	**162**	**1330**	**5193**

Table 2. Summary of the number of groups and the number of dolphins encountered for each months.

Group size

The average group size was five dolphins (4.9 dolphins) with a range of 1-31 dolphins. A one-way ANOVA was used to explore the influence of zones and the time of the day on the mean group size of dolphins. The largest groups were observed in zone 4 (N=8.1), while the smallest groups were observed in zone 1 (N=1.7; $p<0.0001$) (Figure 3A). There was also a significant difference between time of day and the average group size ($p<0.0031$) with, dolphin groups were larger in the afternoon than in the morning (AM: N=4.2; PM1: N=5.1; PM2: N=5.2) (Figure 3B). A one-way ANOVA was also used to explore the influence of months on mean group size. Groups size in April was greater than observed during other months ($p<0.0001$), and lest group size was recorded during the month of August (N=3.6) (Figure 3C).

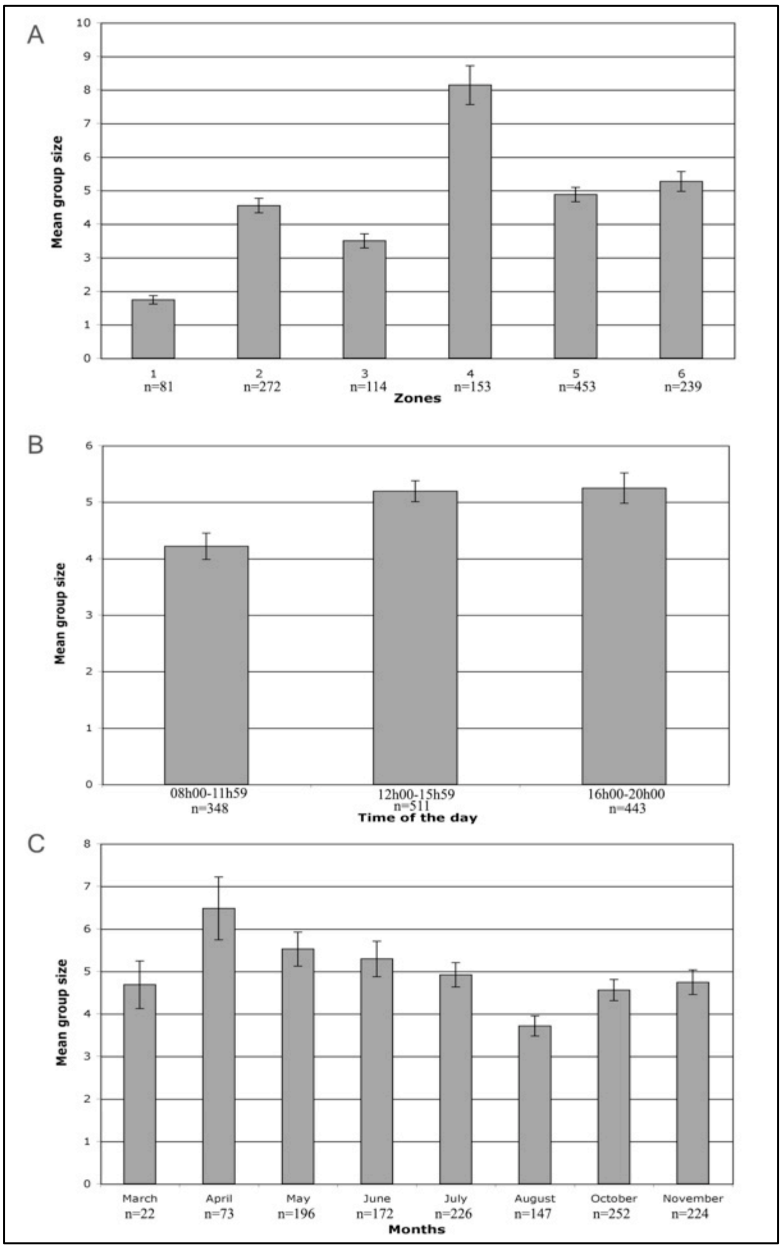


Figure 3. Mean group size, according to A) zones; B) time of the day; and C) months.

Frequency of sightings

Dolphin sightings inside the study area varied with zone. Indeed, the frequency of sightings was the lowest in zones 1 and 3 (10.7% and 8.1%), and highest in zone 6 (30.9%) (Figure 4).

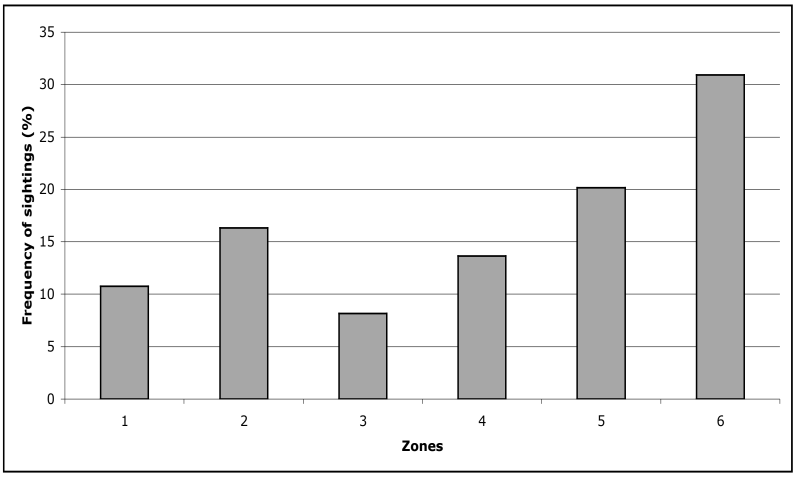


Figure 4. Frequency of bottlenose dolphin observations according zones.

A GLM model was also used to describe the influence of zones and time of the day on the frequency of dolphin sightings. The model shows that zones have significant difference in the variation of frequency of observations, while the time of the day does not influence the frequency of observations (Table 3).

Effect	Num DF	Den DF	F value	Pr > F
Time of the day	2	10	0.33	0.7288
Zone	5	10	10.77	0.0009

Table 3. Results of the GLM model. DF: Free degree; F value= Value of Fisher; Pr > F= Probability of Fisher.

Label	DF	t value	Pr > t
Zone 6 *vs* others	10	5.66	0.0002
Inner zones *vs* outer zones	10	-2.51	0.031
Zone 5 *vs* zone 4	10	1.74	0.1133
Zones 1 & 3 *vs* zone 2	10	-3.2	0.0095
Zone 3 *vs* zone 1	10	-1.5	0.1648
PM1 *vs* PM2	10	0.54	0.6
PM2 *vs* AM	10	-0.6	0.5619

Table 4. Comparison of contrasts realised with the GLM model. The first five contrast investigate the spatial variation in the frequency of observations, and the last two investigate the temporal variation. DF= free degree; T value= Value of the T-test; Pr > t= probability of the T-test.

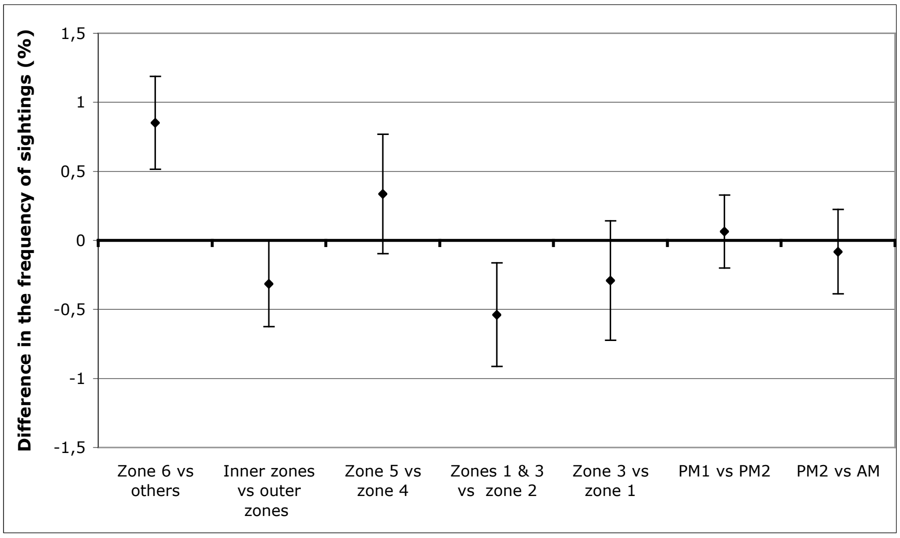


Figure 5. Difference in the frequency observations, with confidence interval (P=0.95), for 7 comparisons of contrast realised on zones and time of the day. AM= 08h00-11h59; PM1=12h00-15h59; PM2= 16h00-20h00.

Results reveal significant difference in the frequency of sightings according zones. Indeed, in the zone 6, the frequency of sighting was on average 0.8 times higher than recorded in other zones. The difference in the frequency observations vary also significantly between inner zones (1, 2 and 3) and outer zones, with frequency of observations on average 0.25 time lower than recorded in outer zones (4 and 5). In zones 1 and 3 frequency of observations were on average lower than recorded in the zone 2. The difference in the frequency of observations between the zone 5 and 4 does not show any significant difference, as well as between zones 3 and 1. Finally, no significant difference was observed when we compare the frequency of observations between time of the day (Figure 5).

The figure 6 shows the repartition of dolphin sightings according zones for each times of the day. In zones 4 and 6, the frequency of observation increased during the day, while they were constant in zone 2. In zone 1, the frequency of dolphin sightings between 12:00 and 15:59 hours (PM1) was low; while in zone 5 the frequency of sighting decreased strongly at the end of the day (PM2), and in zone 3, the frequency was the highest in the morning, between 08:00 and 11:59 hours.

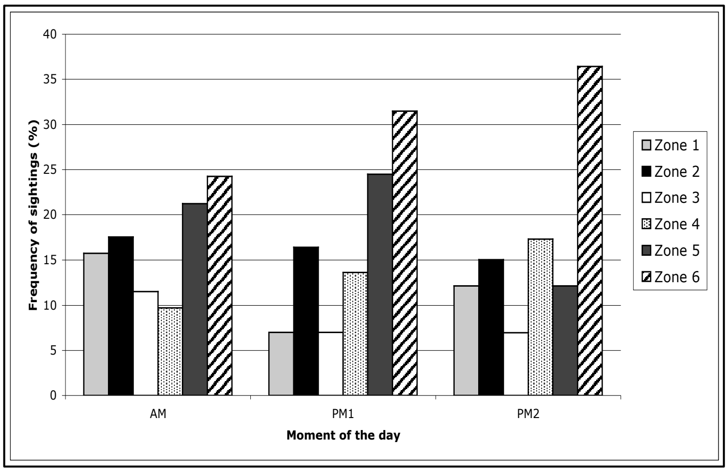


Figure 6. Frequency of bottlenose dolphin observations regarding zones and for each time of the day.

Tidal influence

The presence of bottlenose dolphins in different sectors of the study area has been analyzed in relation to the tidal current. During flood tide, sighting frequency was higher in the interior sector (EXT: 26.7%; INT: 38.6%) while during ebb tide sighting frequency was higher in the exterior sector (EXT: 38.8%; INT: 31.9%) ($p<0.0067$).

Mapping of dolphins sightings

To know the geographical repartition of each dolphin sightings in the study area, and thereby their habitat preference, we reported GPS positions of each sightings on a separate map according to months surveyed between October 2005 and July 2007. Although, dolphin sightings were observed in the whole area, these maps demonstrate, that sightings were mainly concentrated in and around the Channel Entrance (Figure 7). However, the distribution of sightings showed that in November, the greater proportion of sightings was recorded in the Channel Entrance and into the St Andrew Bay, while during other months, dolphins were more frequently observed in the Gulf of Mexico, close to the mouth.

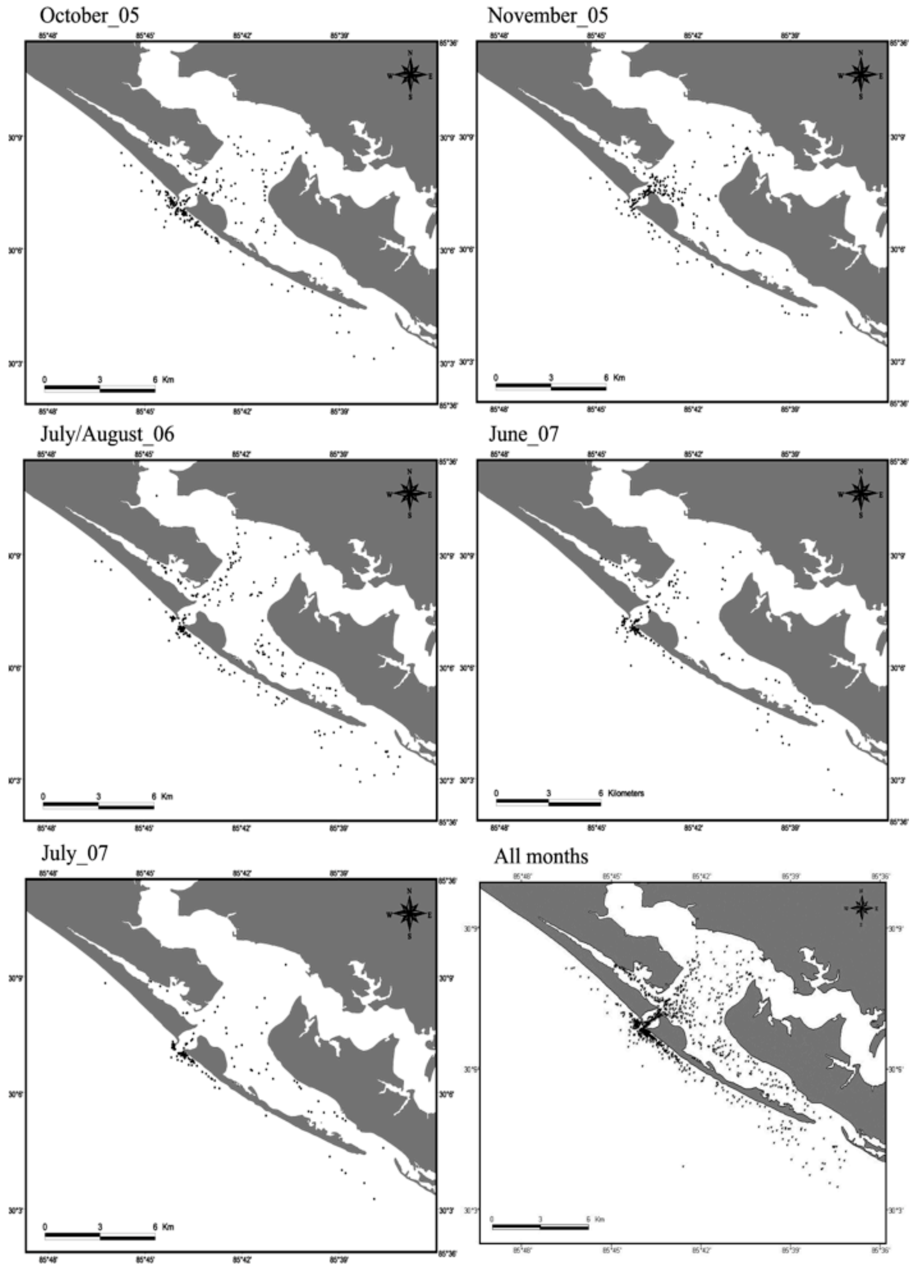


Figure 7. Maps of dolphin sightings located by GPS during the field work conducted between 2005 and 2007 in the Aquatic Preserve of Panama City.

DISCUSSION

Links between fish abundance and dolphin distribution have been highlighted in previous studies around the world (Wells et al., 1980; Barros & Odell, 1990; Acevedo & Burkhart, 1998; Barros & Wells, 1998; Acevedo & Parker, 2000). It appears that bottlenose dolphins favour coastal waters or estuarine systems as feeding areas (Acevedo, 1991; Acevedo & Burkhart, 1998). According to Shane (1990b), dolphins in Aransas Pass, Texas, find benefits from a pass that acts as a funnel to concentrate prey. Therefore, we suggest that dolphins use the channel in Panama City, in a similar way. Indeed, we have observed dolphins using the cooperative hunting technique called “the wall” (Pryor & Norris, 1998), in the channel (zone 6) presumably to compact fish schools in order to trap them between the jetties and the beach located in zone 4.

Our study showed that the presence of dolphins around the channel varied also with tidal. Other studies have also reported that tidal state had a significant influence on the daily distribution of cetaceans (Hansen & Defran, 1993; Mendes et al., 2002) due to the movement of fish along tidal fronts (Johnston et al., 2005). In some places, activities such as feeding have been related to the current strength and the tidal state as dolphins were more abundant during flood tide, especially when the front was stationary (Mendes et al., 2002). In Panama City, sightings were more frequent into the St Andrew Bay during flood tide and into the Gulf of Mexico during ebb tide. These results suggest a similar pattern to that observed in the San Jacinto River, Texas, where movements of bottlenose dolphins occurred against the tidal current (Weeks et al., 1988). Influence of tidal current on other cetacean species has also been documented.

Felleman (1991) showed that killer whales (*Orcinus orca*) moved with the flood tide and against ebb tide. Harbour porpoises (*Phocoena phocoena*), relative density was significantly higher during flood than ebb tide (Johnston et al., 2005). Thus, a general trend seems to be that cetaceans associate with tidal cycles to follow prey.

Group sizes reported for coastal bottlenose dolphins vary widely, with average sizes ranging from three to over 100 individuals (Connor et al., 2000). In Panama City, the mean group size of dolphins was five individuals. These grouping patterns were similar to those reported for dolphins in other protected areas, such as the west coast of Florida (Wells, 1986; Shane, 1990a), in the Northeast Scotland, along the southern coastline of the outer Moray Firth (Culloch, 2004) and in Shark Bay, Western Australia (Smolker et al., 1992). In Panama City, this average number changed according to zones, which could be explained by the characteristics of habitat and the dolphins' activities, as suggested by Shane (1990a) for bottlenose dolphins living in Sanibel, Florida. For instance, foraging activities sometimes required a greater number of dolphins especially when foraging was co-operative (Pryor & Norris, 1998). In a behavioural study conducted in Panama City, our observations highlighted that foraging was most frequently observed in the zone 4 (Bouveroux et al., *submitted b*), where the average group size is the highest. The lowest group size was recorded in zone 1. This zone is characterised by shallow waters with seagrass beds, small oyster reefs, and the presence of several marinas. Taken into account that, low depth associated with probably the low density of prey availability might limit the number of dolphins present in this zone, since it is known that the formation of smaller foraging groups effectively reduces competition among conspecifics when prey density is low (Connor et al., 2000; Gyrax, 2002). It must be pointed that this zone is characterised by a high boating activities, which might disturb large group formation. Most studies on the evolution of group size focus on cost and benefits of behavioural strategies in the contexts of feeding (co-operative foraging), defence of resources against conspecifics, or self-defence against predators. Larger groups use less energy during prey capture (Creel & Creel, 1995), help in the early detection and defense against predators and help in the defence of territory, females, or feeding resources against conspecifics (Connor et al., 2000; Gyrax, 2002). The daily variation of group size might be associated with dolphin activity. Indeed, a behavioural study conducted in Panama City shows that foraging and sexual peaks were observed in the evening (PM2), and yet larger group were recorded during both activities (Bouveroux et al., *submitted b*). Group size of dolphins in Panama City was the largest in April and the lowest in August, while in Turneffe Atoll, Belize, larger groups of bottlenose dolphins were recorded in fall and smaller groups in spring and summer.

This research reveals a preferential distribution of dolphins in the study area, influenced by the time of the day and the tidal current. The habitat preference of dolphins might be related to the prey distribution. Indeed, a greater density of prey coupled with interesting site topography, may represent an advantage in term of energetic cost for catching prey by dolphins. However, additional work is needed to further explore the relation between the distribution of bottlenose dolphins and their prey throughout seasons, and we suggest also to expand the study area for future researches to the West and the East Bay of Panama City.

In terms of conservation, the habitat preference of dolphins inside and around the channel entrance is very important and should be taken into account in conservation management. Indeed, inside the Channel Entrance, a lot of boats are crossing the channel, sometimes with high speeds, that increase risks of collisions between boats and dolphins. Therefore we recommend a maximum speed limit through the channel, in order to limit collisions between boats and dolphins, as well the noise disturbance from boat propellers.

ACKNOWLEDGEMENTS

Special thanks to Douglas Nowacek, from Duke University, in Beaufort, North Carolina, for his encouragement, guidance, and support during this study. Mr. and Mrs. Richard for all their logistic support during fields work. I thank also Sarah Lessire, Audrey Binet and Kim Verbeke for their help in data collecting. Reny Tyson, Stephanie Nowacek, from Duke University, in Beaufort, North Carolina. Jérôme Vrancken from Université catholic de Louvain for his statistical consulting, and Master Goupyl for the best informatics assistance. Jérôme Mallefet is research associate FNRS.

FINANCIAL SUPPORT

Research funding was obtained through donations from *La Fondation Delphus, La Fondation Léopold III pour l'Exploration et la Conservation de la Nature and Communauté Française de Belgique*. *Canon Belgium* provided the photographic material.

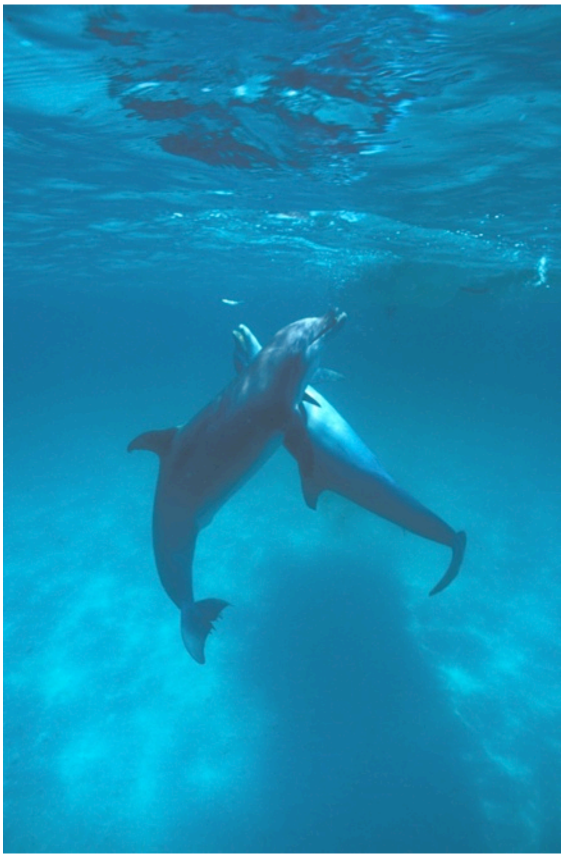
This research was carried out under the General Authorisation GA LOC # 1055-1732 delivery by NOAA Fisheries, and is a contribution to Biodiversity Research Centre (BDIV) of Louvain-La-Neuve.

Article 3:

Behavioural patterns of bottlenose dolphins, *Tursiops truncatus*, in a popular seaside resort: study case of Panama City, Florida.

Bouveroux, Th., Nowacek, D.P., and Mallefet, J.

Submitted to the *journal of Marine Biology*.



Two bottlenose dolphins at meal. Panama City, 2003. Photo by Donald Tipton.

3.1. Context

The second article determined how dolphins were distributed within the study area. Since, the spatio-temporal distribution of dolphins is known, we can study how animals use their habitat in their daily and seasonal activities. Therefore, the third paper aims to characterise how dolphin activities vary with time of the day, zones and months, and to localise areas where vital activities of dolphins are observed. Five natural behaviours (*playing, social, sexual, foraging and traveling*) were analysed. In addition to these, a non natural behaviour generated by humans, «*the begging behaviour*», has been recorded and analysed. GPS data of dolphin behaviours have been plotted on a chart to document the habitat used of these activities.

Results show a significant difference in the diurnal pattern of dolphin behaviours. Significant differences were also observed according to zones and months. Foraging hotspot is found near shore, the West Jetties, and in the Channel Entrance. The non natural behaviour of begging was more frequently observed during the tourist season (April to August), and was highly concentrated at the West end of Shell Island.

3.2. Manuscript

Behavioural patterns of bottlenose dolphins, *Tursiops truncatus,* in a popular seaside resort: study case of Panama City, Florida.

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ABSTRACT

Field surveys were conducted between 2004 and 2007 in the study area of Panama City, Florida, a very popular seaside resort. The aims of this study are to characterise the diurnal and seasonal activities of bottlenose dolphins and to document the habitat use of this bottlenose dolphin population. Behavioural activities of focal groups were recorded each 5 minutes with sample duration of 5 minutes. Systematic surveys following predetermined routes were used to conduct this study. Results show variations in the diurnal patterns of dolphin behaviours, with social behaviour being the dominant activity throughout the day. The number of observations of playing, sexual and begging behaviours increased during the day. Evidence of a feeding peak in the evening is recorded. High proportions of playing activities were recorded near shore Shell Island, while a preferred foraging area has been highlighted near shore the West jetties and in the Channel Entrance. Behavioural patterns of dolphins vary also according to months, social behaviours decrease from May to August and increase during October and November. Begging behaviours, an unnatural behaviour in wild dolphins, were more often observed during the tourism season (April to August), and occurred mainly near shore the East jetties. Significant variation in the group size according to the dolphins' behaviours and zones were observed.

KEYWORDS: *Tursiops truncatus*, behaviour, Florida, begging, human activity, St Andrew Bay, Panama City

INTRODUCTION

Bottlenose dolphins, *Tursiops truncatus* (Montagu, 1821), live in a wide range of habitats from cold temperate to tropical waters, including pelagic waters, coastal shallow waters, estuaries, bays, fjords, lagoons, and sometimes in large rivers (Bräger et al., 1994; Scott et al., 1990a; Wilson et al., 1997; Defran and Weller, 1999; Ingram and Rogan, 2002; Zolman 2002; Lusseau et al., 2003b; Nowacek, 2005). Previous studies have shown that behavioural patterns of dolphins are closely tied to local ecology (prey distribution, predator distribution, bathymetry, tidal influence and human presence) and may thus change from one type of habitat to another (Shane 1990a; Reynolds et al., 2000; Nowacek et al., 2001; Mendes et al., 2002; Constantine et al., 2003; Hastie et al., 2004; Samuels and Bejder, 2004). This behavioural flexibility contributed to their success in diverse habitats, and the best example of the dolphin's flexibility is probably the great diversity recorded in foraging behaviours and techniques (Shane 1990b; Rossbach and Herzing, 1997; Acevedo, 1999; Nowacek, 2002; Sargeant et al., 2005). With the increase of human demography in coastal habitats, marine mammals are more and more exposed to a variety of human activities, and are therefore subject to potential injury or disturbance from anthropogenic activities (Nowacek et al., 2001; Noke and Odell, 2002). Several activities were identified as potentially impacting on marine mammal species at the individual or population level, such as noise pollution from military/industrial activities, coastal degradation, vessel collisions, interactions with fishing gear, and tourism (Wells and Scott, 1994; Wells and Scott, 1997; Nowacek et al., 2001; Jauniaux et al., 2002; Noke and Odell, 2002; Buckstaff, 2004; Laura, 2009). Whether, direct effects of human activities on marine mammals, such as injuries from boat collisions, are easy to observe, indirect effects have been also documented on the behavioural patterns of animals. In the presence of boats, marine mammals may adopt specific responses such as change in dive length, surfacing patterns, foraging habitat selection, shifts in local habitat use or increasing of swimming speed (Nowacek et al., 2001; Glen, 2003).

In Panama City, Florida, the regular presence of the bottlenose dolphins population is well known by tourists who are coming to interact, to swim and to feed dolphins, since along time (Samuels and Spradlin, 1995; Colborn, 1999; Samuels and Bejder, 2004). Therefore, this bottlenose dolphin population is a popular tourist attraction. All of these activities are prohibited by the *Marine Mammal Protection Act (MMPA*) of 1972 as they all cause changes in the dolphins' behaviour (NMFS, 2007). In addition, this dolphin population is also constantly submissive to other significant human activities such as boating, fisheries, military activities, and harbour activities.

Objectives of this present study are to evaluate diurnal and seasonal behaviours as well as the habitat use of bottlenose dolphins in Panama City waters. An important part in the ecology of an animal population is the study of the behaviours. Indeed, an accurate knowledge of the spatial arrangement of the daily and the seasonally behaviours is required to determine how an animal population uses its habitat for their vital activities such as feeding, mating, travelling…?

MATERIALS AND METHODS

Study area

The seaside resort of Panama City (30°07'N, 85°43'O) is located on the Northwest Florida panhandle. Panama City is a very popular tourist location. Indeed, permanent human residents are estimated to be 9,500 but increases to a peak daily population of approximately 90,000 during summer (Official Website of Panama City, Florida - www.pcbgov.com).

The study area was composed by the St Andrew Bay, which is linked to the Gulf of Mexico by a single narrow channel and coastal waters of the Gulf of Mexico. This single communication between the Gulf and the bay may represent a strategic area for this dolphins' population. Therefore, for this study, we limited the survey area of waters in and around the aquatic preserve, which represent a surface area of approximately 323 km^2 and that encompass the Channel Entrance (Figure 1).

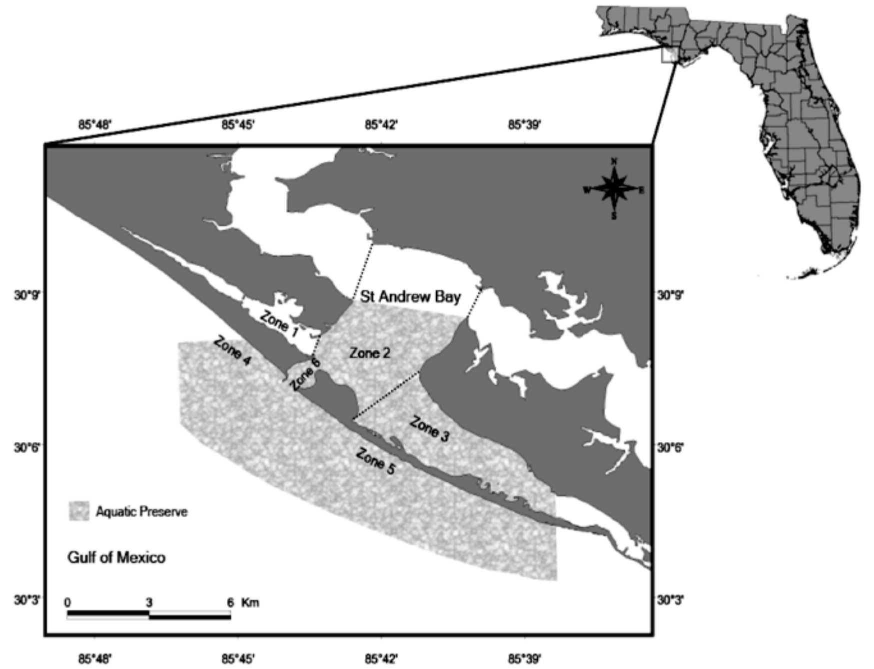

Figure 1. Map of the study area showing the study area divided into six different zones delimited based on easily recognizable landmarks. The Aquatic Preserve is represented in light grey.

To facilitate the geographical location of the dolphins and then to document their spatial distribution, we divided the study area in six parts of different size as zones of observations; these zones were delimited based on the topography of the bay: Zone 1: Grand Lagoon (13.8 km2); Zone 2: St Andrew Bay (109.3 km2); Zone 3: St Andrew Bay South East (76 km2); Zone 4: West Jetties (52.8 km2); Zone 5: East Jetties (71 km2); Zone 6: Channel Entrance (5.7 km2).

Sighting records

The surveys were conducted using small boats powered by 55 to 85 HP outboard engines at a speed around 10 knots. Fieldwork was conducted over four periods:

(1) 20 March to 31 May 2004, (2) 28 September to 31 November 2005, (3) 20 July to 21 August 2006, and (4) 1 June to 25 July 2007. During field periods, 162 survey days were carried out in a Beaufort Sea State of three or less to optimise sightability, and a total of 1062h28 were spent searching for and observing dolphins in the waters of Panama City. Surveys followed predetermined routes (Figure 2) until a group of dolphins was located, whereupon the survey vessel slowly approached the group and ran parallel to its course, avoiding sudden directional changes. These predetermined routes ensure an equal effort since the entire region was surveyed uniformly.

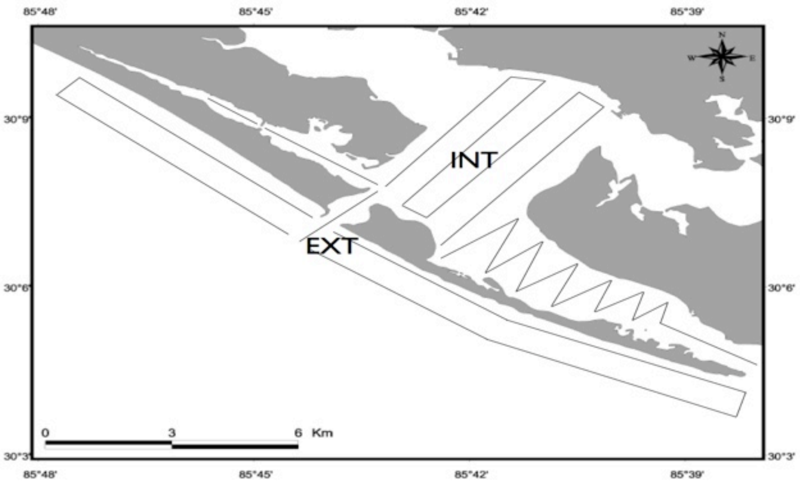

Figure 2. Typical transects used for surveys of bottlenose dolphins during field works between 2004 and 2007. INT= Interior sector, composed by zones 1, 2 and 3 (corresponding to St Andrew Bay waters) and EXT= Exterior sector, composed by zones 4 and 5 (corresponding to Gulf of Mexico waters).

Behavioural data

Behavioural data were recorded every five minutes, with a sampling duration of five minutes that allowed adequate time for both observations and recording of dolphins' activity and then upon a change in group (modified from Shane, 1990a; Samuels and Bejder, 2004). For each group followed, we recorded the time, the zone of observation, geographical position using a GPS, group size and its composition (number of adults, juveniles, calves and new-borns). Observed behaviours were classified into five categories (playing, social, sexual, foraging, travel) according to the definitions adapted by Shane (1999a) and Dudzinski (1996). In addition to these five categories, begging behaviour, which is an unnatural behaviour in wild dolphins, was added. Because the man was feeding dolphins since a long time in Panama City, some of individuals in the population show now begging behaviours. We defined this particular behaviour as "*any dolphin approaching a boat, raising their head out of the water and opening their mouth*". This behaviour was sometimes observed to lead to food intake from humans. Finally, to ease the statistical analyses, data on behaviours were classified into three arbitrary categories of time. Thus, three different time periods were created (Bearzi et al., 1999):

1) AM: 08h00-11h59 hours; 2) PM1: 12h00-15h59 hours; 3) PM2: 16h00-20h00 hours.

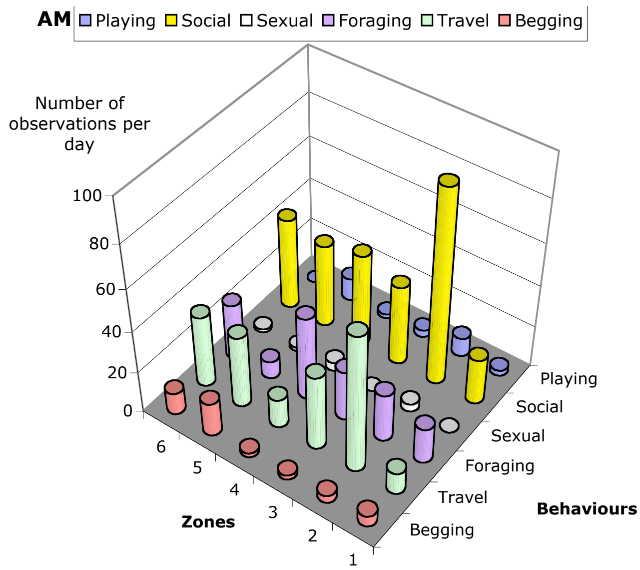

Figure 3a. Repartition of the dolphin activities between 08h00 and 11h59 (AM).

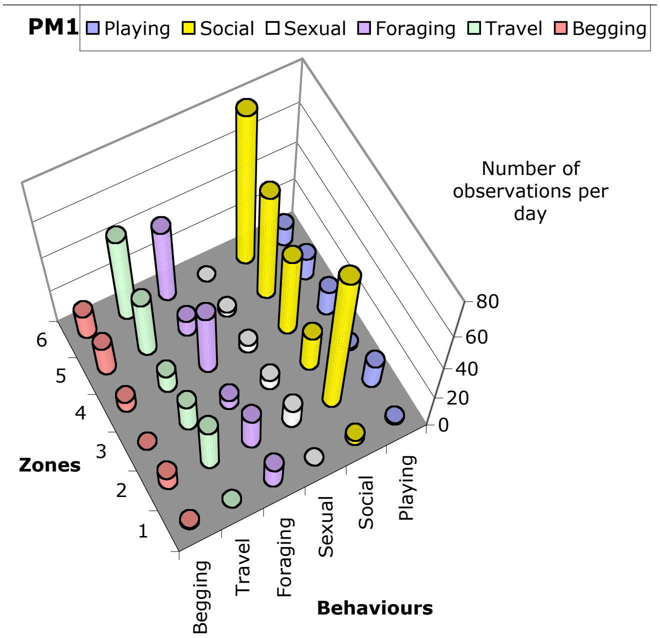

Figure 3b. Repartition of the dolphin activities between 12h00 and 15h59 (PM1).

RESULTS

Diurnal patterns of dolphin behaviours according to zones

To evaluate the daytime pattern of dolphin behaviours in Panama City, we analysed the number of behavioural observations recorded according zones, for each time of the day. Because, zones were different sizes, they have been prospected with different time efforts. Therefore, we weighting the number of observations by the quantity of time spent in each zones and for each times of the day. Our results show that the repartition of the dolphin behaviours throughout the day and according to zones varied strongly. During the morning (Figure 3a), social behaviours were prevailing in each zones, especially in zone 2, while playing and sexual activities were less observed whatever the zone. Foraging behaviours were more observed in zone 4; travelling occurred mainly in zone 2, but was also observed in zones 4, 5 and 6. Begging behaviours were essentially observed in zone 5. In the afternoon (Figure 3b), social behaviours were the main activity, except in zone 1, where the main activity recorded was foraging. The number of playing behaviours observed, increased from the morning, in zones 2, 4, 5 and 6. Sexual behaviours were less observed, but the number of sexual behaviours increased in zone 2, 3 and 4. Foraging activities were less observed than during the morning, but this activity still occurred in zones 4 and 6. Travelling was mainly observed throughout the zone 6, between St Andrew Bay and the Gulf of Mexico, but also along Shell Island (zone 5). Finally, begging behaviours occurred in zones 4 and 6. At the end of the day (Figure 3c), social behaviours were always the most observed activity in zones 2 and 5. The number of playing activities increased strongly in zone 5, while sexual peaks were observed in zones 2 and 5. The number of foraging observations has been increasing during the day, with a peak of foraging observed in zone 4. This activity was also observed in zones 2 and 5. Travelling occurred mainly along Shell Island, but also between zones 2, 3 and 6. During the day, begging behaviour increased and was mainly recorded in zone 5.

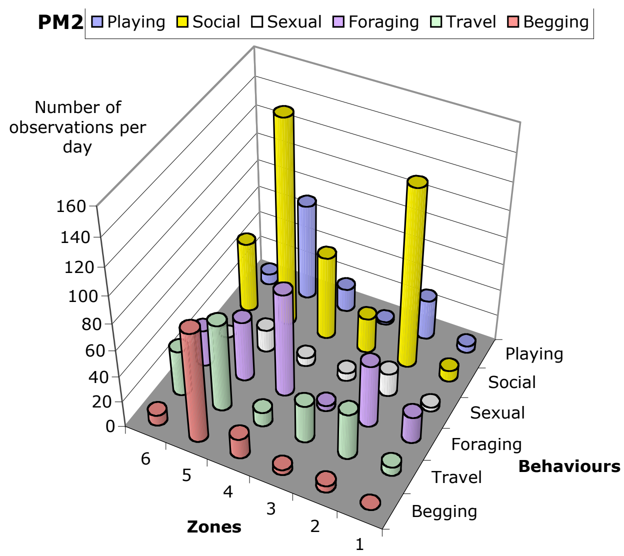

Figure 3c. Repartition of the dolphin activities between 16h00 and 20h00 (PM2).

Mapping of dolphins behaviours

To know the geographical distribution of each behavioural activity in the study area, and thereby the habitat use of Tursiops in Panama City, we reported GPS positions of each behavioural category observed on a separate map of the study area. Analyses of maps show that sightings rates were mainly concentrated in and around the Channel Entrance. Also, we can easily establish that most begging activities, including food intake from humans, were mainly recorded in the West end of Shell Island. Social behaviours were the most widespread behaviour inside the study area. Foraging behaviours were observed in all zones, but occurred more often in both mouth of the channel. Playing behaviours were also more recorded in and around the Channel Entrance. Sexual activities were never observed inside the channel while travelling is highly frequent in the channel (Figure 4).

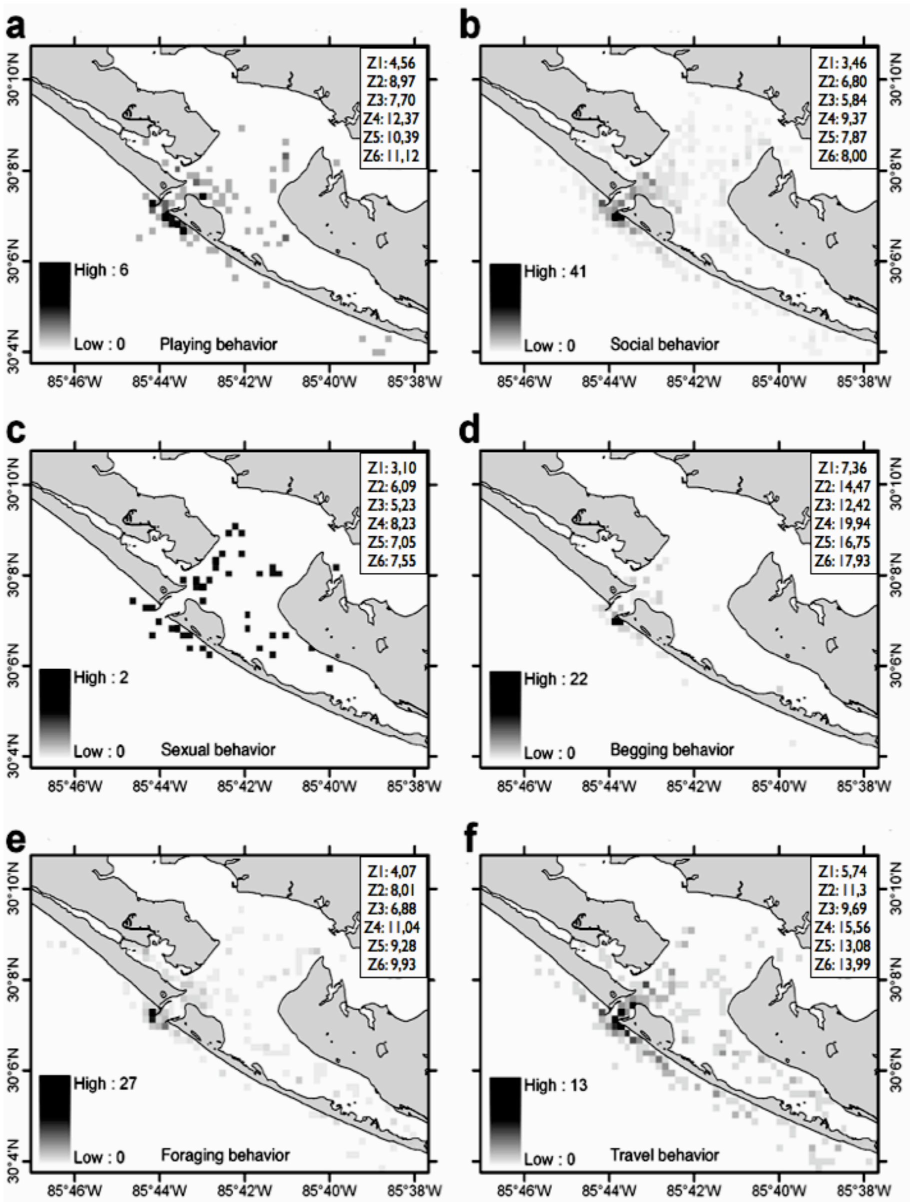

Figure 4. Distribution of sightings for the six behavioural activities studied. a) Playing behaviour; b) Social behaviour; c) Sexual behaviour; d) Begging behaviour; e) Foraging behaviour; f) Travel behaviour. Mean groups size predicted by the model for each zones and for each behaviours are given in the upper right corner.

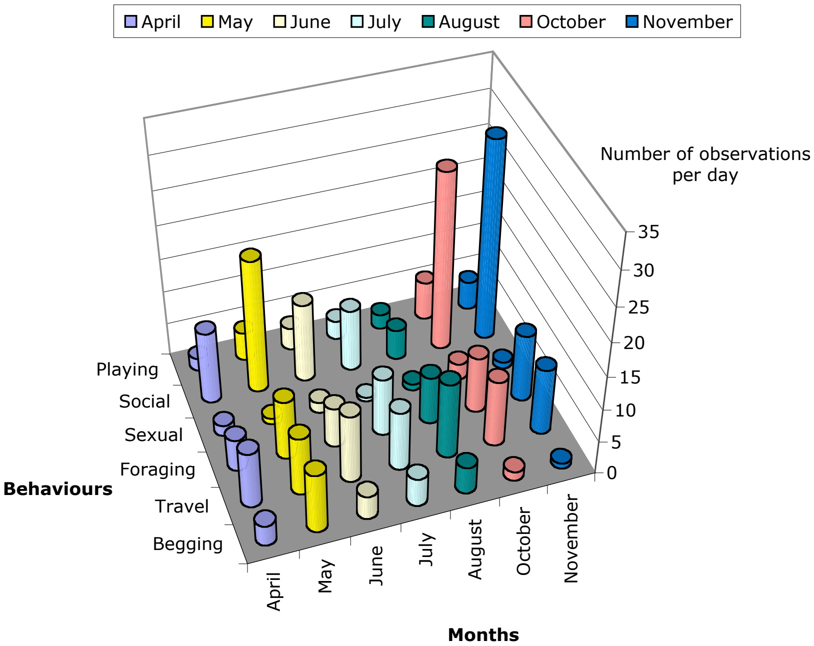

Figure 5. Seasonal distribution of each dolphins behaviours.

Mean group size according to behaviours

Behavioural patterns according to months

The behavioural patterns of dolphins according to months were evaluated as function of the 7 months investigated during fieldwork (Figure 5). Results show that social, foraging and travelling behaviours were dominant whatever the months, while sexual behaviour was the lower activity observed. However, social activities decreased strongly during the tourism season (from May to August), while the number of social activities recorded were the highest during the fall (October and November). The number of observations of foraging and travelling behaviours were similar throughout months. Begging behaviours were less observed in October and November, while the number of begging behaviours was higher between April and August, with a peak recorded in May. During the months of May, October and November, the number of playing behaviours were higher than during other months.

Mean group size changes significantly with behaviours (*ANOVA I: F=13.9, df= 5, P<0.0001*). For playing, social and foraging activities mean group sizes were composed of 6 to 7 dolphins (range between 1-30 individuals). Larger groups were recorded when dolphins were engaged in sexual behaviours. Begging behaviours were observed in groups with less than 4 dolphins in a group. During travelling activities, the mean group size was approximately composed of five dolphins (Figure 6).

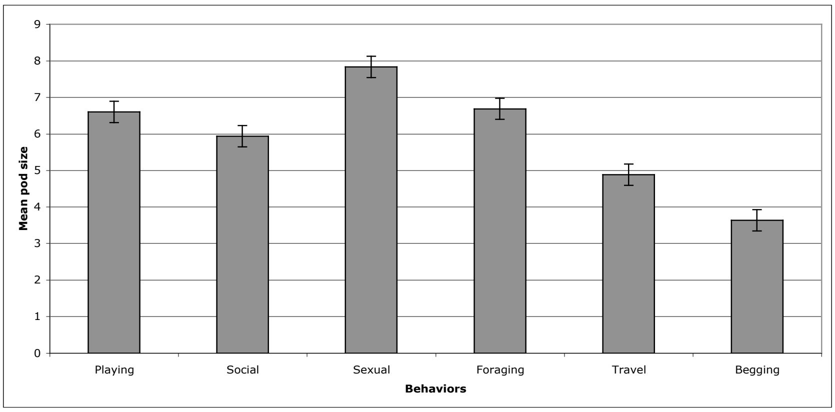

Figure 6. Mean group size observed according dolphin behaviours.

In a previous analysis, we showed that mean group size varied also significantly with time of the day and the observed zone (Bouveroux et al., *submitted a*). Therefore, we evaluated the variation of the mean group size according to behaviours, zones and time of the day, using three different log-linear models.

The first model tested only the influence of the behavioural activity on the mean group size:

Models		**AIC**
Model 1	log (*Gs*)= I + Behaviours + error	2617.4
Model 2	log (*Gs*)= I + Behaviours + Zones + error	2510.4
Model 3	log (*Gs*)= I + Behaviours + Zones + Moment of the day + error	2511.4

Table 1. Akaike's information criterion (AIC) results from the three models built to describe the evolution of the mean group size according to three parameters: Behaviours, Zones and Moment of the day. *Gs*= Group size; I= intercept.

Effect	**Estimate**	**CI Lower**	**CI Upper**	**Std Error**	**Pr > F**
Intercept	2.6954	2.366	3.0247	0.1679	< 0.0001
Playing	-0.2864	-0.4043	-0.1686	0.06005	< 0.0001
Social	-0.564	-0.652	-0.4761	0.04482	< 0.0001
Sexual	-0.6738	-0.8553	-0.4923	0.09253	< 0.0001
Begging	0.1912	0.057	0.3254	0.06839	< 0.0053
Foraging	-0.4	-0.5043	-0.2956	0.05319	< 0.0001
Traveling	-0.05654	-0.1504	0.03735	0.04786	< 0.2377
Zone 1	-0.8906	-1.0837	-0.6975	0.0984	< 0.0001
Zone 2	-0.2142	-0.3393	-0.08903	0.06379	< 0.0001
Zone 3	-0.3673	-0.5243	-0.2104	0.08002	< 0.0001
Zone 4	0.1064	-0.0386	0.2514	0.0739	< 0.0001
Zone 5	-0.06787	-0.1829	0.04719	0.05865	< 0.0001
Zone 6	0	.	.	.	.

Table 2. Results from the best model describing the variation in the mean group size of dolphins. The table shows the contribution of each behaviours and zones on the mean group size. Results are expressed as a logarithm. CI: confidence interval; Std Error: standard error and Pr > F: Probability of Fisher.

(i) $\mathbf{Log(\mathit{Gs_i}) = \mu + B_{1i} + B_{2i} + B_{3i} + B_{4i} + B_{5i} + B_{6i} + \varepsilon_i}$ **;**

In the second model, we tested the contribution of the zones on the mean group size. Since each dolphin's sighting was carried out in only one zone, the model was:

(ii) $\mathbf{Log(\mathit{Gs_i}) = \mu + B_{1i} + B_{2i} + B_{3i} + B_{4i} + B_{5i} + B_{6i} + Z_i + \varepsilon_i}$ **;**

Finally, in the third model, a combination of the three factors was performed: behavioural activity, zones and time of the day:

(iii) $\mathbf{Log(\mathit{Gs_i}) = \mu + B_{1i} + B_{2i} + B_{3i} + B_{4i} + B_{5i} + B_{6i} + Z_i + Ti + \varepsilon_i}$ **;**

where *Gs* is the group size; μ the mean ; *i* the observation number; B_{1i} *to* B_{6i} the behavioural category observed; *Zi*, the zones (1 to 6); Ti, the moment of the day (AM, PM1 or PM2) and ε_i the error.

Model suitability was determined by having the lowest Akaike's Information Criterion (AIC) values (Table 1). Results from the model show that all behaviours, except travelling, influence significantly the mean group size of dolphins. Mean groups size varies also significantly with the observed zone, excepted in the zone 6 that represent the normality inside data set.

With this kind of model, we are now able to make predictions on the mean group size that we could observe in a particular zone when a specific dolphins' activity is observed (Figure 5). For instance, during foraging activities in zone 4, the mean group size will be: Log(Gs)= 2.6954 – 0.4 + 0.1064= 2.4018 and then Gs=exp (2.4018)= 11.04. So, approximately 11 dolphins could be observed when dolphins are foraging in the zone 4 (Table 2 and Figure 5).

DISCUSSION

Diurnal patterns of dolphin behaviours

Dolphin behaviours can be influenced by a number of ecological variables and behavioural responses can differ considerably depending on the habitat in which animals are studied (Shane, 1999a, b). Comparison of behavioural data among study areas is sometimes complicated, because of the methodological differences in data collection or in the definition of behaviours (Shane 1990b; Bearzi et al., 1999; Mann, 1999). However, numerous behavioural studies over the world have revealed diurnal activity patterns in the bottlenose dolphin (Shane, 1990a, b; Hansen and Defran, 1993; Pryor and Norris, 1998; Bearzi et al., 1999; Connor et al., 2000).

This study shows also a diurnal variation in the majority of behaviours and we can note some similarities with other populations of bottlenose dolphins, e.g. in Sanibel Island (Florida) or in Port Aransas (Texas). Travel is the main activity for bottlenose dolphins in these two study areas (Shane, 1990b), and feeding peaks were observed in the morning and in the evening for dolphins in Sanibel and in Port Aransas, (Shane, 1990a, b). According to sites, the diurnal time budget recorded, ranges between 13% to 40% for feeding behaviour and 45% to 67% for travelling (Shane, 1990b, Hansen and Defran, 1993; Reynold et al., 2000). In Panama City, feeding peaks were recorded in the morning and the evening while travelling was more frequently observed in the morning than in the afternoon. Travelling essentially occurs to avoid predators, to go to the resting site(s), or to go to the hunting area(s), given that prey resources are variable in space and time (Hansen and Defran, 1993; Connor et al., 2000). Bottlenose dolphins present a complex social structure with fission-fusion proprieties in which individuals enter into partnership with a small group that can change in composition during the day although, relationships for a long period can exist between individuals in a group, such as males associations and mother-calf associations (Wells et al., 1987; Perrin et al., 2002; Reynolds et al., 2000). Therefore, social behaviours are important components of the daily activities of dolphins in Panama City, reinforcing links between individuals. In other inshore habitats, time budget of socializing range between 4% to 23% (Shane, 1990b; Hansen et Defran, 1993; Reynolds et al., 2000).

Habitat use of bottlenose dolphins

It is known that bottlenose dolphins preferentially use their habitats in accordance to their activities (Wilson et al., 1997; Ingram and Rogan, 2002; Hastie et al., 2004; Hastie et al., 2006; Sargeant et al., 2007). Feeding habits, in particular, have a great importance in shaping the behavioural patterns of Tursiops (Baros and Odell, 1990; Bearzi et al., 1999; Sargeant et al., 2005). The same strategy is found for bottlenose dolphins living in Panama City. Indeed, cartography data of all behavioural activities reveal that the Channel Entrance of Panama City is the most important spot for this population. All behaviours are concentrated in and around the channel and with higher probabilities to be observed than in other parts of the study area. The channel represents the single connection between the Gulf of Mexico and the St Andrews Bay, therefore dolphins use regularly the channel to travel into the study area. Within the channel, deep water, tide currents and waves represent an interesting place for playing behaviours. In addition, human presence is also important in those zones, with boats or big ships that dolphins approach for bow-riding. Whether foraging behaviours have been observed in all zones of the study, yet we can see that the major part of the observations are concentrated in the two mouths of the channel. Links between prey distribution and dolphins' distribution have been highlighted in previous studies around the world (Wells et al., 1980; Barros and Odell, 1990; Acevedo and Burkhart, 1998; Barros and Wells, 1998; Acevedo and Parker, 2000). According to Hastie et al., (2004), feeding behaviours are influenced by the bathymetry, with certain forms of feeding occurring primarily in deeper waters. Shane (1990b), in Aransas Pass, suggested that the pass acts as a funnel that concentrates preys. In Panama City, feeding behaviours may be related to tide current leading fish aggregation in the Channel Entrance. Using the jetties and the beach present around the Channel Entrance, dolphins display a cooperative technique of hunting: the "wall" technique, allowing to trap schools of fishes between the beach and the jetties. Many fishes are present in the Channel Entrance and near the jetties (Bouveroux, 2004), making this zone an interesting feeding area for dolphins.

Behavioural pattern according to months

The annual presence of this dolphin population might be related to the establishment of the Aquatic Preserve in 1972 in the waters of Panama City. Indeed, the St Andrew Bay has a great diversity of marine species and profit from the largest expanse of seagrass beds in the Florida panhandle (Keppner and Keppner, 2005). Moreover, the presence of a large bay, with small lagoons and the single connection between the bay and the Gulf of Mexico, represent strategic habitats for dolphins.

Studies on dolphin behaviours show that seasonal patterns occur in other populations over the world (Shane 1990b; Jacobs et al., 1993; Mann et al., 2000). Indeed, peaks in foraging frequency are observed during the fall for bottlenose dolphins in Port Aransas (Texas) and in Sanibel Island (Florida). Shane et al., (1990b) suggested that these foraging peaks may be related to dolphins building up fat stores in preparation for winter. Social behaviours in Panama City are dominant mainly in May, October and November. Shane (1990a) found in Sanibel Island, that socializing was also more frequently observed in fall and winter, suggesting to be a possible protracted breeding season. In Shark Bay, wild bottlenose dolphins show clearly a breeding peak between October and December (Mann et al., 2000). This present study shows that dolphins were sexually more active in October hence reinforcing the hypothesis of a protracted breeding season in Panama City. However, to confirm those trends, a long-term following survey of dolphin behaviours will be necessary to pursue the study on seasonal patterns of dolphin activities during next years.

If similarities with other populations were found, some differences were nevertheless noticed. In Panama City, travelling is evenly distributed throughout seasons, which is not what is observed in other places such as in Sanibel Island, in Port Aransas, or in the Newport River Estuary (North Carolina) (Shane, 1990b, Jacobs et al., 1993). Assuming that travelling occurs to going to the hunting area(s) or resting site(s) (Connor et al., 2000), the similar seasonal distributions of travel and foraging could be due to the fact that the dolphins in Panama City can find enough food and resting site(s) all year round, limiting their movements in and out of the study area.

The begging behaviour

The bottlenose dolphins in Panama City are exposed to significant human activities and show direct evidence of disturbances from human. Indeed, these repeated interactions have altered dramatically wild behavioural patterns of several individuals in the *Tursiops* population. The best evidence comes from begging behaviours of individuals that regularly approach boats to be provisioned by humans. Begging behaviours mainly occur in the afternoon, especially between 16h00 and 20h00, and this activity is very concentrated around the West end of Shell Island, that was baptised “the interaction beach” in the study conducted by Samuels and Bejder (2004). Among dolphins living in Panama City, only some individuals can be considered to be “regular beggars” hence having interactions with humans on a regular basis. Even if it is very difficult to estimate the exact number of feeding events and its impact on dolphins behaviours in Panama City, some dolphins having regular interactions with human showed serious injuries such as hooks protruding their jaws or even stuck in the eye. The most probable scenario observed is that sometimes dolphins come to steal a fish from fishing lines. We also could observe that the distribution of one female and her calf, was tightly linked to the presence of boats, while other dolphins show a widespread distribution. Similar problems of fishing gear ingestion have been documented in the Indian River Lagoon (Texas), in Shark Bay (Western Australia), and in Sarasota Bay (Florida) (Mann, 1995; Noke and Odell, 2002). Along the central Florida west coast, two cases of fishing gear ingestion, leading directly or not to the death of two of 23 dead-stranded bottlenose dolphins were documented (Gorzelany, 1998). It is important to note that begging may not prevent the mother from teaching to her young dolphin appropriate foraging skills. Indeed, we observed that two young dolphins in Panama City were always begging close to boats and one of them was seen with a hook protruding from the mouth. Moreover, dolphins having interactions with humans and boats, may be less careful to presence of predators. Unsurprisingly, frequencies of begging behaviour are higher during the spring and summer, when tourism activity is more important than during the fall.

Mean group size according to behaviours

The influence of dolphin activities on the mean group size has been already investigated by researchers. In their studies, researchers found that group size was influenced by activity, with larger group engaged in socializing and foraging (Fertl, 1994; Bearzi, 1999; Rogan et al., 2000). For Scott et al. (1990a), larger groups may provide an increased security for young calves or a cooperative foraging effort. In this present study, there is also a significant variation in the group size according to behaviour and zone. However, it seems that our model gives us some inadequate results for begging and travelling behaviours. Indeed, observations on the field show smaller groups than the model predictions. One hypothesis to explain the difference with begging behaviour, could be that begging activities are unnatural in wild bottlenose dolphins population, generated by the human presence, their activities and their behaviours being not predictable. Therefore, in the model, parameters concerning the human presence and activities (number of boats and swimmers, kinds of boat, fishing activities, food providing, etc…) were not taken into account. It is obvious that, model predictions might not reflect field observations. As the P value for travelling behaviour was not significant, we can conclude that travelling behaviour has no effect on the mean group size since the mean group size recorded during travelling activities in all zones (4.88) is equal to the most common group size (4.9; see Bouveroux et al., *submitted a*).

ACKNOWLEDGEMENTS

Special thanks to Eric Le Boulengé, Thierry Jauniaux, Thierry Hance, Hans Van Dyck for providing encouragement, guidance, and support that made this project possible. I would like to thanks Mr. and Mrs. Richard for all their logistic support during fields work. I thank also Sarah Lessire, Audrey Binet and Kim Verbeke for their help in data collecting. Reny Tyson, Stephanie Nowacek, from the Florida State University (Oceanography department, Tallahassee) and Brian Balmer from the University of North Carolina Wilmington. Jérôme Vrancken and Jonathan Jaeger from Université catholic de Louvain for their statistical consulting. Master Goupyl provided informatics assistance.

Research funding was obtained through donations from *Delphus Foundation, the Foundation Léopold III pour l'Exploration et la Conservation de la Nature and Communauté Française de Belgique*. *Canon Belgium* provided the photographic material. Thanks a lot to my family, Lessire's family, all friends and colleagues.

This research was carried out under the General Authorisation GA LOC # 1055-1732 delivery by NOAA Fisheries.
This is a contribution to Biodiversity Research Centre (BDIV) of Louvain-La-Neuve.

Article 4:

Social structure of bottlenose dolphins, *Tursiops truncatus*, in Panama City, Florida.

Bouveroux, Th., and Mallefet, J. (2010)

*J. Mar. Biol. Assoc. of UK***.**

A female adult with a calf in echelon position. Panama City, July 2007. Photo by Donald Tipton.

4.1. Context

This paper on the social organisation of bottlenose dolphins has been published in the *Journal of the Marine Biology Association of the United Kingdom.* Since we are able to identify dolphins in a group by the photo-identification technique, it is now possible to evaluate the relationships between dolphins. This is probably the first study that investigates the social structure of a bottlenose dolphin population in an area with significant human activity. Bottlenose dolphins are long-lived social marine mammals characterised by a fission-fusion society in which individuals associate in small parties that frequently change in composition and behaviour.

In this paper, we investigated coefficients of association (CoA's) of identified dolphins, preferred associations using a cluster, associations by sex using sociograms and temporal stability of dolphins' associations. Unfortunately, data on dolphins' gender was not sufficient to determine accurately the existence of mixed-groups and/or alliances by sex.

The social structure of *T. truncatus* in Panama City shows also a fission-fusion society, with preferred associations between individuals such as pairs or trios of adult males. Males associations are stronger than females, and temporal stability in the social structure of dolphins seems to be observed over the study period with constant companionships.

4.2. Paper

Journal of the Marine Biological Association of the United Kingdom, page 1 of 8.
doi:10.1017/S0025315409991251

Social structure of bottlenose dolphins, *Tursiops truncatus*, in Panama City, Florida

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Social organization is an important attribute of the animal society. We describe the social structure of a bottlenose dolphins population living in Panama City, a seaside resort located on the north-west coast of Florida. Study was conducted with 46 individuals. Dolphins are associated on average half weight index of 0.11. Preferred long-term associations are observed. The proportion of the non-zero association indices suggests that some dolphins seem to avoid others. Associations between and within sex-classes were investigated using only dolphins of known sex and observed at least 4 times. Highly significant differences are found in associations between and within sex-classes (Mantel test, t = 3.7987; P = 1); indeed, male associations are stronger than between inter-sexual associations or between females only. Sociogram of males reveals a complex network with strong associations between pairs or trios that reach up to 0.97, whereas female associations are lower than males. The cluster analysis shows no clear division in the social organization of bottlenose dolphins in Panama City, except for dyads, triads and their multiple networks. The population structure seems to be temporally stable over the study and constant companionships are observed in the dolphin population in Panama City.

Keywords: bottlenose dolphin, *Tursiops truncatus*, social structure, alliances, fission–fusion

Submitted 7 May 2009; accepted 27 August 2009

INTRODUCTION

Social structure of a wide range of mammals, such as baboons (e.g. Packer, 1977), chimpanzees (e.g. Watts, 1998), giraffes (e.g. Le Pendu *et al.*, 2000), bottlenose dolphins (Wells *et al.*, 1987; Connor *et al.*, 1992, 2001), killer whales (e.g. Baird & Whitehead, 2000), long-finned pilot whales (e.g. de Stephanis *et al.*, 2008) or sperm whales (e.g. Lettevall *et al.*, 2002) have been investigated by ecologists for several years. Most mammals live in a society that can be defined as a set of conspecifics that interact more regularly with one another than with members of other societies (Gero *et al.*, 2005). Therefore, inside an animal society, studies on association patterns of individuals and their temporal variations give information about social organization of animal populations (Whitehead, 1995, 2008a).

Bottlenose dolphins are long-lived mammals (~45 years) living in fission–fusion societies where individuals associate in groups that often change in both size and composition, mainly on a daily or hourly basis (Wells *et al.*, 1987; Connor *et al.*, 2000, 2001; Möller *et al.*, 2001). Researches on social structure have showed that inside a bottlenose dolphin community, relationships between individuals can be complex, with several levels of alliances (Connor *et al.*, 2001). The strength and stability of alliances between individuals are probably depending on socio-ecological benefits in behavioural activities such as mating, foraging or predator defence (Gero *et al.*, 2005).

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Two important long-term studies on social organization of bottlenose dolphins were performed in Sarasota Bay, (Florida) (Wells, 1991) and Shark Bay, (Western Australia) (Connor *et al.*, 2001). In both study areas, males form stable alliances of two or three dolphins over long periods that form 'first-order alliances' (Connor *et al.*, 2000, 2001). In Shark Bay, teams of two stable alliances form 'second-order alliances' that attack other alliances in contests over female consorts and defend against such attacks (Connor *et al.*, 1992, 2000, 2001). In both areas, females have large networks of associates. Some live in bands, while others have few or no strong associations with other females (Connor *et al.*, 2000). However, if such long-term associations are observed in Shark Bay and Sarasota Bay, they are not observed in the majority of all bottlenose dolphin populations, where sometimes, there is no evidence of such associations as observed in the Moray Firth, Scotland (Lusseau *et al.*, 2003).

In order to broaden our understanding on social ecology of *Tursiops*, we decided to focus on a population from the north-west coast of Florida. Panama City is a very popular seaside resort with important human activities such as yachting, fisheries, harbour activities and military activities (Bouveroux *et al.*, in preparation). This bottlenose dolphin population is also a popular tourist attraction with many individual dolphins regularly in contact with boats and swimmers who intentionally enter the water to interact with them and to feed them (Samuels & Bejder, 2004; Bouveroux *et al.*, in preparation). This is the first study based on the social organization that is conducted in an area with such human activities. Therefore, studying social structures in a different habitat, having different characteristics and pressures, allows us to broaden our understanding of the range of *Tursiops* social ecology.

In this study we aimed to: (i) characterize the social ecology of a bottlenose dolphin population exposed to human activities; (ii) to evaluate association patterns between individual dolphins in this population; (iii) to assess association depending on sex; and (iv) to estimate the probabilities of association between individuals over time.

MATERIALS AND METHODS

Study area and dolphin population

The study was performed in the seaside resort of Panama City (30°07′N 85°43′W), located on the north-west coast of Florida. It encompasses the waters of the St Andrew Bay and the coastal shallow waters of the Gulf of Mexico. St Andrew Bay is linked to the Gulf of Mexico by a unique connexion, the Channel Entrance (Figure 1). St Andrew Bay estuary is one of the most species diverse estuaries inventoried in the United States and has the largest expanse of seagrass beds in this part of Florida (Keppner & Keppner, 2005).

Field observations

In this study, a total of 65 days were devoted to studying dolphin alliance inside of this coastal bottlenose dolphin population. We used data collected on group composition from 383 groups well identified and encountered during surveys. Fieldwork was conducted over three periods: 28 September to 31 November 2005; 20 July to 21 August 2006; 1 June to 25 July 2007.

Group composition was determined by standard photo-identification (photo-ID) techniques, using natural marks on dorsal fin of dolphins, a non-invasive tool which is frequently used to study the social structure of social marine mammals (Würsig & Würsig, 1977; Würsig & Jefferson, 1990; Bejder *et al.*, 1998). To avoid problems associated with pseudo-replication, the photo-ID survey was not carried out on all days (Wilson *et al.*, 1999). Therefore, we have divided each fieldwork into several spaced sessions of photo-ID and these were evenly distributed over the whole stay. Sessions of the three-year study were performed as follows: six photo-ID sessions of five days in 2005, three sessions of five days in 2006 and four sessions of five days in 2007.

Individuals are considered as associated if found together in a group where they are no more distant than 100 m of each other, moving in the same direction and engaged in similar activities (Wells *et al.*, 1987; Shane, 1990).

For each group observed, we recorded the hour, the zone of observation, geographical position using a GPS, pod size and composition (number of adults, juveniles, calves and new-borns), tidal current and finally the tourism activity (number of boats and swimmers) close to the focal-group. Dolphin sex was determined by direct observations of the genital area or during sexual behaviours with male dolphins exhibiting erections. Females were also indicated by the constant presence of a small animal presumed to be her calf.

For a faster identification of individuals, we used a codification system. We have indeed assigned a code XYZ to each identified dolphin:

where, X, is the age-class (A, adult; J, juvenile or C, calf); Y, represents the sex (M, male; F, female or X, unknown); and Z, the individual number.

For instance, AF30 is the thirtieth identified dolphin, which is a female adult. A photo-ID catalogue was thus created, indexing all recognized individuals. To facilitate the comparison of dorsal fins in the photo-ID catalogue and with other catalogues that come from other study areas, we used the classification system of dorsal fins designed by Urian (Urian *et al.*, 1999).

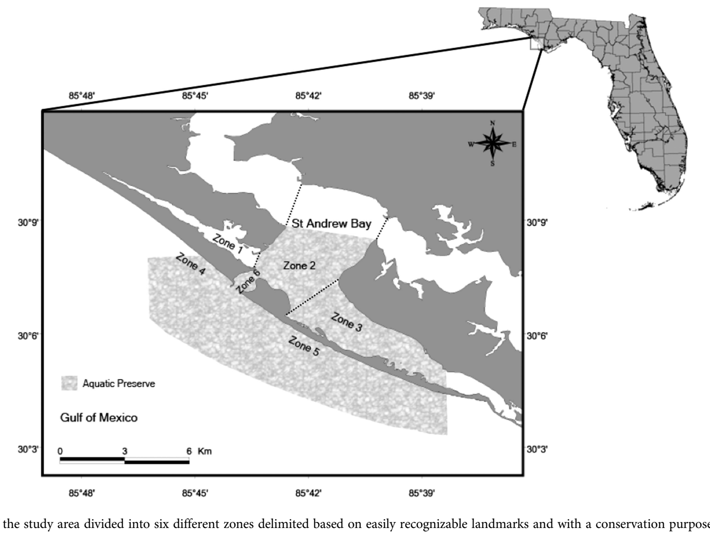

Fig. 1. Map of the study area divided into six different zones delimited based on easily recognizable landmarks and with a conservation purpose.

With a boat smaller than 5 m powered with 55 to 85 HP outboard engines and at a speed around 10 knots, we performed our surveys by following predetermined routes until a dolphin group was localized. Then, nearby the dolphins, we slowed down the vessel and we ran it in parallel to animal course in order to avoid sudden directional changes (Figure 2).

Analyses

Dolphins that were individually identified by at least ten occasions were selected for calculating pairwise association using the half-weight index (HWI) which is also called coefficient of association (CoA):

$$X/(X þ 0.5(Ya þ Yb))$$

where, X, the number of times both individual a and b were seen together in the same group; Ya, the number of times individual a was seen but not individual b; Yb, the number of times individual b was seen but not individual a.

This index is commonly used to describe associations of dolphins and it accounts the best for observer biases inherent in photo-ID techniques (Möller *et al.*, 2001; Quintana-Rizzo & Wells, 2001; Lusseau *et al.*, 2003; Gero *et al.*, 2005). These CoAs range from 0 (for two dolphins never seen together in a group) to 1 (for two individuals that were always observed together). To determine wheter the patterns of associations between individuals were different from random, we built an association matrix from calculated CoAs between individuals, using SOCPROG version 2.3 (for MATLAB 7.1) (Whitehead, 2006). A frequently useful null hypothesis is that individuals have no preference for social partners, with the alternative that there are preferred and/or avoided associations between some pairs of individuals (Whitehead, 2008b). A permutation test, introduced by Bejder *et al.* (1998), was used to determine if individuals associate preferentially with other members inside the population and/or avoided one another. The number of permutations performed was increased until the *P* value became stabilized. To determine whether there were differences in the patterns of associations between and within sex-classes, we performed the Mantel test, with 1000 permutations. The social organization of the population was graphically presented using a hierarchical cluster analysis of the HWI matrix. Finally to investigate the stability of associations among individuals, we calculated variations in lagged association rates for all associations and for each sex-class of associations (male–male; female–male; female–female). Thus, we estimated the probability that if two animals are associated at some time, they will also be associated after various time lags (Baird & Whitehead, 2000).

RESULTS

Bottlenose dolphins are observed in Panama City throughout the year with an estimated population size ranging between 58 and 177 individuals varying with the seasons, with a mean pod size of 4 to 5 dolphins. A total of 263 different dolphins have been photo-identified in the study area between March 2004 and July 2007 (Bouveroux *et al.*, in preparation).

Association pattern

We examined associations for 46 individuals sighted at least 10 times (11 males, 9 females, 26 of unknown sex with two juveniles and one calf). The distribution of CoAs for all individuals (N ¼ 2116) was skewed towards lower values so

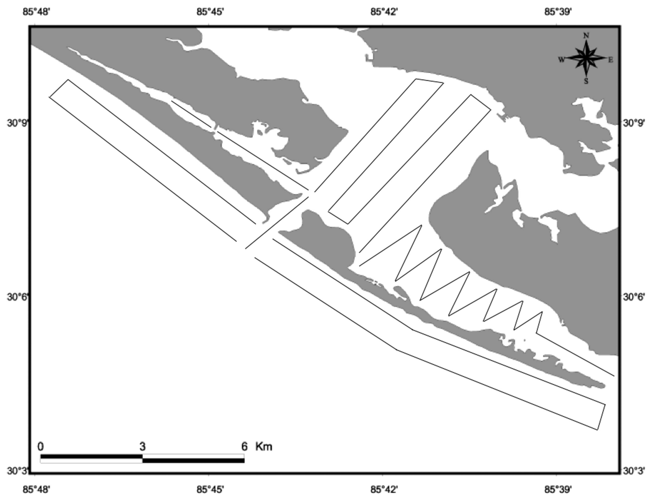

Fig. 2. Typical transects followed for surveys of bottlenose dolphins during the 3-year study (2004–2007).

indicating no association. Calculated CoAs ranged from 0 to 1 (Figure 3A); mean CoAs were found to range from 0.02 to 0.16 (Figure 3B) and maximum CoAs ranged from 0.25 to 1 (Figure 3C). All individuals were associated on average HWI of 0.11 (SD = 0.04).

Preferred long-term associations between individuals were tested using coefficients of variation between the real dataset and random dataset. Association datasets were randomly permuted 20,000 times. We observed that individuals preferentially associated with other individuals, indeed mean association, standard deviation (SD) and coefficient of variation (CV) are higher in the real data set (mean: 0.10782; SD: 0.13798; CV: 1.2798) than in the random data set (mean: 0.10724; SD: 0.11415; CV: 1.06433). Moreover in this dolphin population, some individuals seem to avoid others, since the proportion of the non-zero association indices in the real data set (proportion of non-zero: 0.65314) is lower than the random data set (proportion of non-zero: 0.69225). Associations between and within sex-classes were investigated using only dolphins of known sex, 13 males and 13 females that were observed at least 4 times. Highly significant differences were found in associations between and within sex-classes (Mantel test, $t = 3.7987$; $P = 1$). Male associations were found to be stronger than between inter-sexual associations (Table 1).

Sociograms of male and female associations reveal that males gather in a complex network with strong alliances between pairs or trios that reach up to 0.97 (AM02–AM07; AM37–AM48-AM55 and AM34–AM01). All males in the sample have a considerable number of associations with variable strength, whereas females do not show a similar pattern. The male AM37, AM48 and AM55 showed multiple associations with other males, and they formed a strong triad between themselves (CoA = 0.9). The strongest association observed was between individuals AM48 and AM55 (0.97) (Figure 4). CoAs between females are weaker than between males, with the highest HWI equal to 0.45 (AF30–AF53). Females have only few associates (two or three), with a maximum of 6 companionships observed for AF49, while for males, the highest number of associations in this sampling was 12 associates, as observed for individuals AM48 and AM55.

The cluster analysis shows no clear division in the social organization of bottlenose dolphins in Panama City, Florida, except for dyads, triads and their multiple networks (Figure 5).

Interesting trends in social organization of *Tursiops* are observed in Panama City. Firstly, cluster analysis reveals

Table 1. Mean and maximum half-weight indices (HWI) between and within sex-classes. SD, standard deviation.

Relationships	Mean HWI (SD)	Maximum HWI (SD)
All individuals	0.10 (0.05)	0.49 (0.27)
Female–female	0.06 (0.02)	0.29 (0.10)
Male–male	0.19 (0.07)	0.67 (0.26)
Female–male	0.07 (0.04)	0.21 (0.09)

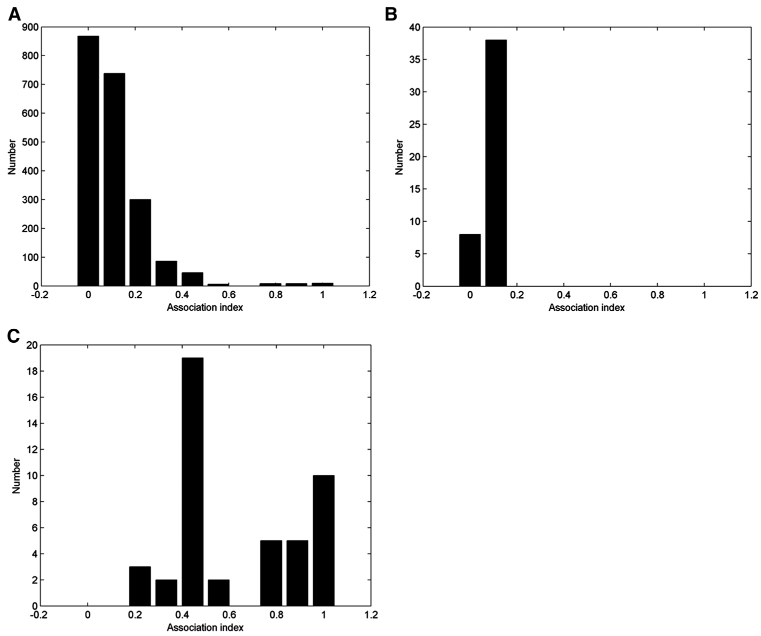

Fig. 3. (A) Distribution of CoAs for 46 bottlenose dolphins (*Tursiops truncatus*) sighted at least 10 times during surveys; (B) distribution of mean CoAs for each individual sighted at least 10 times during surveys; (C) distribution of maximum CoAs for each individual sighted at least 10 times during surveys.

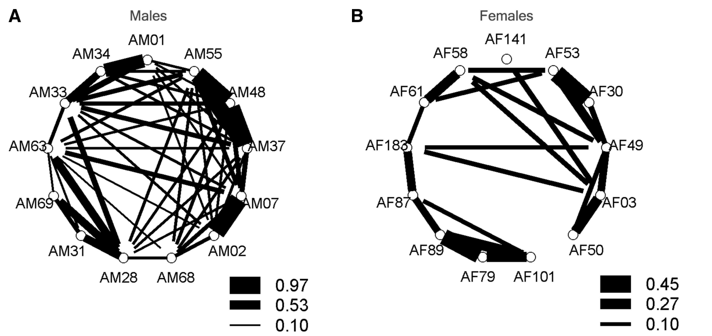

Fig. 4. Sociogram representations of (A) males–males and (B) females–females CoAs. Dolphins are identified by their ID-code. Lines of increasing thickness correspond to the increasing strength of pairs associations.

nine strong dyads or triads of individuals with coefficient association superior to 0.7. The pair AX41–AX42 was never observed separately. Among these nine strong associations, five of them are composed of at least one male, and three of them are composed of male pairs or trios (AM02–AM07, AM01–AM34 and AM48–AM55–AM37). Secondly, nine females are represented on the cluster. Six of them are associated in pairs with another female and have both one calf with same body size; two females have relationships with a dolphin of unknown sex that could be female (AF61–AX24 and AF03–AX06); the last female association represented on this cluster is a strong female–calf association (AF49–CX136). Thirdly, the cluster shows two main mixed groups, the first one composed of 17 dolphins (Group A) and the second one composed of 18 dolphins (Group B). Group A is composed of eight males, with some of them having very strong associations (more than 0.9). In Group B, most of the dolphins have never been sexed. Only three males and four females have been identified.

Lagged association rates

We investigated the temporal stability of dolphin associations in the population using all data sets without any restriction on the number of times that dolphins were observed. Associations were quite stable throughout the study (Figure 6A). Female–female and female–male associations demonstrated a similar pattern (Figure 6B, D), however male–male associations showed a higher rate than female–male (Figure 6C). Most of the measured association rates illustrate well the fission–fusion model for the dolphin population in Panama City. They indeed revealed short term association of individuals over a short period of time (a day) with rapid dissociation (Figure 6A).

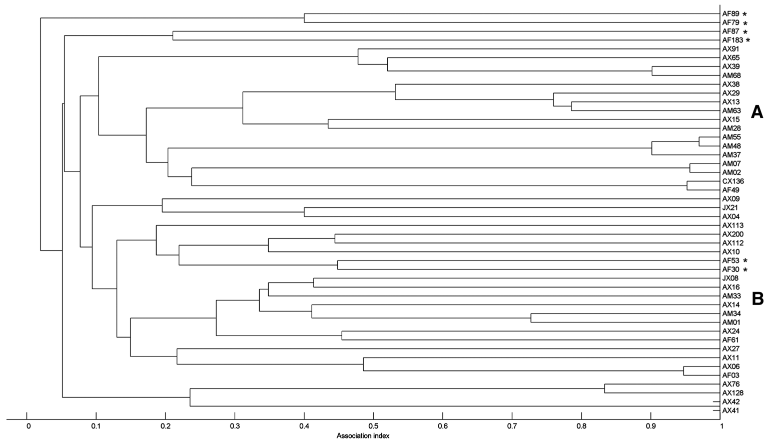

Fig. 5. Cluster showing the average-linkage cluster analysis of associations between identified bottlenose dolphins seen at least 10 times, in Panama City during fieldwork from 2005–2007. Groups A and B are represented. *, indicate female dolphins observed with a calf.

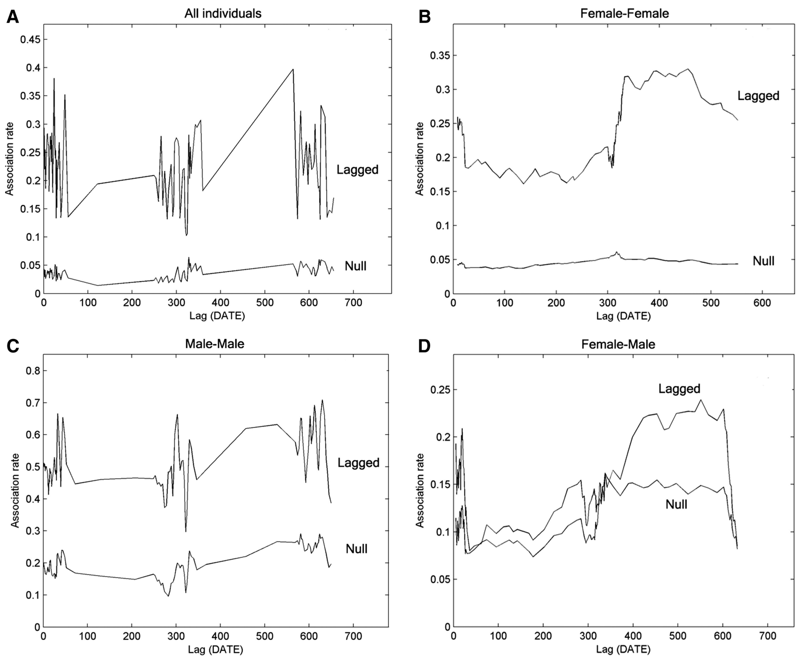

Fig. 6. Lagged association rates for (A) all individuals; (B) female associations; (C) male associations; and (D) female–male associations. Lag(DATE) represents the number of days elapsed between the first photo-ID session in October 2005 and the last one in August 2007.

DISCUSSION

Bottlenose dolphins are social mammals that maintain relations between members of the same population but they can associate with individuals coming from another dolphin population. These relationships can occur between individuals having the same sex or not. Several populations were studied during a long period in order to understand how and why dolphins build relations between individuals (Wells *et al.*, 1987; Connor *et al.*, 1992, 1999; Félix, 1997; Gero *et al.*, 2005; Lusseau *et al.*, 2003). Scientists found that bottlenose dolphin populations have generally four levels of organization: (i) female bands; (ii) male pairs or trios; (iii) mother–calf pairs; and (iv) sub-adult groups (Wells *et al.*, 1987; Félix, 1997; Connor *et al.*, 2000). However, Lusseau and colleagues found that the organization of the bottlenose dolphin community in Doubtful Sound was quite dissimilar to that seen in other populations; they indeed observed an organization in large mixed-sex groups (Lusseau *et al.*, 2003). Alliances of two or three male bottlenose dolphins have been reported in Shark Bay (Western Australia) and Sarasota Bay (Florida); these alliances are strong and stable over a long period (up to 12 years in Shark Bay and 20 years in Sarasota Bay). The same strong alliances between males were found in Panama City over our three years of fieldwork. No clear sub-units were observed in the dolphin population, yet two groups of individuals seem to be associated more often together than with other members. Inside these two groups, some strong associations were observed between pairs or trios. Some females did not have any close associates while few females had only one associate. Our cluster reveals the presence of three female pairs. Each of these six females were accompanied with a calf and inside a female pair; we observed that calves showed a similar body size that can be interpreted as having the same age. In fact, in other places, the formation of female bands seems to depend on the reproductive state of females (Wells *et al.*, 1987; Lusseau *et al.*, 2003), and may provide benefits from bonds with other females to cooperate against harassing males or to protect against predators (Connor *et al.*, 2000). Within bands, females with calves of similar age tend to associate with each other, as do females without calves (Wells *et al.*, 1987; Connor *et al.*, 2000). Therefore, we can suggest that females in Panama City associate according to their reproductive state.

As observed in Panama City and in other places throughout the world, mean group size of bottlenose dolphins depends on the behavioural activities (Shane, 1990; Chilvers & Corkeron, 2002; Bouveroux *et al.*, in preparation). Indeed, some activities need dolphin aggregation such as in feeding cooperation where dolphins take advantage in locating and controlling schools of prey. A study conducted by Gero and colleagues (2005) showed that some dolphins preferentially associate with certain individuals when foraging and others when socializing. In Panama City, we noted alliances of several stable pairs or trios of dolphins during activities such as foraging, mating or socializing (Bouveroux et al., in preparation). If food acquisition drove the social structure of this population, both sexes will have similar associations. However, on nine females seen at least 10 times, six of them are associates in female pairs that seem to have the same reproductive state, since they have been observed with a calf having the same body size and thus the same age. Therefore, we suggest that as observed in Shark Bay, social organization of the dolphin population in Panama City can be mainly dictated by reproductive strategies.

The average HWI from other studied bottlenose dolphin populations range from 0.1 to 0.2 (Wells et al., 1987; Smolker et al., 1992; Quintana-Rizzo & Wells, 2001; Chilvers & Corkeron, 2002). The same trend was also observed for the dolphin population living in Panama City (mean HWI: 0.11) and this low mean suggests a fluid network between dolphins sharing the study area, except for pairs and trios that are characterized by high-level and stable associations.

Long-lasting associations are also a feature of the dolphin population structure as found in the Doubtful Sound (New Zealand) (Lusseau et al., 2006), Sarasota Bay (Florida) (Wells et al., 1987) and Shark Bay (Western Australia) (Connor et al., 1992). This stability was especially observed in Panama City within male associations.

In conclusion, we demonstrated that in a popular seaside resort, bottlenose dolphins show also a fission–fusion model. Interestingly, the bottlenose dolphin population living in the St Andrew Bay, Panama City, Florida is composed of dolphins, living in small groups of two or three associates that can be compared to the first order of alliance described by Connor et al. (1992) in Shark Bay, Western Australia. These alliances regularly associate with other pairs or trios of dolphins or sometimes assemble in larger groups that can have a reproductive purpose, a defensive purpose toward predators or simply for hunting strategies.

In our three years study, the proportion of dolphins with known gender was not sufficient to determine accurately the existence of mixed-group, female bands or the presence of second-order of alliances as described by Connor in Shark Bay after more than nine years of research (Connor et al., 1992, 1999, 2001). Several studies suggest that some alliances are based on kinship (Möller et al., 2001; Lusseau et al., 2006). Therefore, it will be very interesting to undertake a study on sex determination and kinship using genetic methods.

ACKNOWLEDGEMENTS

Special thanks to Jérôme Mallefet and Douglas Nowacek for providing encouragement, guidance, and support that made this project possible; Dr Hal Whitehead and Dr David Lusseau for their statistical advice and review. I would like also to thank Mr and Mrs Richard for all their logistic support during fieldwork; Brian Balmer from the University of North Carolina Wilmington for sharing all information needed for this study; Julie de Wever and Galia Stypers were English reviewers. Research funding was obtained through donations from La Fondation Delphus, La Fondation Léopold III pour l'Exploration et la Conservation de la Nature and Communauté Française de Belgique. Canon Belgium provided the photographic material. Thanks a lot to my family and colleagues. This research was carried out under the General Authorization GA LOC # 1055-1732 delivery by NOAA Fisheries. This is a contribution to the Biodiversity Research Centre (BDIV) of Louvain-La-Neuve.

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DISCUSSION

A leap of a female bottlenose dolphin at the end of Shell Island. Photo by Th. Bouveroux, Panama City, October, 2005.

IV.Discussion

The present study provided information on abundance, residence patterns, spatio-temporal distribution, habitat use and social structure for a bottlenose dolphin population inhabiting in a geographic region recently affected by several Unusual Mortality Events (UME's), and where growing human activities increase the disturbance of dolphins.

Results on population size and site fidelity showed that bottlenose dolphins used not the study area with the same occurrence: some individuals are resident on a year-round basis, some are seasonal residents, while a high proportion of dolphins is considered as transient dolphins At this time, it is difficult to determine whether bottlenose dolphins in Panama City represent a population or a community. Indeed, bottlenose dolphins have been observed in the West and the East Bays during opportunistic surveys (personal communication), but to date, we have no way to assess how individuals, that share the region of Panama City, interact socially or genetically together. In addition, dolphins movement have been observed between St Joseph Bay and Panama City. According to Nowacek (2008), two distinct communities live in Apalachicola Bay as they showed separate home range with very few interactions between the two communities observed. Therefore, we may suggest that bottlenose dolphins in Panama City, also belong to distinct communities (maybe two or three) that share a part of the selected study area, but to confirm this hypothesis, data must be collected in the West and East Bays. The year-round presence of dolphins in Panama City, shows that Panama City is an important area for dolphins in this region, finding sufficient food and protected are for mating, calving and nursing. This studied community associates in small group of 5 dolphins, but this common group size varies according to the observed zone, the moment of the day and the behaviour. Preferred long-term associations have been observed, especially between pairs or trios of individuals, that sometimes associates together during a short period of time for mating strategies or cooperative feeding techniques mainly, since groups size increase when these both behaviours are observed. This dolphin community showed preferential distribution and habitat use in and around the Channel Entrance, that may act as a funnel which concentrate prey. Indeed, dolphins show a preferential foraging area located in and around the channel. From long-term interactions between human and dolphins, several individuals show begging behaviours towards boats and fishermen. These unnatural behaviours are mainly observed at the West end of Shell Island, with higher occurrence during the touristic season (April to August).

In following sections, I will first discuss deeply the results and the choice of the model used to estimate dolphin abundance as well as results on site fidelity. The second section will be devoted to the relations between the spatio-temporal distribution, groups size and the behaviours of dolphins observed. A third section will focus on the social structure and relationships between and within sex classes. Finally, special attention will be drawn to the importance of a conservation plan for a better management of this dolphins community.

4.1. The dolphins abundance, site fidelity and the photo-ID catalogue

The aims of this part were to estimate the number of bottlenose dolphins constituting the population of Panama City, to describe their site fidelity patterns and to create the first photo-ID catalogue that index all identified dolphins in the study area. The estimate population size was performed using mark-recapture methods, applied to photo-ID data, because it is the best non invasive method, increasingly used in cetacean studies (Hansen and Defran, 1990; Würsig and Jefferson, 1990; Urian et al., 1999; Read et al., 2003b; Balmer et al., 2008). The choice of the Robust design model to estimate the population size was suitable, since movements of dolphins between St Joseph Bay and Panama City have been observed during the study. In addition, during the initial study period of 2004 and 2005, several births and stranded died dolphins have been seen. Henceforth, unlike most studies (Wilson et al., 1999; Campbell et al., 2002; Read et al., 2003b; Culloch, 2004), models for closed population cannot be used here with accuracy under the assumption of no migration which required closed population models such as Lincoln-Peterson, Schnabel or derived closed models. Moreover, according Pollock (1982) in wildlife populations, capture probabilities may vary according to age, sex, social status and life history of individuals. Indeed, the presence of regular beggars dolphins in Panama City, has introduced unequal probabilities of captures between individuals. Therefore, we used the model of heterogeneity to thwart the violated assumption of the equal probability of capture between individuals.

In the present study, it was not possible to determine accurately whether the population of bottlenose dolphins in Panama City is subject to seasonal variations in the abundance, because of a lack of repeated data for each month across the years. For logistic reasons, it was not possible to collect data several time per year, because this kind of research is quite time consuming and expensive. Nevertheless, our results suggest some variations in the population size, ranging between 57 and 178 individuals according to months. Data collected reveals lower abundances in March-April and May (2004) and higher abundances in September-October 2005 and in June 2007. Studies conducted by Balmer (Balmer, 2007; Balmer et al., 2008) showed a seasonal variation in the dolphins abundance of St Joseph Bay, with lower abundance recorded in July 2005 and February 2006, and higher abundance in April 2005, May 2005 and September-October 2006. These variations observed in St Joseph Bay are exactly the opposite results of those found in Panama City, except in February, where no data was collected in Panama City. Indeed, dolphins abundance increase in St Joseph Bay during the months of April and May, while the abundance in Panama City decrease during these months. In the same way, dolphins abundance in St Joseph Bay is low in July, while in Panama City, the abundance is relatively high. Studies on coastal populations of bottlenose dolphin in other regions showed that populations tend to be composed of approximately 60 to 150 individuals (Wells, 1991; Williams et al., 1993; Wilson et al., 1999; Baird et al., 2001; Culloch, 2004; Kerr et al., 2005). For example, the bottlenose dolphin in Sarasota Bay, Florida, has an estimated population size of approximately 155 individuals (Wells, 1991; Wells, pers. comm., 2004), nevertheless larger population are reported in Shark Bay, for instance (Connor et al., 1999). For example, a summary of estimated populations size found throughout the world is described in the following table (Table 4.1).

Country	Location	Estimated population size	ǂ of identified dolphins	Mean group size	Method	Source
United State	Sarasota Bay, Florida	140	-	7,0*	CMR - Photo-ID	*Wells et al., 1987 Wells (pers. com., 2004)
	St. Vincent Sound / Apalachicola Bay - Apalachicola Bay, Florida	*Summer*: 182 +/-58 *Winter*: 178 +/-77	115	-	CMR - Photo-ID	Tyson, 2008
	St. George Sound / Alligator Harbor - Apalachicola Bay, Florida	*Summer*: 365 +/-164 *Winter*: 359 +/-87	232	-	CMR - Photo-ID	Tyson, 2008
	St Joseph Bay, Florida	*June/July*: 84 *May*: 313	313	-	CMR - Photo-ID	Balmer et al., 2008
	Pensacola, Florida	18	-	-	Aerial Survey	Baylock and Hoggard, 1994
	Galveston Bay, Texas	152	> 1000	4,4*	Photo-ID	Baylock and Hoggard, 1994 *Bräger *et al.* 1994
	North Carolina, bays, sounds and estuaries	1033	306	-	CMR - Photo-ID	Read et al., 2003b
	Barataria Bay, Louisiana	238	133	5,9	CMR - Photo-ID	Miller, 2003
	Around Maui and Lana'i, Hawaii	134	63	-	CMR - Photo-ID	Baird et al., 2001
Australia	Shark Bay, Western Australia	> 400	-	4,8*	Photo-ID	*Smolker et al., 1992 Connor et al., 1999
	Jervis Bay, South eastern Australia	*Summer*: 61 *Winter*: 108	118	12,3	CMR - Photo-ID	Möller et al., 2001
	Port Stephens, South eastern Australia	160	155	6,8	CMR - Photo-ID	Möller et al., 2001
Scotland	Moray Firth	62	-	-	Land based, coordinated count	Hammond et al., 1991
	Inner + outer Moray Firth	129 +/-15	73 *(left)*; 80 *(right)*	6,3*	CMR - Photo-ID	*Wilson et al., 1993; Wilson et al., 1999
	Outer Moray Firth	108	76	10		Culloch, 2004
Belize	Turneffe Atoll	122	115	2,9	CMR - Photo-ID	Kerr et al., 2005
Wales	Cardigan Bay	178 +/- 22	154	5,8*	CMR - Photo-ID	*Lott, 2004 Posada, 2006
Ireland	Shannon Estuary	113 +/- 16	287	6,6*	CMR- Photo-ID	*Ingram, 2000 Rogan et al., 2000
New Zealand	Doubtful Sound	65	83	17,2	CMR- Photo-ID	Lusseau et al., 2003

Table 4.1. Summary of the estimate populations size, number of identified dolphins, the mean group size by locations. * = the links between results and bibliography.

The sighting history data, which are temporally correlated with the abundance estimates, provide insight into site fidelity patterns of dolphins in Panama City. This study on site fidelity showed that all animals do not use the study area with the same frequency; some individuals reveal high site fidelity indices, but the major proportion of individuals shows low site fidelity indices. Indeed, the larger proportion of individuals have been observed only once, and across the 17 capture sessions, 75% were considered as «rare» animals. However, along with the presence of dolphins movements between St Joseph Bay and Panama City, the low proportion of resident dolphins in the study can also be explained by: (1) the study area of 323 km^2, the size of which was selected on purely logistic grounds, could represent only a portion of the home range of all individuals. Important influx of individuals into the selected study area may occur between the East and the West Bay and St Andrew Bay, and thus show overlapping in individual ranges; (2) differences in behaviours, with some individuals being more site specific and others more ranging according to ecological, social, sexual or age differences; (3) the combination of these factors.

The comparison of the photo-ID catalogues between Panama City and St Joseph Bay revealed that 26% of individuals seen in Panama City have been also observed in St Joseph Bay. Therefore, we suggest that the abundance fluctuation in both study areas are closely tied to spring movements of dolphins into St Joseph Bay and with movements occurring during the fall and the early summer into Panama City.

4.2. The distribution of dolphins and the habitat use

The characterisation of the spatio-temporal distribution of dolphins coupled with the behavioural study, allowed us to determine the preferred habitats within the study area and its uses for wild behaviours.

During the survey, dolphins were observed all day in the study area. Bottlenose dolphins were observed in all zones but they were not equally distributed. GPS positions of dolphin sightings reveal a hotspot located in and around the Channel Entrance. In this area, the number of behavioural observation per day were higher and all dolphin activities have been observed, except for sexual behaviours. According to Würsig and Würsig (1978), Shane (1990a) and Wilson et al. (1997), coastal bottlenose dolphins tend to aggregate around entrances to estuaries, channels, lagoons and bays. Indeed, these kinds of habitat may offer enough food to dolphins, a low energetically cost to catch prey, as well as protected areas towards predators. Panama City benefit of small shallow lagoons that may offer to dolphins some protected areas against predators, especially for calves. Moreover, the presence of the channel may act as a funnel that concentrate prey as suggested by Shane (1990b). Indeed, the behavioural study revealed that foraging behaviours were also more important in this area. Using the jetties and the beach present around the Channel Entrance, dolphins frequently display a cooperative technique of hunting: the "wall" technique. This technique that requires a greater number of dolphins and allows trapping schools of fishes between the beach and the jetties, and to catch them at low energetically cost. The Channel Entrance represents also the single connection between the Gulf of Mexico and the St Andrew Bay, and that dolphins use to travel between these two areas. Therefore, we can confirm that Panama City represent an ideal area to shelter a bottlenose dolphins population.

The spatial distribution of dolphins behaviours have showed that most begging behaviours occurred mainly in the place already called «interaction beach» in the study conducted by Samuels and Bejder (2004), and which is located at the West end of Shell Island. This site is characterised by a great number of recreational boats and fishing boats that beggar's dolphins alternately visit to be fed by humans. During the study, it was not rare to see dolphins with fishing hooks in their jaws, tongue and even in the eye. The proximity of beggars dolphins to boats propellers, also increase the risk of injuries, when dolphins swim and wait close to boats. Although, the MMPA prohibits dolphins harassment and thus swim and feeding activities with dolphins, we suggest strongly to reinforce and to ensure the right application of existing laws on human-dolphin interactions.

On average, groups were composed of five dolphins, but vary significantly according to zones, the time of the day and months. Moreover, the behavioural study reveals also that group size may vary with the observed behaviours. In social marine mammals such as in the bottlenose dolphin, some activities as for instance, cooperative hunting or sexual behaviours, require a greater number of individuals. Temporary associations between individuals change throughout the day lasting from minutes to hours (Wells et al., 1987; Connor et al., 2000), and that depend on strategies adopted by individuals in a given time in relation to their environmental parameters (e.g. predation risk, food distribution) and their activities (e.g. foraging, mating or begging). According to the locations, groups size of bottlenose dolphins vary on average from 2 dolphins in Sanibel, Florida (Shane, 1990a), to 17 dolphins on average in Doubtful Sound, New Zealand (Lusseau et al., 2003). For example, mean groups size recorded in study areas throughout world are given in the following table (Table 4.1).

4.3. The social organisation of bottlenose dolphins in Panama City

The social structure of a marine mammal population is a fundamental component of its biology and ecology. Indeed, studies reveal that mating strategies, foraging techniques and defense strategies against predators are in relation with the association patterns occurring between individuals inside a population (Connor et al., 2001; Gero et al., 2005; Magileviciute, 2006). Most information available on bottlenose dolphins social organisation originates from three long-term studies in Sarasota Bay, Florida (Wells, 1991), Shark Bay, Western Australia (Smolker et al., 1992; Connor et al., 2000) and Moray Firth, Scotland (Wilson, 1995; Eisfeld, 2003).

The classical fission-fusion society, characterised by temporary associations lasting from minutes to hours is also observed in Panama City. The average Half-Weight-Index (HWI) of Panama City is similar to that found in other studied bottlenose dolphin populations which range between 0,1 and 0,2, underlying the predominantly fluid nature of this society (Wells et al., 1987; Smolker et al., 1992; Bräger et al., 1994; Connor et al., 2000; Quintana-Rizzo and Wells, 2001; Chilvers and Corkeron, 2003). However, preferred companionships with long-lasting associations were also recorded within the population, with several strong bonds of pairs or trios. However, there is a low proportion of individuals with sex determined in the sample. Therefore, it was not possible to make clear assumptions on relationships occurring between and within sex classes. Indeed, the cluster shows only three pairs or trios of strong males associations that have been well characterised (AM01-AM34; AM02-AM07 and AM37-AM48-AM55), while other pairs of individuals still remains fully or partially of unknown sex (AX41-AX42; AX76-AX128; AX15-AM28; AX29-AX13-AM63; AX39-AM68). However, we may suggest that in Panama City, males associate in pairs or trios similarly to what has been described in Shark Bay and Sarasota Bay (Wells et al., 1987; Connor et al., 1999; Connor et al., 2000). In both areas, male alliances principally were related to mating strategies. Indeed, sexually mature males of bottlenose dolphins may form several levels of alliances. First level concern pairs or trios of male dolphins that cooperate as stable «*first-order alliances*» to sequester and control reproductive females (Smolker et al., 1992; Connor et al., 1992; Connor et al., 1999). As found in Panama City, these male associations are strong, with CoAs ranging between 0,7 and 1, and these associations are stable over a period ranging up to thirteen years in Sarasota Bay (Wells et al., 1987). Each pair and trio maintained moderately strong associations (CoAs of 0,2-0,6) with one or two other pairs or trios (Wells et al., 1987; Smolker et al., 1992, Connor et al., 2000). Cooperation between male dolphins has been also reported from bottlenose dolphins (*Tursiops aduncus*) in Port Stephens, South eastern Australia (Möller et al., 2001), where pairs or triplets were also observed separating females from their groups. In Panama City, we suggest that «*first-order alliances*» are also a characteristic of male associations, but their implications to sequester females have not been currently highlighted.

In Shark Bay, teams of pairs and trios sometimes cooperate to form «*second-order alliances*» that attack other first alliances or defend against attacks (Connor et al., 2001). Moreover, some males choose sometimes a different strategy by forming large «*superalliances*» of approximately fourteen individuals to attack first and second-order of alliances in contest over females. Although males do not form strong alliances with males outside the superalliances, they do occasionally associate with some of them during episodes of resting, travelling or socialising, but these associations are labile, as members often switch partners between consortships (Connor et al., 1999; Connor et al., 2001; Magileviciute, 2006). However, second-order of alliances and superalliances, are not a characteristic of all bottlenose dolphins populations throughout the world, but seem to be limited to Shark Bay only. Indeed, such cooperative associations between alliances were never documented for Sarasota Bay, Doubtful Sound (New Zealand) or Port Stephens, despite extensive studies (Wells et al., 1987; Möller et al., 2001; Lusseau et al., 2003). In highest latitude, such as in the Moray Firth, Scotland, or in the Cardigan Bay, Wales, strong bonds of bottlenose dolphins have not been found among any adults (Eisfield, 2003; Lott, 2004; Magileviciute, 2006). As suggested by Wilson et al., (1993) low predation risk, food distribution or the lower rate of interactions between rival males might explain the lack of male alliances and female alliances among bottlenose dolphins in these areas.

Association patterns of female bottlenose dolphins also show a large variability. Some females live in bands, while others have few or no strong associates with most females living on a continuum between these two extremes (Connor et al., 2000). According to Mann et al. (2000), female-female bonds are weaker and more variable than male-male ones. The formation of female bands seems also largely depends on the reproductive state of individuals. Indeed, within bands, females with calves of similar age tend to associate with each other, as do females without calves (Wells et al., 1987; Connor et al., 2000). In Panama City, females associations are also weaker than males, and show fewer associations than observed within the males network. Nevertheless, stronger relationships occur between three females (AF79, AF89 and AF101) showing a similar reproductive status, since they were observed with a calf of approximately the same body size. This observation suggest therefore a reproductive strategies in female associations that focus on calf protection (from predators and/or conspecifics). However, in Panama City, a stronger association occurs also between two regular females beggars, AF30 and AF53. These two females were also observed both accompanied with a calf. However, in this case, we suggest that associations may be based on a closer behavioural personality, since they are frequently seen begging together. Relation between sex classes in Shark Bay and Sarasota Bay, were also strongly tied with the females reproductive status, and males and females adults associated much more often during the mating season in Sarasota Bay (Wells et al., 1987; Connor et al., 2000). In Panama City, associations between sex classes have been also observed, but these associations are weak.

Although similarities are found in the social structure of bottlenose dolphins throughout the world, the organisation of the bottlenose dolphin community in Doubtful Sound is dissimilar to that seen in other bottlenose dolphin populations (Lusseau et al., 2003). This society lives in large mixed-sex groups, with strong associations occurring within and between sex classes. Long-lasting associations are also a strong feature of the community structure (Lusseau et al., 2003). This stability in the dynamics of association was observed within and between sex. Seasonal factors such as mating behaviour and care of the young that affects other bottlenose dolphin populations (Connor et al., 2000) do not play a major role in the associations patterns of the Doubtful Sound population. Therefore, Lusseau et al., (2003) proposed the hypothesis of food acquisition and not mating strategies as a driving force for the social organisation in Doubtful Sound.

Associations between mother and calf have been also studied, and not surprisingly, calves associates strongly with their mothers for their first few years (Wells et al., 1987). One of the possible explanations comes from the fact that foraging skills develop slowly. While the social behaviour develops rapidly during the first six months, it appears to take several months to practice before a calf actually catches fish, and years before it can forage independently (Mann and Sargeant, 2003).

Several studies suggest that kinship could play a role in the structuring of male alliances (Wells et al., 1987; Möller et al., 2001; Krützen, 2002). Kin-selection focuses on a positive correlation between genetic relatedness and the degree of cooperation (Krützen, 2002). According to Krützen (2002) males in first and second-order of alliances are strongly related, while inside a superalliance, the strength of the association of partners was not correlated with their genetic relatedness. In Sarasota Bay, up to four generations of kin associates are found in the same sex groups. The lack of genetical data does not allow us to make any assumption on the relatedness of individuals involved in observed association in Panama City. However, a study conducted by Gero et al. (2005) suggests that preferred associations are formed in relation with the behavioural states of individuals. In this study, it seems that associates are chosen to maximise efficiency or benefits when carrying out specific behaviours. For instance, it is likely that individuals using same foraging strategies would maximise foraging efficiency by associating preferentially with individuals that forage in a similar manner.

4.4. Proposal for conservation and management

Growing human activities around the globe have increased interactions between wildlife and humans. Many studies have provided evidence that habitat degradation can cause population decline (Harzen and Brunnick, 1997; Eguchi, 2003; Bejder et al., 2006; NMFS, 2007). In many areas, bottlenose dolphin is a protected species. For instance, Mediterranean 'subpopulation' of bottlenose dolphins are qualified as 'Vulnerable' according to the International Union for Conservation of Nature (IUCN) Red List criteria (Bearzi and Fortuna, 2006), while in the U.S. waters, all marine mammals are protected since 1972, by the Marine Mammal Protection Act, amendments by the U.S. National Marine Fisheries Service (NMFS). According to the NMFS, the terms "conservation" and "management" means *the collection and application of biological information for the purposes of increasing and maintaining the number of animals within species and populations of marine mammals at their optimum sustainable population* (NMFS, 2007). The biological information needed for a conservation and management purposes are conceptually simple, consisting of baselines data on: (a) the abundance, the distribution and habitat use of the concerned species; (b) the type and the intensity of human activities in the area likely to affect cetaceans; and (c) the know or likely impacts of such activities on these mammals (Notarbartolo-di-Sciara, 2008).

One conservation tool that is increasingly reported as a useful way of protecting cetaceans from threats, is the designation of Marine Protected Areas (MPA) (Cañadas et al., 2008). In areas in which marine mammals are locally abundant, protected areas usually try (1) to spatially or temporally segregate fisheries or other pervasive human activities such as commercial tourism, recreational vessels, military activities and engineering works (e.g. seismic surveys, dredging, drilling, underwater explosions) that may disturb marine mammal populations, or (2) to manage areas in which these activities are particularly present (Finn, 2005).

Criteria to identify MPAs include: areas used by marine mammals for (i) foraging, breeding, calving, nursing and social behaviour; (ii) migration routes and corridors; (iii) resting areas; (iv) areas of importance to marine mammal prey; (v) natural process that support continued productivity of marine mammal foraging species (upwellings, fronts…) and (vi) topographic structure favourable for enhancing foraging techniques (Notarbartolo-di-Sciara, 2008). Once these areas are characterised, anthropogenic threats such as intensive fishing activities, frequent bycatch, intensive whale watching or swim with dolphins, military exercises, pollution runoff (organochlorine, heavy metals,...) have to be limited. Therefore, combined results on dolphins distribution and behaviours provide thus a valuable tool to identify important habitats for dolphins (Hastie et al., 2003b), that should be selected for implementing effective boundaries of a marine protected area within the selected study area. Bottlenose dolphins use the study area on a year-round basis, and show preferential habitats for some of their behaviours such as foraging and begging activities. Indeed, the Channel Entrance and its surrounding area provide the most intensively used areas by bottlenose dolphins within the study area. Therefore, the highly frequented area by dolphins, the presence of a unique connection between the Gulf and the St Andrew Bay, the probable higher prey abundance, the interesting topography of this site that facilitate the capture of prey and the presence of harassing human activities, such as swim-with-dolphins and the illegal feeding events by humans that still occur, must be taken into account when building management plans, with particular care needed to mitigate dolphins harassment against human activities. According to the

NMFS, the term "harassment" means *any act of pursuit, torment, or annoyance which—(i) has the potential to injure a marine mammal or marine mammal stock in the wild; or (ii) has the potential to disturb a marine mammal or marine mammal stock in the wild by causing disruption of behavioral patterns, including, but not limited to, migration, breathing, nursing, breeding, feeding, or sheltering* (NMFS, 2007).

Because, dolphins harassment have been daily recorded, while the violation of law currently in force by the NMFS that may engender a maximum fine of $20,000 and one year in jail, we suggest the following proposals that could be brought to the attention of the competent authorities.

For an effective and sustainable management it will be important to focus on the following measures to protect bottlenose dolphins in Panama City:

(a) Implementation of education and awareness programmes;

(b) Enforcement and monitoring of law currently in force to ensure that rules are respected and measures are correctly implemented;

(c) Establishment of a Marine Protected Area in the highly frequented area by dolphins, located in and around the Channel Entrance;

(d) Establishment of an idle speed/no wake zone in the Channel Entrance;

(e) Regulation and mitigation measures to maintain potentially harmful human activities and pollutants within acceptable levels;

(f) Monitoring and periodic review to ensure that the objectives are being met;

(g) Continue research activities to allow management adaptiveness and increase management effectiveness, as well as the monitoring of the population size;

4.5. Critical experimental

To better performed a such study in the future, it is interesting to bring a critical view of this research and to discuss about limitations encountered during this research.

Studying marine mammals in wild is sometimes complicated. Indeed, (i) cetaceans spend most of their time underwater, limiting the observations to few seconds when animals swim to the surface to breath, and a lot of information on their activities are not accessible to scientist. In the behavioural study, we only focused on six behavioural modes (playing, social, sexual, foraging, traveling and begging). Other dolphin behaviours such as aggressive behaviours or resting were not recorded because it was often complicated to well define these behaviours from the behavioural units observed during surveys. Moreover, from a study to another, definition of behaviours may be different, and dolphins may also exhibit diverse adaptations in their behaviours in response to local conditions. In several studies on dolphin behaviours, scientists have created the behavioural mode of «milling» that can be define as *a dolphin or a group of dolphins moving in varying direction in one location but showing no surface behaviours and no apparent physical contact between individuals; usually staying close to the surface* (Shane, 1999a). Therefore, when it is difficult to well define what dolphins are really doing, scientists often attribute these behaviours to the behavioural mode of milling.

(ii) Researchers depend on weather and sea conditions during surveys, that make difficult to perform surveys all days. Moreover, according to the region where the study is conducted, weather and seas conditions may vary strongly between seasons. Therefore, it is sometimes difficult to performed each fieldwork with the same effort throughout months. During the summer, the northern part of the

Gulf of Mexico is hitting by thunderstorms on daily basis, while between May and November, hurricanes may be also observed in this region, that both limit the fieldwork.

(iii) Studies on marine mammals are also often time consuming and expensive in materials (boat, camera, trips to the fieldwork…). Unfortunately, during this study, budget have been limited, and it was not possible to investigate the study area more than a season per year. However, without repeated data for each months, we are not able to investigate accurately the seasonal variation in the dolphin population size, the seasonal distribution and habitat use as well as the seasonal patterns on dolphins behaviour in Panama City. The lack of funds has also limited methods and techniques, that could be used to collect accurate information on this dolphin population, such as level of pollutants found in the blubber or sex determination from genetical analyses.

(iv) Finally, in most of cetaceans, sexual dimorphism is not obvious, and the distinction between males and females often occurs by direct observations of the abdominal region of animal (Reynolds et al., 2000; Dierauf and Gulland, 2001). Although 263 different dolphins have been identified, only 37 dolphins have been sexed (15 males and 22 females). Here again, the lack of funds has limited the investigation that could be made to determine a larger proportion of dolphins sex, and thus to better characterise the relationships within and between sex classes. Two methods can be used to determine the sex of a dolphin: (1) the video recording methods, that needs a waterproof camera to record dolphins underwater. (2) the genetic methods, which involves biopsy samples and analyses in a laboratory.

A bottlenose dolphin at sunset. Photo by Th. Bouveroux. Channel Entrance of Panama City. November, 2005.

VI. Perspectives

This first study on bottlenose dolphins conducted in Panama City, has achieved basic ecological data of this dolphins population such as, (i) how many individuals constitute the population? (ii) Which is the proportion of resident animals in the study area? (iii) Are there places in the study area that are favoured by individuals for their daily activities? (iv) Finally, what are the characteristics of the social structure of dolphins observed in Panama City? With this study, new questions and suggestions of interest may be developed for future research.

5.1. What about the East and the West Bay?

No data have been collected in the West Bay and the East Bay, while they are both linked to the St Andrew Bay. Yet, bottlenose dolphins may be present, extending or limiting their home range to one of the other bay, as it was observed in Apalachicola Bay, where dolphins present form a part of two distinctive communities (Tyson, 2008). Therefore, for a global plan of conservation and management of bottlenose dolphins in Panama City, it is essential to characterise if dolphins belong to several communities or constitute a unique population? We suggest strongly to extend future researches to both bays, to answer questions about dolphins abundance, distribution and habitat use. Thus, in addition to the photo-identification works that must be achieved in both bays, it should also be important to start surveys on dolphins distribution coupled with a behavioural study in order to supplement our data on habitat preference and habitat use by dolphins in all of the waters of Panama City, using multiple boats to sample all strata simultaneously. By extending the study area to both bays, we will be able to characterise home range of this dolphin population.

5.2. Continued year-round study on dolphins abundance

Since data on dolphins abundance are now available, we recommend strongly to pursue efforts realised with regular photo-ID surveys, including the winter months. Continued year-round monitoring of this population, submitted to human pressures and sometimes to environmental troubles (especially red tide), is necessary to detect possible declines in dolphins abundance. Future research is also needed to assess the seasonal fluctuations in dolphins abundance and to help determine potential causes of these changes.

5.3. Do dolphins distribution is influenced by prey distribution?

Our results suggest that the spatio-temporal distribution of dolphins seem to be influenced by prey distribution. Therefore, a better characterisation of resource availability will increase our understanding on dolphins distribution and diet in Panama City. A variety of approaches have been developed to investigate feeding ecology in bottlenose dolphins. One of the best method, is an application of stable-isotope techniques that measure the isotopic ratio of elements (e.g., carbon, nitrogen) in tissues of predators and prey (Barros and Wells, 1998). Stable-isotope provide a long term indication of the feeding history of the animal. However, these techniques lack the ability to distinguish specific prey. Therefore, a combination of complementary techniques should be useful to examine trophic relationships of dolphins. Moreover, the role of additional environmental variables on the distribution patterns of dolphins such as water temperature and bathymetry could enhance our insights into possible influence of ecological factors on dolphins' distribution.

5.4. Social Structure

In studies conducted in Shark Bay, Western Australia, males organisation show alliances of second-order, that attack other alliances in contests over female consorts and defend against such attacks (Connor et al., 1992; Connor et al., 2000; Connor et al., 2001). Moreover, only few studies suggest that some alliances are based on kinship (Möller et al., 2001; Krützen, 2002). Therefore, it is necessary to undertake a study on the sex determination and kinship using genetic methods and inspection of the genital area of individuals of unknown sex to determine if second-order of alliances, mixed groups, females bands are present within the social structure of Tursiops in Panama City.

5.5. Movements of dolphins between populations

Several bottlenose dolphin populations live all along the West coast of the Gulf of Mexico (Figure i). Close to Panama City, studies on bottlenose dolphins have been conducted in two adjacent bays, such as St Joseph Bay (Balmer et al., 2008) and Apalachicola Bay (Tyson, 2008), where catalogues of dorsal fins have been also created. Since evidence of bottlenose dolphins movements have been recorder in Panama City, with tagged dolphins around St Joseph Bay by Balmer (2007). A first comparison between photo-ID catalogues of St Joseph Bay (n=316) and Panama City (n=263), revealed that 69 different dolphins have been photo-identified in both study area.

We suggest to extend our research to estimate the proportion of migrant dolphins between populations, to identify them and thus to better characterise each population of dolphins in the region. Therefore, we propose to develop one dynamic database using a website platform, to index all identify dorsal fins and information about individuals, organised by study areas and classified using the

Urian's method. A free access to scientists working in this region of the Gulf of Mexico, with regular update of the database, will provide a very interesting tool to study dolphin movements between study areas, and definition of dolphins stock along the West coast of Florida.

5.6. Health assessment

With the growing of human activities (military, fishery, yachting, harbour activities), many sources of pollution may be present in the marine ecosystem and thus accumulated in the body of dolphins (i.e. heavy metals, organochlorines, etc...) (Wells et al., 2004). Indeed, dolphins are a top predator in the food web, and can concentrate pollutants which come from the accumulation of pollutants in its food (Shoham-Frider et al., 2009). Therefore, concentrations of anthropogenic chemicals such PCB's and DDT and its metabolites can reach levels of concern for bottlenose dolphin health and reproduction (Schwacke et al., 2002). The increased exposure to anthropogenic compounds may also reduce immune function in bottlenose dolphins (Lahvis et al., 1995), or may have an impact on the reproduction (Wells et al., 2005).

Therefore, we suggest to start a program of health assessment from living and dead-stranded dolphins to determine which is the level of pollutants present in dolphins tissues.

5.7. Behavioural study

a) What dolphins do at night ?

Currently, ethological studies conducted on bottlenose dolphins document strictly the diurnal and the seasonal activities, but what happens during nigh time still remains unknown. Therefore, to complete our knowledge on Tursiops ecology, it is important to initiate a scientific research on the dolphin behaviours as well as the habitat preference during night time. The St Andrew Bay with its calm and shallow waters, give a real good opportunity to start such a study.

b) Behavioural personality

A preliminary study on the behavioural personality in bottlenose dolphins have been initiated. Since, we are able to identify individuals in the population using the photo-identification, it is now possible to investigate the «personality» of identified dolphins. Currently, no information is available on the literature about individual difference of *T. truncatus*. Then, we suggest to extend this preliminary study to more individuals in the dolphins population of Panama City.

This first descriptive study on bottlenose dolphins in Panama City, Florida provide a baseline on the dolphin ecology in this popular seaside resort. The present results could be used by the National Marine Fisheries Service to help in their stock-assessment process and help in the management of the animals in this region more appropriately under the Marine Mammal Protection Act (NMFS, 2007). These results can also be used as a baseline from which future modifications of the ecosystem might be gauged if potential threats (increased development and activity by humans, red tide, future UMEs, etc.) occur in this region of Florida.

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A leap of a bottlenose dolphins at sunset. Photo by Th. Bouveroux. St Andrew Bay, November 2005.

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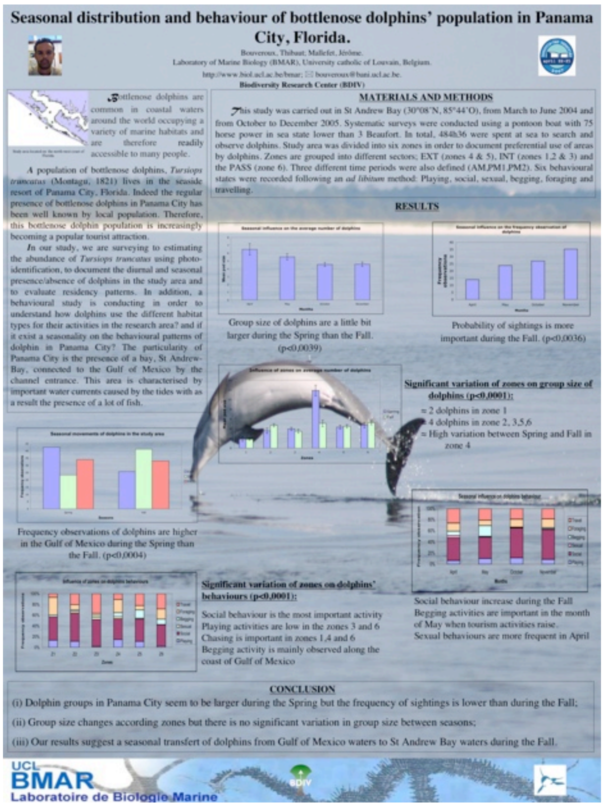


Poster presented at the 21th Conference of the European Cetacean Society, San Sebastian, Spain.

Posters

Study of population of bottlenose dolphins, *Tursiops truncatus*, resident in Panama City, Florida: abundance, distribution and behaviour in relation to human interaction.

Bouveroux, Th. , Mallefet, J. 2004

Poster presented at the *11th Benelux Congress of Zoology*. Louvain-La-Neuve. Belgium

The seaside resort of Panama City, Florida, in the Gulf of Mexico, is famous for its population of bottlenose dolphins, *Tursiops truncatus*, living in the waters of S^{t} Andrew Bay. Although little is known about this dolphin population, it has become a major tourist attraction. A field survey was conducted from March to June 2004 in order to document the abundance as well as the distribution of bottlenose dolphins in this area. Moreover a behavioural study has been initiated to assess tourism impact on dolphins' behaviour. Photo-identification and mark-recapture techniques were used to conduct this survey. The dolphin population was estimated to 51 individuals, among which 2 calves were observed. During the studied period, 101 dolphins have been photo-identified. Bottlenose dolphins were more often observed outside the bay and in the Pass. Behavioural results do not revealed any diurnal pattern in the activities of this dolphin population. Despite this fact, some trends emerged: (i) travelling was more frequent during the morning; (ii) hunting was more frequently observed at the end of the day in the West Pass area; (iii) frequency of spy hopping and begging was greatly increased while more than one ship was present and a decrease of social activities occurred in that situation. These results suggest that behavioural changes are induced by tourism activity.

Ecology and behaviour in relation to human interaction of bottlenose dolphins (*Tursiops truncatus)* in Panama City, Florida.

Bouveroux, Th.; Le Boulengé, E. and Mallefet, J. 2005

Poster presented at the *20th Conference of the European Cetacean Society*, Gdynia, Poland.

The seaside resort of Panama City, Florida, in the Gulf of Mexico, is famous for its population of bottlenose dolphins, *Tursiops truncatus* (Montagu, 1821), living in the waters of St Andrew Bay. Although little is known about this dolphin population, it has become a major tourist attraction. A field survey was conducted from March to June 2004 in order to document the abundance as well as the distribution of bottlenose dolphins in this area. Moreover a behavioural study has been initiated to assess tourism impact on dolphins' behaviour. Photo-identification and mark-capture-recapture techniques were used to conduct this survey. The dolphin population was estimated to 51 individuals, among which 2 calves were observed. During the studied period, 101 dolphins have been photo-identified. Bottlenose dolphins were more often observed outside the bay and in the Pass. Behavioural results do not revealed any diurnal pattern in the activities of this dolphin population. Despite this fact, some trends emerged: (i) travelling was more frequent during the morning; (ii) hunting was more frequently observed at the end of the day in the West Pass area; (iii) frequency of spy hopping and begging was greatly increased while more than one ship was present and a decrease of social activities occurred in that situation (iv) flippering was more observed when number of ship increase. These results suggest that behavioural changes are induced by tourism activity.

Seasonal distribution and behaviour of bottlenose dolphins' population in Panama City, Florida

Bouveroux, Th. & Mallefet, J. 2006

Poster presented at the *21th Conference of the European Cetacean Society*, San Sebastian, Spain.

We evaluated the seasonal variation of the distribution and behaviour of a coastal population of bottlenose dolphin, *Tursiops truncatus*, living in Panama City, Florida. This study was carried out in St Andrew Bay (30°08'N, 85°44'O), from March to June 2004 and October to December 2005. Systematic surveys were conducted using a pontoon boat with 75 horse power in sea state lower than 3 Beaufort. In total, 484h36 were spent at sea to search and observe dolphins. Study area was divided into six zones in order to document preferential use of areas by dolphins. Six behavioural states were recorded following an *ad libitum* method: Playing, social, sexual, begging, foraging and travelling. Results indicate that the mean group size is not different during the day and is approximately of 5 individuals ($p<0.0898$), however the presence of dolphins is not equally distributed in zones ($p<0.0001$). Diurnal behavioural patterns were observed in this dolphin population ($p<0.005$). In this case, foraging and begging activities are more frequently observed at the end of the day (16h00-20h00) and travel does not cease to decrease during the day. A seasonality of behavioural activities is revealed ($p<0.0001$): social behaviours are more often observed during October and November than April and May, when human activities are lower. Begging behaviours are more frequently observed during April and May while a decrease of foraging activities is established in the month of May. Sexual behaviours are mostly observed during April. The presence of new-born occurred only during the summer. Analysis of behaviours within the different zones is highly significant ($p<0.0001$): Begging behaviours are higher in zone 5 and zone 6 while foraging activities increase in zones 1, 4 and 6; travel budget shows a predominance of occurrence in zones 3 and 6.

Behavioural syndromes or when dolphins show some individual differences in their behaviours: preliminary study.

Bouveroux, Th. & Mallefet, J. 2007

Poster presented at the *21th Conference of the European Cetacean Society*, Egmond-aan-Zee, Netherlands.

In this study, we evaluated the individual differences in behaviours of bottlenose dolphins living in Panama City, Florida (30°08'N, 85°44' W). The dolphin population in Panama City, has been fed by human during several years. Despite of his prohibition by the *Marine Mammal Protection Act*, this practice is still observed in Panama City. Moreover, it is not rare to see some dolphins begging. Recent studies conducted by ethologist have documented 'animal personalities' in a broad range of organisms, including arthropods, birds and mammals. Therefore, to evaluate if dolphins have also some individual differences in their behaviours, we analysed the behavioural patterns of ten dolphins easily recognizable in the population. Among those; we are able to identify 4 males, 3 females but 3 individuals remained of unknown sex. Seven behavioural categories were observed: playing, social, sexual, spy hopping, begging, foraging and travelling. Our results show some differences in the behaviour frequencies between individuals, especially in the frequency of spy hopping and begging. Indeed, some dolphins seem to be 'regular beggars' while others dolphins never showed begging activities. We have also recorded the behavioural reactions of dolphins facing the presence of boats. Dolphins reactions were categorized as (i) get near the boat(s), (ii) have a neutral reaction or (iii) avoid the boat(s). Here again, analysis established that dolphins do not show the same behaviours: some of them avoid more often than others the presence of boats.

APPENDIX

Photography of a dolphin in bowriding. Photo by Th. Bouveroux. Channel Entrance of Panama City, October, 2005.

Appendix A
General Authorisation from NMFS (NOAA)

UNITED STATES DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
NATIONAL MARINE FISHERIES SERVICE
Silver Spring, MD 20910

JUN 30 2006

Thibaut Bouveroux
Laboratory of Marine Biology
3, Place Croix du Sud
1348 Louvain-la-Neuvre
Belgium

Dear Mr. Bouveroux:

The Office of Protected Resources' Permits, Conservation and Education Division has approved the request we received on May 31, 2006 to add you as a Co-Investigator to the General Authorization (GA) of Dr. Doug Nowacek (File No. 1055-1732). Therefore, your Letter of Intent (LOI) for a GA Letter of Confirmation (File No. 1096-1841), received in the Permits Division on April 5, 2006 is being returned, as the research activities proposed by this request will now be carried out under Dr. Nowacek's GA.

If you have any questions in reference to your returned LOI or require assistance with other marine mammal permit matters please do not hesitate to call Amy Hapeman at 301/713-2289.

Sincerely,

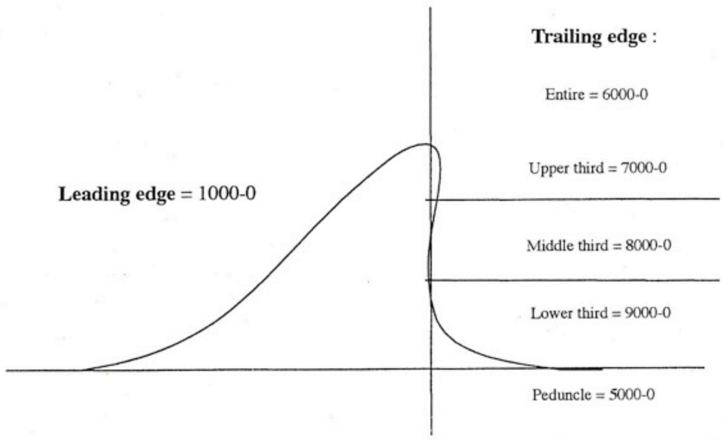
P. Michael Payne
Chief, Permits, Conservation
& Education Division
Office of Protected Resources

Enclosure

Printed on Recycled Paper

Appendix B
Urian's ID coding system
(Urian et al., 1999)

ID CODING SYSTEM FOR DUML/UNCW PHOTO-ID CATALOG



Freezebrand = FB-000 Mutilation = 2000-0 Fin shape = 3000-0 Scar = 4000-0
Right Bend
Left bend
Unique

An unmarked calf is identified by the number code of its mother with the last digit indicating the serial position of this calf in its mother's offspring history, (e.g., 1000-1 is the first known calf of presumed female, 1000-0).

The categories are organized based on the location of the most prominent feature on the dorsal fin. Location is determined by examining the fin, beginning at the anterior insertion of the dorsal fin and following along the fin contour to the posterior insertion of the dorsal fin, and using the following key.

	DUML/UNCW Category	
1. a) Dolphin has a freezebrand on dorsal fin and/or body	**Freezebrand**	**[FB-000]**
2. a) The most prominent feature is located on the dorsal fin............3		
b) The most prominent feature is located on the peduncle	**Peduncle**	**[5000-0]**
3. a) Dorsal fin is intact, with "typical" shape..................................4		
b) Dorsal fin is not intact or does not have "typical" shape: A		
A. Fin has notch, nick or slice on the leading edge	**Lead**	**[1000-0]**
B. Fin is cut off, top or tip of fin is missing	**Mutilation**	**[2000-0]**
C. Fin has unique shape or is canted/bent/curled	**Left/Right Bend**	**[3000-0]**
4. a) Dorsal fin has scarring, pigmentation pattern, healed wound	**Scarring**	**[4000-0]**
b) Dorsal fin does not have scarring...5		
5. a) Fin has prominent feature on trailing edge: A		
A. equally distinctive features in up, mid & lower thirds	**Entire**	**[6000-0]**
B. distinctive features in upper third of fin	**Upper third**	**[7000-0]**
C. distinctive features in middle third of fin	**Middle third**	**[8000-0]**
D. distinctive features in lower third of fin	**Lower third**	**[9000-0]**

Measurement of Photographic Quality and Dolphin Distinctiveness for the NMFS Mid-Atlantic Bottlenose Dolphin Photo-ID Catalog. Kim Urian, Curator. (1999).

OVERALL PHOTOGRAPHIC QUALITY

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

The Overall Photographic Quality score is based on an evaluation and sum of the following characteristics (these scores are absolute values, not a sliding scale):

Focus/Clarity

Crispness or sharpness of the image. Lack of clarity may be caused by poor focus, excessive enlargement, poor developing or motion blur; for digital images, poor resolution resulting in large pixels.

Based on the scale: 2= excellent focus; 4= moderate focus; 9= poor focus, very blurry.

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.

Based on the scale: 1= ideal contrast; 3= either excessive contrast or minimal contrast.

Angle

Angle of the fin to the camera.

Based on the scale: 1= perpendicular to camera; 2= slight angle; 8= oblique angle.

Partial

A partial rating is given if so little of the fin is visible that the likelihood of re-identifying the dolphin is compromised on that basis alone. Fins obscured by waves, *Xenobalanus*, or other dolphins, would be evaluated using this rating.

Based on the scale: 1= fin is fully visible, leading & trailing edge;
8= fin is partially obscured

Proportion of the frame filled by the fin
An estimate of the percentage area the fin occupies relative to the total area of the frame.

Based on the scale: 1= > than 5%; subtle features are visible 5= < than 1 %; fin is very distant
To score Overall Photographic Quality, sum the scores for each characteristic:

6 -9:	Excellent quality	=> Q-1
10-12:	Average quality	=> Q-2
>12 :	Poor quality	=> Q-3

OVERALL DISTINCTIVENESS

Overall Distinctiveness is based on the amount of information contained on the fin; information content is drawn from leading and trailing edge features, and pattern, marks, and scars.

D-1 - Very distinctive; features evident even in distant or poor quality photograph

D-2 - Average amount of information content: 2 features or 1 major feature are visible on the fin

D-3 - Not distinctive; very little information content in pattern, markings or leading and trailing edge features

These measurements are derived from:
Friday et al. 2000. Measurement of photographic quality and individual distinctiveness for the photographie identification of humpback whales, *Megaptera novaeangliae*. *Marine Mammal Science* **16**: 355-374.

Appendix C
List of the studied behaviours in bottlenose dolphins

CODE	NAME	DEFINITION
	PLAY	
BRL	Barrel roll	Roll body 360° in movement or stationary
PLO	Play with object	Dolphins play with object such as jelly-fishes, fishes, humans, algaes, bubbles...
SRF	Surf	Planing toward shore at the surface of a well-formed wave or the swell
BWR	Bow riding	One dolphins or more swim in front of a boat or a ship with or without jumps
JMP	Jump	Dolphins jumping out of water and falling back in the side
	SOCIAL	
NUR	Nursing	Mother-calf pair swimming closely together, with the calf in echelon position
SYB	Synch breathe	Two or more dolphins synchronously surface & breathe
APP	Approach	One dolphin approaches another
RUB	Rubbing	One dolphin rubs its body on another's body
CTP	Contact position	Pectoral fin of one dolphin placed on lateral side of another dolphins
	FORAGING	
FED	Feeding	Animal(s) feeding
FER	Feeding rush	One or more dolphins increase its speed suddenly for 10-20m

CODE	NAME	DEFINITION
SCK	Fish Mounting	Mouthing fish but not eating fish
FSP	Feeding splash	Splash made as dolphins make a final grab for a fish it has pursued
FST	Fish toss	Fish thrown into air by dolphin using its melon or rostrum
	TRAVELLING	
SWM	Swim	Dolphins are steadily swimming with a constant speed in the same direction
	BEGGING	
SPY	Spy hop	Move head up and out of water to pecs or only one side of the head
MDT	Mendicity	Move head up and out of water with open jaws
ITK	Intake	Dolphin(s) get food from hand of humans
	SEXUAL	
ERE	Erection	The turgid, firm & erect position of a dolphin penis oriented or not towards another dolphin or object
BUP	Belly up	Belly fully exposed to surface of water
BTB	Belly to Belly	Dolphins swimming belly to belly
INT	Intromission	Copulation success
GOS	Goose	Rostrum to genital behaviour between two dolphins

Appendix D
Behavioural personality in bottlenose dolphins or when animals show some individual differences in their behaviours: A preliminary study.

INTRODUCTION

Recently, researchers investigated a new aspect of the behavioural ecology of animals based on individual differences (Dall et al., 2004; Sasha et al., 2004; Sih et al., 2004; Dingemanse and Réale, 2005; Highfill and Kuczaj, 2007). Although many studies on dolphins behaviour have been published, very little is known about the behavioural personality of wild bottlenose dolphins. However, psychologists have long been interested in the role of individual differences in the behaviour of many species, such as chimpanzees (*Pan troglodytes*), gorillas (*Gorilla gorilla*), dogs (*Canis familiaris*), cats (*Felis catus*), rats (*Rattus rattus*), guppies (*Poecilia reticulata*), and octopi (*Octopus rubescens*), and how the differences in individual behaviour might reflect temperament or personality in individuals. Nevertheless, studies of animal personality are limited because of the subjects' lack of language, which excludes the use of methods such as self-reports, life-stories, attitude reports, and identity reports (Highfill and Kuczaj, 2007). In general, the terms "personality" and "temperament" are distinguished in human psychology but not in animal personality research. In researches on animal personality, the term "personality" is used to refer to an individual distinguishing patterns of behaviour that remain consistent over time and across situations (Pervin and John, 1997; Highfill and Kuczaj, 2007).

In human society, consistent individual differences in personality are easy to understand. For example, some people are generally more bold, whereas others are generally more shy in a situation (Sih et al., 2004). Studies on dolphins have indicated also some individual differences during feeding, swimming, and mothering behaviors. For example, Hill et al. (2007) suggested that dolphin mothers exhibit consistent individual differences in parenting styles, while maternal styles may affect the development of a calf's personality. Other situations may also reflect individual difference in dolphin behaviours. Dolphins are extremely social animals and live within a social hierarchy where some animals take on more dominant roles while others take on more submissive positions. The existence of different social roles also creates many occasions for consistent individual behavioural differences (e.g., Herman et al., 1993; Connor et al., 2001; Xitco et al., 2004; Delfour & Marten, 2005; Kuczaj & Walker, 2006; Kuczaj & Yeater, 2006). For example, a dolphin may maintain dominance over another by biting, chasing, and fluke-slapping. Consequently, the lower ranking dolphin can either choose to fight back or swim away (Herman, 1980). These kind of dolphins reaction toward a conspecific could reflect a certain personality type. Furthermore, dolphins can establish strong social bonds with other individuals (Wells, 1991). In dolphin society, males often form pair bonds that last a lifetime. The formation of pair bonds may depend on the compatibility of each dolphin's personality (Gero et al., 2005).

The above examples of dolphin behaviour demonstrated that all dolphins are not the same, and they support the possibility that individual differences among dolphins might reflect individual personalities. Unfortunately, the possibility of personality differences in bottlenose dolphins (*Tursiops truncatus*) has not been currently subjected to scientific study. Therefore, this preliminary study investigates the behavioural pattern of ten dolphins easily recognisable in the population in order to contribute to the emerging field of animal personality and to improve our knowledge of bottlenose dolphin ecology. We suggest that the presence of personality differences may affect how animal populations respond to change in their environment. Indeed, from an adaptive perspective, it makes sense for individuals to adjust their behaviours (Dall et al., 2004), especially in area where animals are subject to significant human activities that may change the natural behaviour of some individuals in the population. Thus, Panama City might represent an interesting area to document how human activities could influence the personality of individuals.

MATERIALS AND METHODS

Data were collected in the coastal waters of Panama City, Florida (30°08'N, 85°44'O), between October to December 2005, July/ August 2006 and June/July 2007. Systematic surveys were conducted using a small boat in sea state lower than 3 Beaufort. We used photo-ID technique to identify individuals present in a group. We attributed for each dolphins, an identification code **XYZ**: **X** for the age class: A= adult; J= juvenile or C= calf**;** **Y** for the sex: M= male; F= female or X= unknown**;** **Z** for the individual number. To facilitate the comparison of dorsal fins in the photo-identification catalogue, we used the classification system of dorsal fins based on the methods of Urian et al. (1999). Such a codification allows faster identification. To investigate the behavioural personality in bottlenose dolphins, we analysed the frequency behaviours of ten adult dolphins easily recognisable in the population. Among those, three females, six males and one individual of indeterminate sex were chosen. Six behavioural modes were recorded: playing, social, sexual, begging, foraging and travelling. Finally, we have also noted the behavioural response of dolphins facing the presence of boats. Dolphins reactions were categorised as (i) dolphins approaching the boat(s), (ii) have no response or (iii) avoid the boat(s). A more detailed description of sampling method and survey design to investigate dolphins behaviours as well the method use to identify individuals are described in Bouveroux et al. (*submitted a,* see chapter 3 and Appendix C).

RESULTS

Results reveal that the behavioural patterns of the studied individuals show a great variation in term of frequency of observations (Figure 1). Indeed, some individuals seem to be more playful than others (AM01 and AM34 *vs* AM68). Sexual behaviours are never observed in AF30, AF53 and AX06. Conversely, some dolphins are more sexually active than others (AM01, AM34 and AM33). These results show also that begging behaviours are observed in most individuals of this sample. Indeed, of ten dolphins, only two individuals are never seen to beg (AF79 and AX06). Conversely, two females dolphins (AF30 and AF53) devote a very high percentage of time to begging (59.5% and 41.6%, respectively). Foraging budget is lower for two females AF30 (3.05%) and AF53 (6.6%) than for other individuals of this sample. Finally, travelling budget of AF79 and AM02 is higher than others individuals (25% and 25.9%).

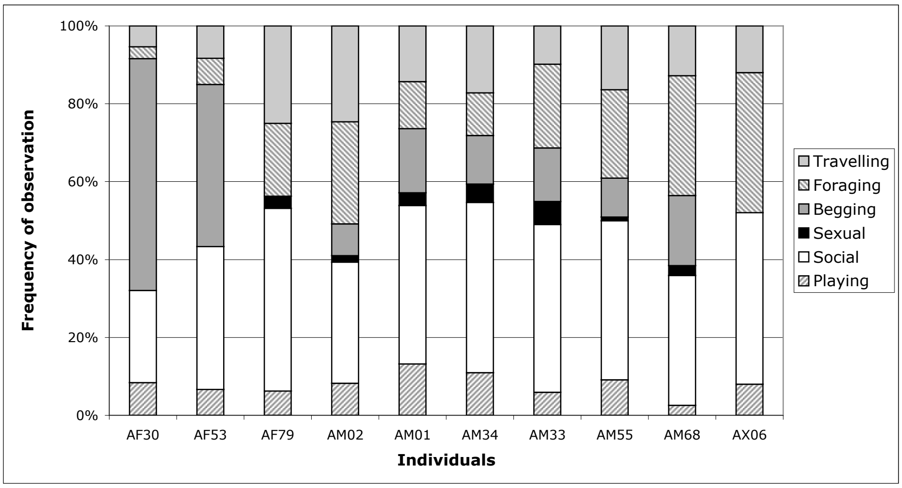


Figure 1. Individual patterns in behaviours of then dolphins easily recognised in the population.

The behavioural responses towards boats are quite different between individuals within the sample. While «no response» is the main reaction for most individuals towards boats, eight of the individuals were observed approaching boats, especially AF30, who comes close to boats in approximately 70% of cases. Conversely, only one female adult (AF79) shows a larger tendency to avoid boats when they are present in proximity.

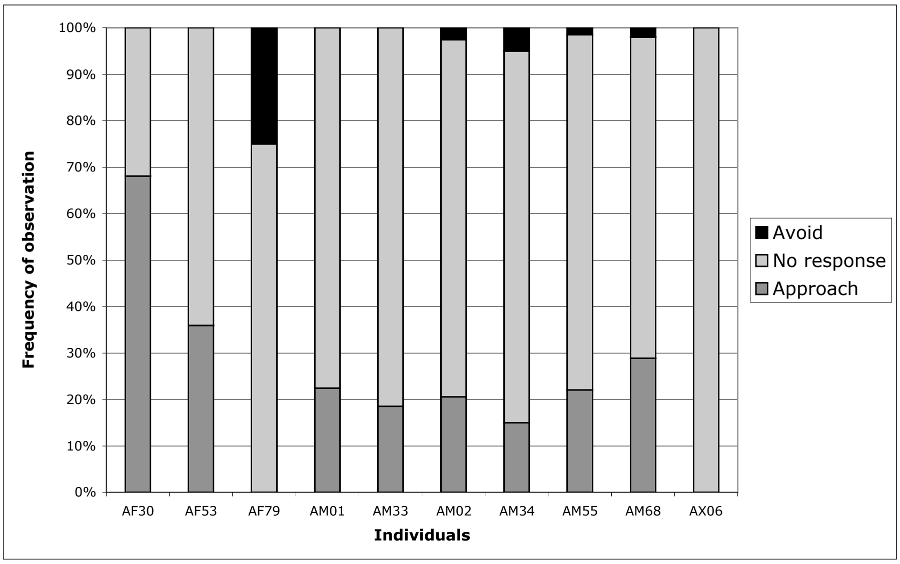


Figure 2. Individual response toward boats for then dolphins easily recognised in the population.

DISCUSSION

This preliminary study suggests some difference in the personality of dolphins. While, social activity budget is quite similar through the individuals, some dolphins seem to be sexually more active that other. These variations may be caused by the age of individuals, the sex of individuals, the hormonal rates or by the reproductive status. Indeed, the two females AF30 and AF53, were never observed in sexual behaviour with other dolphins, because they were already accompanied by a calf when our study started. Some individuals in the population are considered as "regular beggars" (AF30, AF53, AM01, AM33, AM34 and AM68) and these dolphins show chronic interactions with boats and humans. Our study also revealed that, dolphins responses towards boats are different between individuals inside the population. Indeed, some individuals are more "shy" toward human presence while others show a real interest in humans by taking food, that well illustrate the adaptability of individual dolphins to environmental change such as increased human activities. It is possible that dolphins find advantage in terms of energy by taking food from humans, and we can observe that these individuals also devoted less time to search and catch prey themselves. However, the high percentage of time spent close to boats may be harmful for dolphins. Indeed, several studies reveal that collisions between cetaceans and boats may have increased (Wells and Scott, 1997; Nowacek, 1999; Laist et al., 2001), as well as the acoustic pollution generated by boat engines that can change the distribution and the behaviour

Figure 3. Photography of two bottlenose dolphins, a female (AF30, left) and her male calf (AM73) during begging activities. Panama City, August, 2006. Photo by Th. Bouveroux.

of dolphins (Nowacek et al., 2001; Hastie et al., 2003a; Buckstaff, 2004). In Panama City, the kind of food that regular beggars receive from humans is as diverse as fresh fish from fishermen, frozen fishing bait, chips, hotdogs and even beer, have been observed (pers. obs.). Therefore, questions about the real impacts of feeding activities on the health of dolphins should be investigated, since it is known that their proximity with exhaust fumes (Stringer et al., 2000) and the quality of food that dolphins receive from humans might be harmful for dolphins. Moreover, feeding has been reported to have created problems for dolphins, such as learning to approach boats for food, with the risk of entanglement with fishing gear when present, the risk of collision with the boat or the propeller. After Hill et al., (2007), maternal styles may affect the development of a calf's personality. Monkey Mia, Western Australia, is also well known for the provisioned dolphins population that inhabit shallow waters. In this area, two provisioned females produced female calves that became provisioned. In Panama City, similar findings have been observed for the calves of the two regular beggars, AF30 and AF53 (Figure 3), only a few months after their births. Therefore, these observations illustrate well the influence of maternal styles on the development of the calf's personality, and underlines again the problem of feeding dolphins, especially in females that learn these practice to calves.

In order to improve our knowledge of dolphins behaviour, we suggest a deeper investigation of the behavioural differences in individual dolphins.