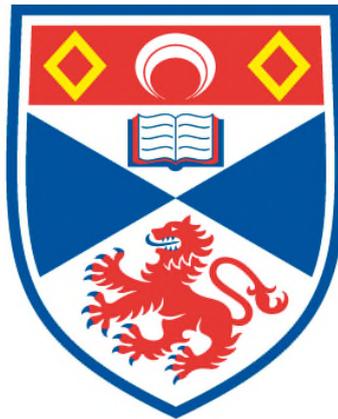


**ECOLOGY OF THE GUIANA DOLPHIN (SOTALIA  
GUIANENSIS) IN THE SOUTHERN AREA OF THE GULF OF  
MORROSQUILLO, COLOMBIA:  
IMPLICATIONS FOR CONSERVATION**

**Beatriz Salomé Dussán Duque**

**A Thesis Submitted for the Degree of PhD  
at the  
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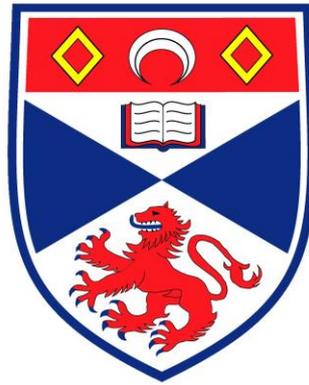
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**Ecology of the Guiana dolphin (*Sotalia guianensis*) in the Southern area of the Gulf of Morrosquillo, Colombia: implications for conservation**

Beatriz Salomé Dussán Duque, MSc



This thesis is submitted to the University of St Andrews for  
the degree of Doctor of Philosophy

Scottish Oceans Institute  
Sea Mammal Research Unit  
School of Biology

July 2013



## **Declaration**

I, Beatriz Salomé Dussán-Duque, hereby certify that this thesis, which is approximately 60,000 words in length, has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree. I was admitted as a research student in October 2007 and as a candidate for the degree of Doctor of Philosophy in October 2008; the higher study for which this is a record was carried out in the University of St Andrews between 2007 and 2013.

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**Group of Guiana dolphins, Gulf of Morrosquillo, Colombia, March 12, 2004. *Photograph***  
*by Salomé Dussán-Duque*



*A Luna y su especie, "Que la nuestra es agua de río mezclada con mar."*

*(Anonymous)*

*A mis padres, Rafael y Beatriz, "Porque vengo de dos ríos que van al mar."*

*(Jorge Manrique)*



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## Abstract

*Sotalia guianensis* is listed as “Data Deficient” by the IUCN and as “Vulnerable” in Colombia. This study aimed to advance understanding of the ecology of this species and its habitats, and to provide information to conservation management in the southern Gulf of Morrosquillo, Colombia. Systematic boat-based surveys were conducted during 395 days in 2002-2006 and 2009-2010, following established routes. Total survey effort was 15,199 km in an area covering  $\sim 310\text{km}^2$ . Fine scale habitat use and behavioural modelling, photo-identification and mark-recapture techniques were used to analyze the ecological patterns for this species. The most recent abundance estimate of dolphins using the study area during dry and rainy seasons, varied from 225 (CV = 0.34; 95% CI: 118-426) to 232 (CV = 0.32; 95% CI: 127-246). Annual survival rate is estimated at 0.948 (95% CI = 0.876-0.980). Overall density was  $0.74/\text{km}^2$ . Dolphins were present year-round in the whole study area. Results indicate that they do not use the study area uniformly and that the use of particular zones is related to eco-geographic variables. Dolphins showed a preference for waters greater than 3m in depth with a slightly increased preference for waters about 5m and 15-25m deep. The average group size was nine individuals. Some individuals show long-term high site fidelity to some zones within the study site boundaries. Even though the site fidelity to feeding areas varied individually, all the individuals focused primarily on one specific area. Foraging was among one of the most predominant behaviours observed. The individual movements show that some dolphins use both bay and gulf waters. Dolphins show a range surface cooperative foraging and feeding strategies. These cooperative behaviours were influenced by zone, group size and prey type. Based on these results an area of special management for the species will be created in Colombia.

**Key words:** *Sotalia guianensis*, vulnerable, habitat modelling, abundance, survival rate, site fidelity, cooperative feeding, conservation.



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We did it! Thank you very much; I humbly leave in your hands “my little white Ganesha”.

*“...Quiero que tus sueños y los míos se encuentren en el tiempo, quiero ser tu pensamiento...te estoy buscando, quiero que vuelvas, que me has dejado aquí, solo en la Sierra...”* (Carlos Vives).



## **Chapter 1 – Introduction**



## 1.1. Estuarine ecosystems and their conservation

“Living organisms and their abiotic environment are inseparably interrelated and interact upon each other forming ecosystems or units” (Odum 1971). In the last century, anthropogenic pressures have moulded and changed many ecosystems (e.g. Cox *et al.* 2000, World Health Organization 2005, McMichael *et al.* 2006). These changes were initially more noticeable for terrestrial ecosystems, where the changes made by humans were more obvious. But in recent decades changes in marine ecosystems became more visible and raised concerns (e.g. Béthoux *et al.* 2002, Orth *et al.* 2006, Moellmann *et al.* 2009). Species and biodiversity were being lost at a faster rate than before. The centre of attention focussed on efforts to recover and protect species, as individual independent units. These efforts were only partially successful and remained so until species started to be considered as integral parts of an ecosystem in which everything is connected through the transfer of energy (e.g. Nyström *et al.* 2000, Aide & Grau 2004). With marine ecosystems, it has taken longer to see them as limited connected systems.

Coastal and estuarine marine ecosystems have been for decades more affected by anthropogenic pressures because of their proximity to terrestrial ecosystems (e.g. Vasconcelos *et al.* 2007, Borja *et al.* 2008, Duarte *et al.* 2008). We have transformed them and treated them as part of the land, without consideration of the long term consequences for the species that inhabit them, including humans (World Health Organization 2005). There are at least five different type of estuaries based on geomorphology, water circulation and system energetics (Margalef 1965, Odum 1971). Tropical estuaries, for example, were and still are considered by many people that inhabit them as “bad lands”. They do not have sandy beaches, they have thick mangrove forest that makes access to the ocean difficult. Nothing can be grown on them for human consumption and they are covered with mosquitos. Estuaries have been one of the ecosystems most misunderstood by us. We did not “like” estuaries, so we had to transform them to be able to live in and use them.

Estuaries have a number of special features. An estuary is a semi-enclosed coastal ecosystem with connection to the sea, and within the ocean water is mixed with water from land (e.g. rivers’ mouths, channels, coastal bays and tidal marshes) (Odum 1971). Estuaries are one of the most productive and stable ecosystems and their physical and biological attributes are unique (Margalef 1965). Many terrestrial and marine species inhabit estuarine waters. These

species are well adapted to deal with natural stressors (e.g., temperature, salinity, anoxia, high light gradients). However, because they live close to their tolerance limits, estuarine species may be particularly sensitive to disturbances created by anthropogenic activities (Kathiresan & Bingham 2001).

In tropical and sub-tropical latitudes estuarine ecosystems have vast forest areas called mangroves. There may be no other group of plants that is so highly adapted to extreme conditions (Robertson & Alongi 1992). Mangroves create unique ecological environments rich in species biodiversity, starting in their immersed roots (Kathiresan & Bingham 2001). The muddy sediments and the channels within the mangal (immersed mangrove roots) support communities of phytoplankton, zooplankton and fish (Holguín *et al.* 2001). They have been called nurseries for juveniles of fish, the adults of which occupy other habitats (Ellison & Farnsworth 1996). Estuarine mangrove ecosystems are among the most endangered because of anthropogenic pressures. The early human communities that inhabited these ecosystems perceived the richness of them. They were willing to modify them in order to inhabit these “harsh” areas. The first thing that needed to be transformed was the mangrove forest to be able to construct human settlements. In recent decades, the destruction of mangrove forests is comparable to that of tropical forests around the globe.

Sirenians, and delphinids are among the animal species that inhabit marine mangrove estuarine waters. Some of these species are apex predators together with several species of sharks and some crocodiles. Because of the fragility and loss of their ecosystems and the continuous overuse by humans, several of these species have declined in numbers in recent decades. The role of apex predators is crucial in maintaining the health of their ecosystems. Apex predators affect prey species' population dynamics and therefore the energetic balance of ecosystems. Ecological impacts of eliminating top predators can be far-reaching in any ecosystem (e.g. Merrick 1997, Post *et al.* 1999, O'Connell *et al.* 2007, Mayers *et al.* 2009).

The Gulf of Morrosquillo is an open mixed mangrove estuarine ecosystem located in the Caribbean Sea of Colombia (9°-10° N and 75°-76° W). A detail description of its geomorphological characteristics is given in Chapter 2. Three marine mammal species inhabit the Gulf of Morrosquillo: *Thrichechus manatus* (Caribbean manatee), *Tursiops truncatus* (bottlenose dolphin), and *Sotalia guianensis* (Guiana dolphin). The Caribbean manatee population is listed as Endangered in Colombia due to low population numbers caused by habitat loss and degradation and high human consumption (Rodríguez *et al.* 2006).

Nothing is known about the population status of the bottlenose dolphin in Colombia. The Guiana dolphin was listed as Vulnerable in 2006 (Trujillo *et al.* 2006) due to habitat loss and degradation and absence in zones where it was previously reported abundant. It is also classified as Data Deficient on the IUCN Red List 2013.

This study aimed to advance understanding of the ecology of Guiana dolphins and its habitats to inform its conservation in Colombia. Data in Colombia about the ecology of this species is almost non-existent, due to the lack of resources available for it coupled with a social and political conflict which has made some areas of the country almost inaccessible over the last two decades. Only one long-term study of these species has been conducted prior to this one (Avila 1995). Avila's work is highly informative but, being a bachelor thesis, has remained unpublished. Most current knowledge of the species comes from studies conducted in Brazil over the last 30 years.

## **1.2. Biology of Guiana dolphins**

### **1.2.1. Systematics and distribution**

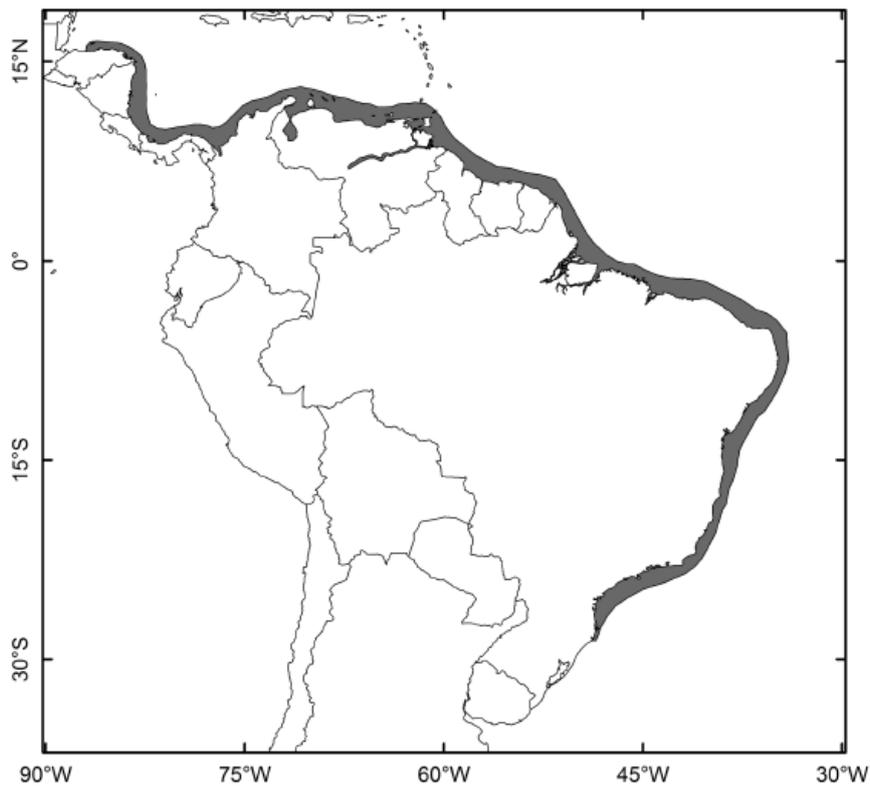
The majority of marine mammal species belong to the Order Cetacea which includes whales, dolphins and porpoises. Two major groups are recognized: the suborder Mysticeti, or baleen whales and the suborder Odontoceti, or toothed whales, to which the Family Delphinidae belongs (Bertha & Sumich 1999).

*Sotalia guianensis* belongs to the Order Cetacea, Suborder Odontoceti, Superfamily Delphinoidea and Family Delphinidae (Rice 2002). The taxonomy of the Genus *Sotalia* has been controversial. In the late 1800s up to five species were described, three from riverine specimens and two from coastal specimens (Rice 1998).

Until 2007, *Sotalia guianensis* was recognized as the marine ecotype of the species *Sotalia fluviatilis* and its scientific name was *Sotalia fluviatilis guianensis* (Flores 2002, Caballero *et al.* 2007). The concept of one species with two ecotypes, one marine and one riverine, was recently changed based on morphological characteristics (Monteiro-Filho *et al.* 2002) and genetic divergence (Cunha *et al.* 2005, Caballero *et al.* 2007).

Two species are now recognized: *Sotalia fluviatilis* or tucuxi, which inhabits the Amazon river and most of its tributaries (Leatherwood & Reeves 1983, da Silva and Best 1996,

Flores 2002), and *Sotalia guianensis* or Guiana dolphin, which is distributed along the Caribbean and Atlantic coasts of South America, from Nicaragua (Carr and Bonde 2000, Edwards & Schnell 2001) and possibly Honduras (Edwards & Schnell 2001) to Florianopolis in southern Brazil (Geise and Borobia 1987, Borobia *et al.* 1991). It has also been reported in some Caribbean islands including Trinidad and Tobago (da Silva and Best 1996). One population has also been described in Maracaibo Lake (Hershkovitz 1962). Although the distribution of *S. guianensis* seems to be continuous along the coast, the number of distinct populations that might exist is unknown (Caballero 2006) (Figure 1.1).



**Figure 1.1 - General distribution of the Guiana dolphin in South and Central America. From Flores *et al.* (2010).**

### **1.2.2. Conservation status of the Genus *Sotalia***

*Sotalia* is classified as Data Deficient on the IUCN Red List 2013, and is listed in Appendix I of CITES. It is also listed in Appendix II of the U.N. Convention on Migratory Species.

The classification of Data Deficient (DD) is given by the IUCN to a taxon when there is inadequate information to make a direct or indirect assessment of its risk of extinction based on its distribution and/or population status. Listing of taxa in this category indicates that more information is required and acknowledges the possibility that future research will show that threatened classification is appropriate. It is important to make positive use of whatever data are available on the species (Cetacean Specialist Group 1996). This lack of information reinforces the importance of conducting long-term studies about its ecology.

Appendix I of CITES lists species that are the most endangered among CITES-listed animals and plants (see [Article II, paragraph 1](#) of the Convention). They are assessed as threatened with extinction and CITES prohibits international trade in specimens of these species except when the purpose of the import is not commercial (see [Article III](#)), for instance for scientific research. In these exceptional cases, trade may take place provided it is authorized by the granting of both an import permit and an export permit (or re-export certificate). Additionally, [Article VII](#) of the Convention provides for exemptions to this prohibition and these requirements (UNEP-WCMC 2008).

Appendix II of the Convention on Migratory Species (2006) list migratory species that have been assessed as having unfavourable conservation status or would benefit significantly from international co-operation organized by tailored agreements. For this reason, the Convention encourages the Range States to conclude global or regional agreements for the conservation and management of individual species or, more often, of a group of species listed in Appendix II. The agreements may range from legally binding treaties to less formal instruments, such as Memoranda of Understanding, and can be adapted to the requirements of particular regions (Convenio sobre especies migratorias 2006).

In Colombia the species *Sotalia guianensis* is listed as a Vulnerable species under the IUCN criteria A2cd (Trujillo *et al.* 2006). This categorization is supported nationally by Resolution 0572 of 2005 of the Ministry of Environment. With this Resolution the previous categorization of this species as Data Deficient was changed. In the IUCN Red List Categories & Criteria version 3.1 (2013) a taxon is Vulnerable (VU) when it is not Critically Endangered or Endangered, but is facing a high risk of extinction in the wild in the medium-term future, as defined by any of the criteria. The criteria given to *Sotalia guianensis* in Colombia (A2cd) corresponds to:

A) Reduction in population size base on:

2) An observed, estimated, inferred or suspected population size reduction of  $\geq 80\%$  over the last 10 years or three generations, whichever is the longer, where the reduction or its causes may not have ceased OR may not be understood OR may not be reversible, based on (and specifying):

(c) a decline in area of occupancy, extent of occurrence and/or quality of habitat.

(d) actual or potential levels of exploitation.

After the recognition in 2007, by the scientific community, of the existence of two species in the Genus *Sotalia*: one marine *Sotalia guianensis* and one riverine *Sotalia fluviatilis*, there have not been any changes given specifically to the status of each species in particular. These changes will help the *Sotalia* researchers to refine in a better way the future actions to be taken to conserve both species.

### **1.2.3. The natural history of *Sotalia guianensis* ( P. J. Van Bénédén, 1864)**

The Guiana dolphin is listed as insufficiently known (Data Deficient) by the IUCN. The lack in the data about this species corresponds mainly to three factors: firstly that research has been conducted only in two countries of its known distribution: Brazil and Colombia; secondly that long-term studies with this species started to be developed only two decades ago; and thirdly that only Brazilian studies on *S. guianensis* have been published.

#### **1.2.3.1. Common name and general description**

Alexander von Humboldt was the first naturalist to document the presence of coastal dolphins that entered the mouths of rivers in Venezuela, South America. During his travels to this region between the XVIII and XIX centuries, he noted the presence of small dolphins with prominent dorsal fins, around 130 km up from the mouth of the Orinoco River (Humboldt von 1889, Hershkovitz 1962).

*Sotalia guianensis* was previously known by its common and popular name tucuxi, which comes from *tucuchi-una* after de Tupi language of the Mayanas Indians from the Amazon region of Brazil (Flores 2002). Along its distribution *S. guianensis* is locally known by several different names that correspond to the different languages spoken in various range states. The most recent proposal (Flores *et al.* 2010) was to leave the common name of tucuxi for *Sotalia fluviatilis* or the riverine species, and to give the common name of Guiana dolphin to *Sotalia guianensis* or the coastal species.

The Guiana dolphin is similar to *Tursiops truncatus*, bottlenose dolphin, but much smaller (maximum length of 210 cm reported) and stubbier, with a less falcate dorsal fin, that is almost triangular, and sometimes slightly hooked at the tip. Its coloration is light to bluish gray on the dorsal area and pinkish to light grey on the ventral region, with a distinctive boundary from the mouth gape to the flipper's leading edge. On the sides it has a lighter area between the flippers and the dorsal fin, another one in the middle body at the anus level, and may have sometimes another light grey rounded streak on both sides of the caudal peduncle. It has a moderately slender long beak, a rounded melon, and 26-36 teeth in each mandibular ramus (Leatherwood & Reeves 1983, Flores 2002) (Figure 1.2).



**Figure 1.2-** *S. guianensis* external morphology and coloration. *Photograph by Salomé Dussán-Duque.*

### **1.2.3.2. Ecological aspects of the species**

*S. guianensis* is found mainly in estuaries, bays and other protected shallow coastal waters (Edwards & Schnell 2001, M.C. de O. Santos *et al.* 2001, Dussán-Duque *et al.* 2003, Flores 2003, Da Silva *et al.* 2010). Its presence is recorded throughout the year in many coastal locations such as Baía Norte, Cananéia estuary and Baía de Guanabara, Baía de Todos os Santos, and Fortaleza, all of them in Brazil, as well as Bahía Cispatá and Golfo de Morrosquillo in Colombia (Flores 2003). Photo identification studies in some of these areas have demonstrated that at least some animals are residents year-round for up to 7 continuous

years (Avila 1995, Flores 1999, Dussán-Duque *et al.* 2006). The Guiana dolphin undertakes mainly local movements, remaining within a limited home range (Leatherwood & Reeves 1983, Flores 2003, García & Trujillo 2004, Dussán-Duque & Wells 2007, Rossi-Santos *et al.* 2007, Wedekin *et al.* 2007). In many areas of its distribution, this species shows seasonal variations in spatial usage, possibly associated with prey distribution (Ávila 1995, Flores 2003, Dussán-Duque *et al.* 2003 2006, De Freitas Azevedo *et al.* 2004, García & Trujillo 2004, Wedekin *et al.* 2007).

Guiana dolphins are very social, often found in groups of 2-9 individuals (Flores 2002, 2003, Dussán-Duque *et al.* 2003); the tightness of their swimming formation suggest that they have strong social ties (Leatherwood & Reeves 1983) (Figure 1.3).



**Figure 1.3- Guiana dolphin group, Gulf of Morrosquillo, Colombia. Photograph by Salomé Dussán-Duque.**

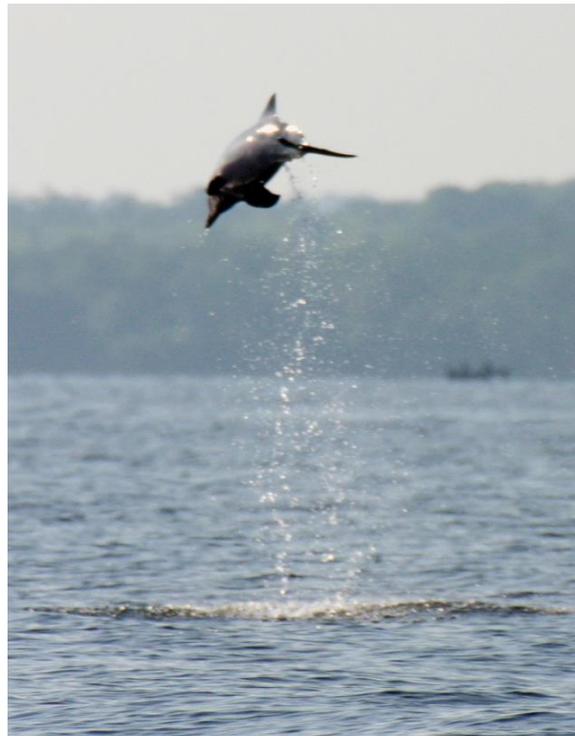
Larger aggregations are usually engaged in cooperative feeding, in these aggregations groups up to 50 or 70 animals are found (Flores 2003, Dussán-Duque & Wells 2007). Aggregations of up to 200 are reported in Baía de Sepetiba (Flach *et al.* 2008), and around 400 individuals in Baía da Ilha Grande on the southeastern Brazilian coast (Lodi & Hetzel 1998). Feeding occurs in two general ways: in pairs and cooperatively in large groups or sub-groups when different strategies are employed (Flores 2003, Dussán-Duque unpublished data). During feeding activities associations between Guiana dolphins and birds often occurred. The most common birds species are: the brown booby *Sula leucogaster*, terns (*Sterna* spp), frigate *Fregata magnificens* and kelp gull *Larus dominicanus* (Avila 1995, Flores 2002, Dussán-Duque *et al.* 2003).

From the results of stomach contents analysis from stranded animals from Brazil, it has been possible to establish that this species feeds mainly on neritic prey that inhabits coastal areas.

These prey species are abundant year round in the study areas, and have low commercial value (Rosas *et al.* 2010). The prey species are pelagic, demersal or pelagic-demersal, which

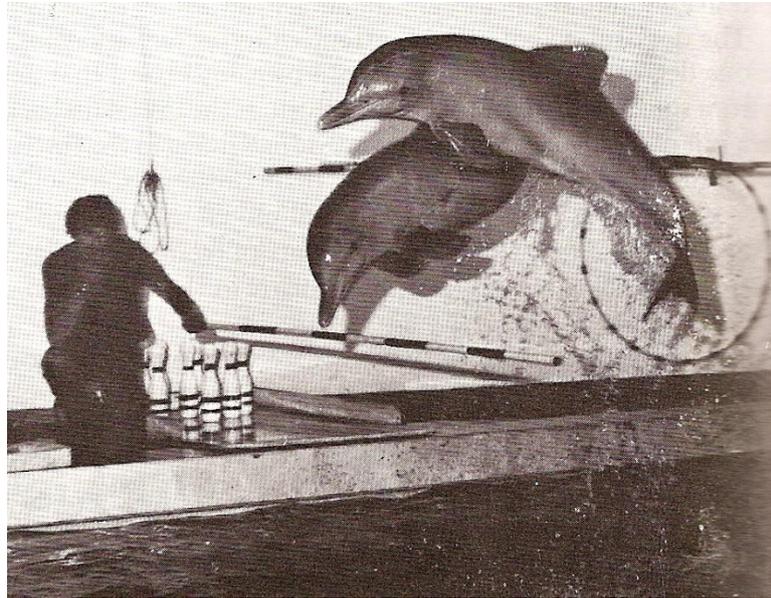
indicates that Guiana dolphins capture their prey at different water depths in the water column (Di Benedetto & Siciliano 2004). The most frequently found species were the teleost fishes *Trichiurus lepturus*, *Cynoscion guatucupa*, *Isopisthus parvipinnis*, and *Porichthys porossimus*, but at least 17 different species of fish have been identified (Borobia & Barros 1989). Back calculations of prey sizes indicated that they feed mainly on young specimens (Di Benedetto & Ramos 2004). In addition, neritic cephalopods (family Loliginidae), shrimps and flounders are occasionally taken (Di Benedetto *et al.* 1998). Differences in the foraging habits of the Guiana dolphin between the areas that it inhabits, are probably related to environmental features and consequently to the prey species abundance and distribution (Carvalho 1963, Geise & Gomes 1988, Flores 2002, Santos *et al.* 2002, Di Benedetto & Ramos 2004).

Behaviour reported in wild populations includes aerial displays such as vertical and lateral full jumps (Figure 1.4), somersaults, spy-hopping, tail-lobbing, lying on the surface belly up and hitting the water with flippers and flukes, surface rolling, and porpoising (Avila 1995, García 1998, Flores 2002 2003, Dussán-Duque unpublished data).



**Figure 1.4.-** Guiana dolphin calf leaping out of the water in Cispatá Bay, Gul of Morrosquillo.  
*Photograph by Salomé Dussán-Duque.*

They do not bow ride but may surf in waves or wakes produce by passing boats (Borobia 1984, Geise 1984 1989, Da Silva & Best 1996, Araujo *et al.* 2001). On the other hand, captive specimens rarely show voluntary aerial displays (Terry 1983 1986) (Figure 1.5).



**Figure 1.5.- Guiana dolphins in captivity being trained in the Duisburg Zoo, Duisberg, Germany. From: The Sierra Club handbook of whales and dolphins, pp. 186. These dolphins were captured in Cispatá Bay, Gulf of Morrosquillo (Bössenecker 1978).**

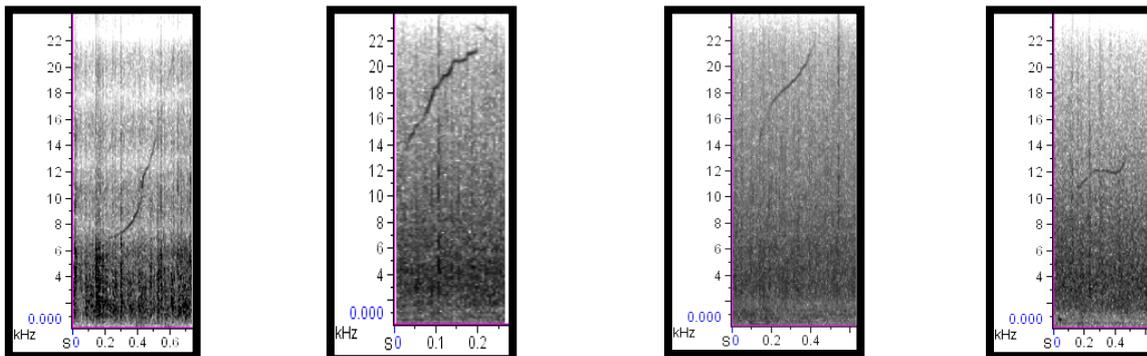
There have been only a few studies of the bioacoustics of this species, mostly from Brazil, and only two have been conducted in Colombia; there are no studies in other areas of its distribution. The intense, rapidly repeated clicking sounds made by this dolphin probably allow it to echolocate in a visually opaque medium such as estuarine waters (Leatherwood & Reeves 1983).

The Guiana dolphin has a varied repertoire of whistles, but the signals are simple in form, and whistles with 0 or 1 inflection point are more abundant. The whistles are characterized to be mainly upsweep or ascending, and despite their similar characteristics to other delphinids, whistles produced by this dolphin were shorter and less complex in shape. The average minimum frequency of the whistles is reported to be  $9.22 \pm 3.44$  kHz and the average maximum frequency is reported to be  $19.05 \pm 2.97$ , but the whistles can reach frequencies greater than 24 kHz. This species emits whistles with fundamental frequencies above 24 kHz

more frequently than other odontocetes previously studied. The whistle duration is short ( $308 \pm 137$  ms) (Azevedo & van Sluys 2005).

There are variations in the magnitude of whistle characteristics between northern and southern areas of the Brazilian coast. The northern populations have higher whistle frequencies than those in the south. It has been suggested that these variations may be caused by isolation of the populations, as well as differences in the social and acoustic environments (Azevedo *et al.* 2005, Rossi-Santos & Podos 2005).

In one of the studies conducted in the Gulf of Morrosquillo of Colombia, four typical whistles contours were present (Figure 1.6). The mean duration of the vocalization was 0.253 s. whistles with up to 3 inflection points were found and 2 inflections were present in the most common vocalization made during group feeding activities. Ascending whistles made up 86% of the recordings. Whistles with 0 and 1 inflections made up 66% of the sounds emitted. The maximum frequency recorded was 23.8 kHz and the minimum was 5.08 kHz (Bernasconi *et al.* 2005).



**Figure 1.6.- Whistle contours of the vocalizations Guiana dolphins vocalizations (Bernasconi *et al.* 2005).**

The second study conducted in the Gulf of Morrosquillo was the first one to obtain and report high frequency recordings of this species' vocalizations. Whistles were short (duration =  $169 \pm 117$  ms), ascending (64%), and ultrasonic ( $f_{min} = 17.3 \pm 6.0$  kHz,  $f_{max} = 24.5 \pm 6.4$  kHz,  $N = 251$ ). Four whistles extended beyond 45 kHz, showing that even a 96 kHz sampling rate is not enough to capture the whole frequency range of Guiana's dolphin whistle fundamental frequencies. Echolocation clicks seem to be bimodal with regular inter-click intervals (ICI)

greater than 30ms, and energy starting at about 20kHz that extends beyond 250kHz. Burst pulses started at about 8.8kHz, with an ICI of approximately 1.4ms (Bazúa-Durán *et al.* 2009).

The Guiana dolphin often travels at high speeds near the surface of the water. Surfacing is often accompanied by explosive breathing, where the animals exhale forcefully, and movements through the water that produced rooster-tails (Edwards & Schnell 2001). Dive times are about 1.5 to 2 minutes with shorter surfacings every 5-10 sec in between (Avila 1995, García 1998, Flores 2002, Dussán-Duque unpublished data).

The body length at which this species reaches sexual maturity is 170-180cm in males and 160-169cm in females, and the age of sexual maturity occurs at 6-7yr in males and 5-7yr in females (Rosas *et al.* 2010). Adult size is attained when there are five or more growth layer groups in the dentine (Weber-Rossas *et al.* 2003). According to growth layer groups, the lifespan can reach 30 years (Borobia 1989). Natural mortality rates are unknown (Flores 2002). The breeding system is polyandrous and involves sperm competition (Best & Da Silva 1984), with mating involving tactile contact and copulation occurring belly to belly. Gestation is estimated to be around 11-12 months with calves ranging from 90 to 100 cm at birth. Calving is year-round, and the calving interval is believed to be 22-23 months (through photo-identification data) (Flores 2003).

Potential predators are killer whales (*Orcinus orca*) and various species of coastal sharks (Figure 1.7). However, there is no record of any predation (Flores 2003).

*S. guianensis* interacts to some extent with *T. truncatus* in areas of their distribution in which their home ranges overlap (Avila 1995, García 1998, Flores 2002 2003, Dussán-Duque in progress). These species have been engaged in apparent mating behaviour in Costa Rica (P. Forestell, personal communication).



**Figure 1.7.- Juvenile tiger shark (*Galeocerdo cuvier*) captured and killed in a gillnet in Cispatá Bay, Gulf of Morrosquillo. Photograph by Salomé Dussán-Duque.**

### **1.3. Conservation threats of the species**

Along its estuarine habitats, the species is subject to a variety of human activities that threaten its conservation. Interactions include: incidental mortality in different types of nets (gillnets causing the highest mortality rates); the use of dynamite in fisheries direct catches and resource competition with local fisheries (Lodi & Capistrano 1990, Pinhero & Cremer 2004, Dussan-Duque *et al* 2006); bycatch is reported in Brazil with the use of blubber as bait for long-lines (Siciliano 1994); contaminant concentrations have been reported within the normal range of coastal species (Laison-Brito *et al.* 2000); habitat destruction and loss due to populations being present in areas of major human development. Other environmental conflicts reported for Guiana dolphins include the construction of dams and hydroelectric power facilities that may fragment the populations by isolation, and interrupt fish migration as well as reduce fish abundance (Ferreira 1984).

Incidental mortality in local and commercial fishing gear such as gill nets and seines is the main direct threat (Figure 1.8) (Leatherwood & Reeves 1983, Avila 1995, Flores 2005, Dussán-Duque *et al.* 2003). In some localities they are killed occasionally for shark bait or human consumption (Figure 1.9) (Flores 2003, Dussán-Duque unpublished data).



**Figure 1.8.-** *S. guianensis* individual entangled and killed in an artisanal fishing gillnet, Cispatá Bay, Gulf of Morrosquillo. *Photograph by Salomé Dussán-Duque.*

### **1.3.1. Guiana dolphins in Colombia**

The first report about the populations of this species in Colombia was by Bössenecker (1978). In this document, the author reported the legal catch of dolphins of this species in Colombia.

He reported as well that the largest schools of Guiana dolphins were seen near the mouth of the Magdalena River, near Barranquilla in the northern tip of Colombia. Since then, there have not been any reports about the presence of this species in that area.

It was decided to capture dolphins in Cispatá Bay in the Gulf of Morrosquillo where the fisherman reported the daily presence of several dolphins in very shallow waters. In total about 80 dolphins were captured, of which 24 were selected to be transported to Europe; several of them died during the capture process, and in the pools (A. Arevalo, H. Beltrán, personal communication).

Bössenecker (1978) mentioned hepatic degeneration, lung problems and severe vascular thrombosis in Guiana dolphins caught on the Gulf of Morrosquillo. The dorsal fin, flippers and flukes of this species can be severely injured, due to trauma related to net entanglements resulting in partial or complete amputations and deformations (Rosas *et al.* 2010).

The species has been maintained in captivity in the USA, Europe, Brazil and Colombia (Flores 2002). Today only a few remain in captivity in Colombia, where illegal direct catch is

still operating (Figure 1.10). The last individual of this species held in captivity in Europe died in 2012 (Professor Dehnhardt, personal communication). This individual was the last one alive of the ~80 animals captured in Cispata Bay, Gulf of Morrosquillo (Bössenecker 1978). Guiana dolphins die easily due to capture stress, during transportation or handling. Under captivity conditions this species rarely exhibit aerial behaviour and usually show common aggression toward other males of the same species and other species (Flores 2002).



**Figure 1.9.-** Guiana dolphin calf, entangled in an artisanal gillnet (“trasmallo”) before being consumed by the local fishermen. Isla Fuerte, Atlantic Sea, Colombia. *Unknown photographer.*



**Figure 1.10.-** Guiana dolphins' individuals held in captivity in two facilities in Isla Palma and Isla Múcura in the northern area of the Gulf of Morrosquillo, Colombia. *Photographs by Salomé Dussán-Duque.*

The Gulf of Morrosquillo is the only area of Colombia where Guiana dolphins have been reported since 1978. The main threats for this species in Colombia are: regional changes in prey abundance (IVEMAR 2005), progressive loss of habitat (INVEMAR 2002, Sánchez-Páez *et al* 2004), contaminants (REDCAM 2005), direct capture for national illegal marketing and display (Dussán-Duque *et al.* 2003), and incidental entanglement in gillnets (Avila 1995, Dussán-Duque 2003).

## **1.4. Thesis aim and objectives**

### **1.4.1 Main aim**

To advance understanding of the ecology of *Sotalia guianensis* and its habitats in the southern area of the Gulf of Morrosquillo, Colombia, to inform its conservation.

### **1.4.2 Objectives**

- To model the distribution, habitat use and selection of *S. guianensis* in the study site, with an emphasis on feeding areas.
- To estimate the survival rates and seasonal abundance of the Guiana dolphins using the southern Gulf of Morrosquillo.
- To explore the long-term site fidelity of *S. guianensis* in the study site.
- To study the cooperative surface foraging and feeding strategies of Guiana dolphins.

## **1.5. Thesis structure**

This work presents the first long-term study of the ecology of the Guiana dolphins in Colombia. All chapters are based on data collected in the Gulf of Morrosquillo during systematic boat-based surveys from 2002-2006 and 2009-2010.

Chapter 2 describes the study area and the general materials and methods use in the collection of the data.

Chapters 3 to 6 are specific investigations in response to reasearch questions that required different methodologies and analyses in order to be answered.

In Chapter 3, habitat models were constructed to investigate the distribution, habitat use and selection of this species in the study site with an emphasis on feeding areas. These models were built based on sighting and environmental data collected during boat surveys.

Chapter 4 uses sighting histories of naturally marked individuals that use the study area, to estimate survival rates and seasonal abundance using mark-recapture methods.

In Chapter 5, the long-term site fidelity patterns of the species is explored through the sighting histories of the marked individuals with the highest sighting frequencies during the study period.

In Chapter 6, data acquired during sightings in which dolphins were foraging and feeding were used to analyze the coordinated surface foraging and feeding strategies used by the species in the study area.

Chapter 7 synthesizes the results of Chapters 3-6 and place them in an wider ecological and research context. This Chapter also sets guidelines for management and long-term conservation of the species and future research.

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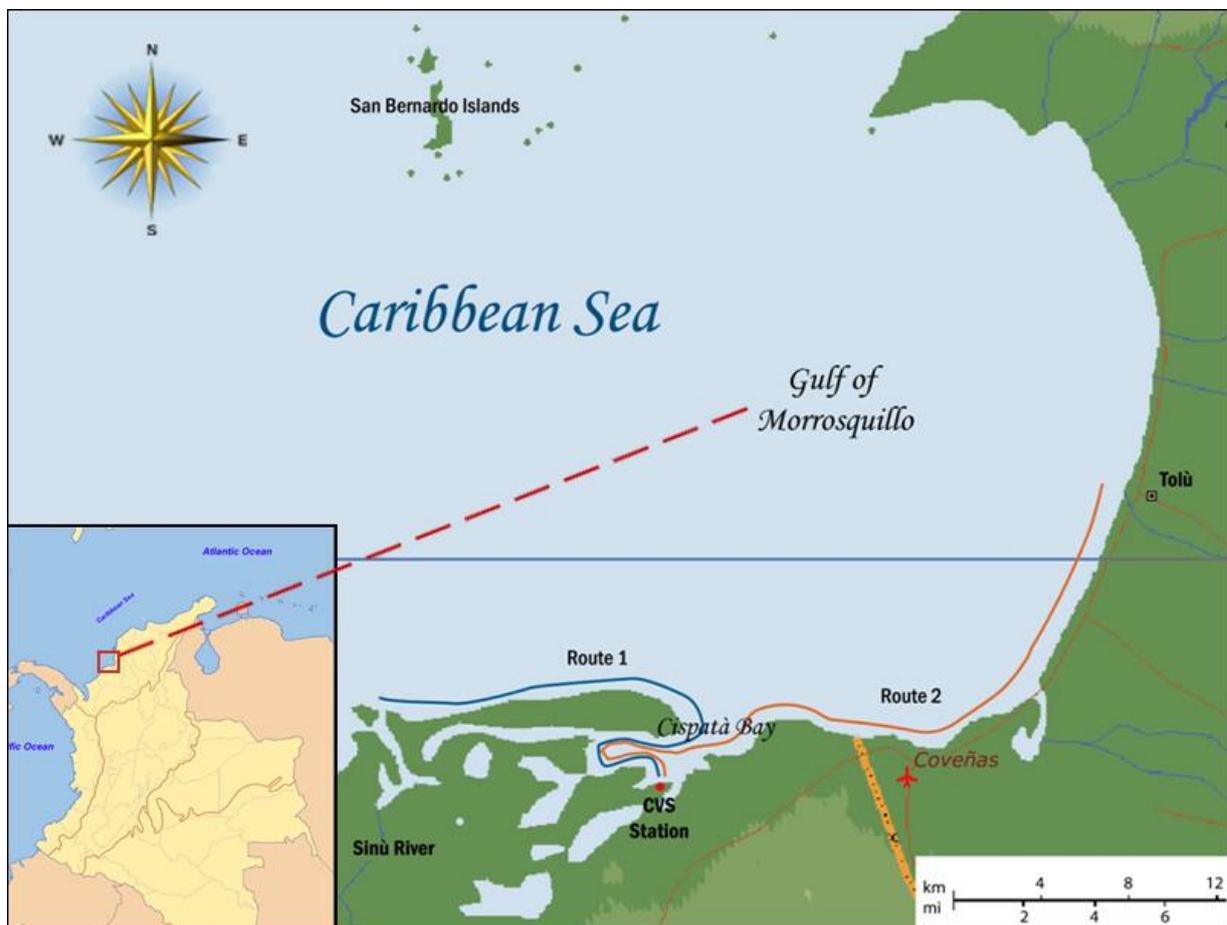
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## **Chapter 2 – Materials and Methods**



## 2.1. Study area: The Gulf of Morrosquillo

The Gulf of Morrosquillo is an open mixed estuarine system located in the Caribbean Sea of Colombia (9°- 10° N and 75°-76° N) between two states: Córdoba and Sucre. From west to east it encompasses approximately 80km. Its limit in the south is Boca de Mireya, the first mouth of the Sinú River delta. In the north its limit is the archipelago of San Bernardo Islands, comprising eight islands (Figure 2.1) (Patiño-Corredor & Flórez-Amaya 1993).



**Figure 2.1 - Gulf of Morrosquillo, Caribbean Sea, Colombia.**

The natural processes related with the Sinú River delta, the fluctuations of the sea level and the marine and climatic dynamic, have transformed this ecosystem substantially over the last 63 years. Cispatá Bay used to be the Sinú River delta before 1942 (Patiño-Corredor & Flórez-Amaya 1993, INVEMAR 2003). The inhabitants of the bay witnessed the slow

migration of the river towards the south, with all the consequent ecological implications and the transformation of the landscape units. The biotypes also changed, with the transformation of the environment, into dense mangrove areas with a stronger presence of marine species (Cispatá Bay inhabitants, personal communication, 2003).

The gulf is located in the band of low equatorial pressure (Oster 1975), characterized by high humidity levels, an annual average temperature of 26.7°C, persistent winds from the north to the northeast and an annual precipitation of 900-1,200 mm (Instituto Geográfico Agustín Codazzi 1975). It has two main climatic seasons: the dry season from December to April and the rainy season from May to November, with a semi-dry season in the month of July. The semi-dry season is called like this because it is characterised by a reduction in precipitation (Patiño-Corredor & Flórez-Amaya 1993). The Gulf of Morrosquillo is under the influence of the Trade winds and the Inter-tropical convergence zone (ITCZ). In the dry season, the winds blow constantly and strongly from the northeast and simultaneously the Caribbean current moves towards the west. On the other hand, during the wet season, the winds are very light and move in different directions (Patiño-Corredor & Flórez-Amaya 1993).

Inside the gulf the bathymetry ranges from 0m to  $\leq 50$ m, presenting high sedimentation parallel to the coastal line (Patiño-Corredor & Flórez-Amaya 1993).

Tides are semidiurnal with an amplitude  $\leq 50$  cm. Every two weeks, the amplitude of the tides increases, causing very high tides and very low ones. The hydrographic pattern of the gulf gives rise to high water levels from September to December and low levels from January to July. The delta of the river covers a very large area during the rainy season. Throughout the gulf, the sea surface temperature ranges from 27.0°C to 32.0°C, the surface transparency ranges from 0.8m to 10.0m and the salinity ranges from 25.0‰ to 36.0‰.

The drainage basin of the gulf is approximately 2,100 km<sup>2</sup>, with Cispatá Bay at the south, five swamps and six marshes with depths between 1 and 5m, with muddy sediments (Patiño-Corredor & Flórez-Amaya 1993). The transport of sands lead to two trends: from the islands towards la Boca del Francés; and from Cispatá Bay towards Tolú (Vernette 1985).

The Gulf of Morrosquillo is one of the most popular tourist areas of Colombia, due to its white sand beaches and coral reefs. Tolú and Coveñas are the largest cities of the gulf, supporting a minimum of 80,000 tourists per year (Villaraga 2012).

The National Government of Colombia approved in 1993 the construction of the Urrá I hydroelectric plant. Its main water source is the Sinú River and its tributaries, which rise in the Natural National Park Paramillo. Its discharged capacity is 9,500m<sup>3</sup>/s (Urrá SAEPS 2000). The dam has not only affected the ecosystem in the upper part of the Sinú River; the lower ecosystems and their inhabitants have been even more affected (Fernández 2007): Destruction of the artisanal fisheries due to displacement and collapse of stocks (INVEMAR 2003 2005), irreversible degradation of the soils near the river delta, salt penetration into the river, salinization of the marshes close to the delta (CVS 2004 2005) and alteration of the normal water flux towards Cispatá Bay are some of these consequences (WRM 2001, Marquez-Calle 2001 and Vélez-Flórez 2009).

Personal communication in 2003 with the permanent inhabitants of the gulf revealed that 60% of their basic necessities are unsatisfied; 90% of the population depends upon the artisanal fisheries and agriculture. A large proportion of the population is illiterate and the people struggle for daily survival. The fast growth of these communities is causing the levels of poverty to increase rapidly stocks (INVEMAR 2003 2005).

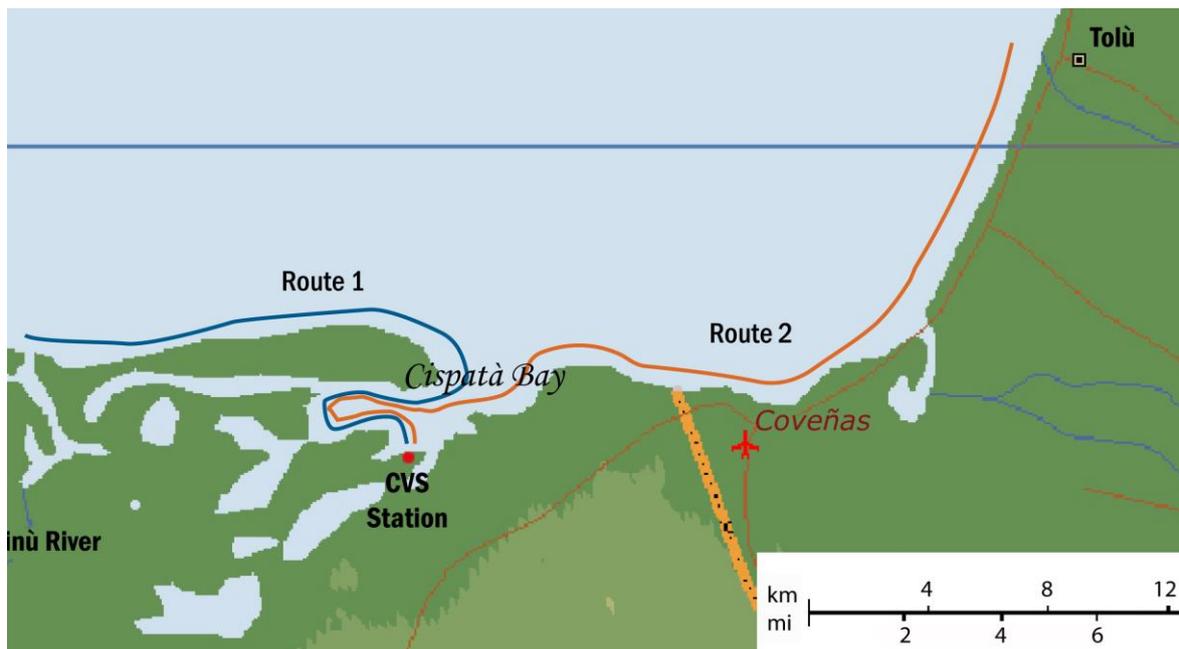
In recent years, due to the difficulties for human survival, the gulf has become one of the routes for narco-traffic groups to export drugs and guns to Central America. At present, the Gulf of Morrosquillo is one of the most violent areas of Colombia (El Tiempo 2013).

## 2.2. Survey protocol

Due to the extensive size of the Gulf of Morrosquillo, and the impossibility of surveying the whole area using the type of boat used for this project, the surveys were limited only to the southern area of the gulf (Figure 2.2), where *S. guianensis* is reported to be seen more often. The survey area included the first Sinú River mouth (Boca Mireya) (9.45291° N, -75.91764° W) to Tolú (9.44004° N, -75.63604° W), covering approximately 43 km of shore line. This area is characterized by an estuary surrounded by a very large mangrove system connected to the Sinú River by a number of small channels and marshes.

Two survey routes were established (Figure 2.2) in order to ensure a homogenous coverage of the study area. One route was chosen daily, alternating between them each day. When the environmental conditions did not allow the survey of the scheduled route (e.g. strong wind coming from the north), the easiest one was surveyed.

The routes were not straight lines parallel to the coast. Instead, they served more as guidelines to cover the routes. Each daily survey was tailored by the researcher, depending upon the environmental conditions prevailing on the day. On some days the survey routes were conducted in a zigzag pattern. On other days a line parallel to the coast line was surveyed until the end of the routes. Then, a line out to 20m isobaths was surveyed, followed by a line back to the Corporación Autónoma Regional de los Valles del Sinú y del San Jorge station (CVS).



**Figure 2.2 - Study area in the Gulf of Morrosquillo with the surveying routes.**

A 5.2 m fiberglass boat with an outboard 45 hp engine was used to conduct systematic surveys by the researcher and a boat driver, at a constant speed of 9 km/hour in good weather conditions: Beaufort state  $\leq 3$  and none or little precipitation (Figure 2.3).

The researcher was located at the prow of the boat and with the help of the boat driver continuously scanned the area around the boat, sometimes using binoculars.



**Figure 2.3 – Boat CIMACI, Corporación Autónoma Regional de los Valles del Sinú y del San Jorge (CVS), used to survey the study area from 2002 to 2010. *Photograph by Salomé Dussán-Duque.***

Surveys were conducted during a total of 395 days, parallel to the 43 km of shore line, during the three climatic seasons: rainy, dry and semi-dry in 2002-2006 and 2009-2010. The effort per day was recorded using the tracking function of the GPS and downloaded later onto a map. The total survey effort was 15,199 km. The study area was divided in six zones, from the first mouth of the Sinú River (Boca Mireya) to Tolú, including five of the zones defined previously by Avila in 1994 (Figure 2.4).

These zones were established based on the work of Avila in 1994 (Figure 2.5), with the addition of zones 5 and 6. The geographic limits of the zones were different from Avila's study, but very similar in zones 1, 2, 3 and 4. All the zones were divided in accordance with their oceanographic characteristics as follows:



- **Zone 1: Cispatá Bay**

Between Punta Terraplen and Punta Resguardo. Estuarine water ecosystem with an approximate surface area of 10.5km<sup>2</sup>, and an average depth of 2.0m. Surrounded by mangroves mainly of the species *Rhizophora mangle*. Fine and extra fine sediments (Patiño-Corredor & Flórez-Amaya 1993).

- **Zone 2: External zone of the bay**

From Punta Mestizos to Playa Blanca. Depth between 1.5m and 16m. Direct action from the sea currents, with high erosion present. There is a channel present in Punta Mestizos, at less than 1m from the coastline, demarking an abrupt change of depth from 1.5m to 8m (personal observation).

- **Zone 3: Ciénaga Mestizos**

From Punta Mestizos to Ciénaga Icotea. This zone is characterized by the presence of two main marshes: Mestizos and Icotea. Composed of internal channels surrounded by mangroves, with diverse phreatic levels depending on the season of the year (personal observation).

- **Zone 4: Boca Tinajones**

From Ciénaga Icotea to the first river mouth, Boca Mireya. Sinú River delta, characterized by high sedimentation and the lowest salinities of the study area.

- **Zone 5: Playa Blanca**

From Playa Blanca to Boca de la Ciénaga. White sand beaches surrounded by mangroves. The marshes of La Caimanera display high movement of sand sediments and during the dry season a wall of sediments. This wall closes the movements of the water from the marshes to the sea (Patiño-Corredor & Flórez-Amaya 1993). This zone is the one that is most affected by tourists in the southern area of the Gulf.

- **Zone 6: Muelle de Coveñas**

From Boca de la Ciénaga to Tolú. This area is characterized by a vast continental platform, with waters no greater than 20m deep. The water transparency in this zone

is higher than in the other zones, as is salinity (Personal observation). This zone has two important characteristics: it holds the Coveñas pier, which is used mainly for the transport of petroleum from the pipeline Caño Limón- Coveñas, in deep water vessels. Second, due to the presence of the petroleum company, it is a restricted area. Special permits are required to enter the marine restricted area even by local fishermen. In the last decade there have been minor petroleum spills in this zone.

## **2.3. Data collection**

The survey forms used were design by Sarasota Dolphin Research Program (SDRP 2002). Each day two forms were completed: one with the hourly taken environmental information, and the other with the information on the dolphin sighting(s).

### **2.3.1. Chapter 3: Modelling the habitat preferences and distribution**

Data on 20 eco-geographic explanatory variables were taken *in situ* (Table 2.1) before starting the survey and subsequently every hour or before if the conditions changed (e.g. precipitation, high wind). The geographic positions where these variables were measured were marked in the GPS unit as dolphin absences.

When a sighting was made, the same variables were taken but marked in the GPS unit as dolphin presences.

### **2.3.2. Chapter 4 and 5: Survival rates, seasonal abundance and site fidelity**

When dolphins were encountered, the motor was turned off, and we approached the dolphins by paddling. All measurements were made as close as possible to where dolphins were first sighted. The following information on the sighting was taken:

- Dolphin species: *Sotalia guianensis* or *Tursiops truncatus*.
- Dolphins heading: Initial, general and final.
- Activity: First recording the event by scan sampling of all individuals present (Altmann 1974). The activity recorded was the one shown by >50% of the individuals involved in the sighting. Groups were defined as individuals with distances between them of  $\leq 1$  m. The events were: foraging, feeding, or other. After the record of the event, only foraging and feeding behavioural states were recorded every two minutes by focal group sampling methodology (Altmann 1974). For the purpose of this study, foraging behaviour was

defined as that which is required for the dolphins to search for food. Whole group foraging was indicated by changes in the direction of movement. The whole group search was conducted along a complex trajectory with dolphins in a group moving synchronously (Bel'kovich *et al.* 1991). Feeding, on the other hand, was defined as an activity when at least one individual in a group was seen with a fish in its mouth (Barros & Wells 1998).

- Field estimates: Maximum, minimum and best number of adults, calves and young of the year was recorded. A calf was defined as a dolphin approximately one third of the body size of an adult. A young of the year had foetal fold marks.

Photographs of dolphin dorsal fins and body marks were taken for photo-identification. A total of 74,226 pictures were taken, with an average of 188 pictures per survey day. In 2002 and 2003 the pictures were taken with a Canon EOS 7 Elan camera with 75-300mm lens and slide film (64 speed Ektachrome, 100 speed Sensia, and 100 speed Provia). From 2003 through 2006 the pictures were taken with a Canon Rebel digital camera using 75-300 mm or 100-400 mm lenses. In 2009 and 2010 pictures were taken with an EOS 40D Canon camera and a 100-400 mm lens. The researcher attempted to photograph all the individuals within a group without bias for distinctive marks.

### **2.3.3. Chapter 6: Cooperative surface foraging and feeding strategies**

If the dolphins were engaged in foraging or/and feeding events, data on the following additional variables were taken: Behaviour, strategy, prey species, recognized individuals engaged in the activity (*ex situ*: through photo-identification). The observational method used to sample the foraging and feeding states was the focal-group sampling. Focal group sampling refers to any sampling method in which: all occurrences of specified interactions of a group of individuals are recorded during each sampling period (Altmann 1974). The strategies were documented on digital video and photographs when possible.

Every survey day after coming back to the field station, tracks and waypoints were downloaded into the ArcView 3.3 (ESRI) map, photo-identification data were saved in external hard drives (except for years 2002 and 2003 when the data were slides), and the GPS and camera memories were cleared for the following day.

**Table 2.1. – Eco-geographic variables recorded during boat-based sightings and habitat surveys in the southern area of the Gulf of Morrosquillo.**

Response variables	Name	Type	Description	Measurement method	Unit and range
Absence/presence of dolphins	ABPRE	Binary	Absence/presence of dolphins	Visual observation	1/0
Number of adult dolphins present	ADULTS	Count	Adult animals present in groups and sub-groups	Visual observation/ binoculars	
Number of calves present	CALVES	Count	Calves present in groups and sub-groups	Visual observation/ binoculars	
Absence/presence of foraging or feeding events	FORAGING FEEDING	Binary	Absence/presence of dolphins foraging or feeding	Visual observation/ binoculars	1/0
<b>Explanatory variables</b>					
Julian day	JULIAND	Continuous	Day of the of the year	Day transform in julian day	1-365
Month	MONTHF	Factor	Month of the year	Current month	2-11
Year	YEARF	Factor	Year	Current year	2002-2006/2009-2010
Season	SEASONF	Factor	Rainy, dry, semi-dry	Current season of the year	Rainy =1, Dry =2, Semi-dry =3
Hour of the day	TIME	Continuous	Current hour of the day	Hour transform into decimal hour	
Tide	TIDEF	Factor	Tide state present	Tide chart Coveñas (IDEAM-Colombia)	In =1, Out =2, Hi =3, Low =4
Zone	ZONEF	Factor	Study area divided in zones	Avila (1995)	1-6
Latitude and longitude	LAT-LONG	Continuous	Geographic position expressed in UTM coordinates (E,-N)	Hand held GPS Garmin	UTM
Beaufort wind force scale	BEAF	Factor	Wave heights in the scale	Visual observation of sea conditions	Flat =0, Ripples without crest =1, Small wavelets, crest of glassy appearance =2, Large wavelets, scattered white caps =3
Depth	DEPTH	Continuous	Water depth at the location where the dolphins are first sighted or the data taken	Depth sounder	m
Sea surface temperature	SST	Continuous	Surface water temperature	Bucket and thermometer	°C
Salinity	SALINITY	Continuous	Surface water salinity	Refractometer	ppm
Distance to shore	DTS	Continuous	Linear distance to nearest coast	Extrapolated from ArcView GIS	m
Distance to the Sinú river	DTR	Continuous	Linear distance to the river	Extrapolated from ArcView GIS	m
Effort per zone per day in distance	EFFORTD	Continuous	Distance surveyed per zone per day	Extrapolated with the ArcView measuring tool	Km
Effort per day in hours	EFFORTH	Continuous	Hours of effort per day		Hours and minutes
Cloud cover	CLOUDSF	Factor	Clear or few, partly cloudy, overcast, rain	Visual observation	Clear or few=0, Partly cloudy=1, Overcast=2, Rain=3
Glare	GLAREF	Factor	None, little, some, much	Visual observation	None =0, Little =1, Some =2, Much =3
Sightability	SIGHTAF	Factor	Excellent, good, fair, poor	Visual observation	Excellent =0, Good (unlike to miss dolphins) =1, Fair (may miss some dolphins) =2, Poor (probably missing dolphins) =3

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**Chapter 3 – From where to why: Modelling the distribution, habitat use and selection of *Sotalia guianensis*, with an emphasis on feeding areas**



### 3.1. Introduction

Habitat is defined as the resources and conditions present in an area that produce occupancy, including survival and reproduction, by an organism (Hall *et al.* 1997). The heterogeneity of marine environments usually leads to a patchy and clumped distribution of suitable habitat which meets species-specific and individual-specific requirements (Stevick *et al.* 2002).

The special and characteristic ways in which an animal interacts with its habitat are defined by the concepts of habitat use, selection and preference. Habitat use patterns are the ways than an animal uses a collection of biotic and abiotic resources to meet life-cycle needs of survival and reproduction in order to maximize fitness (Hall *et al.* 1997, Stevick *et al.* 2002). Habitat selection is the hierarchical process involving a series of innate and learned behavioural decisions made by an animal at different geographic scales to determine a location to acquire resources. It usually reflects a trade-off between the benefits of resource gain and the threat of predation (Lima & Dill 1990, Hall *et al.* 1997, Bjørge 2001). These decisions are reflected in the habitat preferences of the individuals of an animal community, which result in disproportional use of some biotic resources over others (Hall *et al.* 1997).

Likewise, resource selection occurs in a hierarchical way, from the geographical range of a species to a selection of a feeding site by a population (Manly *et al.* 1993). Feeding habitats are selected by an animal or a population in a complicated way that implies many decisions to be made with the use of as little energy as possible. If the resources have equal availability through time, the possibility that a population shifts its feeding habitats is highly unexpected. If something happens within the ecosystem that changes this resource's availability, then the probability that a population may shift its distribution increases.

The use of habitat modelling to define important habitats has increased in recent decades (Gregs & Trites 2001, Ingram & Rogan 2002, Yen *et al.* 2004), and it has been used to define areas suitable as marine protected areas (MPAs) for several species of cetaceans (Hooker *et al.* 1999, Reeves 2000, Cañadas *et al.* 2005, Cañadas & Hammond 2006), including *S. guianensis* in southern Brazil (APAA Decreto Federal N° 528 1992).

The lack of information on the ecology of *S. guianensis* in Colombia represents one of the major problems for its conservation. Only two studies have been conducted on this species until now, Avila (1995) and García (1998). Several things have changed in this coastal region

since Avila's and García's results were reported, and a number of species have been affected in the process. The data analysed in this study represent the most extensive on Guiana dolphins in Colombia. This chapter explores through habitat modelling the habitat use and selection of this species in the southern Gulf of Morrosquillo. In addition, this chapter aims to explore if the changes that have taken place in the study site affected the distribution of this species in the study site, with an emphasis on feeding areas.

## **3.2. Aim and objectives of the Chapter**

### **3.2.1. General aim**

To model the distribution, habitat use and selection of *S. guianensis* in the southern area of the Gulf of Morrosquillo in relation to eco-geographic variables, with an emphasis on the feeding areas.

### **3.2.2. Objectives**

- Identify which combination of the measured eco-geographic variables influenced the distribution, abundance and habitat use of Guiana dolphins' adults and calves in the study area.
- Explore if distribution and habitat use fluctuated seasonally or annually during the study and the nature of these fluctuations.
- Investigate the relationships between the eco-geographic variables and the number of dolphins feeding and the distribution of feeding events.
- Explore differences from previous studies in the habitat use and distribution of Guiana dolphin in the study area.

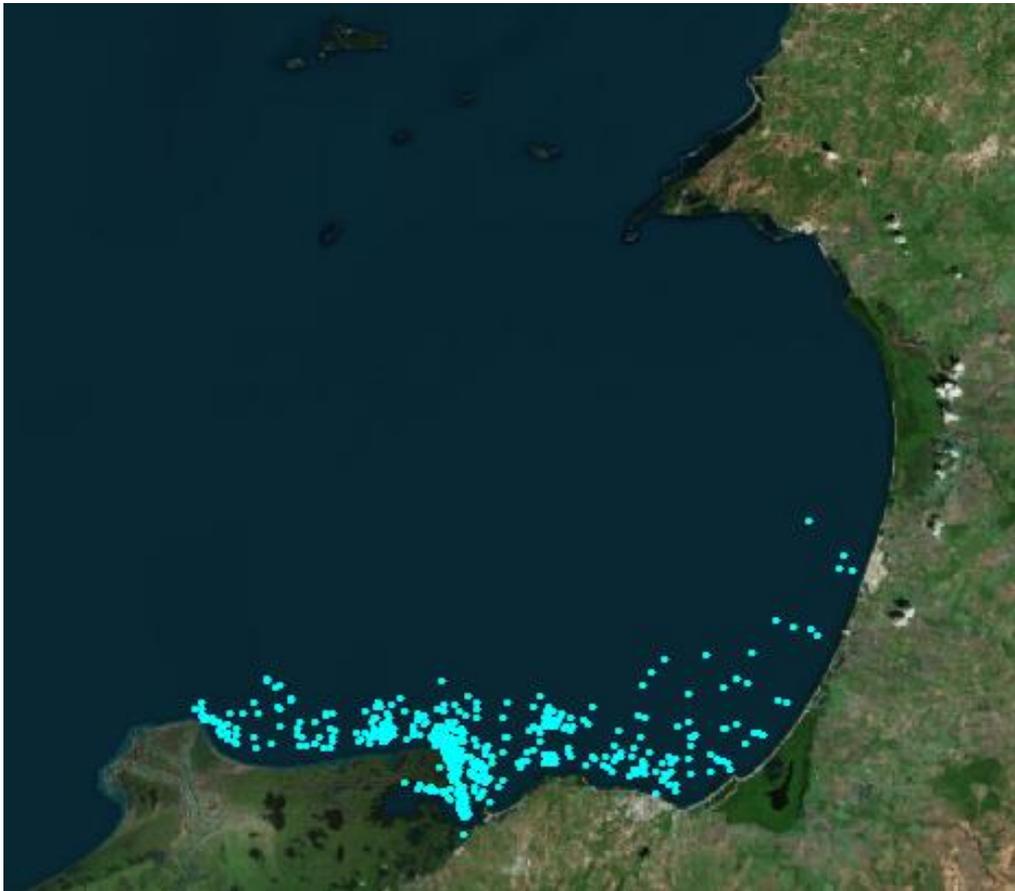
### 3.3. Materials and Methods

Survey methods and data collection methods are described in Chapter 2.

### 3.4. Data Analysis

#### 3.4.1. Unit of analysis

Data acquired from boat surveys in 2002-2006 and 2009-2010 were used in ArcView 3.3 to build the absence and presence GPS waypoints for Guiana dolphins in the study area (Figure 3.1).



**Figure 3.1-** Data locations from 2002-2006 and 2009-2010 downloaded from the GPS in the study area. The map was downloaded from Bing cartography 2013.

There were 852 data points used in analysis, 318 of them corresponding to dolphin sightings or presence points. The dolphins were followed for periods ranging from a few minutes up to three hours. The full dataset of eco-geographic and sighting-related explanatory variables included: Julian day, month, year, season, time of day, tide, sea surface temperature, salinity, depth, distance to the river, latitude, longitude, zone, distance to nearest shore, Beaufort sea state, glare, clouds and sightability. Except for distance to the river and distance to shore, all the other explanatory variables were measure *in situ*. The response variables were: absence or presence of dolphins, adult and calf counts, and counts of dolphins feeding. All the data were recorded on a standardized form (Chapter 2) and the full dataset was used in the habitat use and feeding modelling analysis.

### **3.4.2. Pre-modelling exploratory data analysis**

The explanatory variables were divided into two main groups: the variables that affected detection of the dolphins or survey effects (Beaufort, glare, clouds and sightability), and those that may explain the absence or presence of dolphins, their numbers and their behaviour (Julian day, month, year, season, time of day, tide, sea surface temperature, salinity, depth, distance to the river, distance to shore, latitude, longitude and zone). The division of the covariates in this way was so that the variable(s) that affected detectability could first be found so that they could be included thereafter as a covariate(s) in all subsequent models.

The possibility of collinearity between the continuous explanatory variables was inspected through the correlation coefficient using the `cor.test` function in software R 2.15.2 (R Development Core Team 2012). The only variables that showed any collinearity were distance to shore (DTS) and depth (DEPTH), correlation coefficient = 0.57. Depth was chosen to be included in the models because it was collected *in situ* whilst distance to shore was extrapolated from ArcView 3.3 (ESRI software).

Histograms and boxplots, produced in R 2.15.2 (R Development Core Team 2012), were used to inspect the distribution of each of the explanatory variables, including the presence of outlier points. Each covariate was summarised by its mean, median, minimum and maximum values, lower and upper quartiles and standard deviation to measure the spread of the data. A scatterplot matrix of all the variables plotted against each other was produced to provide a further check for the correlation between them because a correlation coefficient is a measure of the strength of a linear relationship and can be misleading if the relation is not linear (Crawley 2005).

### 3.4.3. Model Building

The basic aim of building a model is to determine the values of the parameters that ultimately lead to the fit of the best model to the data. The definition of “best” can be based on maximum likelihood and the best model is the minimal adequate model to describe the dataset. “All models are wrong, some models are better than other ones; the correct model can never be known with certainty and the simpler the model, the better it is” (Crawley 2005).

All the modelling analysis was conducted in software R 2.15.2 (R Development Core Team 2012).

The main aim of this study was to find out which environmental characteristics explain best the observed habitat use of *S. guianensis* in the study area. Because all the variables were measured *in situ*, and this is the only information that exists about these variables in the Gulf of Morrosquillo because of the lack of remotely sensed oceanographic data, prediction was not able to be applied to the entire study area. Similarly, using the models to predict potentially important areas of habitat outside the study site boundaries was not possible.

To determine the nature of the relationships between each response variable and the explanatory variables, two types of models were used: Generalised linear models (GLMs) and Generalised additive models (GAMs).

GLMs have three important properties: the error structure of the response variable; the linear predictor, which introduces the effect of the covariates on the mean of the response variable; and the link function, which transforms the mean of the response variable to its linear predictor (Crawley 2005, Matthiopoulos 2010).

GLMs can be used when the error distribution of the response variable is not Normal. For count data, the error structure is Poisson distributed. However, count data are often over-dispersed, with more zeros present in the dataset than expected from a Poisson distribution causing the variance to be greater than the mean. In such cases, the error structure of the response variable can be assumed to be quasi-Poisson. GLMs generally deal well with this issue (Crawley 2005, Wood 2006 and Zuur *et al.* 2009). Count data tend to be heterogeneous and are always non-negative (Zuur *et al.* 2009). The model is fitted with a log link to ensure that the fitted values are bounded below (Crawley 2005). The resulting GLM is called a log-linear model (Matthiopoulos 2010). For presence/absence data, the appropriate error structure is binomial and the appropriate link function is the logit.

GLMs were used to obtain parametric descriptions of the relationships between each response variable and the explanatory variables, to check diagnostics for evidence of clear non-linearity in any relationships, and to explore the over-dispersion in the dataset.

GAMs are more flexible than GLMs; they are essentially GLMs with a linear predictor that includes the sum of smooth functions of covariates (Hastie & Tibshirani 1986, 1990). Because GAMs are more flexible, they can be appropriate for modelling ecological datasets, where the relationship between the response and explanatory variables is not always linear (Guisan *et al.* 2002, Wood 2006 and Zuur *et al.* 2009). GAMs have the advantage of letting the dataset dictate the shape of the relationship by the fitting of non-parametric smooth terms. Therefore, after a first approach using GLMs, GAMs were considered for building the final models. GAMs were fitted using the *mgcv* package in R (Wood 2006). Models for count data were run with a Poisson error structure first, and then with quasi-Poisson error structure to check for over-dispersion.

For investigating the relationships between feeding dolphins and explanatory covariates, a two-model approach was used.

First, a GLM/GAM with binomial error structure and logit link function was used to model the presence/absence of dolphins of all ages, to estimate the probability of occurrence of dolphins as a function of the covariates. The logit link function maps the response data onto linear space and ensures the model predictions are bounded by zero and one.

Second, a GLM/GAM with a Poisson/quasi-Poisson error structure and log link was used to model the counts of dolphins feeding conditional on the probability of occurrence (as estimated by the first model).

To obtain a final prediction for any combination of the model covariates, the predicted probability of occurrence and the predicted count of animals feeding are multiplied to give a prediction of the abundance of dolphins feeding given the probability they were present. This method of two-stage modelling approach (Borchers *et al.* 1997) was followed because the single model of counts of dolphins was over-dispersed (dispersion parameter of 4.07).

#### **3.4.4. Model Fitting and Selection**

The selection of which covariates to retain in the models was based on Akaike's Information Criterion (AIC) (Akaike 1973):

$$AIC = -\{2l(model|data)\} - 2K$$

Here, the term  $\{2l(model|data)\}$  is the maximum log likelihood of a model under the observations. This quantity increases (i.e. the model gives a better fit to the data) as the number of parameters in the model increases. Therefore, the value of the criterion is penalised by the number of parameters ( $K$ ) in the model. The best model is the one with the smallest AIC (Matthiopoulos 2010). Burnham & Anderson (2002) provide guidance on the interpretation of differences in AIC between models. If the difference (delta-AIC) between two models is less than 2, these models have effectively the same support from the data. If delta-AIC is greater than 2 then the model with the lower AIC has better support from the data. For models fitted with quasi- error structure for the response variable, a quasi-AIC (QAIC) can be calculated.

The first group of response variables considered were those that affected the encounter rate of the dolphins: Beaufort, glare, clouds and sightability (see Evans & Hammond 2004). Investigation of how these variables affected the count of all dolphins and the count of calves was done first to select the covariate(s) of this group to be included in all future models. This was done using forward stepwise selection. Poisson and quasi-Poisson models were run for this group of explanatory variables to check for over-dispersion and to find out which covariates had a significant effect on the counts.

The only explanatory covariate that was retained in the models of counts of adults and calves was Beaufort. The AIC was smaller when Beaufort was included as a factor variable than when it was included as a continuous variable. Therefore, Beaufort as a factor (BEAF) was included as a covariate in all subsequent models for adults and calves.

The same procedure was conducted with the second group of explanatory variables (Julian day, month, year, season, time of day, tide, sea surface temperature, salinity, depth, distance to the river, distance to shore, latitude, longitude and zone) to investigate which eco-geographic variables had an influence on counts of adults and calves: Poisson models to find the AICs, and quasi-Poisson models to get the dispersion parameter values.

Latitude and longitude were not included as covariates at this stage, because they correlate spatially with environmental characteristics of the habitat (Redfern *et al.* 2006).

To investigate if there were temporal patterns of habitat use by Guiana’s dolphins in the southern area of the Gulf of Morrosquillo, data for all years and the three climatic seasons were modelled together. Month, Season, Year, Zone, Tide and Beaufort were included in the models as factors. Models were fitted for adult counts, calf counts, presence/absence of dolphins, and counts of feeding dolphins conditional on probability of presence. GLMs were first fitted through forward selection and then GAMs were fitted using backward selection.

After finding the best-fitting GLMs for adults and calves a check for collinearity in the covariates in the fitted model was conducted through estimation of Variance Inflation Factors (VIFs) (Brauner and Shacham 1998) using the library `car` in R 2.15.2. No collinearity was present among any of the variables in the fitted models (Table 3.1).

**Table 3.1 - GVIF score assessing the collinearity in the covariates of the fitted models for adults, calves, presence/absence and animals feeding. For full model results, see section 3.5.**

	ADULTS GVIF	CALVES GVIF	AB/PRE GVIF	DOLPHINS GVIF
Time of day	1.17	1.17	1.35	
Salinity	1.27	1.33		
Depth	1.33	1.47	2.09	1.40
YearF	1.83	1.84	2.86	
BeaufortF	1.20	1.22	1.56	1.27
ZoneF	1.89	2.09	3.41	2.16
SeasonF			1.60	
TideF				1.34

The dredge function in R 2.15.2 was run to find the best fitting GAMs because AIC cannot be calculated. This function requires two libraries: `MUMIn` and `mgcv`. Dredge performs automated model selection with subsets of the supplied ‘global’ model, and optional choices of other model properties (such as different link functions (Package `MuMin`) using a specified model selection criterion, in this case QAIC. In order to run the dredge function, two models have to be run: first a Poisson or Binomial model (depending on whether the data are count data or presence/absence data), and second a quasi-Poisson or quasi-Binomial model. The results of the dredge function are all the possible models in ascending order by QAIC.

The best models ( $\Delta\text{QAIC} < 2$ ) from the GAMs dredge were chosen for: adult counts, calf counts, presence/absence of dolphins and counts of dolphins feeding. Model selection was then conducted in a stepwise backward procedure by minimising the unbiased risk estimator

(UBRE) for models with a Poisson error structure and the GCV criterion for models with a quasi-Poisson error structure. UBRE and GCV are equivalents to AIC that trade off goodness-of-fit against model complexity (Wood 2006).

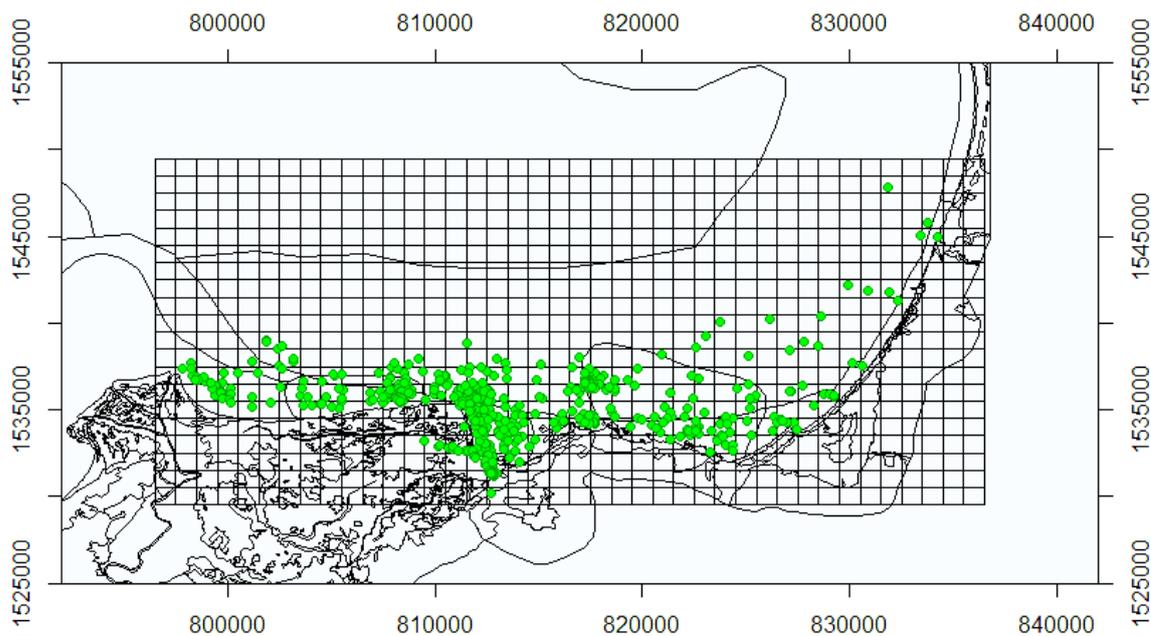
The most appropriate error structures for the response variable for each model were chosen based on the dispersion parameters estimated by the quasi-Poisson GLMs for each model of each dataset. Over-dispersion in the residuals was detected in two of the four models with a Poisson error structure: adult counts and feeding dolphin counts. For these two response variables, the over-dispersion in the residuals of the models was accounted for by using a quasi-Poisson GAM. Conversely, the residuals of the other two models: calf counts and presence/absence of dolphins did not show any over-dispersion. Therefore, Poisson error structure and binomial error structure were assumed for these models, respectively.

In the GAMs, the continuous explanatory variables were introduced into the models as smooth terms with the default maximum number of knots ( $k=10$ ). Knots are equivalent to degrees of freedom and define how smooth or “wiggly” a smoothed relationship is. When necessary (to smooth a fitted relationship that appeared unnecessarily wiggly), the maximum number of knots was minimised one by one, until a more biologically realistic smooth function was obtained for each covariate (Embling *et al.* 2010). The value of  $\gamma$  (*gamma*) was set at 1.4. The function  $\gamma$  of is to penalise the model for using too many degrees of freedom and to reduce over-fitting (Wood 2006). A “ts” smoothing base was used to fit the model in cases where the explanatory covariates could potentially be reduced to linear functions. A “ts” is the same than a thin plate regression spline (TPRS) but with shrinkage, meaning that the smoothing can be eliminated if it is not supported (Wood 2006). In cases where this produced a linear relationship, the smoothing of this covariate was taken out of the final model.

Latitude and longitude were not included in the final models because latitude was correlated with depth and longitude was correlated with zone; if included in the final models they would compete with these two covariates. Nevertheless, if the models can be used for prediction, longitude could take the place of zone in the model because longitude will be predicted at a finer scale suitable for mapping.

A map grid was created under R 2.15.2 and R 3.0.1, using the libraries: sp, maptools, rgdal and RcolorBrewer (Blight 2013). The projection used was projection Bogota 1975 / Colombia Bogota zone (<http://spatialreference.org/ref/epsg/21897>), and the chart used was

created by INVEMAR in 2002. The study area was divided into grid cells of 1km latitude x 1km longitude (Figure 3.2). The grid was composed of 800 cells, the majority of them with zeros for all the covariates because they were never visited during the surveys and there are no other data for these areas. Averages and summaries of each explanatory and response covariate were calculated per cell. The presence of so many cells with no data was the reason that model results were not predicted onto maps to show habitat usage areas for the species inside and outside the boundaries of the study site.



**Figure 3.2 - Map of the study area with absences and presences waypoints 2002-2006 and 2009-2010 downloaded from the GPS (Rozo 2002, Blight 2013).**

### 3.5 Results

Boat surveys were conducted on 395 days, along 43 km of shore line, during the three climatic seasons: rainy, dry and semi-dry in 2002-2006 and 2009-2010. The effort per day was recorded using the tracking function of the GPS and downloaded later into the map (see Figure 2.4 in Chapter 2). The study area was divided into six zones, from the first mouth of the Sinú River (Boca Mireya) to Tolú. The total survey effort covering the six zones was 15,199 km. As described in Chapter 2, the size of the zones differed considerably, hence

survey effort in km also varied significantly among zones. Likewise, survey effort was not consistent among years, and the zones covered per survey were highly dependent on the weather conditions (Table 3.2).

A total of 318 sightings of *S. guianensis* and 534 environmental variables points were recorded and used for modelling habitat use and distribution of the species in the study area (Figures 3.2 and 3.3, Table 3.2).

**Table 3.2 - Summary of survey effort and sightings information of Guiana dolphins by zone during 2002-2006 and 2009-2010 in the southern area of the Gulf of Morrosquillo.**

<b>Zone Number</b>	<b>Distance surveyed (km)</b>	<b>Number of dolphin sightings</b>	<b>Number of adults</b>	<b>Number of calves</b>	<b>Total number of dolphins</b>	<b>Number of dolphins feeding</b>
1	693.52	28	132	30	162	120
2	1,700.52	182	1,258	195	1,453	686
3	4,327.52	36	258	35	293	174
4	2,358.42	15	59	11	67	40
5	2,244.67	53	295	38	333	142
6	3,874.7	4	75	7	82	60
<b>Total</b>	<b>15,199.35</b>	<b>318</b>	<b>2,077</b>	<b>316</b>	<b>2,390</b>	<b>1,222</b>

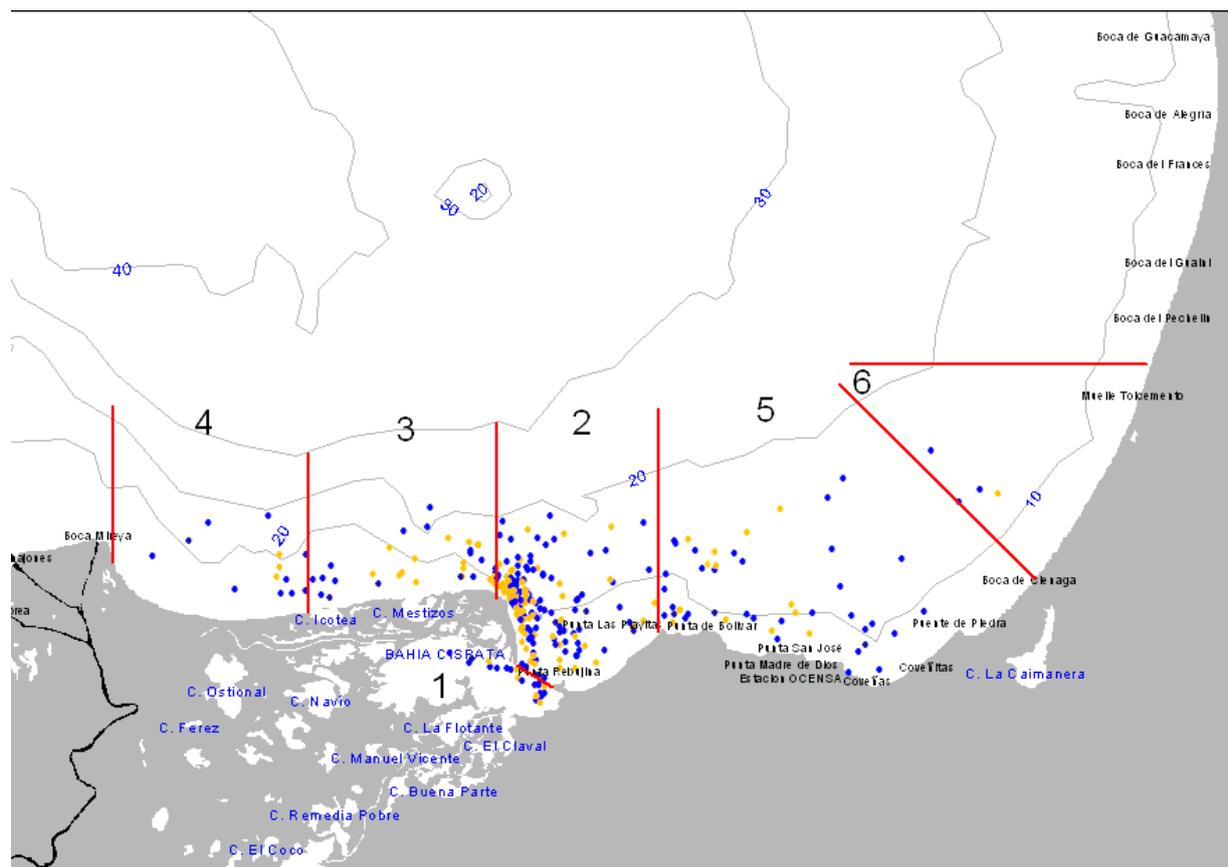
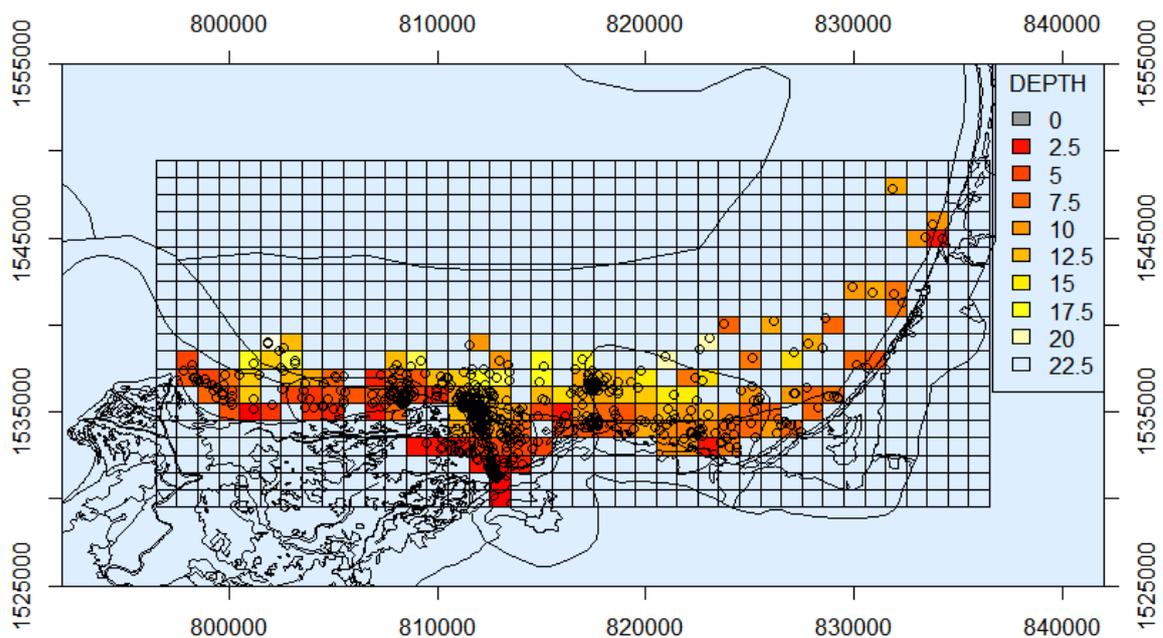


Figure 3.3 - Distribution of sightings of Guiana dolphins from 2002-2006 and 2009-2010 in the study site. Blue dots represent the rainy and semi-dry season, yellow dots the dry season.

Table 3.3 - Sightings of Guiana dolphins by zone and season during 2002-2006 and 2009-2010 in the southern area of the Gulf of Morrosquillo.

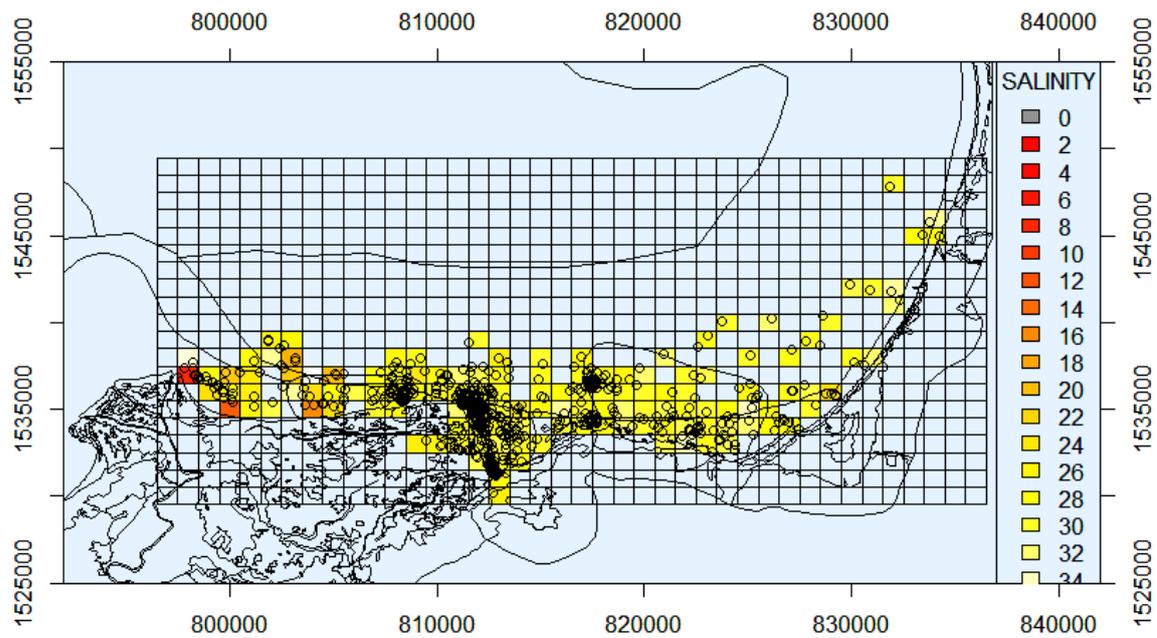
Zone Number	Number of sightings			Total sightings
	Rainy season	Dry season	Semi-dry season	
1	19	9	0	28
2	96	77	9	182
3	19	16	1	36
4	11	4	0	15
5	39	13	1	53
6	1	1	2	4
<b>Total</b>	<b>223</b>	<b>95</b>	<b>13</b>	<b>318</b>

Figure 3.4 shows the counts of Guiana dolphins in relation to depth in the study area by grid cell. As also shown in Table 3.2 and Figure 3.3, the majority of adult sightings were in zone 2 during all the climatic seasons. The summary statistics of adult counts, range from 0 adults per cell to 332, with an average of 15 adults per cell. The range of depths was from 1.40m to 25.00m. The average depth was 9.35m. During the opportunistic surveys conducted outside the boundaries of the study area (isobath <25m), there were no sightings of Guiana dolphins. These opportunistic data were not included in the modelling.



**Figure 3.4 - Counts of Guiana dolphins in relation to depth in the study area from 2002-2006 and 2009-2010.**

As seen in Figure 3.5 the salinity in the study area varied from 2.00 ppm to 36.00 ppm. The lowest salinities were present closer to the Sinú River delta. Apart from the salinities close to the river, those in the rest of the study site had a range between 26 ppm and 36 ppm, the highest values being in shallower waters close to shore and to the 10m bathymetry contour. The average salinity was 28.53 pp.



**Figure 3.5 - Counts of Guiana dolphins in relation to salinity in the study area from 2002-2006 and 2009-2010.**

Surveys were conducted mainly between 06:00 and 16:00 hours, with some surveys conducted inside the bay between 16:00 and 18:00 hours. As seen in Table 3.4 dolphins were present throughout the study area during 06:00 and 18:00 hours, but the number of sightings per zone changed depending on the time of day. This may indicate daily movements of the dolphins within the study area (Chapter 4), resulting in a different use of the zones depending on the time of day. There was a peak in sightings in the hours between 08:00 and 10:00, with an average hour at 09:50.

**Table 3.4 - Sightings of Guiana dolphins by time of day by zone during 2002-2006 and 2009-2010 in the southern area of the Gulf of Morrosquillo.**

Time of day	Sightings per zone						Total sightings
	1	2	3	4	5	6	
6:00-8:00	8	40	6	1	0	0	55
8:00-10:00	12	80	17	7	16	0	132
10:00-12:00	4	41	12	5	21	3	86
12:00-14:00	1	12	1	2	12	1	29
14:00-16:00	2	6	0	0	4	0	12
16:00-18:00	1	3	0	0	0	0	4
<b>Total</b>	<b>28</b>	<b>182</b>	<b>36</b>	<b>15</b>	<b>53</b>	<b>4</b>	<b>318</b>

The observed group size varied from 1 to 60 individuals (Figure 3.6). The mean group size was 9 individuals ( $n = 1-60$ ) and the interquartile range was 5 (turquoise dots in Figure 3.6) and this group size was found mainly in zones 2, 3 and 5, but they were predominantly during the dry season in zone 3 (Figure 3.3). Solitary dolphins were only found in zones 1 and 2 (black dots), and only during the dry season. Adult pairs (orange dots), were found mainly in zones 2 and 5, with one sighting in zone 3 during the dry season and two sightings in zone 4 during the rainy season. Groups of 11-16 individuals (pink dots), were found mainly in zones 2 and 5. There was one sighting in zone 3 and another one in zone 4 and two in zone 6, all of them during the rainy season. Groups of 17 and 22 (dark blue dots) were found only in zone 2 during both the rainy and dry seasons. Groups of 23-28 individuals (purple dots) were found mainly in zone 2 with only one sighting in each of zones 3, 4 and 5. The sighting in zone 4 was during the rainy season, whilst in zone 3 and 5 they were during the dry season. There were only three sightings of groups between 29 and 41 individuals (bright green dots), two of them in zone two and one in zone 3, all of them following the contour of the 20m bathymetry line. All three were during the rainy season. Only one group of 60 individuals was present during all the surveyed years (red dot), it was present during the rainy season in zone 6.

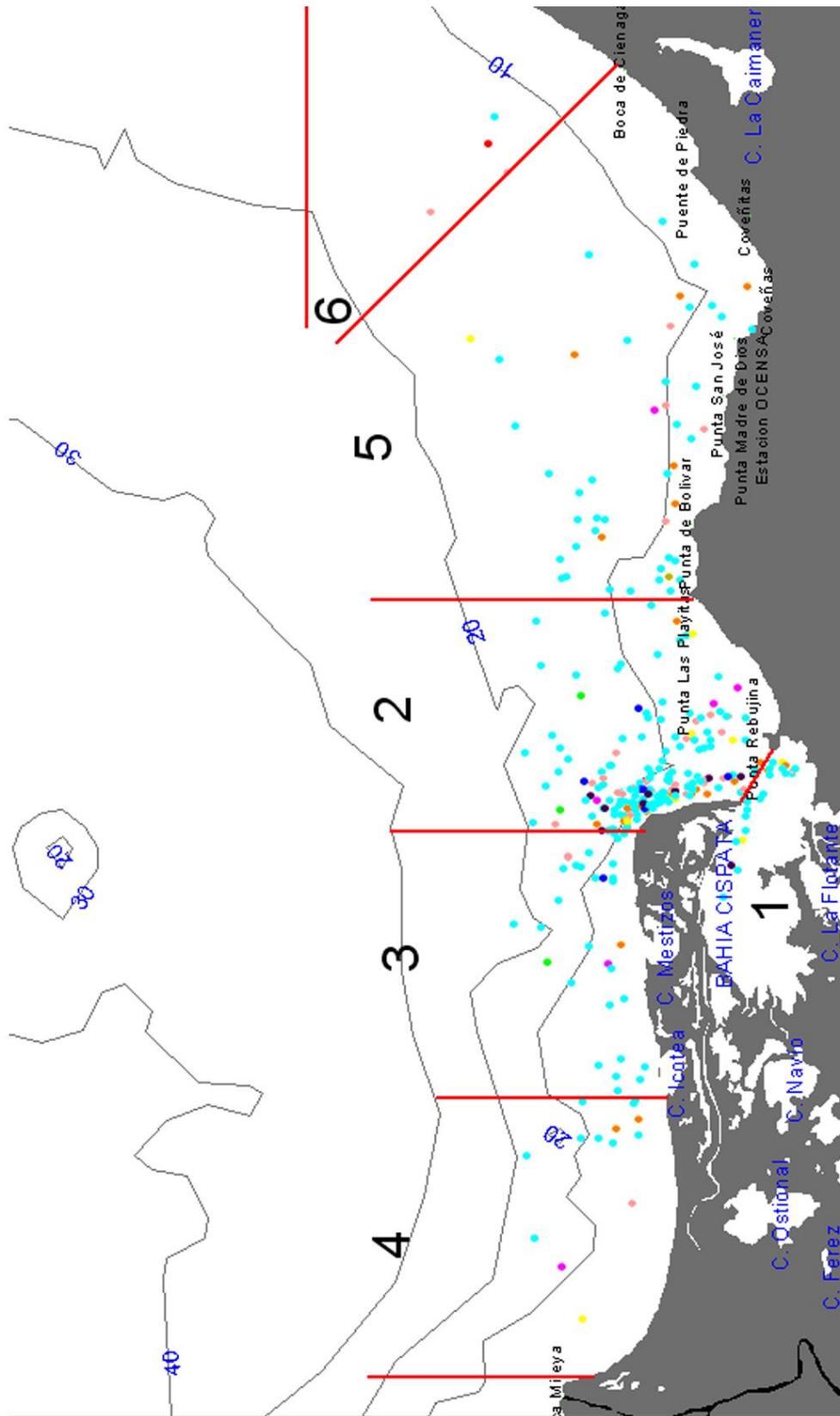
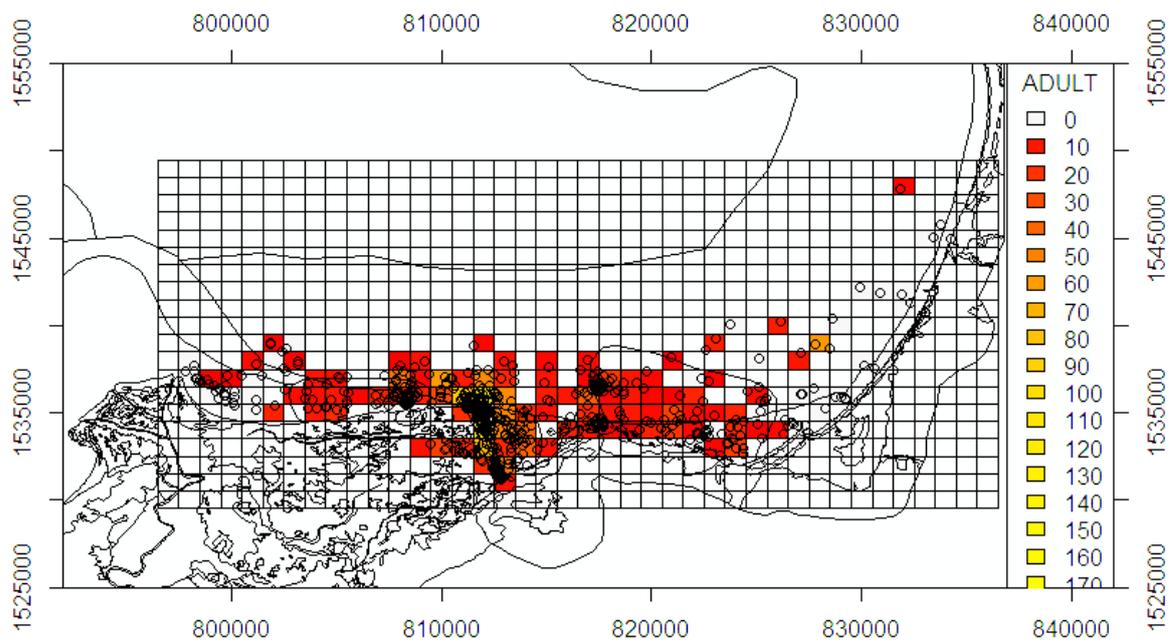


Figure 3.6 - Group size of Guiana dolphins present in the study area during both rainy and dry seasons from 2002-2006 and 2009-2010. Solitary dolphins (black dots), mothers and calf pairs (bright yellow dots), adult pairs (orange dots), average group size (turquoise blue dots), groups sizes between 11 and 16 (pink dots), groups sizes between 17 and 22 (dark blue dots), groups sizes between 23 and 28 (purple dots), group sizes between 29 and 41 (bright green dots), 60 individuals (red dot).

### 3.5.1 Adults

Figure 3.7 shows the distribution of sightings of adults in the study area by grid cell. As also shown in Table 3.2 and Figure 3.3, the majority of adult sightings were in zone 2 during all seasons. The summary statistics of adult counts, range from 0 adults per cell to 332, with an average of 15 adults per cell.

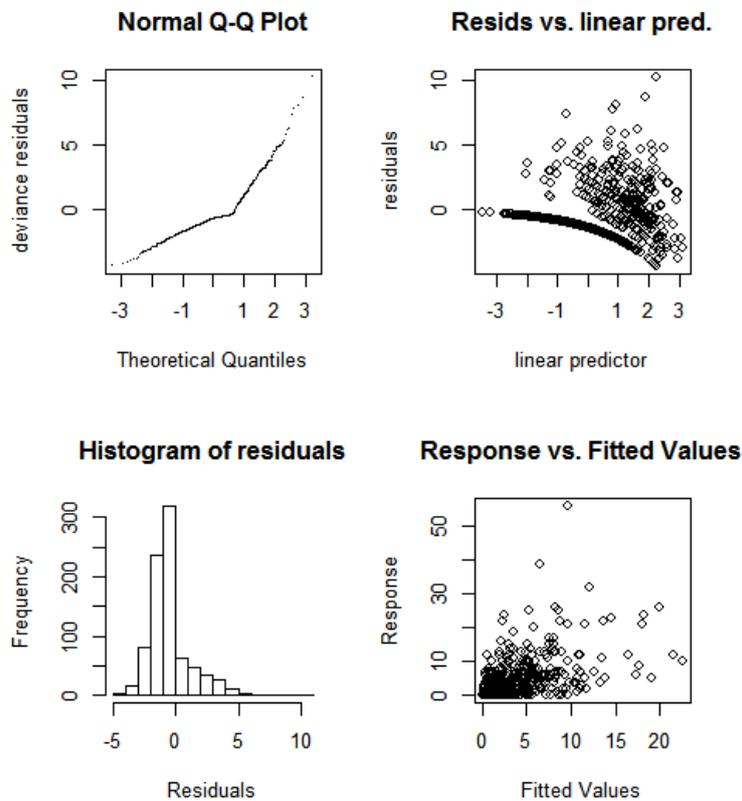


**Figure 3.7 - Distribution of sightings of adult Guiana dolphins from 2002-2006 and 2009-2010 in the southern area of the Gulf of Morrosquillo presented by grid cell.**

For adult counts, the best-fitting GLM obtained through forward selection differed from the best-fitting GAM obtained through backwards selection only in one explanatory variable: time of day. The relationship between adult counts and one covariate (depth) showed a non-linear response so the GAM was chosen as the best model. The final GAM for adult counts retained five explanatory bio-geographic covariates and one sighting-related covariate of the total of 20 measured during the surveys: time of day, salinity, depth, year, zone and Beaufort.

**Adult counts** ~ Time of day + Salinity + s (Depth) + Year (as a factor) + Zone (as a factor) + Beaufort (as a factor), *family = quasi-Poisson*

The final model explained 48.2% of the deviance (Table 3.5) and fitted the data moderately well (adjusted  $r^2 = 0.332$ ). All covariates retained were significant (Table 3.5). The range of the variables is given in Table 2.1 in Chapter 2.



**Figure 3.8 - Diagnostics for the GAM for the adult counts model.**

Figure 3.8 shows the standard diagnostics for the fitted GAM. The Q-Q plot shows a “broken stick” shape indicating that the structure of the model did not allow a good fit across the range of the data. The residuals are not evenly spread indicating increasing variance as the counts increase. This is also shown in the observed response vs fitted values plot. The histograms of residuals are skewed. Overall, the diagnostics show the model did not fit very well but that it did capture some of the variability in the data.

**Table 3.5 - Summary results of the final model of adult counts. Year, Beaufort and zone were modelled as factors. Significance codes: \*  $0.01 < p < 0.05$ ; \*\*  $0.001 < p < 0.01$ ; \*\*\*  $p < 0.001$ . edf are the estimated degrees of freedom for the smoother.**

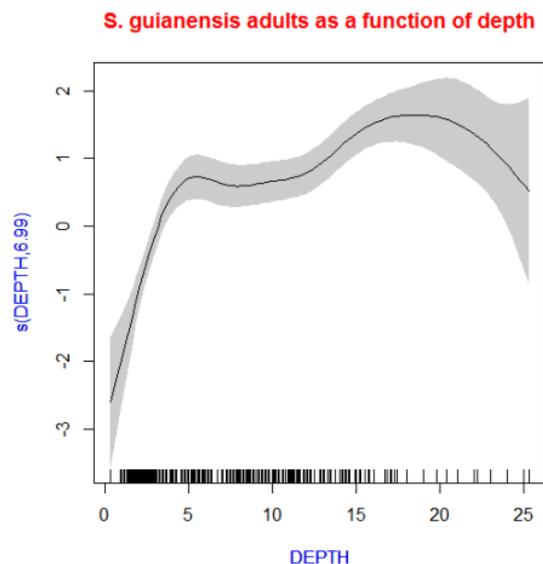
<b>Variable</b>	<b>coefficient</b>	<b>SE</b>	<b>p</b>	
(Intercept)	-2.061	0.5174	<0.001	***
Time of day	0.049	0.0224	0.029	*
Salinity	0.041	0.0122	0.001	***
Year 2003	0.519	0.1965	0.008	**
Year 2004	0.456	0.1913	0.017	*
Year 2005	0.821	0.2072	<0.001	***
Year 2006	0.379	0.2631	0.149	***
Year 2009	0.947	0.2064	<0.001	***
Year 2010	0.798	0.1975	<0.001	***
Beaufort 1	-0.366	0.0976	<0.001	***
Beaufort 2	-0.858	0.132	<0.001	***
Beaufort 3	-1.257	0.1981	<0.001	***
Zone 2	1.087	0.284	<0.001	***
Zone 3	0.739	0.2865	0.01	*
Zone 4	0.001	0.3752	0.997	
Zone 5	0.08	0.3098	0.794	
Zone 6	1.229	0.3644	<0.001	***
	<b>edf</b>		<b>p</b>	
s(Depth)	6.986		<0.001	***

Zone had a strong effect on adult counts as shown by the large variation in the coefficients among the zones (Table 3.5). Zones 2, 3 and 6 had the strongest positive impact on adult counts. The result for zone 2 is supported by the observed data but the result for zone 6, especially, is not (Tables 3.2, 3.3 and 3.4, Figure 3.4).

As shown in Table 3.5, the effects of Beaufort are negative and increase as Beaufort increases, as expected.

The differences among the years are not particularly strong as shown by the lack of variation in the coefficients. However, there was a stronger positive relationship between adult counts and the years 2005, 2009 and 2010 (Table 3.5).

The relationship between counts of adults and depth is shown in Figure 3.9 and Table 3.5. Adults appear to prefer waters greater than about 3m (the curve between 3 and 25m is all above zero on the y-axis) with a slightly increased preference for waters about 5m deep and 15-25m.



**Figure 3.9 - Adult counts of *S. guianensis* as a smooth function of depth. Shadow areas show the 95% confidence intervals. The rug plot along the x-axis shows the spread in the data.**

Figure 3.9 shows that the probability of sighting adults in the study area decreased in waters greater than about 23m but there are few data to support the fitted relationship in this range of

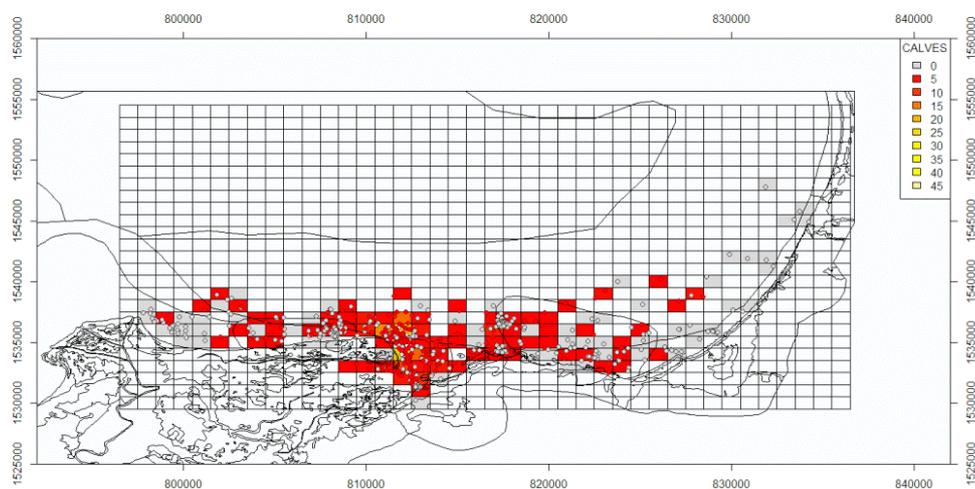
depths. The data showed a tendency for a strong inshore distribution for Guiana adult dolphins in the southern area of the Gulf of Morrosquillo, but this is less supported by the model results.

The effects of time of day and salinity on counts of adults were weak (Table 3.5). The results indicated that adult dolphins were distributed uniformly with respect to salinity and time of day in the study area. The results of the model with respect to time of day were not supported by the observed data (Table 3.4).

### 3.5.2 Calves

Figure 3.10 shows the distribution of sightings of calves in the study area by grid cell. As also shown in Table 3.2 and Figure 3.3, the majority of calves sightings were in zone 2 during all seasons. The summary statistics of calf counts range from 0 adults per cell to 52, with an average of 2 calves per cell.

Mother and calf pairs (bright yellow dots) (Figure 3.6), were found in zones 1, 2, 4 and 5, but predominantly at the border between zones 2 and 1, with only one sighting in zone 4 and one in zone 5. All sightings of mothers and calf pairs were made during the rainy season.

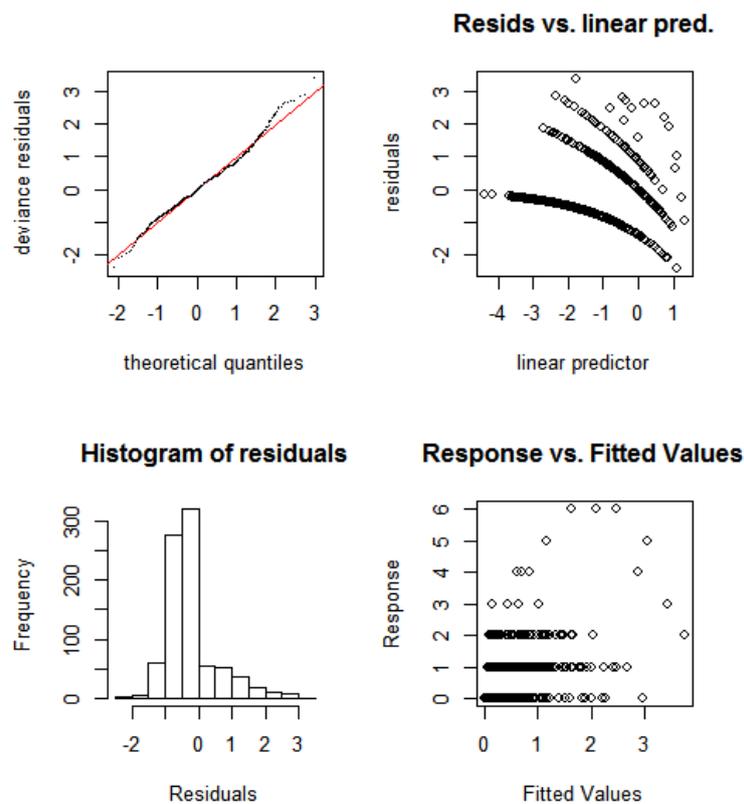


**Figure 3.10 - Distribution of sightings of calves of Guiana dolphins from 2002-2006 and 2009-2010 in the southern area of the Gulf of Morrosquillo, presented by grid cell.**

For calf counts, the best-fitting GLM obtained through forward selection differed from the best-fitting GAM obtained through backwards selection only in one explanatory variable: time of day. The error family used for this model was Poisson because no over-dispersion was found in the data (dispersion parameter = 1.08). The relationship between calf counts and one covariate (depth) showed a non-linear response so the GAM was chosen as the best model. The final GAM model for calf counts retained the same six explanatory covariates as that for adult counts: time of day, salinity, depth, year, zone and Beaufort.

**Calf counts** ~ Time of day + Salinity + s (Depth) + Year (as a factor) + Zone (as a factor) + Beaufort (as a factor), *family = Poisson*

The final model explained 38.6% of the deviance (Table 3.6) and fitted the data moderately well (adjusted  $r^2 = 0.28$ ). Many but not all of the coefficients of the retained covariates were significant (Table 3.6).



**Figure 3.11 - Diagnostics for the GAM for the calf counts model.**

Figure 3.11 shows the standard diagnostics for the fitted GAM. The Q-Q plot shows a straight line indicating a good model fit across the range of the data. The residuals are not evenly spread indicating increasing variance as the counts increase. The observed response vs fitted values plot does not show a very clear relationship. The histograms of residuals are skewed. Overall, the diagnostics show the model fitted the data reasonably well.

**Table 3.6 - Summary results of the final model of calf counts. Year, Beaufort and zone were modelled as factors. Significance codes: · 0.1 < p < 0.1 ; \* 0.01 < p < 0.05; \*\* 0.001 < p < 0.01; \*\*\* p < 0.001. edf are the estimated degrees of freedom for the smoother.**

<b>Variable</b>	<b>coefficient</b>	<b>SE</b>	<b>p</b>	
(Intercept)	-3.366	0.6969	<0.001	***
Salinity	0.026	0.0168	0.115	
Year 2003	0.719	0.2728	0.008	**
Year 2004	0.246	0.2775	0.376	
Year 2005	0.678	0.3003	0.024	*
Year 2006	0.717	0.3400	0.035	*
Year 2009	0.833	0.2904	0.004	**
Year 2010	0.984	0.2720	0.000	***
Zone 2	1.080	0.3594	0.003	**
Zone 3	0.560	0.3697	0.130	
Zone 4	0.051	0.4756	0.914	
Zone 5	-0.143	0.4063	0.724	
Zone 6	0.657	0.5353	0.219	
Beaufort 1	-0.447	0.1359	0.000	***
Beaufort 2	-0.632	0.1737	0.000	**
Beaufort 3	-1.141	0.2629	<0.001	***
Time of day	0.059	0.0304	0.052	·

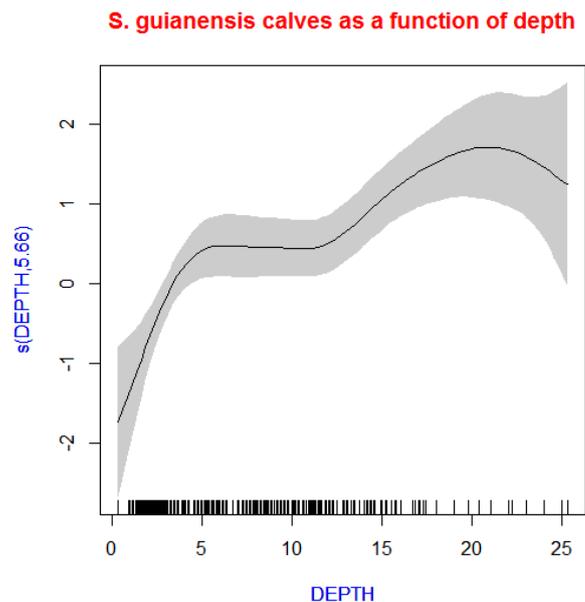
	<b>edf</b>	<b>p-value</b>	
s(Depth)	5.663	<0.001	***

Zone had a strong effect on calf counts as shown by the large variation in the coefficients among the zones (Table 3.6). Zone 2 had the strongest positive impact on calf counts whilst zone 5 had a negative impact. The result for zone 2 is supported by the observed data but the result for zone 5, especially, is not (Tables 3.2 and 3.6, Figure 3.10).

As shown in Table 3.6, the effects of Beaufort are negative and increase as Beaufort increases, as expected.

The differences among the years are not particularly strong as shown by the lack of variation in the coefficients. However, years 2003, 2009 and 2010 have a more significant effect than the other years (Table 3.6).

The relationship between counts of calves and depth is shown in Figure 3.12 and Table 3.6. Calves appear to prefer waters greater than about 3m with an increased preference for waters 12-25m deep.



**Figure 3.12 - Calf counts of *S. guianensis* as a smooth function of depth. Shadow areas show the 95% confidence intervals. The rug plot along the x-axis shows the spread in the data.**

Figure 3.12 shows that the probability of sighting calves in the study area decreased in waters greater than about 23m but there are few data to support the fitted relationship in this range of depths. The data showed a tendency for a strong inshore distribution for calves of Guiana dolphins in the southern area of the Gulf of Morrosquillo, but this is less supported by the model results (Figure 3.10).

The effects of time of day and salinity on calf counts were weak (Table 3.6). The results indicated that calves were distributed uniformly with respect to salinity and time of day in the study area.

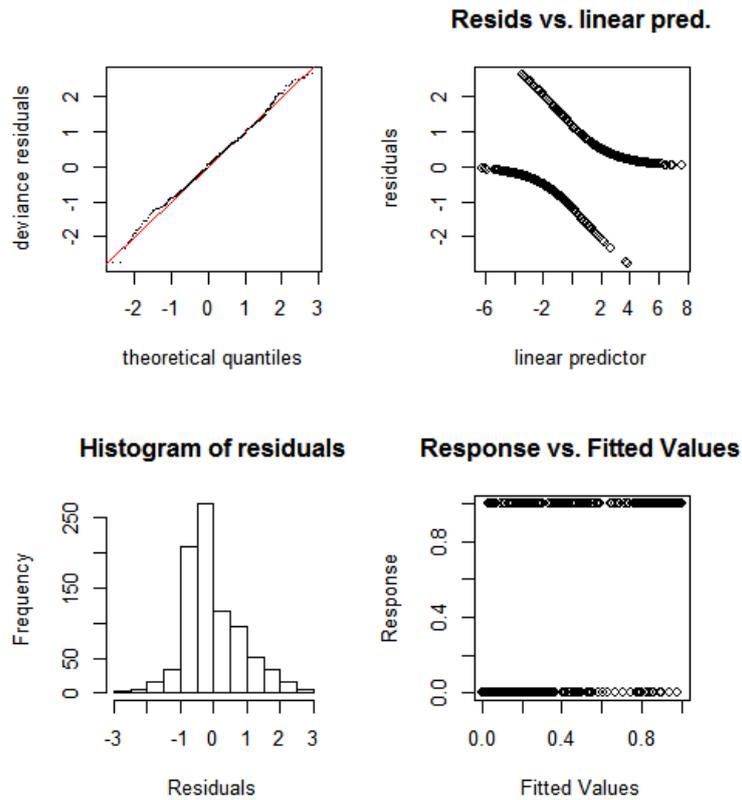
### 3.5.3 Feeding models

#### 3.5.3.1 Model number 1: Presence/absence of Guiana dolphins

For the model of presence/absence of dolphins, the error family used was Binomial. No over-dispersion was found in the data (dispersion parameter = 1.06). Two covariates (depth and time of day) showed a non-linear response so the GAM was chosen as the best model. This model retained five of the same covariates as those retained in the models for adult and calf counts: time of day, depth, year, zone and Beaufort. In addition, one new variable was retained: season. Salinity, a variable that had been retained in the other two models, was not retained. The final model was:

**Presence/absence** ~ Year (as a factor) + s (Depth,  $k = 8$ ) + Season (as a factor) + Beaufort (as a factor) + s (Time of day) + Zone (as a factor), *family = binomial*)

The final model explained 45.7% of the deviance (Table 3.7), and fitted the data moderately well (adjusted  $r^2 = 0.513$ ). Many but not all of the coefficients of the retained covariates were significant (Table 3.7).



**Figure 3.13 - Diagnostics for the GAM for feeding model 1: presence/absence of dolphins.**

Figure 3.13 shows the standard diagnostics for the fitted GAM. The Q-Q plot shows a very straight line indicating a very good model fit across the range of the data. The histograms of residuals show an approximately Normal distribution, also indicating good fit. The residuals and observed response vs fitted values plots are not very informative for binomial data. Overall, the diagnostics show the model fitted the data well.

**Table 3.7 - Summary results of the final model for presence/absence of dolphins. Year, season, Beaufort and zone were modelled as factors. Significance codes: \* 0.01 < p < 0.05; \*\* 0.001 < p < 0.01; \*\*\* p < 0.001. edf are the estimated degrees of freedom for the smoother.**

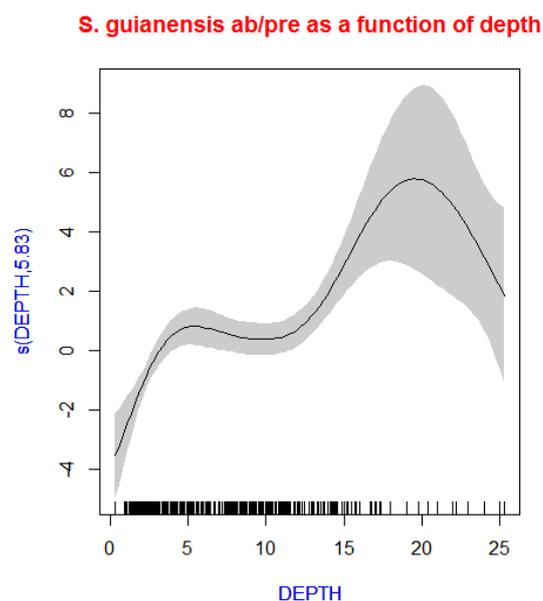
<b>Variable</b>	<b>coefficient</b>	<b>SE</b>	<b>p</b>	
(Intercept)	-2.474	0.5692	<0.001	***
Year 2003	1.394	0.5156	0.007	**
Year 2004	1.653	0.5165	0.001	**
Year 2005	1.609	0.5384	0.003	**
Year 2006	1.554	0.575	0.007	**
Year 2009	2.054	0.5847	<0.001	***
Year 2010	2.371	0.6169	<0.001	***
Season 2	0.075	0.2654	0.779	
Season 3	-0.497	0.531	0.349	
Beaufort 1	-0.884	0.2819	0.002	**
Beaufort 2	-1.299	0.3385	<0.001	***
Beaufort 3	-1.239	0.4217	0.003	**
Zone 2	2.951	0.4976	<0.001	***
Zone 3	0.707	0.4913	0.150	
Zone 4	0.116	0.5872	0.844	
Zone 5	0.255	0.5394	0.637	
Zone 6	0.383	0.7954	0.630	
		<b>edf</b>	<b>p-value</b>	
s(Depth)		5.833	<0.001	***
s(Time of day)		3.191	0.013	*

Zone had a strong influence on the presence/absence of dolphins as shown by the large variation in the coefficients among zones (Table 3.7). The effect of Zone 2 was very strong, as supported by the data and also the models of adult counts and calf counts models (Tables 3.2, 3.5, 3.6 and 3.7).

As shown in table 3.7, the effects of Beaufort were negative. There was an increase in effect from Beaufort 1 to 2 but not between Beaufort 2 and 3.

The variation in coefficients shows that the effect of year was moderate with the strongest positive relationship for 2010 and 2009 (Table 3.7).

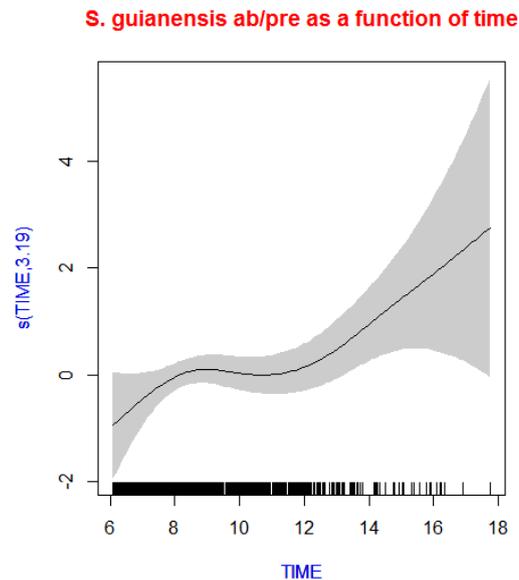
The relationship between presence of dolphins and Depth is shown in Figure 3.14 and Table 3.7. Dolphins appeared to prefer waters greater than about 3m and to have a strong preference for waters 15-25m deep.



**Figure 3.14 - Presence/absence of *S. guianensis* as a smooth function of depth. Shadow areas show the 95% confidence intervals. The rug plot along the x-axis shows the spread in the data.**

Season 3 (the semi-dry season) had a negative impact on presence compared to season 2 (the dry season) (Table 3.7).

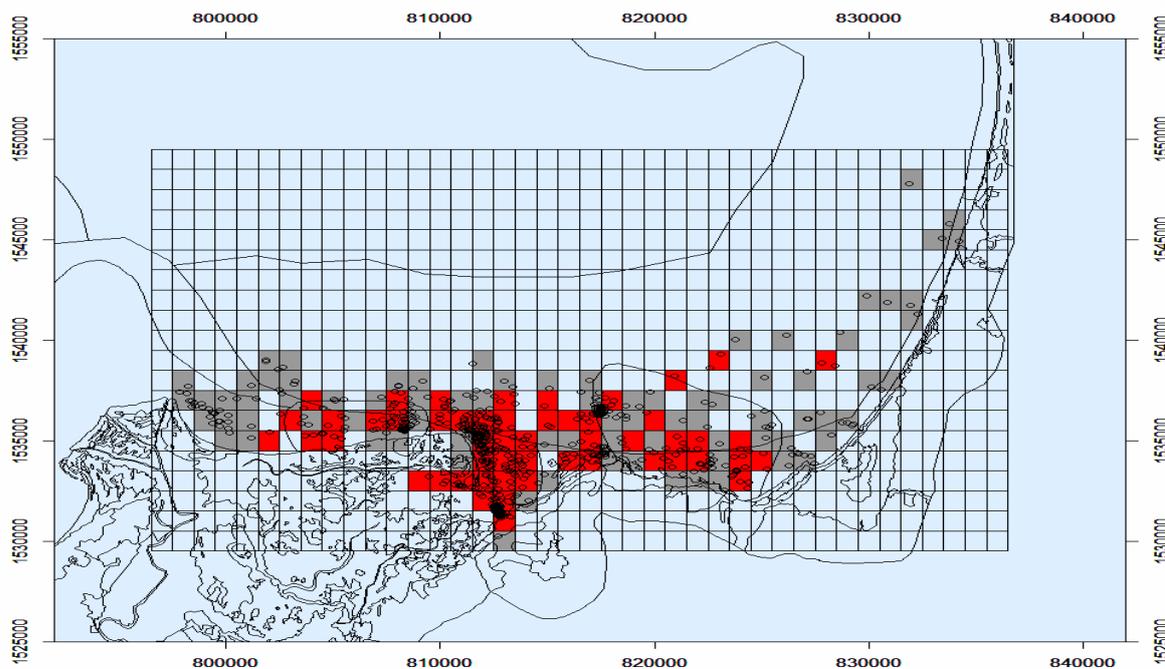
The effects of time of day on presence of dolphins were not very strong, the same results as for adults and calves (Table 3.7 and Figure 3.15). The model shows a tendency for dolphins to be present in the area in the afternoon but the confidence in this relationship is not strong. This result is not supported directly by the observed data (Table 3.4).



**Figure 3.15 - Presence of *S. guianensis* as a smooth function of time of day. Shadow areas show the 95% confidence intervals. The rug plot along the x-axis shows the spread in the data.**

### **3.5.3.2 Model number 2: Number of Guiana dolphins feeding conditional on the presence of dolphins in the area**

Figure 3.16 shows the distribution of feeding areas by grid cell. Dolphins show a clear selection for areas to feed within the 15m bathymetry contour line. The majority of sightings of dolphins feeding were in zone 2, 5 and 3 (Table 3.8). Zone 6 had the largest feeding aggregation ( $n = 60$ ) during the survey years (Table 3.10).



**Figure 3.16 - Distribution of the feeding areas of Guiana dolphins from 2002-2006 and 2009-2010 in the southern area of the Gulf of Morrosquillo presented by grid cell. Red areas show the feeding habitat of the dolphins, grey areas show the areas where the dolphins did not feed.**

**Table 3.8 – Sightings of dolphins and number of dolphins feeding per zone.**

<b>Zone</b>	<b>Sightings</b>	<b>Number of dolphins feeding</b>
1	12	100
2	69	677
3	15	180
4	6	40
5	17	144
6	1	60
<b>Total</b>	<b>120</b>	<b>1,201</b>

Table 3.9 shows how the number of sightings of dolphins feeding in the study area changes depending on the climatic season, as well as the total number of dolphins feeding.

**Table 3.9 – Number of sightings and number of dolphins feeding per season.**

<b>Season</b>	<b>Number of sightings (dolphins feeding)</b>	<b>Number of dolphins feeding</b>
Rainy	65	654
Dry	50	451
Semi-dry	5	96

Groups of more than 15 individuals (average group size = 9), were considered as feeding aggregations (Table 3.10). The zone with the largest number of feeding aggregations was zone 2 followed by zone 3. There was an equal number of feeding aggregations during the rainy and dry seasons. There were only two feeding aggregations during the semi-dry season.

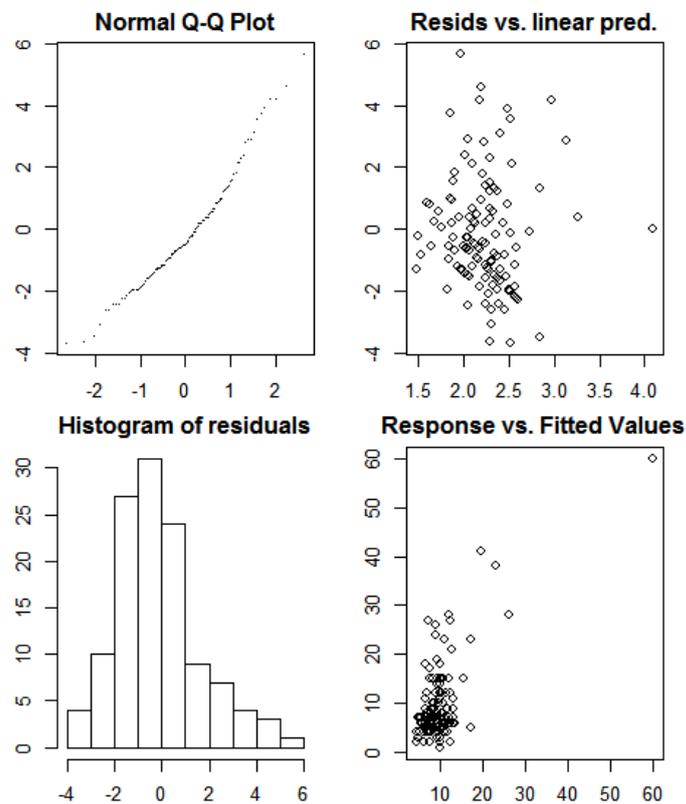
**Table 3.10 – Feeding aggregations by zone, season and tide (In = rising tide, Hi = high tide, Out = receding tide, Low = low tide) from 2002-2006 and 2009-2010 in the southern area of the Gulf of Morrosquillo.**

<b>Group size</b>	<b>Zone</b>						<b>Season</b>			<b>Tide</b>				<b>Total Sightings</b>
	<b>1</b>	<b>2</b>	<b>3</b>	<b>4</b>	<b>5</b>	<b>6</b>	<b>Rainy</b>	<b>Dry</b>	<b>Semi-dry</b>	<b>In</b>	<b>Hi</b>	<b>Out</b>	<b>Low</b>	
15-20	0	7	3	0	2	0	6	5	1	3	1	6	2	12
21-26	1	4	0	0	0	0	3	2	0	1	2	1	1	5
27-38	0	4	1	0	0	0	2	3	0	1	2	2	0	5
41-60	0	0	1	0	0	1	0	1	1	0	1	0	1	2
<b>Total</b>	<b>1</b>	<b>15</b>	<b>5</b>	<b>0</b>	<b>2</b>	<b>1</b>	<b>11</b>	<b>11</b>	<b>2</b>	<b>5</b>	<b>6</b>	<b>9</b>	<b>4</b>	<b>24</b>

The relationship between the count of dolphins feeding and one covariate (depth) showed a non-linear response so the GAM was chosen as the best model. The error family used for this model was quasi-Poisson (dispersion parameter = 4.07). The final GAM for feeding dolphins retained four covariates, three of them in common with the previous three models. However, tide was also retained in this model. The best model was:

**Dolphins feeding** ~ s (Depth, bs = “ts”) + Tide (as a factor) + Zone (as a factor) + Beaufort (as a factor), *family* = *quasi-Poisson*

The final model explained 38.1% of the deviance (Table 3.10), and fitted the data moderately well (adjusted  $r^2 = 0.417$ ). Only a few of the covariates were significant.



**Figure 3.17 - Diagnostics for the GAM for the model of dolphins feeding.**

Figure 3.17 shows the standard diagnostics for the fitted GAM. The Q-Q plot shows a fairly straight line indicating a generally good model fit across the range of the data. The histograms of residuals show an approximately Normal distribution, also indicating good fit. The

residuals plot shows some pattern across the range of data, supported by the observed response vs fitted values plot. The data point representing the one large feeding aggregation is influential. Nevertheless, overall, the diagnostics show the model fitted the data fairly well.

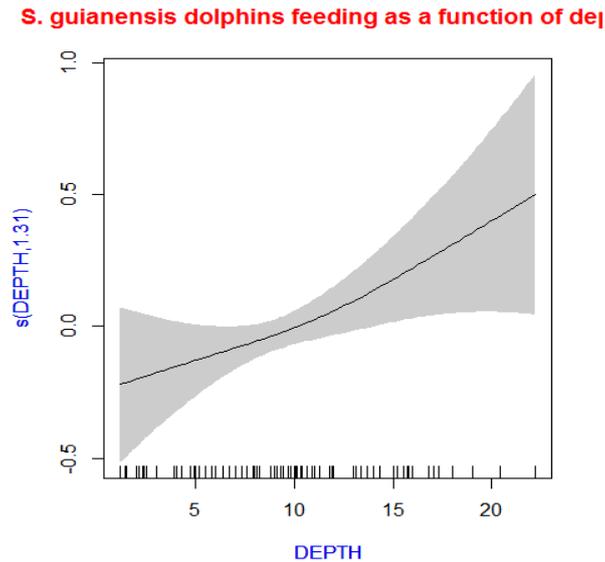
**Table 3.11- Summary results of the final model 2: Dolphins feeding . Tide, zone and Beaufort were modelled as factors. Significance codes: . · 0.1 < p < 0.1; \* 0.01 < p < 0.05; \*\*\* p < 0.001. edf are the estimated degrees of freedom for the smoother.**

<b>Variable</b>	<b>coefficient</b>	<b>SE</b>	<b>p</b>	
(Intercept)	2.394	0.2443	< 0.001	***
Tide 2	-0.194	0.1556	0.215	
Tide 3	0.334	0.1772	0.062	.
Tide 4	-0.115	0.1817	0.529	
Zone 2	0.093	0.2413	0.700	
Zone 3	0.252	0.2640	0.342	
Zone 4	-0.151	0.3650	0.679	
Zone 5	-0.100	0.2901	0.732	
Zone 6	1.904	0.3957	<0.001	***
Beaufort 1	-0.213	0.1298	0.104	
Beaufort 2	-0.391	0.1835	0.035	*
Beaufort 3	-0.755	0.3193	0.020	*
		<b>edf</b>	<b>p</b>	
s(Depth)		1.31	0.023	*

Zone had a very strong effect on the number of dolphins feeding as shown by the large variation in the coefficients among the zones (Table 3.11). Zones 4 and 5 had a negative influence, whilst zones 2, 3 and 6 had a positive influence, as supported by the observed data; zone 6 was where the biggest feeding aggregation of Guiana dolphins seen in the study area (Table 3.8, 3.11 and Figure 3.16). Zone 6 was the only highly significant covariate.

As shown in table 3.11, the effects of Beaufort are negative and increase as Beaufort increases, as expected.

The relationship between the number of feeding dolphins and depth was only slightly non-linear (Figure 3.18). Guiana dolphins seem to prefer feeding in waters greater than 10m deep (Figure 3.18).



**Figure 3.18 - The number of *S. guianensis* feeding as a smooth function of depth. Shadow areas show the 95% confidence intervals. The rug plot along the x-axis shows the spread in the data.**

Tide did not show a strong correlation with the number of feeding dolphins as shown by the limited variation in the coefficients among the different tidal states (Tables 3.10, 3.11). Nevertheless, the relationship was negative for tide factor level 2 (tide going out) and tide factor level 4 (low tide), whilst tide factor level 3 (high tide) shows a positive correlation. Thus, the model shows a tendency for dolphins to feed less when the tide is going out and low and more during high tide.

### 3.6 Discussion

Understanding the factors behind a species distribution is one of the main topics in ecology (MacArthur 1972, Brown 1984, Harte *et al.* 1999, Nogués-Bravo 2009). Habitat usage and selection modelling has been used in ecological studies for decades (Odum 1971, Gilliam & Fraser 1987, Cowlshaw 1997, Gratwicke & Speight 2005, Richard *et al.* 2011, Sunarto *et al.* 2012) and more recently in marine mammals studies (Greg & Trites 2001, Kashner *et al.* 2006, Redfern *et al.* 2006, Cañadas & Hammond 2008, Bailey *et al.* 2009 and Hammond *et al.* 2013). Through modelling the effect of bio-geographic covariates on the distribution of different species, it is possible to investigate from a wider perspective the intrinsic

relationships within diverse ecosystems (Guisan & Zimmerman 2000, Austin 2002, Guisan *et al.* 2002, Freitas *et al.* 2008, Matthiopoulos & Aarts 2010).

However, ecological interactions are highly complex, and habitat models can only explain a part of these relationships between species and ecosystems. Therefore, it is important when using models to describe species-habitat relationships to be aware that they are necessarily a simplistic description of a small part of an ecosystem and that the results should be interpreted in an ecological context before making final conclusions about the patterns (Carpenter *et al.* 1993, Phillips & Dudik 2008 and Matthiopoulos & Aarts 2010). The results and limitations of habitat modelling should be carefully analysed and should not be applied in a generalist manner (Guisan & Thuiller 2005). The background of a model is data, the stronger and more consistent the data are, the higher the probability of the model to fit and somehow explain them (Crawley 2005).

Cetacean species are difficult to study and monitor over long periods of time. Cetaceans are highly mobile and their habitats may extend more widely than those of terrestrial mammals. This characteristic, together with the possibility of seeing them only during certain periods, highlights the utility in the field of conducting habitat modelling studies to better understand the complex processes involved in their habitat use and distribution (Guisan *et al.* 2002, Matthiopoulos & Aarts 2010). In addition, an understanding of the diverse factors behind a species distribution is a very important tool to inform its conservation.

As described in Chapter 1, *S. guianensis*, is listed by the IUCN as “Data Deficient” (IUCN 2012) and as “Vulnerable” in the Red List of Mammals of Colombia. Guiana dolphins are characterised by a highly patchy distribution through all of their range. The Gulf of Morrosquillo is considered the most important place in Colombia that currently holds the largest and most conserved population of this species (Bossenecker 1978, Avila 1995, Garcia 1998, Garcia & Trujillo 2004, Dussán-Duque *et al.* 2003, 2006, Dussán-Duque & Wells 2007).

The results of habitat use, selection and distribution of Guiana dolphins in the southern area of the Gulf of Morrosquillo presented in this chapter is intended to provide practical information to conservation management of this species and its habitats in the study site. It is also intended that the results will help inform ecological understanding and conservation management of this and similar species in other areas.

### 3.6.1 Observed data and model assumptions

The building, selection and fitting of the habitat use models in this chapter were based on the observed data collected during the surveys conducted in the study area from 2002-2006 and 2009-2010 (see Chapter 2). No additional data on the eco-geographic variables measured for this study exist, therefore all the data used in the models were collected *in situ* at a small scale. This made it impossible to make predictions for areas not actually visited within the study area or for areas of *S.guianensis* distribution in the Gulf of Morrosquillo outside the boundaries of the study site. Model prediction based on data averaging outside the study site was not attempted because the bio-geographic characteristics within the Gulf of Morrosquillo are specific to each area and any prediction would thus likely be subject to considerable bias and therefore of no practical value.

On the other hand, because the data were collected at a small spatial scale, habitat use and selection can be analysed at a fine scale. Guiana dolphins are characterized as a coastal, non-migratory species with a high site fidelity to specific areas throughout its distribution (Da Silva *et al.* 2010), so fine scale habitat modelling is highly appropriate. This may not be the case for open water marine mammal species, which may be migratory, highly mobile and/or have low site fidelity (Cañadas *et al.* 2005, Cañadas & Hammond 2008, Panigada *et al.* 2008, Pirolta *et al.* 2011, Anderwald *et al.* 2012). Analysis of fine scale habitat usage patterns, as in this study, is very important to identify core relationships for species with similar characteristics to *S. guianensis*. In this case, the use of habitat models and results had an explanatory purpose which is important for informing conservation policy and action.

Due to the body size and cautious behaviour of the Guiana dolphins, their detectability is low and detecting them is challenging during poor sighting conditions (i.e. wind, rain, etc.) (De O. Santos *et al.* 2010). Surveys conducted for this study were done in good weather conditions following established protocols for working with this species in the field (De O. Santos *et al.* 2010). All data were collected *in situ*, including hourly measurements of the environmental variables in the absence (and presence) of dolphins. Thus, in this study, sampling points were the sampling units, and it was assumed that these sample data represented the habitat use of the dolphins in the study site.

In the Gulf of Morrosquillo, the environmental parameters do not show extreme seasonal fluctuations, unlike those seen in other sites (Heinrich 2006 and Booth 2010). These small fluctuations are one of the characteristics of tropical ecosystems (Odum 1971). The surveys

for this study were conducted during the three climatic seasons that occur through the year in the Gulf of Morrosquillo (dry, wet and semi-dry). Hence, the data are representative of these seasonal environmental changes, as well as the daily fluctuations of these parameters in the study site.

All the habitats surveyed during this study were equally available throughout the years; therefore there was no violation of this assumption for habitat modelling.

Based on the amount of deviance explained by the models, it is possible to confirm that other unmeasured explanatory variables must have influenced the distribution and abundance of Guiana dolphins in the Gulf of Morrosquillo during the surveyed years. It is important to understand that the relationships among environmental variables in an ecosystem may not be direct but some may be proxies for other unmeasured variables (e.g. prey, currents) (Marcot *et al.* 2001, Stenseth *et al.* 2003). Proxy variables can be important because they can be measured more easily than other variables as in this study (Elser *et al.* 2007, Cañadas & Hammond 2008, and Torres *et al.* 2008).

When covariates are retained in a model, it does not necessarily mean that these particular covariates are important, and *vice versa* (Burnham & Anderson 2002).

### **3.6.2. Habitat use and selection of Guiana dolphins**

Guiana dolphins were present in the study area in all the surveyed years, and showed year-round presence as found in previous studies conducted in the study site (Avila 1995, Garcia 1998, Garcia & Trujillo 2004, Dussán-Duque *et al.* 2003, 2006, Dussán-Duque & Wells 2007) and studies conducted in other areas of their range (De Araujo *et al.* 2001, Edwards & Schnell 2001, Flores 2003, De Freitas *et al.* 2004, Rossi-Santos *et al.* 2010, Hardt *et al.* 2010). *S. guianensis* is a non-migratory species, and its distribution is highly influenced by the availability of suitable estuarine habitats (Flores 2002), surrounded by shallow waters (Da Silva & Best 1996) and with a high concentration of prey (Borobia & Barros 1989). All these conditions are met in the southern area of the Gulf of Morrosquillo, as described in Chapter 2.

#### **3.6.2.1 Zone**

The effect of zone on the abundance and distribution of dolphins was generally strong in the four selected models, recognizing the zone as a key environmental factor for Guiana dolphins in the study area. There was a clear preference for zones 2, 3 and 5 during all seasons

throughout all years as shown in previous studies conducted in the area (Figure 3.3) (Avila 1995, Garcia 1998, Garcia & Trujillo 2004, Dussán-Duque *et al.* 2003, 2006, Dussán-Duque & Wells 2007). Zone 2 (see Chapter 2, Figure 2.2) is where a strong oceanic current enters Cispatá Bay (Figures 2.2 and 2.3). Punta Terraplén is located exactly where the majority of sightings were made, and it used to be part of the Sinú River delta in 1942 as described in Chapter 2 (Figure 2.3). This zone still has the characteristics of a delta area and has a continual exchange and mix of estuarine and oceanic waters (INVEMAR, CARSUCRE, CVS 2002). This interchange of waters occurs mainly through all the channels and marshes of estuarine water coming out to the ocean from within the bay and the oceanic current coming directly in front of Punta Terraplén (Figure 2.3).

Punta Terraplén is a zone of daily use for the majority of individuals of *S. guianensis* and *T. truncatus* (Avila 1995, Garcia 1998, Garcia & Trujillo 2004, Dussán-Duque *et al.* 2003, 2006, Dussán-Duque & Wells 2007). From there, the Guiana dolphins coming from zone 3 follow two main routes every day (Avila 1995, Garcia 1998, Garcia & Trujillo 2004, Dussán-Duque *et al.* 2003, 2006, Dussán-Duque & Wells 2007): either they enter the bay or they continue moving towards zone 5. The waters in zone 2, due to the direction of the current, are highly productive estuarine waters in which prey species of Guiana dolphins are present year-round (Parra 1996, INVEMAR 2002, 2003). In addition, this zone has, in Punta Terraplén (Figure 2.3), a channel caused by the influence of the oceanic current flowing against the coast (Patiño- Corredor & Flórez-Amaya 1993). This channel confers an advantage to the feeding strategies displayed by Guiana dolphins and bottlenose dolphins in the study site (Chapter 6).

The models showed an inshore distribution for Guiana dolphin calves in the southern area of the Gulf of Morrosquillo as reported in previous studies (Avila 1995, Garcia 1998, Garcia & Trujillo 2004, Dussán-Duque *et al.* 2003, 2006, Dussán-Duque & Wells 2007, Wedekin *et al.* 2007, Cremer *et al.* 2009 and Rossi-Santos *et al.* 2010). There was a negative relationship between zone 5 and calves, specifically. This zone (Figure 2.3) is the one with the largest continental shelf within the study area boundaries. This means that the area has a larger distance between the coast and the 20m bathymetry contour making it a more “open” environment than zones 1-4. Guiana dolphin mother and calf pairs have a tendency, throughout the range of the species, to prefer calm, shallow and “protected” waters more than “open” ones (Flores 2002, Daura-Jorge *et al.* 2004, Da Silva *et al.* 2010).

Mother and calf pairs were found predominantly along the border between zones 2 and 1. These zones contain a high density of prey in very shallow waters. All the sightings of mother and calf pairs occurred during the rainy season, which is the season that calves are born in the southern area of the Gulf of Morrosquillo (Avila 1995, Dussán-Duque & Wells 2007).

Zone 6, based on the models, had the strongest positive influence on the counts of dolphins. This result may have been because of the sighting in this zone of the largest feeding aggregation seen during the study. On the other hand, it is important to note that feeding aggregations were not common in this zone but were more common in zones 2 and 3 (Table 3.10). However, from the results it seems that zone 6 may be not such a bad place for dolphins to be and aggregate. Zone 6 has one of the largest preserved marsh areas towards the northern boundaries of the study site: La Ciénaga de la Caimanera (Figure 2.3). This mangrove area and its biodiversity has been systematically studied as part of the management plan for the mangrove areas of the Caribbean of Colombia since 2002 (Sánchez-Páez *et al.* 2004). It is under a process of ecological restoration by the local community and researchers. La Ciénaga de la Caimanera is considered one of the most pristine mangrove areas in the southern part of the Gulf of Morrosquillo (Sánchez-Páez *et al.* 2004). As such, it presents the ecological equilibrium of a mature mangrove area with one of the highest primary productivities in the southern part of the gulf (Odum 1971, Sánchez-Páez *et al.* 2004).

Within the range of possible suitable areas within the study site boundaries, three zones with higher sighting rates were indicated, zones 2, 3 and 6 suggesting these areas as important habitat within the distribution of Guiana dolphins. The results suggest that dolphins of this species do not use the southern area of the gulf uniformly and that the use of particular areas is related to eco-geographic covariates. The results are noteworthy for highlighting the strong habitat selection of this species that should be important for informing the long-term conservation of this species and its habitats within the Gulf of Morrosquillo.

### **3.6.2.2 Inter-annual variation**

Year was retained in the all the final models except in the one for dolphins feeding. This indicates that there were significant variations among years of the study in numbers of Guiana dolphins detected but that the areas used for feeding did not change from year to year. However, the differences among years were not particularly strong as shown by the lack of variation in the model coefficients. Nevertheless, the models did show that 2009 had a

stronger relationship with counts of adults. The reasons for this anomalous year are not understood. For calves instead, the year with the strongest relationship was 2010. If there was an increase in the number of adults during 2009, as the data and the model indicate, this could have led to an increase in calves present in the following year, as seems to be the case. Because 2010 was the last year of surveys, there are no further data to compare and check for the presence of trends.

### 3.6.2.3 Water depth

Salinity, temperature and depth are some of the most important ecological barriers that limit the free movement of marine organisms (Odum 1971). Distribution of marine mammals worldwide is highly influenced by the depth of the water in which they live (Costa 1993, Hooker *et al.* 1999, Cañadas *et al.* 2002, Kaschner *et al.* 2006, Longley *et al.* 2011 and Thorne *et al.* 2011). *S. guianensis* is characterised as having a coastal distribution and being concentrated close to river mouths in estuarine and mangrove areas (M. Di Benedetto *et al.* 2004, Rossi-Santos 2006, Cremer *et al.* 2011) and apparently the species is limited to depths of less than 50m (Fernandes 2005). The results of this study generally indicate that the probability of seeing Guiana dolphins in the study area decreases with increasing depth. Dolphins appeared to prefer areas within the bathymetry contour line of 25m as described in previous studies conducted in this study site (Avila 1995, Garcia 1998, Garcia & Trujillo 2004, Dussán-Duque *et al.* 2003, 2006, Dussán-Duque & Wells 2007) and other sites throughout their distribution (Flores & Bazalo 2004, De O. Santos & Rosso 2007, Rossi-Santos *et al.* 2010). Model results show a preference for waters greater than about 3m with a slightly increased preference for waters about 5m deep and 15-25m. During the opportunistic surveys conducted outside the study site boundaries into open waters, there were no sightings of this species beyond the 25m isobath. However, there was an increase in the sightings of *T. truncatus* (Dussán-Duque & Wells 2007) close to the 40m bathymetry contour. Depth contours and the channel in front of Punta Terraplén (Figure 2.3) seem to be used as vectors of movement by Guiana dolphins. The 10m and 20m contour lines are well used especially in zones 2, 3 and 4 where the continental platform extends not too far from the coast.

The selection by Guiana dolphins of areas of particular depths could be driven by the distribution of prey species in these areas (INVEMAR, CARSUCRE, CVS 2002). This topic is further discussed in the feeding section 3.6.2.7.

#### **3.6.2.4 Salinity**

Salinity was retained in only two of the models: adult and calf counts. However, the relationships between this covariate and Guiana dolphin counts were weak, as supported by the data. The study site is a moderately stratified estuary where fresh water coming from the river delta and the marshes and channels mixes in a mostly equal proportion with the tidal inflow (Odum 1971, CIOH 1994). Therefore, the vertical salinity profile is less steep than in other areas that are not estuarine. In general, the salinity in the study site does not have large annual fluctuations, so the characteristics of the ecosystem are uniform year round, with little change between the dry and rainy seasons. There is a small change during the dry season when salinity increases due to the currents coming from the northern part of the Gulf of Morrosquillo (INVEMAR, CARSUCRE, CVS 2002). The lowest salinities occur closer to the Sinú River delta and this seems to present an ecological barrier for Guiana dolphins because the presence of dolphins decreases towards the Sinú River delta.

#### **3.6.2.5 Sea conditions and time of day**

The effects of sea state (Beaufort) were strongly negative, as expected, showing that the detectability of dolphins decreased as Beaufort increased. Sea state has been shown to influence detection probability in previous studies of *S. guianensis* and other species (Palka 1995, Palka & Hammond 2001, Evans & Hammond 2004, Embling 2007, De O. Santos *et al.* 2010). As a protocol in field work with Guiana's dolphins, surveys should not be conducted with Beaufort levels higher than 2 (De O. Santos *et al.* 2010, Hammond *et al.* 2013). The study area is located in the “Zone of Intertropical Confluence“ (ZIC), influenced by the Caribbean Trade Winds, which define the two major climatic seasons: rainy and dry. The dry season is characterized by strong northerly winds which influence sea state (Molina *et al.* 1994). During this season there is also a common phenomenon called “mar de leva” caused by the entry into the Caribbean area of the polar front. This phenomenon produces high sea states especially during the months of January and February, sometimes March. It has a

duration of 48 hours and can be repeated during the same month up to four times (CIOH 2001). These characteristics made surveying during these months almost impossible in the study area.

Time of day was retained in all the models except for dolphins feeding but the relationships were not strong. The models showed a tendency for the dolphins to be present in the area in the afternoon hours, which is not consistent with the observed data in the study site (Avila 1995, Garcia 1998, Garcia & Trujillo 2004, Dussán-Duque *et al.* 2003, 2006, Dussán-Duque & Wells 2007). However, this result seems to be a good example of the ability of models to reveal tendencies that may be different to those indicated by the raw data themselves. The study area is characterised by an increase in Beaufort levels in the afternoon due to strong winds coming from the north of the gulf. Hence, it is possible that the dolphins are still present, but that their detectability by the observer is reduced except in areas protected from the wind like Cispatá Bay, and that this is the explanation for the model results.

### **3.6.2.6 Feeding**

Prey availability is a driving force in the distribution, movements, behaviour and habitat selection of predators (Halpin *et al.* 1988, Costa *et al.* 1989, Berstein *et al.* 1991 Eide *et al.* 2004). Foraging ecology, the way that an animal makes choices about prey, feeding areas, etc is one of the most complex areas of behavioural ecology (Krebs & Davies 1984, Begon *et al.* 2006). It is to be expected that, over time, predators acquire knowledge about their habitat and learn about the quality of each patch of prey, travel times between them, etc. Guiana dolphins should be no exception and should be expected to show selectivity in the choice of feeding habitats.

The presence/absence model used as a precursor to the model of feeding dolphins showed that seasonality seems to be an important factor in the habitat use of Guiana dolphins, which is supported very well by the observed data. Seasonality is very important in the estuarine ecosystem of the southern area of the Gulf of Morrosquillo, as in every other estuarine ecosystem (Rudnick *et al.* 1985, Withfield *et al.* 1999, Heidelberg *et al.* 2002). An estuarine ecosystem fauna, from plankton to ichthyofauna, changes markedly depending on the natural floods of the ecosystem, caused by the rainy season (Odum 1971). In Figure 3.3 it is possible to see how the Guiana dolphins use the study area differently depending on the season. For example, the southern and northern extremes of the study site represented by zones 4, 5 and 6 are mostly used during the rainy season. These are the areas closer to the Sinú River and

Ciénaga de la Caimanera (Figure 3.3). This may indicate a different distribution of prey patches, as is expected, during the dry and rainy season.

The model results show that the semi-dry season had a moderate negative effect on the presence of Guiana dolphins in the study area; an important difference from the dry season. As previously described, the semi-dry season is in the middle of rainy season (CIOH 2001), during which there is a change in the patterns of precipitation, which may change the distribution of the dolphins in the study site through changes in the distribution of their prey. As described in previous studies of *S. guianensis* (Avila 1995, Edwards & Schnell 2001, Dussán-Duque *et al.* 2003, 2006, Dussán-Duque & Wells 2007, Flach *et al.* 2008) and studies of other species (Parra 2006, Ingram *et al.* 2007, McCluskey *et al.* 2011, Vigness-Raposa *et al.* 2011, Malinowski *et al.* 2011), the distribution of marine mammals is influenced mainly by the distribution of their prey species.

In the model of dolphins feeding, there was a slightly non-linear increasing relationship between the number of feeding dolphins and depth (Figure 3.18). The selection by Guiana dolphins of areas of particular depths could be driven by the distribution of prey species in these areas (INVEMAR, CARSUCRE, CVS 2002). In other studies, this species has been shown to exhibit long-term high site fidelity for feeding areas in coastal estuarine waters (De O. Santos *et al.* 2001, De Freitas Azevedo *et al.* 2004, Rossi-Santos *et al.* 2007), indicating a feeding specialization for estuarine prey species. When mixed groups of *S. guianensis* and *T. truncatus* were present in the study area, *T. truncatus* was not usually feeding (Dussán-Duque & Wells 2007). There is a clear division based on prey size in the feeding areas and habitat use of these sympatric species (Dussán-Duque & Wells 2007). *S. guianensis* is a small dolphin (maximum length of males 1.80m (Rosas *et al.* 2010) specialized in catching small prey species such as: *Mugil* sp. (De O. Santos 2010), *Caranx crysos*, Engrulidae and Albulidae (Dussán-Duque & Wells 2007). These species are estuarine but also inhabit coastal waters. The estuarine waters of Cispata Bay represent a “nursery” for several species of fishes, molluscs and crustaceans in their larval and juvenile stages. The marine organisms present in this area take advantage of the sediments and detritus present in the roots of the mangroves. Several of these species are known to be prey of Guiana dolphins.

Model results showed that zone had a very strong effect on the number of feeding dolphins. The effect of zones 4 and 5 was negative indicating a lack of feeding in these zones. The

effect of zone 6 was strongly positive indicating a preference for feeding in this zone. Zone 6 was where the largest feeding aggregation of Guiana dolphins was seen in the study area.

Comparing these results with those of Avila's study in 1995, there has been a shift in the usage of zone 4 (zone 5 in his study), as reported previously by Dussán-Duque & Wells (2007). This change of usage in zone 4 seems to be related to the construction of a hydroelectric plant. As described in Chapter 2, the construction of the Urrá hydroelectric plant brought major changes in the ecological patterns of the study site. The natural hydrological cycles were changed and the normal inundations coming with the rainy season, as well as the dryness of certain areas during the dry season, were altered. There was anoxia in channels inside the bay (INVEMAR 2002) and also salinization of estuarine areas due to the water retention by the mangroves. The fishermen still cannot catch fish in places where they used to be abundant; instead they have to travel to places more distant from the coast (Dussán-Duque *personal communication*). It seems that Urrá hydroelectric plant changed the distribution of prey species, and with it the distribution of predators.

The effects of tide on the number of dolphins feeding were not strong, as shown by the lack of variation in the model coefficients among the different tidal states. In the study site, tides have a semidiurnal cycle with an average tidal range < 0.4m (CIOH 1994). The physical action of the tides in the southern area of the Gulf of Morrosquillo is very reduced and does not influence the marine currents (CIOH 1994). Receding and low tides had a negative effect on feeding dolphins, whilst high tide had a positive effect. This pattern is likely to have been influenced by diurnal movements of the dolphins' prey.

Group size varied from 1 to 60 individuals. The mean group size was nine individuals, which is typical for this species (Avila 1995, De O. Santos & Rosso, Dussán-Duque *et al.* 2003, 2006, Dussán-Duque & Wells 2007, 2007, Garcia 1998, Garcia & Trujillo 2004, Flores & Bazalo 2004, Rossi-Santos *et al.* 2010). Mean group sizes were found mainly in zones 2, 3 and 5, but they were predominantly found during the dry season in zone 3 during feeding events. The dry season in the Gulf of Morrosquillo is characterized by low waters, with minimal precipitation <50mm/month and minimal water flow of 100m<sup>3</sup>/sg (Molina *et al.* 1994); this may cause a different prey distribution in the study area during the dry season. The increase in mean group size in zone 3 during the dry season probably reflects a response to predation on larger concentrated patches of prey instead of more scattered smaller ones (Neumann 2001). Instead, during the rainy season the increase in precipitation changes the

flux of the water flow to 800m<sup>3</sup>/sg, and the waters are warmer due to a reduction in the winds and the Colombia-Panamá current has a bigger influence than the polar front (Andrade 2000). These changes in the ecosystem may produce a change in prey abundance and distribution, hence causing a change in group composition and maybe in feeding strategies (Chapter 6) in order to take advantage of the different conditions. Formation of larger groups of predators, in group hunters, is related to larger patches of prey. In these cases all the individuals involved in the event profit of group foraging and hunting. When the prey is distributed in small patches, it is probably more efficient for the dolphins to be distributed in small groups (Chapter 6) (Neumann 2001).

Feeding aggregations were not very common, which may be influenced by the prey being distributed in small patches (Neumann 2001). The zones that had the largest number of feeding aggregations were zones 2 and 3. There was equal number of feeding aggregations during the rainy and dry seasons. Solitary adult dolphins were only seen in zones 1 and 2 and only during the dry season. This may be due to an increase in foraging effort by individuals trying to find suitable prey (Bel'kovich *et al.* 1991). It seems that single dolphins use the habitat differently from groups.

Feeding strategies of mothers and calves are investigated in Chapter 6. It seems that females of Guiana dolphins teach their calves to fish in the mangroves roots present in very isolated and shallow waters of zone 1.

### **3.7. Conclusions and implications for conservation**

The principal goal of this chapter was to identify consistently important regions of distribution of *S. guianensis* in the southern area of the Gulf of Morrosquillo and to improve understanding of the eco-geographic relationships involved in the selection and use of this species' habitats. The models developed in the chapter indicate that the survey methods applied in this study were appropriate in capturing some of the environmental features involved in the daily decisions made by the individual Guiana dolphins in the study site. Some of these features may be proxies for other variables more difficult to measure in the field, which highlights the importance of the use of habitat modelling as a conservation and management tool (Cañadas & Hammond 2008, Matthiopoulos & Aarts 2010).

As expected, the habitat modelling results indicated that the distribution and habitat use of Guiana dolphins was influenced by both fixed and temporally varying environmental parameters in the study site. The most important of these fixed covariates were zone and depth. The temporally varying covariates highlighted by the models were time of day, seasonality and year, especially the last two years of the study. These results indicate that there are important patterns in the habitat use and selection of Guiana dolphins in the southern area of the Gulf of Morrosquillo.

Areas of high occurrence, as indicated by the models, such as zones 2, 3, 5 and 6, indicate habitat selection possibly driven mainly by prey distribution and these zones may encompass the feeding habitat use by this population in the southern area. There seems to be high site fidelity to these areas, especially for feeding, by all the different age groups of this species in the study site. Chapter 5 explores how this habitat selection and site fidelity is more pronounced in some individuals than in others. Chapter 6 investigates feeding strategies of individuals.

The zones highlighted by the models, within the range of all six available zones, suggest the importance of these areas for conservation. Clustering of the dolphins in some zones determined the importance of that specific habitat, thus informing the decisions to be made for the protection and conservation of this species and its core habitats in the southern area of the Gulf of Morrosquillo.

Cetacean habitat models can provide a finer spatial resolution than traditional abundance estimates (Guisan *et al.* 2002, Cañadas & Hammond 2008, Matthiopoulos & Aarts 2010). Through the modelling of feeding habitats in this study site, is possible to hypothesize that the distribution of the Guiana dolphins in the southern area of the gulf is driven by that of their prey species. The results indicate a correlation between dolphins' inshore distribution and the likely relative abundance of their prey. The results also show variability in group size, depending in seasonality, and possibly also driven by the patchiness of the prey. This indicates that altering the natural water cycles of an estuarine ecosystem can also alter the distribution and abundance of top predators, in this case the Guiana dolphins. One aspect not analysed during this study was the impact of the Urrá hydroelectric plant on the distribution of *T. truncatus*, but preliminary results show that is even bigger than that on *S. guianensis* (Dussán-Duque & Wells 2007). Comprehensive knowledge of the ecological factors which contribute to long-term persistence of the feeding grounds for both species is fundamental for

their conservation. The anthropogenic interactions present in the areas highlighted by the models as core areas for Guiana dolphins discussed in Chapter 7.

Through the results of this study, the Ministry of Environment in Colombia had recently approved the integration of the core and buffer areas of habitat usage of this species into the area of special management decreed by the same Ministry in the Gulf of Morroquillo in 2001 (INVEMAR, CVS, CARSUCRE 2002). Several interdisciplinary studies have been conducted with different species in this area of special management (MIZC). Previously there was a lack of information about the dolphin species using this area, but a management plan for these species has now been included as a result of this study.

The work presented in this chapter is the first attempt to explore habitat modelling as a tool to determine distributions and habitat use of marine mammal species in Colombia. As described in Chapter 1, *S. guianensis* is listed as “vulnerable” in Colombia and as “Data Deficient” by the IUCN. This highlights the importance of these results not only in Colombia, where they led to the creation of the Special Management Area in the southern area of the Gulf of Morroquillo but also to help the IUCN improve on its “Data Deficient” listing because there is now information on distribution and year round habitat use of this species from another area outside of Brazil.

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**Chapter 4 – Mark-recapture estimates of survival rates and  
seasonal abundance of the Guiana dolphins using the  
southern Gulf of Morrosquillo**



## 4.1. Introduction

Population dynamics is a central topic in ecology (e.g. Caughley 1977, Royama 1992, Tuljapurkar & Caswell 1997). It studies the fluctuations of populations through time (Royama 1992) with the aim of understanding the effects of intrinsic and extrinsic factors (Aars & Ims 2002). Population dynamics encompasses the study of the life history of individuals and populations through investigating how these intrinsic and extrinsic factors regulate reproduction and survival (e.g. Gaillard *et al.* 1989, Yoccoz & Ims 1999, Gaillard & Yoccoz 2003).

Marine mammals are long-lived animals (Mead & Potter 1990, Ford *et al.* 2002), with low reproductive rates (Perrin & Reilly 1984, Marsh & Kasuya 1986, Barlow 1990) and low mortality rates but with higher mortality rates during the first year(s) of life (Mann *et al.* 2000, Mann & Watson-Capps 2005). The study of marine mammal population dynamics is challenging due to the difficulties involved in monitoring wild populations through long-term studies. It is for this reason that the life histories of the majority of marine mammal species are still unknown. Furthermore, the natural dynamics of many cetacean populations have been affected, in some cases to a large extent, by anthropogenic pressures; e.g. whaling (Howton 1994 & Yablokov 2000), by-catch in fisheries (Read *et al.* 2006) and contaminants (Endo *et al.* 2003, Aguilar *et al.* 2002). Our lack of knowledge of how marine mammal populations are likely to respond to natural or anthropogenic changes in the environment hampers our ability to make accurate decisions about the conservation and management of populations. Although such lack of knowledge of life histories is not necessarily the cause of conservation failures, for example in the cases of the Baiji (*Lipotes vexillifer*) (Zhang *et al.* 2003) and the vaquita (e.g. D'agrosa *et al.* 2000 and Jaramillo-Legorreta *et al.* 2007), the chances of successful conservation are greatly enhanced if we have a solid understanding of species population dynamics.

Mark-recapture studies have been widely conducted on many species of animal to learn about their population dynamics (e.g. Kareiva 1983, Hestbeck *et al.* 1991, Mowat & Strobeck 2000)

and such studies have increasingly been conducted on marine mammal species including cetaceans, pinnipeds and sirenians (e.g. Hammond *et al.* 1990, Pomeroy *et al.* 1994, Flores 1999, Langtimm *et al.* 2004). Survival rates have been estimated through mark-recapture methods for several species of marine mammal (e.g. Langtimm *et al.* 2004, Larsen & Hammond 2004, Mizroch *et al.* 2004, Hernández-Camacho *et al.* 2008, Silva *et al.* 2009, Ramp *et al.* 2010, Cantor *et al.* 2012).

In recent decades anthropogenic factors have affected several species of marine mammals and their habitats, and population numbers have decreased, apparently in response (e.g. Currey *et al.* 2007, Reeves *et al.* 2003). Knowledge of abundance in marine mammal species is a key factor in order to evaluate the conservation status of the populations, and therefore to develop accurate guidelines for their management and conservation. Mark-recapture methods have been used in order to assess the abundance of several marine mammal species, and have proven to be an effective method to do so (e.g. Hammond *et al.* 1990, Flores 1999, Calambokidis *et al.* 2004, Langtimm *et al.* 2004, Fruet *et al.* 2011, Reisinger *et al.* 2011, Cantor *et al.* 2012).

Mark-recapture methods require individuals to be recognized and a variety of identification methods have been used for different marine mammal species in order to study the life history parameters of populations through time (Loughlin *et al.* 2010). Photo-identification is now probably the most widely used method and has proved to be a highly valuable tool for studying the population dynamics of the cetacean species (Hammond 1990, Hammond *et al.* 1990, Wells & Scott 1990, Würsig & Jefferson 1990).

As described in Chapter 1, *S. guianensis* is listed as “vulnerable” in Colombia and as “Data Deficient” by the IUCN. Guiana dolphins are coastal and express strong patterns of long term residency (Chapter 5) and site fidelity especially to feeding habitats (Chapter 3). These characteristics of the species make it appropriate for longitudinal studies (Baker *et al.* 2010), which are necessary because of the estimated longevity of this Genus of approximate 43 years (Rosas *et al.* 2010). Several long-term studies have been conducted on Guiana dolphins in Brazil but only one of them explores the population dynamics of the species (Cantor *et al.* 2012).

This study presents results from the longest ongoing research with Guiana dolphins in Colombia and this chapter analyzes the photo-identification data taken during a seven year period in the southern area of the Gulf of Morrosquillo. Through mark-recapture analysis of these data, two elements of the population dynamics of this species are investigated: annual survival rates and seasonal abundance. The new results from this study will inform its conservation status in Colombia.

## **4.2. Aim and objectives of the Chapter**

### **4.2.1. General aim**

To estimate, through mark-recapture techniques, the survival rate and seasonal abundance of the *S. guianensis* population that uses the southern area of the Gulf of Morrosquillo.

### **4.2.2. Objectives**

- Estimate the survival rate of the Guiana dolphin population using the study area.
- Compare the survival rate estimated from this area with previous studies conducted with the same species and other cetacean species worldwide.
- Estimate the seasonal abundance of the individuals using the study site and identify possible trends.

## **4.3. Materials and Methods**

General survey and data collection methods are described in Chapter 2.

From 2002-2006 and 2009-2010, 395 boat surveys were conducted in the study area that covers approximately 310 km<sup>2</sup> (Figure 3.2). The survey effort was conducted for continuous

periods of a minimum of one month to up to five months. A calendar day was selected as the sampling unit for mark-recapture analyses to estimate abundance within seasons. A year was selected as the sampling unit for estimating survival rates. The aim of surveying during continuous periods of time was to ensure as far as possible that different individuals had an equal probability of being captured within years (Hammond 2009, Baker *et al.* 2010).

Sighting effort was distributed evenly throughout the study site according to the methodology used for Chapter 3 (habitat modelling). Due to the small size of the study site, variation in the probability of being captured during a sampling occasion was minimized (Hammond 2009).

Nonetheless, accomplishing equal probability of capture in each sampling occasion is typically almost impossible (Hammond 2009). For example, studies conducted on various species of marine mammals show that sighting probability is not equal for animals of different age and sex within the population classes (e.g. Wells & Scott 1990, Heppell *et al.*, 2000, Gaspar 2003, Young & Keith 2011). Therefore, even though attempts were made to minimize this in the field, models that allowed for heterogeneity of capture probabilities were explored during data analysis (see below). Notwithstanding this, Carothers (1973) and Gilbert (1973) showed that heterogeneity of capture probabilities becomes relatively unimportant when the average capture probability is high.

#### **4.3.1. Photographic sampling**

An average of 188 photographs was taken per survey day, but pictures were not taken during every sighting because of poor weather conditions. In total, 74,226 photographs of Guiana dolphins' dorsal fin marks were taken for photo-identification (Flores 1999, Wells 2002, Hammond 2009, 2010) during 318 sightings.

An equal effort was made to “capture” the fins of every individual present during a sighting. In any case, it is not possible to recognize individuals of this species in the field, even through the camera lens, at least in this study area. As many pictures as possible of the individuals present were taken during every sighting until the individual or group decided to move to another area. For every encounter the group size was recorded (number of adults and number of calves).

Photographs were graded based on the resolution and focus of the image and the angle of the animal relative to the camera lens. Only good quality pictures of adult individuals with permanent marks on the dorsal fin or body were included in analysis in order to reduce potential biases in estimates resulting from errors in matching photographs of individuals (Hammond *et al.* 1990, Wells 2002). Calves were not included in the analysis because they were either unmarked or insufficiently marked for them to be recognized in a future photograph.

### 4.3.2. Individual identification

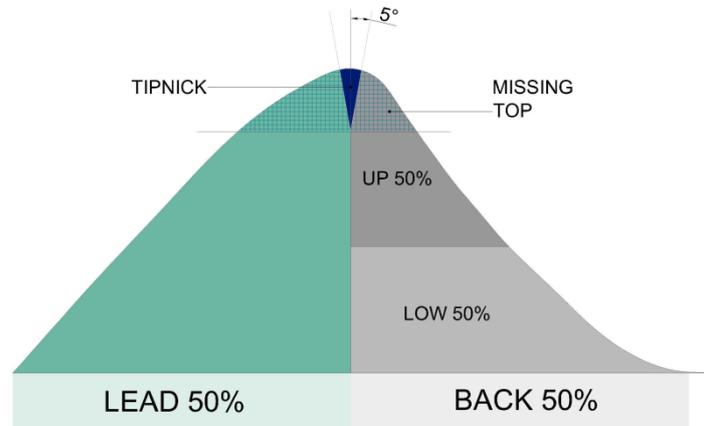
The marks used to identify individual dolphins were: nicks and notches and unusual shapes of the dorsal fin (Figure 4.1).



**Figure 4.1-** Photographs of Guiana dolphins from the study site showing examples of the dorsal fin marks used to identified individuals. *Photographs by Salomé Dussán-Duque.*

The protocol developed by the Sarasota Dolphin Research Program designed to be used in the photo-identification and cataloguing process of *T. truncatus* was initially used to identify and catalogue individuals of *S. guianensis*. However, differences in the size and shape of the dorsal fins between these two species created problems in following this protocol. Dorsal fins of the Guiana dolphins individuals are half of the size of that one's of *T. truncatus* and less falcate. Following this protocol led to false positive matching of some individuals and thus violating one of the assumptions of mark re-capture methodology (Hammond 2009).

Therefore, based on the guidelines of the matching protocol of the Sarasota Dolphin Research Program, a specific protocol for *S. guianensis* was created for dorsal fin photo-identification, using divisions of the dorsal fin shown in Figure 4.2.



**Figure 4.2-** *S. guianensis* dorsal fin schematic with the divisions for the different categories. Each dorsal fin photograph was categorized according to the following key:

<b>Key:</b>	<b>Category</b>
1. a. The most prominent feature is located on the dorsal fin .....2	
b. The most prominent feature is located on the body	<b>Diverse</b>
2. a. Dorsal fin is intact, with usual shape.....3	
b. Dorsal fin is not intact or does not have usual shape.....A	
A. Fin has a notch, nick or slice in the leading edge	<b>Lead</b>
B. Fin is cut off, top or tip of fin is missing	<b>Missing Top</b>
C. Fin is bent	<b>Left/Right Bend</b>
3. a. Dorsal fin has a scarring, pigmentation pattern, wound	<b>Scarring</b>
b. Dorsal fin does not have scarring.....4	
4. a. Tip of dorsal fin has a distinctive mark	<b>Tipnick</b>
b. Fin has a prominent feature on trailing edge below the tip..A	
A. Equally distinctive features in up/low area of the fin	<b>Entire</b>
B. Distinctive features in upper (50%) area of fin	<b>Up</b>
C. Distinctive features in lower (50%) area of fin	<b>Low</b>
D. Extended tip, the fin tip extends past trailing edge	<b>Extended Tip</b>

This key was used to categorize photographs of dorsal fins in a catalogue and database of individual animals. The photographic database was updated regularly to prevent the loss of identities and false marking of the individuals. Due to the small size of the catalogue, a computer matching program was not used for matching. Instead, every picture was analysed visually, and the matching was conducted through visual comparison of the photographs using Adobe Photoshop CS6.

Following this protocol, a catalogue of 98 well-marked adult individuals was created.

For each marked dolphin a capture history was produced in two different ways: one to be used in the analysis of annual survival rates (Figure 4.3), and a second one to be used for the seasonal abundance analysis (Figure 4.4). A capture history compilation is a row of 1s and 0s, that indicates if the animal was seen or “captured” (1) or not seen or “not captured” (0); annually for survival rates and daily for abundance. This is further explained in the following sub-sections.

### **4.3.3 Estimation of annual survival rates**

For the estimation of survival rate, a year was selected as the sampling unit.

The annual survival rate of adult Guiana dolphins using the southern area of the Gulf of Morrosquillo from 2002-2006 and 2009-2010 was estimated using seven years of capture histories of the 98 sampled individuals (Figure 4.3).

The Cormack-Jolly-Seber (CJS) survival model estimator was used to estimate annual survival rate (Cormack 1964, Jolly 1965 and Seber 1965) implemented in Program MARK (White & Burnham 1999). CJS survival estimation uses maximum likelihood estimation (MLE) (Baker *et al.* 2010) to estimate the parameters of a statistical model (Seber 1973). The CJS model makes the following assumptions (Pollock *et al.* 1990):

- Every animal present in the population at the time of the sampling occasion has the same probability of recapture ( $p$ ).

- Every mark animal present in the population immediately after the sample occasion has the same probability of survival ( $\phi$ ) until the next sample occasion.
- Marks are not lost or overlooked.
- All marking is instantaneous and each animal is released immediately after sampling.

The CJS model is unable to distinguish between death and permanent emigration so the estimated parameter of interest is usually referred to as apparent survival rate ( $\phi$ ). Also estimated is the average probability of recapture ( $p$ ) of individuals within each sampling occasion (Hammond 2009, Baker *et al.* 2010).

#### **4.3.3.1 Model fitting and selection**

Models were fitted to the annual recapture histories in program MARK to investigate whether the data supported the estimation of apparent survival rates that were time dependent  $\phi(t)$  or constant over time  $\phi(.)$ . Similarly, models investigated whether recapture probabilities were constant  $p(.)$  or time dependent  $p(t)$ .

There was a 3 year gap in the data between 2006 and 2009 (Table 4.3); this was taken into account in analysis.

The “best” model was selected based on Akaike’s Information Criterion for small sample sizes (AICc) (Akaike 1973). A description of AICc is given in Chapter 3. Models with a difference in AICc (delta-AICc) of less than 2 have effectively the same support from the data. If delta-AICc is greater than 2, the model with the lower AICc has more support from the data.

ID	2002	2003	2004	2005	2006	2009	2010
1			0			0	
2							0
3		0	0			0	0
4	0		0	0			
5		0		0	0	0	0
6	0		0	0	0	0	0
7	0			0			0
8	0		0	0	0	0	0
9	0		0	0		0	0
10	0					0	0
11	0					0	
12	0			0			
13	0						
14	0		0	0		0	0
15	0			0			
16	0					0	
17	0			0			
18	0						
19	0	0				0	0
20	0	0		0	0	0	0
21	0	0		0	0	0	0
22	0	0					
23	0	0		0		0	0
24	0	0		0	0	0	0
25	0	0		0	0		0
26	0	0		0		0	0
27	0	0				0	
28	0	0		0		0	0
29	0	0		0	0		0
30	0	0		0	0	0	0
31	0	0		0	0	0	0
32	0	0		0			
33	0	0					
34	0	0		0	0	0	0
35	0	0		0		0	0
36	0	0					
37	0	0		0			0
38	0	0		0		0	0
39	0	0				0	0
40	0	0		0		0	0
41	0	0		0	0	0	0
42	0	0		0	0	0	0
43	0	0		0		0	0
44	0	0					
45	0	0		0	0	0	0
46	0	0		0	0	0	0
47	0	0		0			0
48	0	0		0		0	0
49	0	0				0	
50	0	0					
51		0	0			0	0
52	0	0		0	0	0	0
53	0	0					0
54	0	0					0
55	0	0			0	0	0
56	0	0	0	0	0	0	
57	0	0					
58	0	0		0		0	0
59	0	0		0		0	0
60	0	0					0
61	0	0	0			0	0
62	0	0	0		0	0	0
63	0	0	0			0	
64	0	0	0			0	0
65	0	0	0		0	0	0
66	0	0	0		0	0	0
67	0	0	0				
68	0	0					0
69	0	0	0			0	0
70	0	0	0				0
71	0	0	0			0	0
72	0	0	0				0
73	0	0	0		0	0	0
74	0	0	0				0
75	0	0	0		0	0	0
76	0	0	0			0	0
77	0	0	0				
78	0	0	0		0	0	0
79	0	0	0		0	0	0
80	0	0	0			0	0
81	0	0	0	0			
82	0	0	0	0			
83	0	0	0	0	0		
84	0	0	0	0		0	
85	0	0	0	0	0		
86	0	0	0	0		0	
87	0	0	0	0			
88	0	0	0	0	0	0	
89	0	0	0	0	0		
90	0	0	0	0		0	
91	0	0	0	0		0	
92	0	0	0	0		0	
93	0	0	0	0			
94	0	0	0	0	0		0
95	0	0	0	0			0
96	0	0	0	0		0	0
97	0	0	0	0			
98	0	0	0	0	0		

Figure 4.3- Annual capture histories of 98 identified adults from the southern area of the Gulf of Morrosquillo from 2002-2006 and 2009-2010. Black represents the capture of a dolphin in that specific year.

#### 4.3.4 Seasonal abundance

There are three climatic seasons in the gulf of Morrosquillo: dry (December to April), semi-dry (July) and rainy (May to June and August to November) (Patiño-Corredor *et al.*1993). Because the semi-dry season is a single month in the middle of the rainy season, it was included in the rainy season for analysis in order to have continuity in the data. As previously mentioned, for the estimation of annual seasonal abundance during the dry and rainy seasons, a calendar day was selected as the sampling unit (Table 4.1).

**Table 4.1- Annual sampling occasions (days) in the Gulf of Morrosquillo during the two climatic seasons from 2002-2006 and 2009-2010.**

<u>Year</u>	<u>Dry season</u>	<u>Rainy season</u>
2002	0	2
2003	2	9
2004	17	14
2005	0	13
2006	0	10
2009	11	15
2010	15	8

In mark-recapture analyses, the estimate of abundance obtained is the number of animals using the study site during the study period (Hammond 2010). The annual seasonal abundance of adult Guiana dolphins using the southern area of the Gulf of Morrosquillo from 2002-2006 and 2009-2010 was estimated using seven years of capture histories of the 98 sampled individuals (Figure 4.4).

ID	R02	D03	R03	D04	R04	R05	R06	D09	R09	D10	R10
1	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0	0	0	0	0
25	0	0	0	0	0	0	0	0	0	0	0
26	0	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0	0	0	0	0
32	0	0	0	0	0	0	0	0	0	0	0
33	0	0	0	0	0	0	0	0	0	0	0
34	0	0	0	0	0	0	0	0	0	0	0
35	0	0	0	0	0	0	0	0	0	0	0
36	0	0	0	0	0	0	0	0	0	0	0
37	0	0	0	0	0	0	0	0	0	0	0
38	0	0	0	0	0	0	0	0	0	0	0
39	0	0	0	0	0	0	0	0	0	0	0
40	0	0	0	0	0	0	0	0	0	0	0
41	0	0	0	0	0	0	0	0	0	0	0
42	0	0	0	0	0	0	0	0	0	0	0
43	0	0	0	0	0	0	0	0	0	0	0
44	0	0	0	0	0	0	0	0	0	0	0
45	0	0	0	0	0	0	0	0	0	0	0
46	0	0	0	0	0	0	0	0	0	0	0
47	0	0	0	0	0	0	0	0	0	0	0
48	0	0	0	0	0	0	0	0	0	0	0
49	0	0	0	0	0	0	0	0	0	0	0

ID	R02	D03	R03	D04	R04	R05	R06	D09	R09	D10	R10
50	0	0	0	0				0	0	0	
51		0	0	0	0			0	0	0	0
52	0	0	0	0		0	0	0	0	0	0
53	0	0	0	0				0		0	0
54	0	0	0	0			0	0	0	0	0
55	0	0	0	0			0		0	0	0
56	0	0	0	0	0	0	0	0	0		0
57	0	0	0	0			0			0	
58	0	0	0	0		0	0	0	0	0	0
59	0	0	0	0		0	0	0	0	0	0
60	0	0	0	0				0	0		0
61	0	0	0	0	0		0	0	0	0	0
62	0	0	0	0	0		0	0	0	0	0
63	0	0	0	0	0		0	0	0	0	
64	0	0	0	0	0		0	0	0	0	0
65	0	0	0	0	0		0	0	0	0	0
66	0	0	0	0	0		0	0	0	0	0
67	0	0	0	0	0		0		0		0
68	0	0	0	0						0	0
69	0	0	0	0	0		0	0	0	0	0
70	0	0	0	0	0				0	0	0
71	0	0	0	0	0		0	0	0	0	0
72	0	0	0	0	0		0	0	0	0	0
73	0	0	0	0	0		0	0	0		0
74	0	0	0	0	0			0	0	0	0
75	0	0	0	0	0		0	0	0	0	0
76	0	0	0	0	0		0		0	0	0
77	0	0	0	0	0		0			0	
78	0	0	0	0	0		0	0	0	0	0
79	0	0	0	0	0				0	0	0
80	0	0	0	0	0			0	0	0	0
81	0	0	0	0	0	0	0				
82	0	0	0	0	0	0	0	0	0	0	0
83	0	0	0	0	0	0	0	0			
84	0	0	0	0	0	0	0	0	0		
85	0	0	0	0	0	0	0		0	0	
86	0	0	0	0	0	0	0	0			
87	0	0	0	0	0	0	0		0	0	
88	0	0	0	0	0	0	0	0	0		0
89	0	0	0	0	0	0	0				0
90	0	0	0	0	0	0	0		0		0
91	0	0	0	0	0	0	0	0			0
92	0	0	0	0	0	0	0	0			0
93	0	0	0	0	0	0	0	0	0		
94	0	0	0	0	0	0	0			0	
95	0	0	0	0	0	0	0			0	
96	0	0	0	0	0	0		0	0	0	0
97	0	0	0	0	0	0	0		0	0	
98	0	0	0	0	0	0	0				

Figure 4.4- Seasonal capture histories of 98 identified adults from the southern area of the Gulf of Morrosquillo from 2002-2006 and 2009-2010. Blue colour represents the rainy seasons (R) and the red ones the dry seasons (D) in that specific year.

For these analyses, it was determined that the length of a season was short enough for births, deaths and permanent immigrations and emigrations to be ignored. Additionally, there was enough time between the sampling occasions (days) for the dolphins to mix in the study area (Hammond 2010). Hence, multi-sample closed population models (Pollock 1991) in program CAPTURE (Otis *et al.* 1978) were used to analyze the seasonal capture histories of the marked individuals (Pollock *et al.* 1990, Hammond 2010). Data analysis is more flexible when working with closed population models than with open models. The different models implemented in program CAPTURE differ in the way that capture probability is modelled allowing three sources of variation in capture probabilities: individual heterogeneity, trap response, and temporal variation among sampling periods (Pollock *et al.* 1990).

#### **4.3.4.1 Model fitting and selection**

Not having heterogeneity in the capture probabilities of the animals sampled is difficult to achieve with marine mammal populations. Heterogeneity can be caused by factors such as the size of the study area (Hammond 2010), and habitat preferences and site fidelity of specific individuals within the population (Chapters 3 and 5). Trap response models were not considered for this analysis because the data used were obtained through photo-identification.

For the rainy season in 2002, there were only two sampling occasions (Table 4.1) and the sample size was very small so it was not possible to estimate abundance for this dataset.

For the rest of the datasets (Table 4.1) four models were implemented that allowed capture probability ( $p$ ) to vary in different ways: the equal catchability model  $M(o)$ , the heterogeneity model  $M(h)$  (Chao *et al.* 1992), the time dependent model  $M(t)$  (Darroch 1958), and the time dependent and individual heterogeneity model  $M(th)$  (Chao *et al.* 1992).

The results of the goodness of fit tests conducted in program CAPTURE were used to select the most appropriate models.

#### **4.3.4.2 Proportion of marked animals in the population**

The mark-recapture analyses estimate the number of well-marked animals in the population.

To obtain estimates of the total population, these estimates must be corrected by the proportion of well-marked animals in the population.

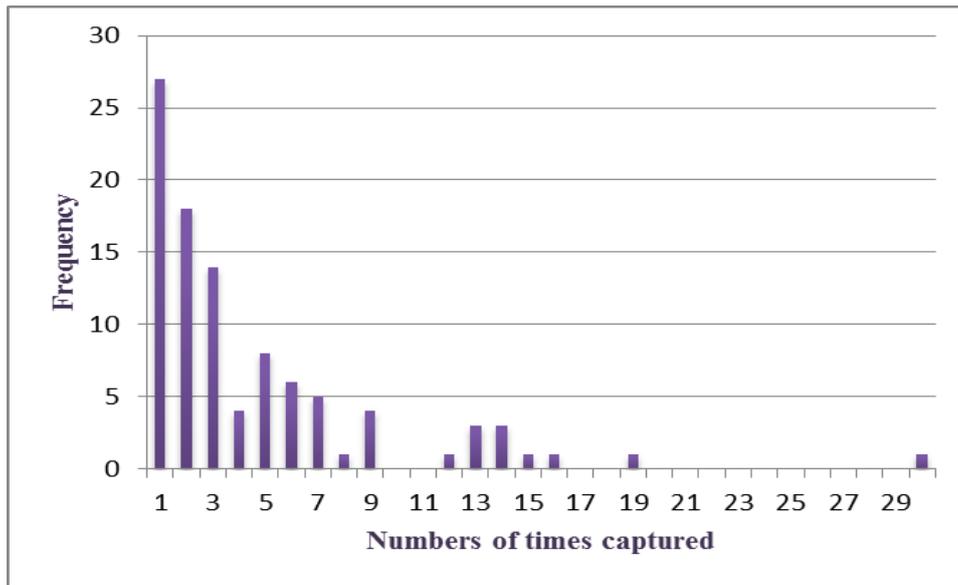
Generalized Linear Models (GLMs) with a binomial error structure, and a logit link function (Chapter 3) were fitted in software R 2.15.2 (R Development Core Team 2012) to estimate the proportion of well-marked animals in the population. A first model assumed that the proportion of well-marked individuals using the southern area of the Gulf of Morrosquillo did not change by year. A second model included year as a factor to estimate annual proportions by year. The best model was chosen based on the Akaike's Information Criterion (AIC) (Akaike 1973). The best-fitting model was run with a quasi-binomial error structure, and a logit link function to check for over-dispersion in the data.

#### **4.3.4.3 Estimates of total abundance**

Total abundance per season and year was estimated by dividing the estimates of well-marked dolphins from the selected mark-recapture models by the proportion of well-marked animals in the population (see Wilson *et al.* 1999). Estimation of the standard errors of these estimates was based on the delta method (Seber 1973). 95% confidence intervals of total abundance were calculated assuming that the estimates were log-normally distributed (Buckland *et al.* 2001).

## **4.4. Results**

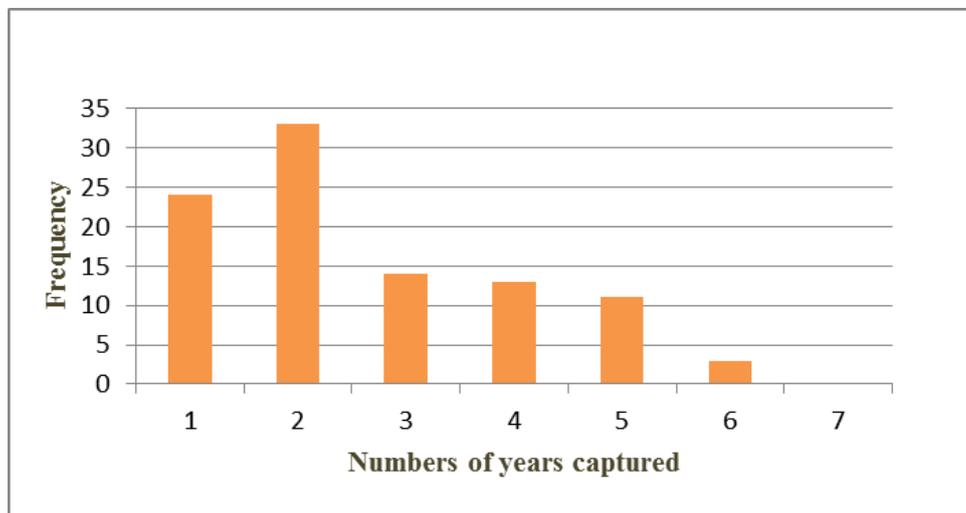
A total of 98 well-marked adults using the southern area of the Gulf of Morrosquillo were identified between 2002-2006 and 2009-2010. Some well-marked dolphins were captured in six of the seven years showing long term residency within the study site (Chapter 5) (Figure 4.3). The daily capture frequency of these dolphins was highly variable indicating heterogeneity of capture probability in the population (Figure 4.5). The presence of marked dolphins in the study site varied from one up to five continuous days, indicating high site fidelity of some of the animals (Chapter 5).



**Figure 4.5-** Capture frequency of the well-marked dolphins using the southern area of the Gulf of Morrosquillo from 2002-2006 and 2009-2010.

#### 4.4.1 Annual survival rates

Figure 4.6 shows the annual capture frequency of the well-marked dolphins.



**Figure 4.6-** Annual capture frequency of the well-marked dolphins using the southern area of the Gulf of Morrosquillo from 2002-2006 and 2009-2010.

Table 4.3 shows the diagnostics for all the models fitted. The best-fitting models were a fully time dependent CJS model (Model 1) and a CJS model with constant survival rate but time varying recapture probability (Model 2). The delta-AICc between these models was less than

2, so both can be considered to have equal support from the data. Models 3 and 4 had no support from the data.

Table 4.4 shows the parameter estimates for Model 1. Two of the annual survival rate parameters have hit their upper bound of 1.0 and were not estimated and the other three were estimated at less than 0.9. The estimated recapture probabilities are high but variable, reflecting the different number of animals seen in different years (Figure 4.3).

Table 4.5 shows the parameter estimates for Model 2. The constant annual survival rate is estimated at 0.948 (95% CI = 0.876-0.980). The estimates of recapture probability are similar to Model 1 but are lower in 2009 and 2010.

Models 1 and 2 have equivalent support from the data. The unrealistic variability in the time-dependent survival rate estimates in Model 1 make Model 2 a more appropriate description of the data and Model 2 is therefore considered the best model of survival rate for Guiana dolphins in the southern Gulf of Morrosquillo.

**Table 4.3- Cormack-Jolly-Seber (CJS) candidate models for apparent survival ( $\phi$ ) and recapture probability ( $p$ ) ranked by AICc. Model notation: constant parameter (.), time dependent (t).**

<b>Model</b>	<b>AICc</b>	<b><math>\Delta</math> AICc</b>	<b>AICc Weight</b>	<b>Number of parameters</b>	<b>Model deviance</b>
<b>1</b> {CJS $\phi$ (t) $p$ (t)}	438.95	0	0.643	9	94.16
<b>2</b> {CJS $\phi$ (.) $p$ (t)}	440.13	1.18	0.357	7	99.62
<b>3</b> {CJS $\phi$ (t) $p$ (.)}	460.64	21.7	0	6	122.25
<b>4</b> {CJS $\phi$ (.) $p$ (.)}	497.96	59	0	2	167.85

**Table 4.4- Summary results for Model 1: {CJS  $\phi(t)$   $p(t)$ }. Full time-dependent Cormack-Jolly-Seber model for survival rate,  $\phi(t)$  and recapture probability,  $p(t)$ .**

Parameter	Estimate	SE	95% Confidence Interval	
			Lower	Upper
$\phi$ 2002-03	1.000	-	-	-
$\phi$ 2003-04	0.892	0.046	0.764	0.955
$\phi$ 2004-05	1.000	-	-	-
$\phi$ 2005-06	0.885	0.165	0.243	0.995
$\phi$ 2006-09	0.779	0.149	0.392	0.951
$p$ 2003	0.667	0.079	0.500	0.800
$p$ 2004	0.945	0.038	0.806	0.986
$p$ 2005	0.489	0.059	0.376	0.604
$p$ 2006	0.597	0.123	0.352	0.802
$p$ 2009	0.368	0.214	0.088	0.779

**Table 4.5- Summary results for Model 2: {CJS  $\phi(\cdot)$   $p(t)$ }. Cormack-Jolly-Seber model for constant survival rate  $\phi(\cdot)$  and time-dependent recapture probability,  $p(t)$ .**

Parameter	Estimate	SE	95% Confidence Interval	
			Lower	Upper
1: $\phi$	0.948	0.024	0.876	0.980
2: $p$ 2003	0.680	0.079	0.511	0.813
3: $p$ 2004	0.932	0.045	0.773	0.982
4: $p$ 2005	0.506	0.063	0.385	0.627
5: $p$ 2006	0.575	0.067	0.442	0.698
6: $p$ 2009	0.198	0.054	0.113	0.325
7: $p$ 2010	0.073	0.033	0.029	0.170

#### 4.4.2 Seasonal abundance

Figures 4.7 to 4.12 show the capture frequencies of all the datasets used to estimate seasonal abundance. In some datasets there is evidence of individual heterogeneity of capture probabilities.

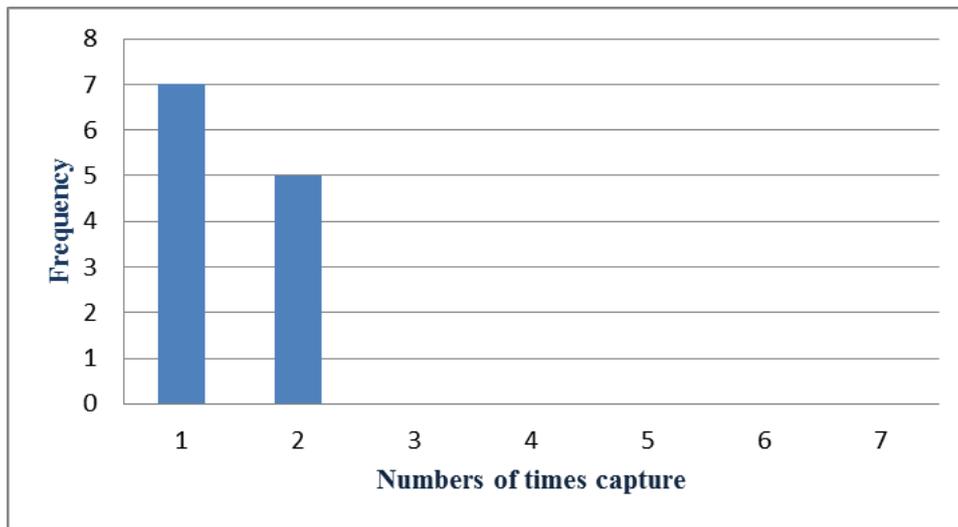


Figure 4.7- Rainy season 2003 capture frequency of well-marked dolphins using the study area.

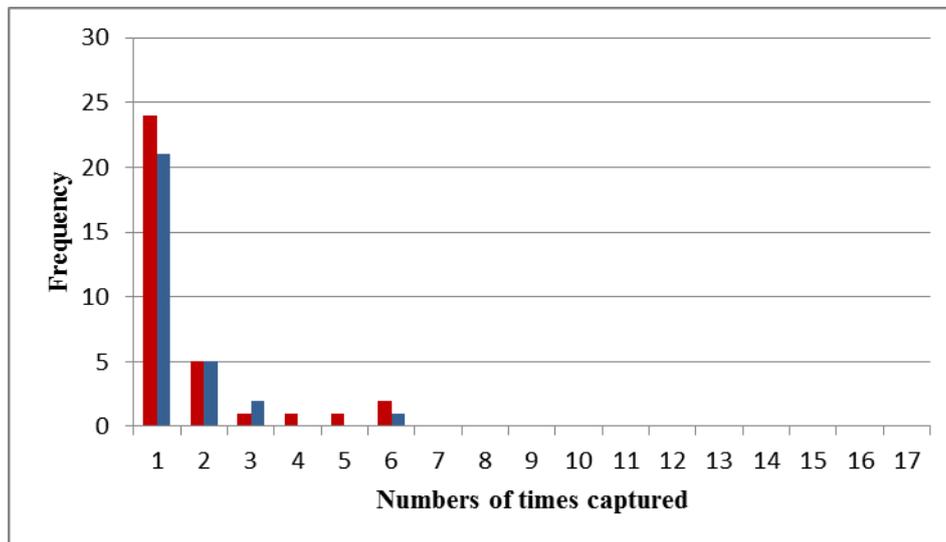


Figure 4.8- Capture frequency of well-marked dolphins using the study area in 2004. Red bars indicate the capture frequency during dry season. Blue bars indicate the capture frequency during rainy season.

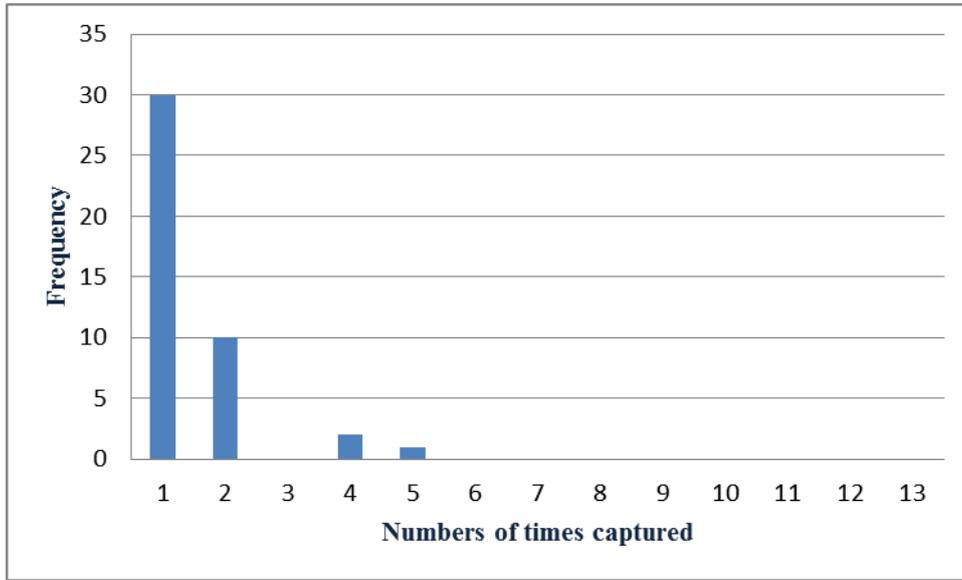


Figure 4.9- Rainy season 2005 capture frequency of well-marked dolphins using the study area.

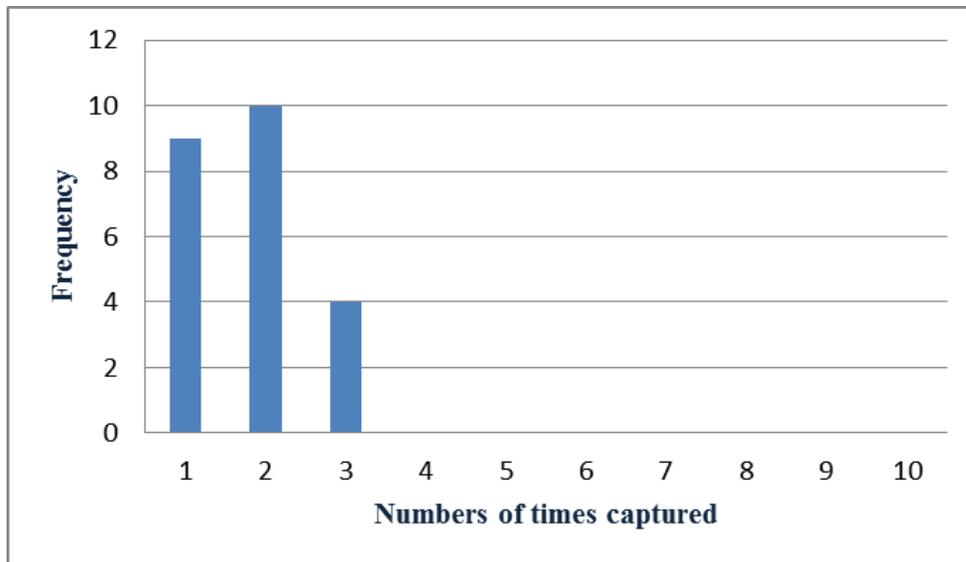
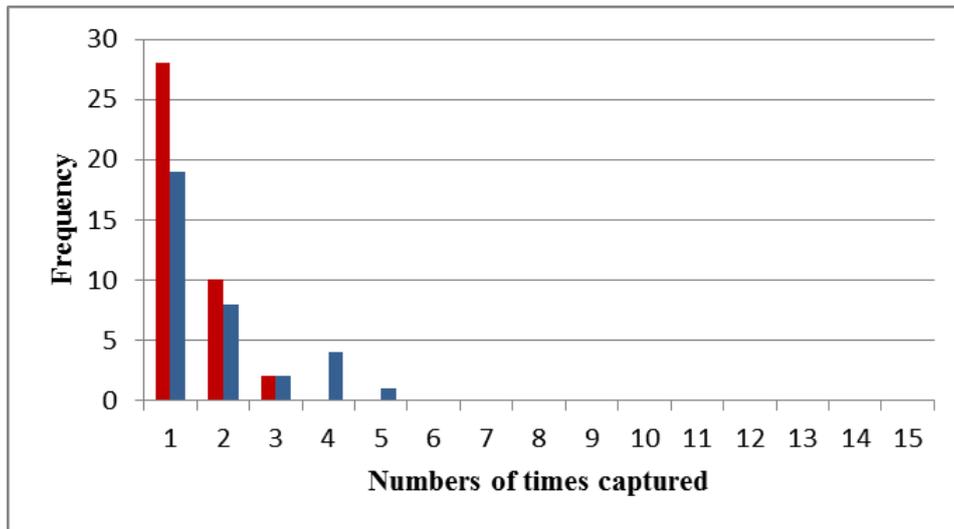
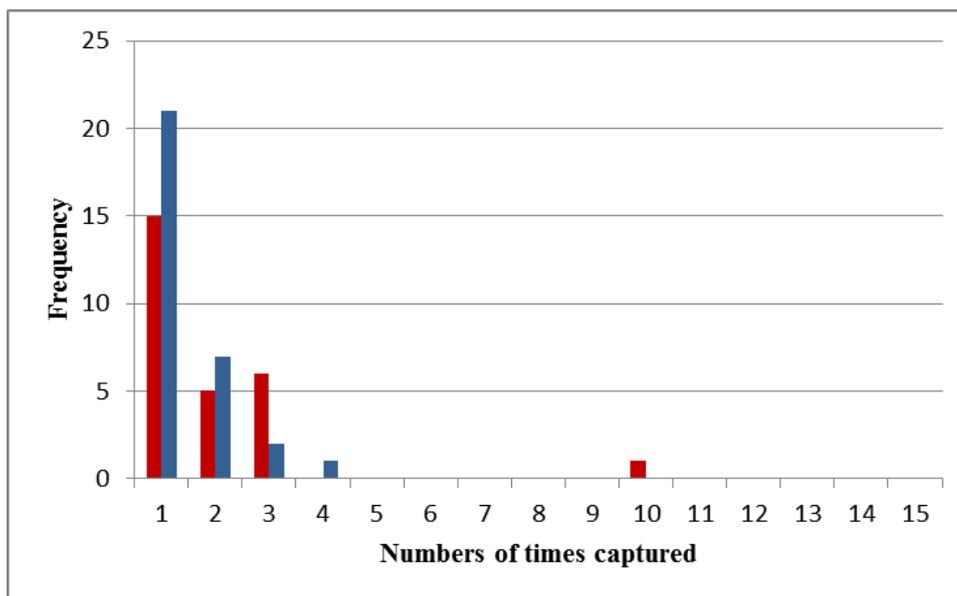


Figure 4.10- Rainy season 2006 capture frequency of well-marked dolphins using the study area.



**Figure 4.11-** Capture frequency of well-marked dolphins using the study area in 2009. Red bars indicate the capture frequency during dry season. Blue bars indicate the capture frequency during rainy season.



**Figure 4.12-** Capture frequency of well-marked dolphins using the study area in 2010. Red bars indicate the capture frequency during dry season. Blue bars indicate the capture frequency during rainy season.

Table 4.6 shows the results for the selected models fitted to the seasonal datasets. The best fitting models were the ones that incorporated individual heterogeneity in the probability of capture ( $p$ ), except in the dry season of 2009 where the difference in the estimates is  $<5$ .

**Table 4.6- Multi-sampled closed population models results for the seasonal abundance in each year. n = total number of identified dolphins. For each season/year, the first model is the best model without heterogeneity of capture probabilities and the second model is the best model including heterogeneity. \* indicates the best model for each season/year. Where both models are indicated with a \*, both models were equally well-fitting.**

Season	Year	Days	n	Model	N	SE	95% CI	Model	N	SE	95% CI
Dry	2004	17	34	M(o)	46	5.9	39-63	M(th)*	104	36.2	61-215
Dry	2009	11	40	M(t)*	73	14.0	55-113	M(th)	78	19.9	55-139
Dry	2010	15	27	M(t)	31	2.5	27-38	M(th)*	60	18.9	39-120
Rainy	2003	9	12	M(o)*	19	6.0	14-41	M(h)*	16	3.6	13-30
Rainy	2004	14	29	M(o)*	47	8.8	37-73	M(h)*	73	28.3	43-168
Rainy	2005	13	43	M(o)*	71	11.3	57-103	M(h)*	88	22.7	61-157
Rainy	2006	10	23	M(o)*	29	3.8	25-41	M(h)*	27	3.6	24-41
Rainy	2009	15	34	M(o)*	43	4.7	38-57	M(h)*	57	13.9	42-102
Rainy	2010	8	31	M(t)	48	8.4	39-73	M(th)*	62	18.3	42-121

The results in Table 4.6 show that in all seasons except one the model that accounts for heterogeneity of capture probabilities is either the best- or equal best-fitting model. In the dry season in 2009, the model without heterogeneity of capture probabilities is the best-fitting model but the estimates are almost the same from both models. Accordingly, for consistency, models accounting for heterogeneity of capture probabilities were chosen as the best models for estimating the number of well-marked animals.

Table 4.7 shows the total population abundance estimates, corrected for the proportion of well-marked animals in each year, for the dolphins using the study area in different seasons and years. The model including year as a factor best predicted the proportion of well-marked animals. The quasi-binomial model showed little evidence for over-dispersion (variance: mean ratio < 2).

The estimated number of dolphins using the study area varies among the years but there is little evidence for either a seasonal difference in abundance or any directional trend in time. In 2004 and 2009 the dry season estimates are higher than the rainy season estimates, but the

wide 95% confidence intervals indicate that there is no real evidence for seasonal variation in abundance.

In 2010, the estimates from the dry (225; CV = 0.34; 95% CI = 118-426) and rainy (232; CV = 0.32; 95% CI = 127-246) season are almost the same. These are the most recent estimates and are therefore the best estimates of the size of the population of Guiana dolphins in the southern area of the Gulf of Morrosquillo.

These results show that density in the surveyed area ( $\sim 310\text{km}^2$ ) is 0.74 Guiana dolphins per  $\text{km}^2$ .

**Table 4.7- Seasonal abundance estimates of the Guiana dolphin population using the southern area of the Gulf of Morrosquillo in each year, “N marked” is the mark-recapture estimate of the number of well-marked animals using the best-fitting model with heterogeneity of capture probabilities (from Table 4.6). “Prop marked” is the estimated proportion of well-marked animals in the population. “N total” is the corrected estimate of total population size. CV is the coefficient of variation.**

Season	Year	N marked	SE	95% CI	Prop marked	SE	N total	SE	95% CI	CV
Dry	2004	104	36.2	61-215	0.285	0.032	365	133.3	182-730	0.37
Dry	2009	78	19.9	55-139	0.330	0.035	236	65.2	139-402	0.28
Dry	2010	60	18.9	39-120	0.267	0.031	225	75.4	118-426	0.34
Rainy	2003	16	3.6	13-30	0.085	0.027	187	72.7	90-390	0.39
Rainy	2004	73	28.3	43-168	0.285	0.032	256	103.3	119-548	0.40
Rainy	2005	88	22.7	61-157	0.224	0.034	393	117.5	221-697	0.30
Rainy	2006	27	3.6	24-41	0.366	0.061	74	15.7	49-112	0.21
Rainy	2009	57	14.0	42-102	0.330	0.035	173	46.2	103-288	0.27
Rainy	2010	62	18.3	42-121	0.267	0.031	232	73.6	127-246	0.32

## 4.5 Discussion

### 4.5.1 Survival

The annual survival rate for the adult Guiana dolphin population using the southern area of the Gulf of Morrosquillo was estimated to be constant throughout the study period and high (0.948; 95% CI = 0.876-0.980). A constant survival rate is expected in long-lived species

(Millar & Zammuto 1993) as a way of maintaining their abundance when facing environmental variation. Adult survival rate is therefore expected to be high and to be the life history parameter that varies least (Zeh *et al.* 2002).

High survival rate was expected for the Guiana dolphins using the study site, based on knowledge of longevity (30+ Years) (Rosas *et al.* 2010). Survival rate across years was consistent with that reported for bottlenose dolphins (0.92-0.98) (Wells and Scott 1990, Gaspar 2003, Silva *et al.* 2009) and also for humpback whales (0.92-0.98) (Barlow & Clapham 1997, Calambokidis & Barlow 2004, Larsen & Hammond 2004).

However, the survival rate of adult Guiana dolphins estimated in this study (0.95) is markedly higher than the only other estimate for this species in Brazil (0.88) (Cantor *et al.* 2012). Even if the expected survival rate should be high for a long-lived species, estimates may be lower due to external factors (e.g. anthropogenic mortality) or internal factors affecting estimation (e.g. heterogeneity of capture probabilities, permanent emigration). In a population with a survival rate of 0.95, 46% of individuals would survive after 15 years but with a survival rate of only 0.88, only 15% would survive after 15 years.

#### **4.5.2 Heterogeneity in capture probabilities**

Heterogeneity in the probability of an animal to be captured is a common violation of conventional mark-recapture models (Hammond 1990, Wells & Scott 1990). Studies conducted with other species of marine mammals show that sighting probability is not equal for animals of different age and sex within the population classes (e.g. Wells & Scott 1990, Heppell *et al.*, 2000, Gaspar 2003, Young & Keith 2011). Notwithstanding this, it was shown by Carothers (1973) and Gilbert (1973) that heterogeneous capture probabilities are relatively unimportant when the average capture probability is high, as is the case of the Guiana dolphins using this site.

The reasons for the heterogeneity in capture probability present among the Guiana dolphins using the study area may be caused by two main factors: the high site fidelity shown by some individuals of the population (Chapter 5) (Buckland 1990, Whitehead 2001) and the movements of some individuals to areas outside the boundaries of the study site (Hammond 1990). A patchy or clumped geographical distribution in the areas primarily used for feeding,

as in the case of Guiana dolphins using the study area (Chapter 3), may be one of the causes of heterogeneity. The estimates of capture probability from the models of seasonal abundance of well-marked animals were quite low. Survey effort was extensive so this may indicate that animals were moving in and out of the study area and were not always available to be captured.

Another factor that may cause heterogeneity in capture probabilities was the use of film cameras in 2002 and 2003 and the shift to digital cameras thereafter, as well as the improvement in camera lenses.

### **4.5.3 Seasonal abundance**

The best-fitting models for seasonal abundance were those that incorporated individual heterogeneity in the probability of capture. As described above, this may be caused by behavioural differences among the Guiana dolphins individuals using the southern gulf of Morrosquillo. Individual heterogeneity, with exceptions, often improves stability in population dynamics at large scales (Hixon *et al.* 2002).

Even though the estimates of the number of dolphins using the study area fluctuated between seasons and among years; there was no real evidence for either a seasonal difference in abundance or any directional trend in time. Characteristically, mangrove tropical estuaries are very stable ecosystems (Chapter 3), with high primary productivity year-round (Odum 1971). Therefore, there is no ecological reason for the abundance of Guiana dolphins to be expected to change between dry and rainy seasons.

The most recent abundance estimate (in 2010) was approximately 230 Guiana dolphins using the study area during both climatic seasons. The abundance estimates from studies of other populations of *S. guianensis* have varied between 54 and 1,067 individuals using Bay and Gulf areas (De O. Santos *et al.* 2010). A preliminary estimate of abundance for this species in the southern area of the Gulf of Morrosquillo was ~90 marked individuals (Dussán-Duque *et al.* 2006, Dussán-Duque & Wells 2007). Corrections for unmarked individuals were not available at the time.

Results from the surveyed area ( $\sim 310\text{km}^2$ ) show an overall density of 0.74 Guiana dolphins per  $\text{km}^2$ . Comparing this result with the density of Guiana dolphins estimated from study areas in Brazil ( $0.18/\text{km}^2$ ,  $0.17/\text{km}^2$ ,  $0.70/\text{km}^2$ ,  $2.88/\text{km}^2$ ,  $7.36/\text{km}^2$ ,  $19.0/\text{km}^2$ ) (De O. Santos *et al.* 2010, Cantor *et al.* 2012), the density of Guiana dolphins in this study site is at the lower end of the range. The reasons behind the low density of this species in the study area need to be explored further. The observed potential threats in the study area are: habitat degradation, loss and fragmentation, overlapping with artisanal fisheries activities, overfishing, boat strikes, direct catch, water contamination and shift in distribution and abundance of prey species (Chapter 7). This species is listed as Vulnerable in Colombia based on: absence in zones where it was previously reported abundant, isolation due to habitat fragmentation and loss, direct catch and declining prey species (Trujillo *et al.* 2006) (Chapter 1).

#### **4.6 Conclusions and implications for conservation**

The principal goal of this chapter was to estimate, through mark-recapture techniques, the survival rate and seasonal abundance of the *S. guianensis* population that uses the southern area of the Gulf of Morrosquillo.

The models developed in the chapter indicate that the surveyed methods applied in this study for the use of photo-identification techniques were appropriate to be applied to the Guiana dolphins using the study site. This study is a good example of long-term monitoring of a species of marine mammal (Wells & Scott 1990, Wells 2002, Hammond 1990, 2009, 2010) to investigate possible trends in survival and abundance.

The results of Chapter 3 indicate that there are important patterns in the habitat use and selection of Guiana dolphins in the southern area of the Gulf of Morrosquillo. This clustering of Guiana's dolphins in certain areas of the study site may be one of the reasons behind the individual heterogeneity in capture probability found in the analyses conducted during the study. The best closed populations models selected were generally those that accounted for individual heterogeneity (Chao *et al.* 1992). Other reasons for heterogeneity in capture probabilities may be the use by some individuals in the population of areas outside the boundaries of the study site. This result is important to take into account when considering

the boundaries of the Special Management Area for this species in the Gulf of Morroquillo, decreed in recent months by the Ministry of Environment of Colombia (Chapter 3).

The lack of evidence for a difference in abundance between the two climatic seasons shows that Guiana dolphins use the study area consistently year-round.

The survival rate of the individuals using the southern Gulf of Morroquillo was high, but the density estimates were relatively low when comparing with previous studies. A decline in the presence of Guiana dolphins in certain areas of Colombia was the reason to move them to the vulnerable species status (Trujillo *et al.* 2006). The results of this study support the need for the implementation of the Special Management Area in the southern area of the Gulf of Morroquillo. It should help the IUCN to improve on its “Data Deficient” listing of this species because there is now information on survival rates and seasonal abundance of this species from another area outside the geographic boundaries of Brazil.

Mark re-capture techniques can be applied satisfactorily with diverse cetacean species (Hammond *et al.* 1990, Langtimm *et al.* 2004, Larsen & Hammond 2004, Mizroch *et al.* 2004, Hernández-Camacho *et al.* 2008, Silva *et al.* 2009, Ramp *et al.* 2010, Cantor *et al.* 2012). These provide accurate information about estimates of the populations’ survival rate and abundance and their conservation status. Estimates of demographic parameters and abundance are necessary to inform conservation and to implement adequate management measures to protect cetacean species and their ecosystems.

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**Chapter 5 – Long-term site fidelity of Guiana dolphins in the southern Gulf of Morrosquillo**



## 5.1. Introduction

Site fidelity, can be described as a tendency of an animal to return to a previously occupied area after long absences or to re-use the same places through time (Switzer 1993). Site fidelity is a wide-spread behaviour among numerous animal species from insects through marine mammals (e.g. Warkentin & Hernández 1996, Craig & Herman 1997, Simões-Lopes & Fabian 1999, Jakob *et al.* 2000, Parra *et al.* 2005, Foote *et al.* 2010). Site fidelity and associated movements of species can be important to successful breeding, optimal foraging and social interactions, and the evolution of population structure (Hoelzel 2009). The ecological and evolutionary implications of site fidelity should not be ignored in the conservation of species (Hoelzel 2009).

Site fidelity of an individual or a group is directly affected by the habitat use expressed by this individual or group. Therefore, taking into account the energetic cost of moving and finding new suitable habitats (Hoelzel 2009), if a habitat provides for successful fitness, the individual or group may return to the same habitat or stay in it over long periods of time (Chilvers 2008). Basic animal habitat selection models assume that for each “settlement” decision an animal evaluates all the available habitats and selects the one with the highest quality or suitability (e.g. best habitat) (Switzer 1993). However, these predictable models are not as simple as one may assume. The selection of certain sites by an animal and the re-use of them is conducted at an individual level and does not only depend on environmental factors. Certain habitats may not be preferred equally by all individuals within a population (Switzer 1993, McConnell *et al.* 1999). As stated by Switzer (1993): “fine-scale site fidelity constitutes an important structural component on animal societies by setting limits to an individual social interaction space”.

Two main aspects of site fidelity have been studied in the past of a number of species: site fidelity for feeding grounds; and the social implications of site fidelity at the population structure level (e.g. Hestbeck *et al.* 1991, Baird *et al.* 2009, Foote *et al.* 2009).

Marine mammals are long-lived animals (Mead & Potter 1990 and Ford *et al.* 2002), characteristic that makes them suited for long-term studies of site fidelity. However, one of the problems to face in studying the site fidelity patterns of marine mammals is the logistical difficulties involved in analyzing the spatial patterns of these species through long periods of time. The majority of studies have been conducted with species of pinnipeds (e.g. McConnell *et al.* 1999, Matthiopoulos *et al.* 2004, Chilvers 2008,) and coastal dolphins (e.g. Wells *et al.* 1987, Maze & Würsig 1999, Smolker & Connor 1985) and some with open water cetaceans (e.g. Baird *et al.* 2008, McSweeney *et al.* 2008, Valenzuela *et al.* 2008).

Guiana dolphins are coastal and strong patterns of long term site fidelity have been reported for the species in Brazil (e.g. De Oliveira Santos *et al.* 2001, De Freitas Azevedo *et al.* 2004, Rossi-Santos *et al.* 2007). Flores (1999) reported the longest site fidelity for the species known to date; ten years of fidelity of an individual to a study site in Brazil.

As described in Chapter 1, *S. guianensis* is listed as “vulnerable” in Colombia and as “Data Deficient” by the IUCN. This study presents the longest ongoing research with Guiana dolphins in Colombia. Four years of site fidelity for some individuals was reported in the same area by Avila (1995). Comparisons between Avila’s (1995) catalogue of identified individuals and that compiled in this study will be conducted in the future. This chapter uses photo-identification data to investigate the long-term site fidelity of those individuals with the greatest frequency of sightings between 2002-2006 and 2009-2010 in the southern area of the Gulf of Morrosquillo. Through analysis of the site fidelity to their feeding habitats of individuals in this population, it explores the conservation implications of site fidelity for the species throughout its distributional range.

## **5.2. Aim and objectives of the Chapter**

### **5.2.1. General aim**

To use the distribution of individual Guiana dolphins in the southern Gulf of Morrosquillo to investigate site fidelity and use of specific areas for feeding during the study period.

### 5.2.2. Objectives

- To investigate whether individual dolphins use particular areas consistently; in general and for feeding.
- To explore the variability in spatial patterns of site fidelity to assess how individuals use the study area overall.

### 5.3. Materials and Methods

General survey and data collection methods are described in Chapter 2.

From 2002-2006 and 2009-2010, 395 boat surveys were conducted in the study area that covers approximately 310 km<sup>2</sup> (Figure 3.2) with a total survey effort of 15,199 km. The survey effort was conducted for continuous periods of a minimum of one month to up to five months. Sighting effort was distributed evenly throughout the study site during the three climatic seasons: rainy, dry and semi-dry. This fieldwork yielded 318 dolphin sightings (see Figure 3.16 in Chapter 3). A total of 74,226 photographs of Guiana dolphins' dorsal fins marks were taken for photo-identification. Photographs were not taken on every sighting due to the field conditions. An equal effort was made to photograph the dorsal fins of every individual present during a sighting. As many pictures as possible of the individuals present were taken during every sighting until the individual or group decided to move to another area. Photographs were graded based on the resolution and focus of the image and the angle of the animal relative to the camera lens. Only good quality pictures of adult individuals with permanent marks on the dorsal fin or body. For the individual identification and matching protocol, refer to Chapter 4. From the catalogue of 98 well-marked adult individuals, the 10 individuals with the highest sighting frequencies were chosen to investigate site fidelity.

### 5.4. Data analysis

Site fidelity of individual dolphins to the predetermined zones (Chapter 2, Figure 2.6) was quantified by a Sighting Index by Zone (SI<sub>ZONE</sub>), following the methodology

described by Flores in 2003 (Flores & Fontouran 2006). This index was calculated as the number of times a specific individual was sighted in each specific zone as a proportion of its total number of sightings.

The site fidelity of individual dolphins to feeding areas was quantified by a Feeding Index by Zone ( $FI_{ZONE}$ ). This index was calculated as the number of times a specific individual was sighted while feeding in each specific zone as a proportion of its total number of feeding sightings.

The site fidelity of individual dolphins to certain areas in other behaviour events was quantified by a Behavioural Index by Zone ( $OBI_{ZONE}$ ). This index was calculated as the number of times a specific individual was sighted engaged in other behaviours different than feeding in each specific zone as a proportion of its total number of sightings other behaviours.

## **5.5 Observations of individuals**

### **5.5.1. Sighting histories**

Figures 4.2 and 4.4 in Chapter 4 show the years the identified dolphins were sighted and the climatic seasons by ID number. The following tables (Tables 5.1 – 5.10) show the details of all sightings, including month, year, season, zone and behaviour of the following individuals: ID-018, 022, 013, 032, 012, 027, 011, 057, 044, and 015, from 2002-2006 and 2009-2010. Figures 5.1- 5.20 show identification photographs of the ten dolphins and the distribution of the sightings of these individuals downloaded from the GPS to maps.

**Luna (018)** (Figure 5.1).



**Figure 5.1- Individual dolphin Luna (ID-018), southern Gulf of Morrosquillo. Photograph by Salomé Dussán-Duque.**

As seen in Table 5.1, dolphin ID-018 was sighted 30 times from 2003 to 2006 and 2009 to 2010. Out of the 30 sightings, 17 were feeding events mainly in zones 1 and 2. The others were of different behavioural events (see Chapter 2). This individual had the highest sighting rate among all the 97 identified Guiana dolphins in the study area.

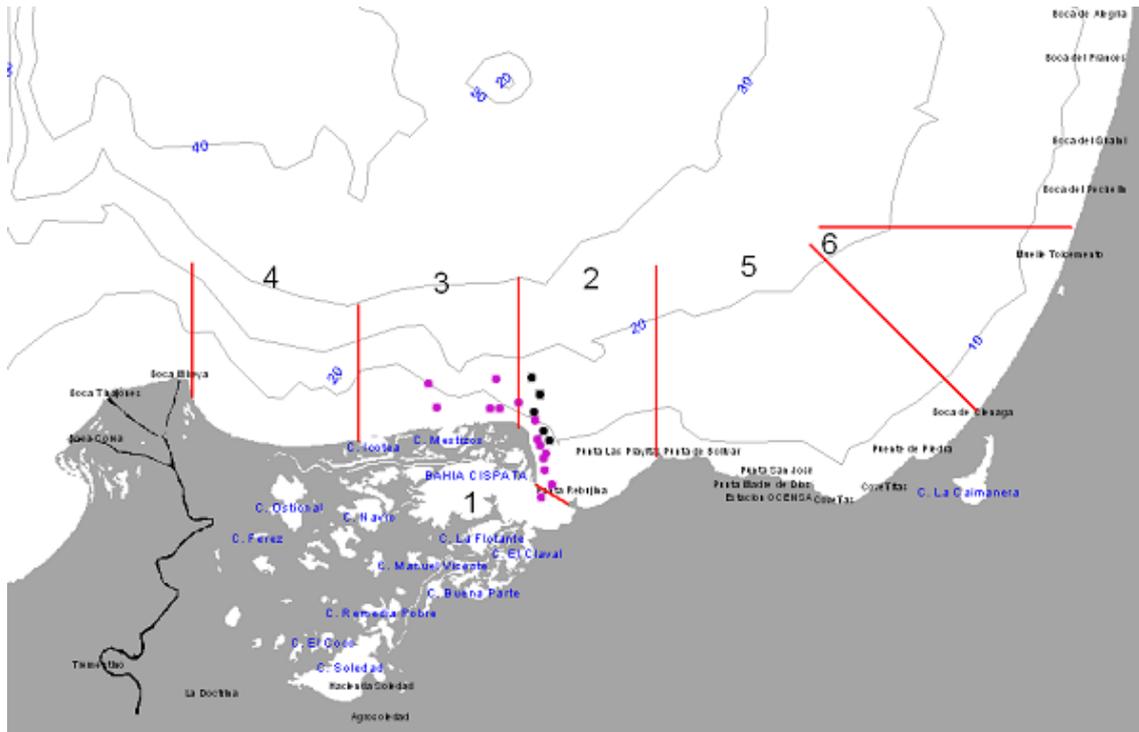
**Table 5.1- Sighting history of individual ID-018 from the first until the last date sighted in the southern gulf of Morrosquillo.**

<b>Day</b>	<b>Month</b>	<b>Year</b>	<b>Season</b>	<b>Zone</b>	<b>Behaviour</b>
18	8	2003	1	2	Feeding
7	5	2004	1	2	Other
11	5	2004	1	1	Feeding
14	6	2004	1	5	Feeding
29	9	2004	1	2	Feeding
23	10	2004	1	2	Feeding
9	8	2005	1	1	Feeding
30	8	2005	1	2	Feeding
16	5	2006	1	1	Feeding
18	5	2006	1	2	Other
26	3	2009	2	2	Other
11	4	2009	2	2	Other
8	9	2009	1	5	Other
17	9	2009	1	2	Feeding
22	9	2009	1	1	Feeding
24	9	2009	1	2	Feeding
5	4	2010	2	2	Feeding
6	4	2010	2	2	Feeding
7	4	2010	2	5	Other
10	4	2010	2	2	Other
11	4	2010	2	1	Feeding
12	4	2010	2	2	Feeding
13	4	2010	2	2	Other
14	4	2010	2	2	Feeding
22	4	2010	2	2	Other
24	4	2010	2	5	Other
27	4	2010	2	2	Other
4	5	2010	1	2	Other
8	5	2010	1	2	Other
15	5	2010	1	2	Feeding



**Table 5.2- Sighting history of individual ID-022 from the first until the last date sighted in the southern gulf of Morrosquillo.**

<b>Day</b>	<b>Month</b>	<b>Year</b>	<b>Season</b>	<b>Zone</b>	<b>Behaviour</b>
12	3	2004	2	1	Feeding
31	3	2004	2	2	Feeding
4	4	2004	2	3	Feeding
6	4	2004	2	2	Feeding
7	4	2004	2	2	Other
21	4	2004	2	3	Feeding
19	5	2004	1	3	Feeding
17	6	2004	1	2	Feeding
2	11	2005	1	2	Feeding
18	5	2006	1	2	Other
20	5	2006	1	2	Feeding
29	5	2006	1	2	Feeding
26	3	2009	2	2	Feeding
23	4	2010	2	3	Feeding
24	4	2010	2	3	Feeding
27	4	2010	2	3	Feeding
5	5	2010	1	2	Other
8	5	2010	1	2	Other
16	5	2010	1	2	Other



**Figure 5.4-** Sightings of dolphin ID-022 from 2004 to 2006 and 2009 to 2010 in the southern Gulf of Morrosquillo. Purple dots represent the feeding events and black dots the other behaviours.

**Blach (013)** (Figure 5.5).

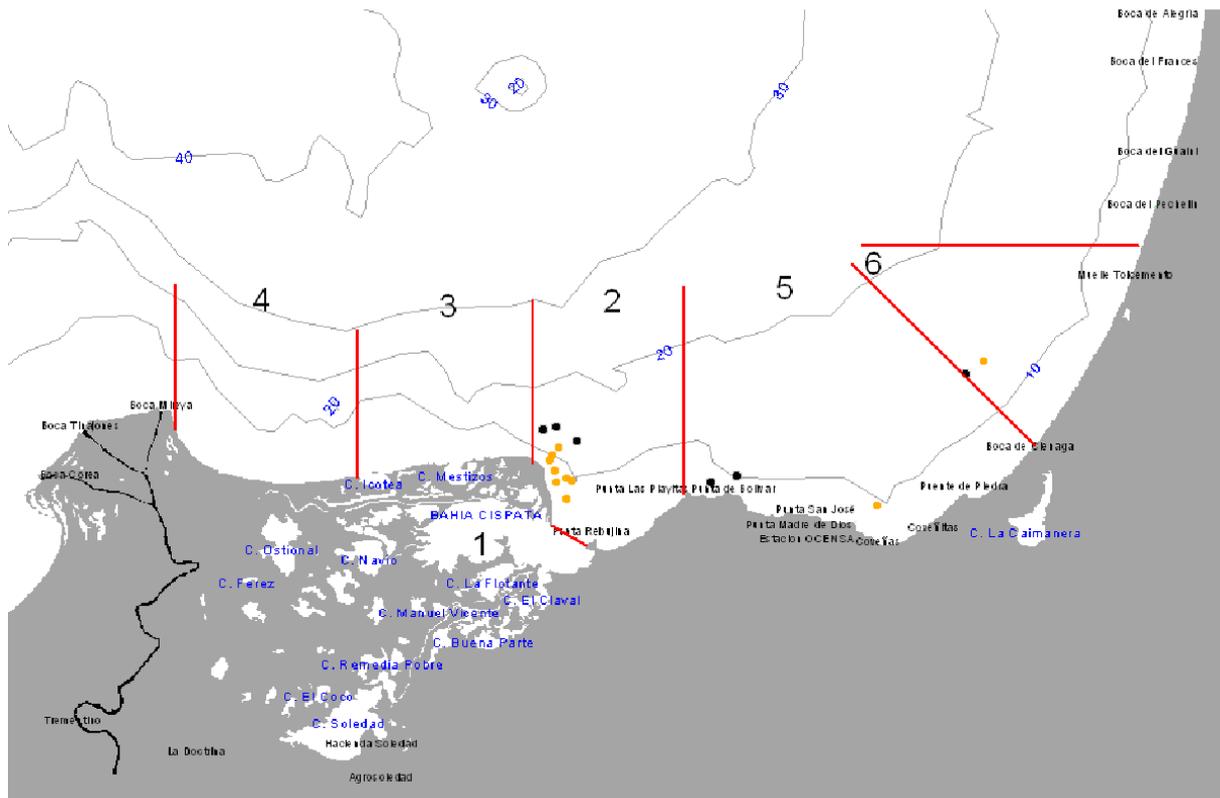


**Figure 5.5-** Individual dolphin Blach (ID-013), southern Gulf of Morrosquillo. *Photograph by Salomé Dussán-Duque.*

As seen in Table 5.3, dolphin ID-013 was sighted 16 times from 2003 to 2006 and 2009 to 2010. Out of the 16 sightings, 10 were feeding events in zones 2 and 6.

**Table 5.3- Sighting history of individual ID-013 from the first until the last date sighted in the southern gulf of Morrosquillo.**

<b>Day</b>	<b>Month</b>	<b>Year</b>	<b>Season</b>	<b>Zone</b>	<b>Behaviour</b>
4	6	2003	1	2	Feeding
2	7	2003	3	6	Feeding
12	3	2004	2	2	Feeding
13	10	2004	1	2	Other
28	7	2005	3	2	Feeding
3	8	2005	1	5	Feeding
19	8	2005	1	2	Feeding
3	11	2005	1	2	Other
10	5	2006	1	2	Feeding
24	5	2006	1	6	Other
25	5	2006	1	2	Feeding
16	9	2009	1	5	Other
26	9	2009	1	2	Feeding
3	5	2010	1	2	Feeding
5	5	2010	1	5	Other
6	5	2010	1	2	Other



**Figure 5.6-** Sightings of dolphin ID-013 from 2003 to 2006 and 2009 to 2010 in the southern Gulf of Morrosquillo. Orange dots represent the feeding events and black dots the other behaviours.

**Mercu (032)** (Figure 5.7)

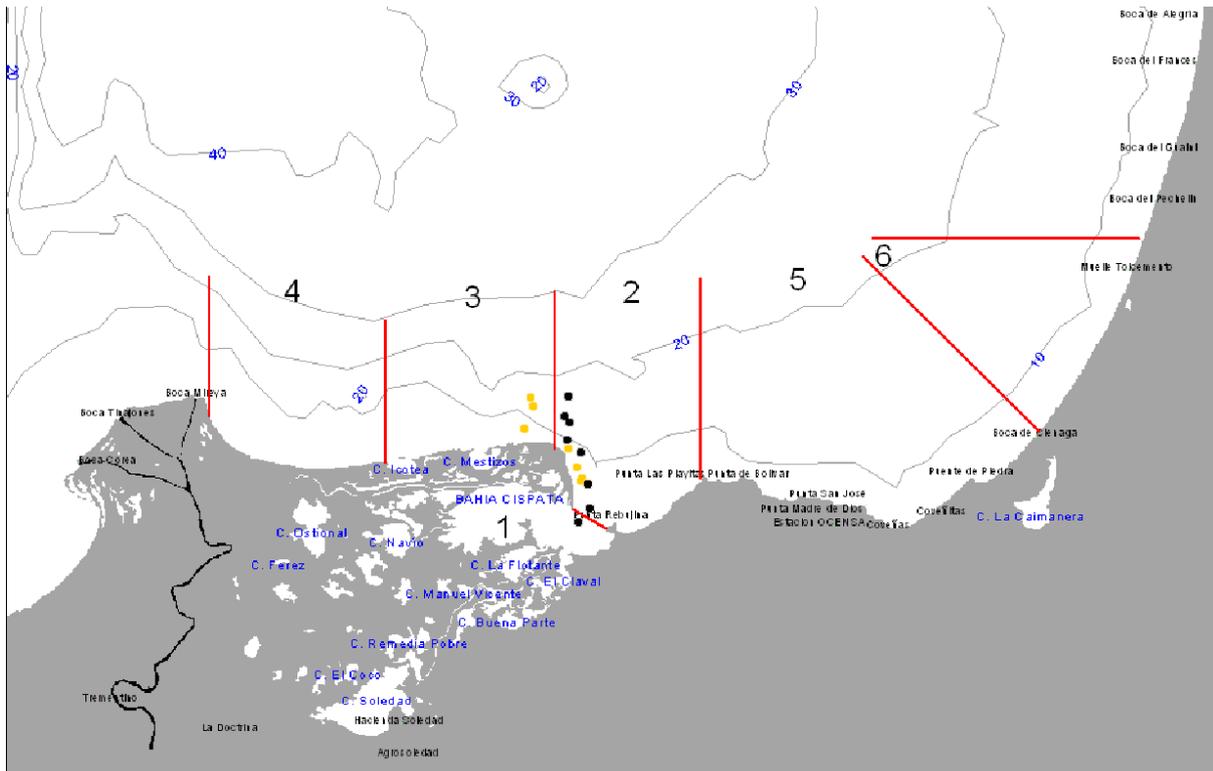


**Figure 5.7-** Individual dolphin Mercu (ID-032), southern Gulf of Morrosquillo. *Photograph by Salomé Dussán-Duque.*

As seen in Table 5.4, dolphin ID-032 was sighted 15 times from 2004 to 2006 and 2009 to 2010. Out of the 15 sightings, 7 were feeding events in zones 2 and 3.

**Table 5.4- Sighting history of individual ID-032 from the first until the last date sighted in the southern gulf of Morrosquillo.**

<b>Day</b>	<b>Month</b>	<b>Year</b>	<b>Season</b>	<b>Zone</b>	<b>Behaviour</b>
31	3	2004	2	3	Feeding
6	4	2004	2	2	Feeding
19	4	2004	2	2	Feeding
24	4	2004	2	1	Other
26	4	2004	2	2	Other
26	5	2006	1	2	Other
4	4	2009	2	2	Feeding
11	4	2009	2	2	Feeding
16	9	2009	1	2	Other
23	9	2009	1	2	Other
24	4	2010	2	3	Feeding
17	4	2010	2	2	Other
27	4	2010	2	3	Feeding
4	5	2010	1	2	Other
16	5	2010	1	2	Other



**Figure 5.8-** Sightings of dolphin ID-032 from 2004 to 2006 and 2009 to 2010 in the southern Gulf of Morrosquillo. Yellow dots represent the feeding events and black dots the other behaviours.

**Cumbal (012)** (Figure 5.9).



**Figure 5.9-** Individual dolphin (ID-012), southern Gulf of Morrosquillo. *Photograph by Salomé Dussán-Duque.*

As seen in Table 5.5, dolphin ID-012 was sighted 14 times from 2003 to 2004 and 2009. Out of the 14 sightings, 7 were feeding events in zones 2 and 3.



**Sinú (027)** (Figure 5.11)

**Figure 5.11-** Individual dolphin (ID-027), southern Gulf of Morrosquillo. *Photograph by Salomé Dussán-Duque.*

As seen in Table 5.6, dolphin ID-027 was sighted 14 times from 2004 to 2006 and from 2009 to 2010. Out of the 14 sightings, 10 were feeding events in zones 2 and 3.

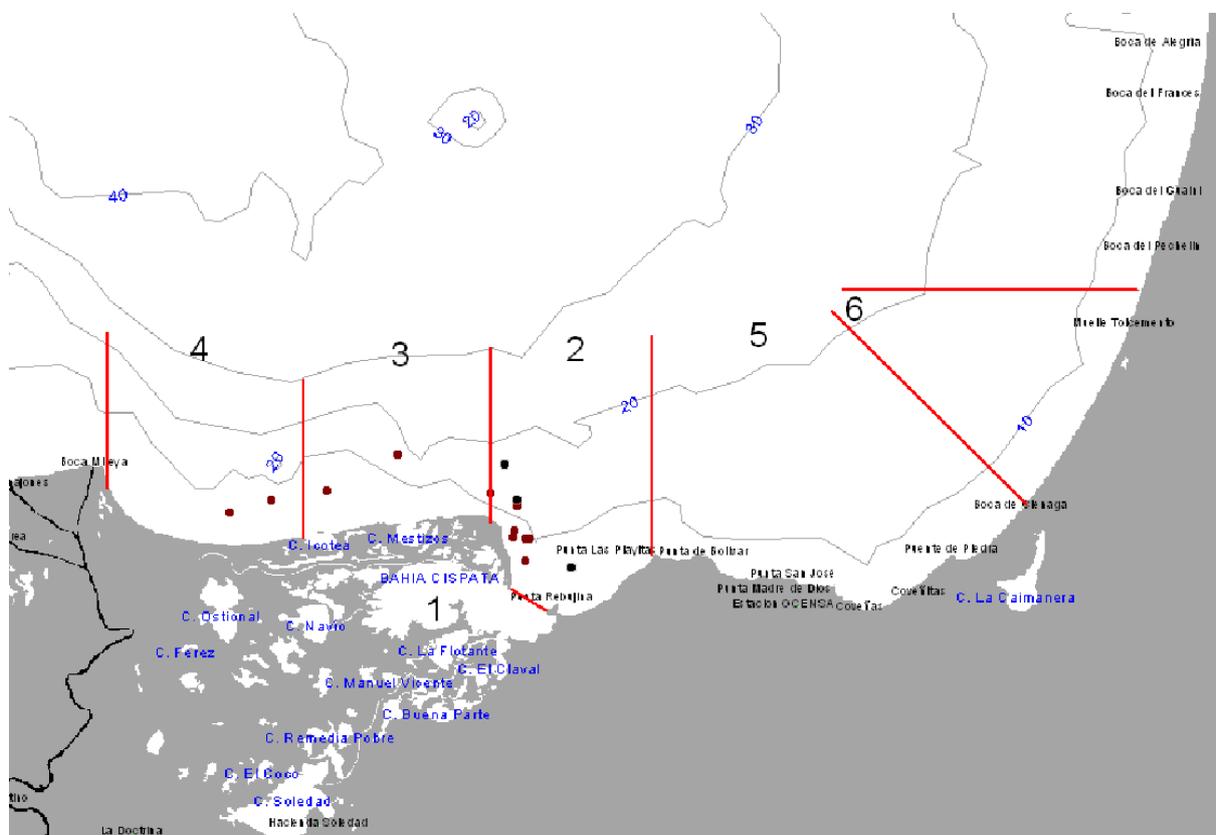
**Table 5.6-** Sighting history of individual ID-027 from the first until the last date sighted in the southern gulf of Morrosquillo.

<b>Day</b>	<b>Month</b>	<b>Year</b>	<b>Season</b>	<b>Zone</b>	<b>Behaviour</b>
12	3	2004	2	2	Feeding
31	3	2004	2	2	Feeding
22	4	2004	2	2	Other
18	8	2005	1	2	Feeding
30	8	2005	1	2	Feeding
26	10	2005	1	2	Other
2	11	2005	1	2	Feeding
10	5	2006	1	2	Feeding
11	4	2009	2	3	Feeding
9	9	2009	2	2	Other
17	9	2009	1	2	Feeding
15	4	2010	2	2	Other
23	4	2010	2	3	Feeding
24	4	2010	2	3	Feeding



**Table 5.7 - Sighting history of individual ID-011 from the first until the last date sighted in the southern gulf of Morrosquillo.**

Day	Month	Year	Season	Zone	Behaviour
14	5	2003	1	3	Feeding
29	9	2004	1	2	Feeding
13	10	2004	1	2	Other
28	10	2004	1	4	Feeding
30	8	2005	1	2	Feeding
2	11	2005	1	2	Feeding
17	5	2006	1	2	Feeding
20	5	2006	1	4	Feeding
11	4	2009	2	3	Feeding
15	4	2009	2	2	Feeding
22	9	2009	2	2	Feeding
4	5	2010	1	3	Feeding
8	5	2010	1	2	Other
14	5	2010	1	2	Other



**Figure 5.14- Sightings of dolphin ID-011 from 2003 to 2006 and 2009 to 2010 in the southern Gulf of Morrosquillo. Brown dots represent the feeding events and black dots the other behaviours.**

**Tolú (057)** (Figure 5.15).

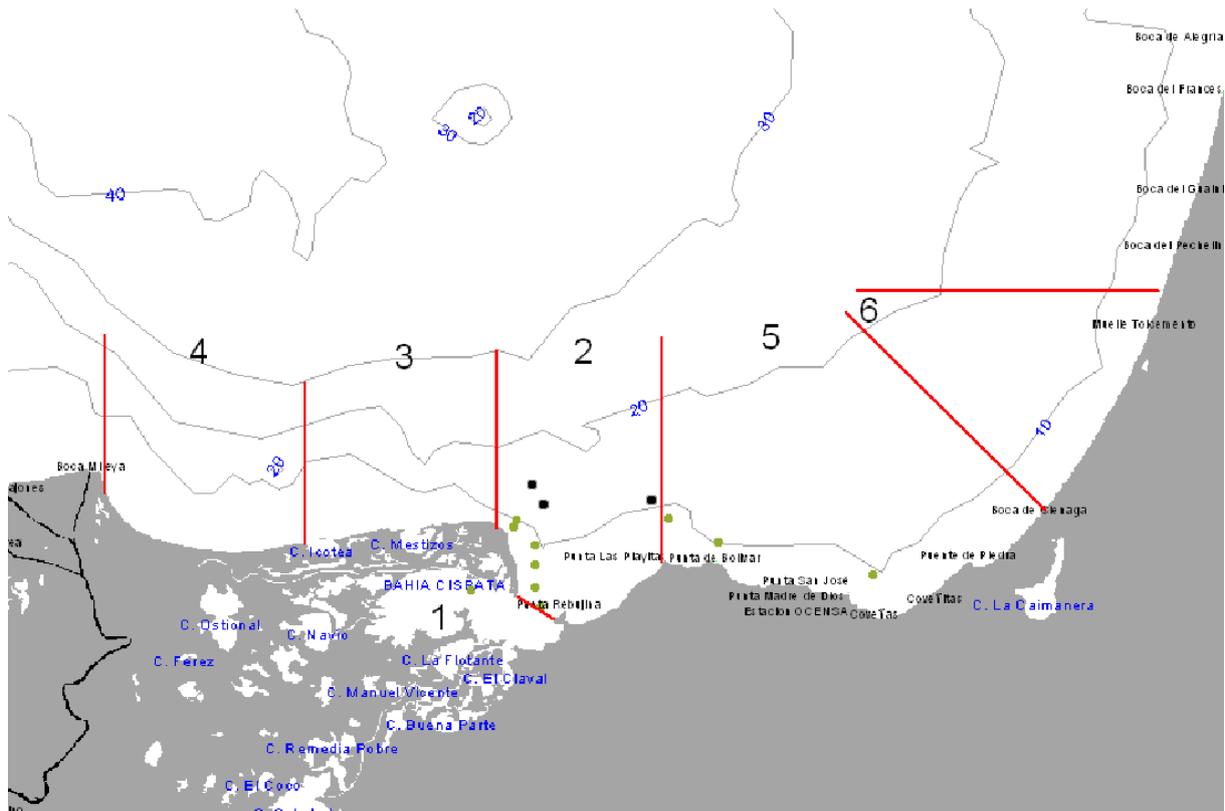


**Figure 5.15-** Individual dolphin (ID-057), southern Gulf of Morrosquillo. *Photograph by Salomé Dussán-Duque.*

As seen in Table 5.8, dolphin ID-057 was sighted 13 times from 2004 to 2005 and from 2009 to 2010. Out of the 13 sightings, 8 were feeding events in zones 1, 2 and 5.

**Table 5.8 - Sighting history of individual ID-057 from the first until the last date sighted in the southern gulf of Morrosquillo.**

<u>Day</u>	<u>Month</u>	<u>Year</u>	<u>Season</u>	<u>Zone</u>	<u>Behaviour</u>
15	10	2004	1	5	Feeding
28	10	2004	1	2	Feeding
28	7	2005	3	2	Feeding
29	7	2005	3	2	Feeding
3	8	2005	1	5	Feeding
9	8	2005	1	1	Feeding
15	8	2005	1	2	Feeding
2	4	2009	2	2	Feeding
8	9	2009	1	2	Other
10	9	2009	1	2	Other
4	5	2010	2	2	Other
14	5	2010	2	5	Feeding
15	5	2010	2	2	Feeding



**Figure 5.16-** Sightings of dolphin ID-057 from 2004 to 2005 and 2009 to 2010 in the southern Gulf of Morrosquillo. Green dots represent the feeding events and black dots the other behaviours.

**Equi (044)** (Figure 5.17).

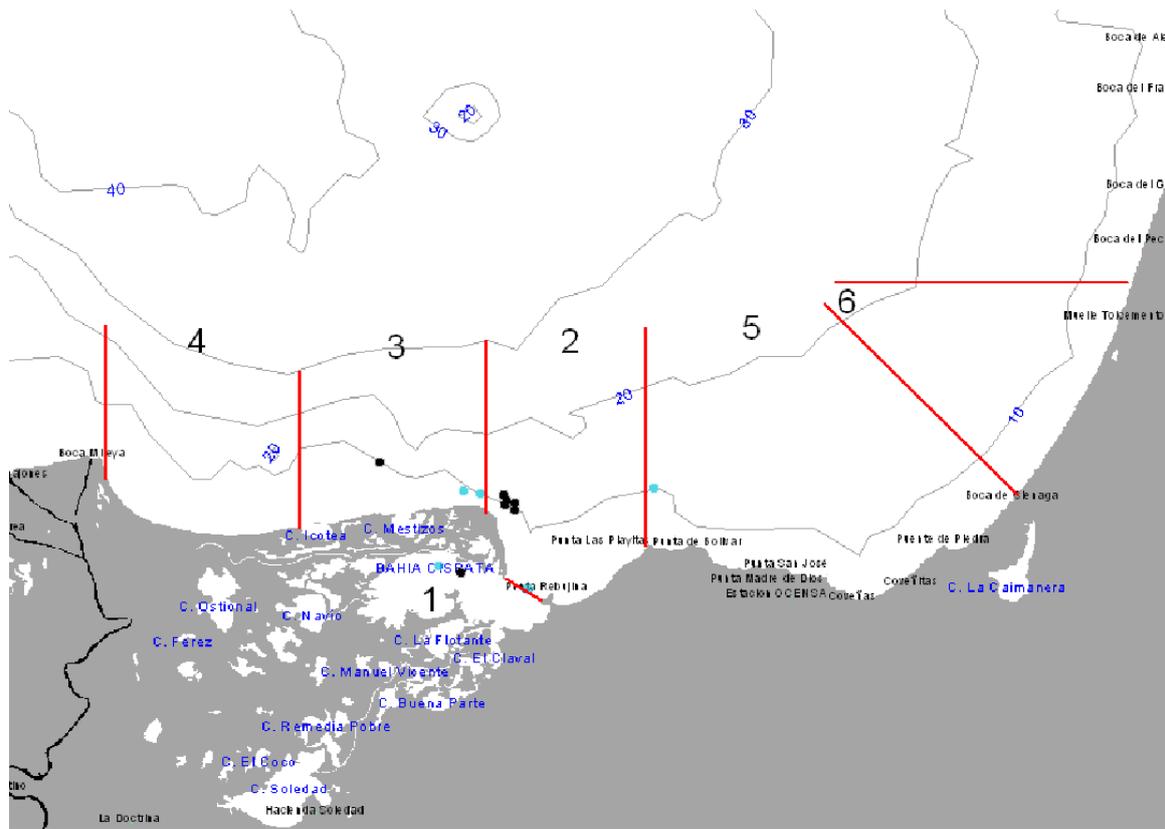


**Figure 5.17-** Individual dolphin (ID-044), southern Gulf of Morrosquillo. *Photograph by Salomé Dussán-Duque.*

As seen in Table 5.9, dolphin ID-044 was sighted 13 times from 2004 to 2006 and from 2009 to 2010. Out of the 13 sightings, 6 were feeding events in zones 2 and 3.

**Table 5.9 - Sighting history of individual ID-044 from the first until the last date sighted in the southern gulf of Morrosquillo.**

Day	Month	Year	Season	Zone	Behaviour
21	4	2004	2	3	Feeding
22	4	2004	2	2	Other
7	5	2004	1	2	Other
19	5	2004	1	3	Feeding
29	9	2004	1	2	Feeding
9	8	2005	1	1	Feeding
18	5	2006	1	2	Other
21	5	2006	1	5	Feeding
26	3	2009	2	2	Feeding
16	9	2009	1	2	Other
26	9	2009	1	3	Other
15	4	2010	2	1	Other
10	5	2010	1	2	Other



**Figure 5.18- Sightings of dolphin ID-044 from 2004 to 2006 and 2009 to 2010 in the southern Gulf of Morrosquillo. Blue dots represent the feeding events and black dots the other behaviours.**

**Bruj (015)** (Figure 5.19).



**Figure 5.19-** Individual dolphin (ID-015), southern Gulf of Morrosquillo. *Photograph by Salomé Dussán-Duque.*

As seen in Table 5.10, dolphin ID-015 was sighted 13 times from 2003 to 2006 and from 2009 to 2010. Out of the 13 sightings, 10 were feeding events in zones 2, 3 and 5.

**Table 5.10 - Sighting history of individual ID-015 from the first until the last date sighted in the southern gulf of Morrosquillo.**

<b>Day</b>	<b>Month</b>	<b>Year</b>	<b>Season</b>	<b>Zone</b>	<b>Behaviour</b>
28	7	2003	3	2	Other
19	3	2004	2	2	Other
24	3	2004	2	3	Feeding
14	6	2004	1	2	Feeding
17	6	2004	1	2	Feeding
15	10	2004	1	2	Feeding
23	10	2004	1	2	Feeding
4	4	2009	2	3	Feeding
11	4	2009	2	2	Feeding
13	4	2009	2	2	Feeding
24	4	2010	2	2	Feeding
27	4	2010	2	3	Feeding
11	5	2010	2	5	Feeding



**Table 5.11 – Sighting Index by Zone ( $SI_{ZONE}$ ) of the dolphins with the highest sighting frequencies from 2002-2006 and 2009-2010 in the southern Gulf of Morrosquillo.**

<b>ID</b>	<b>Zone 1</b>	<b>Zone 2</b>	<b>Zone 3</b>	<b>Zone 4</b>	<b>Zone 5</b>	<b>Zone 6</b>	<b>Total</b>
Luna-018	0.16	0.70	0	0	0.13	0	1
Triz- 022	0.05	0.63	0.32	0	0	0	1
Blach-013	0	0.69	0	0	0.18	0.13	1
Mercu-032	0.07	0.73	0.20	0	0	0	1
Cumbal-012	0	0.57	0.29	0	0.14	0	1
Sinu-027	0	0.79	0.21	0	0	0	1
Tuchin-011	0	0.64	0.21	0.15	0	0	1
Tolu-057	0.08	0.69	0	0	0.23	0	1
Equi-043	0.15	0.54	0.23	0	0.08	0	1
Bruj-015	0	0.69	0.23	0	0.08	0	1

### **Feeding Index by Zone ( $FI_{ZONE}$ )**

Table 5.12 shows the summary results for the feeding index by zone ( $FSI_{ZONE}$ ) of all the individuals. As seen in the Table, Zone 2 was the main zone used by all these individuals to feed but there was considerable variation among individuals. The use of other zones for feeding varied among individuals, showing evidence of individual variation in feeding site fidelity during the study period. Zone 3 was used by most dolphins for feeding but Zones 1 and 5 were used by only about half of the animals. Zones 4 and 6 were only used by one dolphin each for feeding; Tuchin (ID-011) and Blach (ID-013), respectively.

**Table 5.12 – Feeding Index by zone ( $FI_{ZONE}$ ) of the dolphin individuals with the highest overall sighting frequencies from 2002-2006 and 2009-2010 in the Southern Gulf of Morrosquillo.**

<b>ID</b>	<b>Zone 1</b>	<b>Zone 2</b>	<b>Zone 3</b>	<b>Zone 4</b>	<b>Zone 5</b>	<b>Zone 6</b>
Luna-018	0.29	0.65	0	0	0.06	0
Triz- 022	0.07	0.5	0.43	0	0	0
Blach-013	0	0.8	0	0	0.1	0.1
Mercu-032	0	0.57	0.43	0	0	0
Cumbal-012	0	0.57	0.43	0	0	0
Sinu-027	0	0.7	0.3	0	0	0
Tuchin-011	0	0.55	0.27	0.18	0	0
Tolu-057	0.1	0.6	0	0	0.3	0
Equi-043	0.17	0.33	0.33	0	0.17	0
Bruj-015	0	0.64	0.27	0	0.09	0

The results of the ( $FI_{ZONE}$ ) show clear feeding site fidelity by the individual dolphins to some zones among all the zones within the study site boundaries. As seen in Tables 5.1-5.10 not all the individuals used the zones all the years, but they re-used the same zones throughout the study period.

### Other Behavioural events Index by Zone ( $OBI_{ZONE}$ )

Table 5.13 shows the summary results for the other behavioural events index ( $OBI_{ZONE}$ ) of all the individuals. As seen in the Table, Zone 2 was also used by all the individuals when engaged in behavioural events other than feeding. There was also some variation in the use of other zones when engaged in other behaviours; five dolphins only used Zone 2 and the others used one or two other zones. However, sample sizes were small for these behavioural observations.

**Table 5.13 – Other Behavioural events Index by Zone ( $OBI_{ZONE}$ ) of the dolphin individuals with the highest sighting frequencies from 2002-2006 and 2009-2010 in the Southern Gulf of Morrosquillo.**

<b>ID</b>	<b>Zone 1</b>	<b>Zone 2</b>	<b>Zone 3</b>	<b>Zone 4</b>	<b>Zone 5</b>	<b>Zone 6</b>
Luna-018	0	0.77	0	0	0.23	0
Triz- 022	0	1	0	0	0	0
Blach-013	0	0.5	0	0	0.33	0.17
Mercu-032	0.12	0.88	0	0	0	0
Cumbal-012	0	0.57	0.14	0	0.29	0
Sinu-027	0	1	0	0	0	0
Tuchin-011	0	1	0	0	0	0
Tolu-057	0	1	0	0	0	0
Equi-043	0.14	0.72	0.14	0	0	0
Bruj-015	0	1	0	0	0	0

### 5.6.2 Results for individual dolphins

**Luna (018)** (Figure 5.1).

As shown in Table 5.14, Luna (018) showed high site fidelity for Zone 2 and a moderate fidelity for Zones 1 and 5. This dolphin fed primarily in Zone 2 and also Zone 1 (Figure 5.2) but only Zones 2 and 3 were used for other behavioural events.

**Table 5.14- Sighting Index by Zone ( $SI_{ZONE}$ ) of individual Luna (018) divided between feeding and other behavioural events from 2003-2006 and 2009- 2010.**

<b>Luna (018)</b>	<b>Zone 1</b>	<b>Zone 2</b>	<b>Zone 3</b>	<b>Zone 4</b>	<b>Zone 5</b>	<b>Zone 6</b>
Feeding	0.29	0.65	0	0	0.06	0
Other	0	0.77	0	0	0.23	0

**Triz (022)** (Figure 5.3).

As shown in Table 5.15, Triz (022) occurred in Zones 1, 2 and 3 but showed highest site fidelity for Zone 2. This individual fed mostly and almost equally in Zones 2 and 3 (Figure 5.4) but only Zone 2 was used for other behavioural events.

**Table 5.15- Sighting Index by Zone ( $SI_{ZONE}$ ) of individual Triz (022) divided between feeding and other behavioural events from 2004 to 2006 and 2009 to 2010.**

<b>Triz (022)</b>	<b>Zone 1</b>	<b>Zone 2</b>	<b>Zone 3</b>	<b>Zone 4</b>	<b>Zone 5</b>	<b>Zone 6</b>
Feeding	0.07	0.5	0.43	0	0	0
Other	0	1	0	0	0	0

**Blach (013)** (Figure 5.5).

As shown in Table 5.16, Blach (013) showed high site fidelity for Zone 2 but was also seen in Zones 5 and 6 where it also fed (Figure 5.6). This dolphin used the same zones for other behavioural events.

**Table 5.16- Sighting Index by Zone ( $SI_{ZONE}$ ) of individual Blach (013) divided between feeding and other behavioural events from 2004 to 2006 and 2009 to 2010.**

<b>Blach (013)</b>	<b>Zone 1</b>	<b>Zone 2</b>	<b>Zone 3</b>	<b>Zone 4</b>	<b>Zone 5</b>	<b>Zone 6</b>
Feeding	0	0.8	0	0	0.1	0.1
Other	0	0.5	0	0	0.33	0.17

**Mercu (032)** (Figure 5.7)

As shown in Table 5.17, Mercu (032) showed high site fidelity for Zone 2 but also used Zone 3 to feed (Figure 5.8). This dolphin used Zones 1 and, primarily, 2 for other behavioural events.

**Table 5.17- Sighting Index by Zone ( $SI_{ZONE}$ ) of individual Mercu (032) divided between feeding and other behavioural events from 2004- 2006 and 2009- 2010.**

<b>Mercu (032)</b>	<b>Zone 1</b>	<b>Zone 2</b>	<b>Zone 3</b>	<b>Zone 4</b>	<b>Zone 5</b>	<b>Zone 6</b>
Feeding	0	0.57	0.43	0	0	0
Other	0.12	0.88	0	0	0	0

**Cumbal (012)** (Figure 5.9).

As shown in Table 5.18, Cumbal (032) showed highest site fidelity for Zone 2 but also Aone 3, both of which were used to feed (Figure 5.10). Znes 2, 3 and 5 were used for other behavioural events.

**Table 5.18- Sighting Index by Zone ( $SI_{ZONE}$ ) of individual Cumbal (012) divided between feeding and other behavioural events from 2003- 2004 and 2009.**

<b>Cumbal (012)</b>	<b>Zone 1</b>	<b>Zone 2</b>	<b>Zone 3</b>	<b>Zone 4</b>	<b>Zone 5</b>	<b>Zone 6</b>
Feeding	0	0.57	0.43	0	0	0
Other	0	0.57	0.14	0	0.29	0

**Sinú (027)** (Figure 5.11)

As shown in Table 5.19, Sinú (027) showed high site fidelity for Zone 2 and moderate site fidelity to Zone 3, both of which were used to feed (Figure 5.12). This dolphin used only zone 2 for other behavioural events.

**Table 5.19- Sighting Index by Zone ( $SI_{ZONE}$ ) of individual Sinú (027) divided between feeding and other behavioural events from 2004- 2004 and 2009-2010.**

<b>Sinú (027)</b>	<b>Zone 1</b>	<b>Zone 2</b>	<b>Zone 3</b>	<b>Zone 4</b>	<b>Zone 5</b>	<b>Zone 6</b>
Feeding	0	0.7	0.3	0	0	0
Other	0	1	0	0	0	0

**Tuchín (011)** (Figure 5.13).

As shown in Table 5.20, Tuchín (011) showed high site fidelity for Zone 2 and moderate site fidelity to Zones 3 and 4; all of which were used to feed (Figure 5.14). This dolphin used only zone 2 for other behavioural events.

**Table 5.20- Sighting Index by Zone ( $SI_{ZONE}$ ) of individual Tuchín (011) divided between feeding and other behavioural events from 2003- 2006 and 2009-2010.**

<b>Tuchín (011)</b>	<b>Zone 1</b>	<b>Zone 2</b>	<b>Zone 3</b>	<b>Zone 4</b>	<b>Zone 5</b>	<b>Zone 6</b>
Feeding	0	0.55	0.27	0.18	0	0
Other	0	1	0	0	0	0

**Tolú (057)** (Figure 5.15).

As shown by Table 5.21, Tolú (057) showed high site fidelity for Zone 2 and moderate site fidelity for Zone 5, which were also the main zones used to feed (Figure 5.16). This dolphin used only Zone 2 for other behavioural events.

**Table 5.21- Sighting Index by Zone ( $SI_{ZONE}$ ) of individual Tolú (057) divided between feeding and other behavioural events from 2004- 2005 and 2009-2010.**

<b>Tolú (057)</b>	<b>Zone 1</b>	<b>Zone 2</b>	<b>Zone 3</b>	<b>Zone 4</b>	<b>Zone 5</b>	<b>Zone 6</b>
Feeding	0.1	0.6	0	0	0.3	0
Other	0	1	0	0	0	0

**Equi (044)** (Figure 5.17).

As shown in Table 5.22, Equi (044) showed highest site fidelity for Zone 2 but only moderate site fidelity for Zones 2 and 3 and low for Zones 1 and 5 to feed (Figure 5.18). Zones 1, 2 and 3 were used for other behavioural events. This dolphin was the only one to be seen in four different zones.

**Table 5.22- Sighting Index by Zone ( $SI_{ZONE}$ ) of individual Equi (044) divided between feeding and other behavioural events from 2004- 2006 and 2009-2010.**

<b>Equi (044)</b>	<b>Zone 1</b>	<b>Zone 2</b>	<b>Zone 3</b>	<b>Zone 4</b>	<b>Zone 5</b>	<b>Zone 6</b>
Feeding	0.17	0.33	0.33	0	0.17	0
Other	0.14	0.72	0.14	0	0	0

**Bruj (015)** (Figure 5.19).

As shown in Table 5.23, Bruj (015) showed high site fidelity for Zone 2 and moderate site fidelity for Zone 3 overall and to feed (Figure 5.20). Only Zone 2 was used for other behavioural events.

**Table 5.23- Sighting Index by Zone ( $SI_{ZONE}$ ) of individual Bruj (015) divided between feeding and other behavioural events from 2003- 2006 and 2009-2010.**

<b>Bruj (015)</b>	<b>Zone 1</b>	<b>Zone 2</b>	<b>Zone 3</b>	<b>Zone 4</b>	<b>Zone 5</b>	<b>Zone 6</b>
Feeding	0	0.64	0.27	0	0.09	0
Other	0	1	0	0	0	0

## 5.6 Discussion

The data from this study show that some individual Guiana dolphins use the southern area of the Gulf of Morrosquillo year after year. All the ten individuals used for this analysis were re-sighted after the three year gap in the effort from 2006 to 2009. Examination of the data used for this analysis show high fidelity for the study area, by some individuals. The northern boundary of the study area is not a physical boundary as it is for the southern border: the Sinú River (Figure 2.3 Chapter 2). Therefore, connectivity between the southern area and the northern area was assumed from the beginning of this study. Ballance (1992) suggested that individual ranges of dolphins were of a minimum of 65 km of coastline. The study area comprised ~ 43km of coastal line, so there is a big probability that the dolphin individuals which use the study site are using as well the habitats in the northern area as it was expected.

Groups of up to ~100 animals have also been reported in the northern Gulf of Morrosquillo by local fishermen (*personal conversation*). The population of individuals that used the study site was estimated to be ~230 dolphins (Chapter 4). The results of this chapter show that some Guiana dolphin individuals show long-term high and moderate site fidelity for some zones within the study site boundaries. The aggregation of dolphins of this species in Cispatá Bay (Zones 1 and 2) has long been reported Bössenecker (1978). He and his team conducted one of the biggest direct captures of *S. guianensis* to date in the shallow waters of Cispatá Bay (Chapter 1).

The data also show that some individuals use the study site regularly, remaining mainly within Zone 2 for up to five consecutive days (Figure 2.3 Chapter 2 and Table 5.1). This behaviour of the species has been observed widely in Brazil, where dolphins stay within very small areas for up to a week (e.g. Santos *et al.* 2001, De Freitas-Azevedo *et al.* 2004, Flores & Bazzalo 2004). Individuals came back to particular zones within the study site boundaries, especially to feed, showing localized patterns of preferential use of some zones for foraging and feeding individuals. Use of feeding habitat by the whole population is analysed in Chapter 3.

Site fidelity has been documented for several coastal dolphin species including bottlenose dolphins (e.g. Wells 1991, Ballance 1992, Connor *et al.* 2000). From these and other studies we know that areas of high site fidelity have two things in common: they are protected from predators and they have abundant food resources. The level of site fidelity may therefore be a function of prey availability. In areas where prey species are abundant, dolphins do not have

to move long distances for foraging (Karczmarski, 1999). This behaviour results in a high level of site fidelity.

The southern area of the Gulf of Morrosquillo is a large estuarine system receiving freshwater input from the Sinú River and creeks. As in any tropical estuarine area, its primary productivity is high and different prey species are abundant year-round (INVEMAR 2005). Foraging is among one of the most predominant behaviours observed in the study area being surpassed only by travelling. There are eight different species of sharks reported to be found inside Cispatá Bay (Figure 2.3 Chapter 2). All of them are endangered due to high catches for human consumption (INVEMAR 2005). The local fishermen fish the sharks when they are still juveniles, so few individuals reach reproductive age (personal observation). Therefore, the shark species that used to be predators of *S. guianensis* in the area are no longer predators.

Hence, the environmental characteristics of this habitat (low predation and high prey density) suggest that individuals may return regularly to the study area because they have higher chances of finding prey without danger of predation. Site fidelity seems to be inversely related to heterogeneity in habitat quality and positively related to the predictability of the outcome (Switzer 1993), meaning foraging or feeding in this case. In a heterogeneous environment like the one in the Gulf of Morrosquillo, it may be possible that the Guiana dolphins remain closer to (or return to) areas where they know they can easily feed. As reported previously by Avila (1995), García & Trujillo (2004), and Dussán-Duque *et al.* (2006) the Guiana dolphins that use the southern area of the Gulf of Morrosquillo, “enter “ the adjacent areas of Cispatá Bay every day in the morning and the afternoon to feed.

However, they do not stay after feeding as has been reported for the majority of populations in Brazil (Santos *et al.* 2001, De Freitas-Azevedo *et al.* 2004, Flores & Bazzalo 2004). The individual movements show that some dolphins use the estuary waters and also waters outside the bay as was reported as well by Rossi-Santos *et al.* 2007. This result provides evidence that this species uses a variety of habitats from the shallow waters inside the bays to the island waters in the northern Gulf. High site fidelity may increase the knowledge of the characteristics of the local environments and allow the individuals to use predictable prey areas as well as to facilitate social interactions among the individuals (Wolf and Trillmich 2007).

This chapter also shows that site fidelity in Guiana dolphins varies among individuals; this may lead to individual differences in foraging and feeding strategies (Chapter 6). The site

fidelity of Guiana dolphins to feeding areas varied individually, but all of the individuals focused on one specific area: Zone 2. Thus, the site fidelity of the animals overlaps intensively in Zone 2 as was also reported by Flores and Bazzalo (2004) for the same species in Brazil. Reasons for individual variability may be endogenous or external (McConnell *et al.* 1999). For example, some Guiana dolphin individuals maybe using the extreme shallow waters of Zone 1 to feed upon prey that hides under the mangrove roots. This behaviour was observed in mother and calf pairs, showing individual specializations and evidence of cultural transmission (Chapter 6). Some other individuals do not go inside Cispatá Bay, but instead used the isobaths to feed. Some of them moved longer distances between the feeding patches than the others.

Site fidelity may cause feeding specializations that can reduce the gene flow in the species influencing the population structure especially of coastal dolphins (Hoelzel 2009). The apparent intrinsic isolation of individuals due to the resources they follow may have important conservation and management implications (Block *et al.* 2007).

## **5.7 Conclusions and implications for conservation**

In Colombia, *S. guianensis* is listed as Vulnerable based on: absence in zones where it was previously reported abundant, isolation due to habitat fragmentation and loss, and declining prey species (Trujillo *et al.* 2006)

Coastal dolphin populations, due to their restricted distribution and a fine-scale population genetic structure, are highly susceptible to environmental changes caused by anthropogenic pressure (Hoelzel 2009). Species with high levels of site fidelity like the Guiana dolphin are vulnerable to population declines due to habitat degradation and loss of coastal habitats. The loss of habitat may increase habitat fragmentation as well as the distances to find appropriate prey. Returning to the same region may not lead to the discovery of suitable habitat resulting in a decrease of the survival probability particularly among habitat specialists (Switzer 1993).

Estimation of the population abundance of the individuals that use the southern Gulf of Morrosquillo (Chapter 4) showed that the density of the Guiana dolphins in the study site is among the lowest ones of its distributional range (Santos *et al.* 2010, Cantor *et al.* 2012).

Potential threats that require monitoring include those related to chemical pollution, boat strikes, bycatches, overfishing, and loss of mangrove areas. These activities may have long-term effects and may operate cumulatively (Whitehead et al 2000). Taking into account that *S. guianensis* is vulnerable in Colombia, more uncontrolled changes in the habitat may seriously affect the fitness of this population in the southern Gulf of Morrosquillo.

Studies about spatial structure enlarge our understanding of how this species uses a patchy heterogeneous complex environment such as the Gulf of Morrosquillo. Evidence of strong site fidelity provides an opportunity to conservation and management agencies to monitor these populations (Shillinger et al 2008). Actions to maintain the population need to include management of anthropogenic pressures outside the study site boundaries; we do not know anything about the populations of *S. guianensis* in Colombia outside the boundaries of this study site. Even though this species is protected by law in Colombia there is a lack of real management action to assure its long term survival through the protection of its habitats.

Further research in areas in the northern area of the Gulf of Morrosquillo and monitoring of the southern areas needs to be conducted to be able to manage the Gulf of Morrosquillo as a whole. There is a need to improve our capacity to provide effective management actions towards the conservation of this species and its habitats in the Gulf of Morrosquillo.

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**Chapter 6 – Cooperative surface foraging and feeding strategies  
of Guiana dolphins in the southern Gulf of Morrosquillo**



## 6.1. Introduction

Cooperative behaviour is described as the action of an animal investing resources in a common interest shared by other group members (Chase 1980). Likewise, cooperation has been defined for dyadic social interactions, as behaviour whose final outcome is increased fitness in all the participants in the behaviour (Busse 1978).

Cooperative group foraging and feeding has been described for some mammalian species, but the majority of them are non-cooperative (Packer & Ruthan 1988). The optimal foraging and feeding strategy for social hunters is one which employs a group size that will maximize the return of energy to every individual in the group (Nudds 1978). Prey and predators share a history of co-evolution (Begon *et al.* 2009) and the evolution of fast-moving prey favoured the evolution of mammalian social hunters (Nudds 1978). Different characteristics of the prey may cause predators to express differing cooperative behaviours. For example, cooperative hunting appear to be a key cause in grouping in species that kill multiple prey in a single effort (Pulliam & Caraco 1984) or when an individual has a low probability of capturing the prey alone due to size (Packer & Ruthan 1988). Therefore, cooperative hunting is favoured when prey capture and handling requires more than one individual and when all the individuals can be satiated (Busse 1978).

Resource selection occurs in a hierarchical way, from the geographical range of a species to a selection of a feeding site by a population or an individual (Manly *et al.* 1993). Feeding habitats are selected by an animal or a population in a complicated way that implies many decisions to be made with the use of as little energy as possible. Successful foraging and feeding strategies may be related to specific eco-geographic variables, group size, prey species size and availability, and specific individuals.

Cooperative feeding has been described for several species of delphinid: killer whales (e.g. Baird *et al.* 1992, Similä 1997, Nøttestad *et al.* 2002), dusky dolphins (e.g. Würsig & Würsig 1980), bottlenose dolphins (e.g. Wells *et al.* 1980, Bel'kovich *et al.* 1991, Nowacek 2002, Torres & Read 2009) and Guiana dolphins (e.g. Avila 1995, Rossi-Santos 1997, Tardin *et al.* 2011) among others. Collective behaviour may enhance individual feeding opportunities in

the encounter of patchy and unpredictable prey (Norris & Dohl 1980). Intraspecific variation in foraging and feeding strategies behaviour has also been documented across diverse species of mammals, but the impact of these specializations on the ecological and social dynamics of the populations has not received much attention (Bolnick et al. 2003).

High site fidelity, can lead to individual differences in the foraging and/or feeding activity of some animal species (individual specializations) depending on the habitat (Hoelzel 2009) (Chapter 5). If they are dependent on different prey types, foraging and or feeding specializations may affect the dispersal pattern behaviour of the species through the social facilitation of such specializations (Hoelzel 2009). Thus, the individuals may engage in cooperative hunting groups to learn certain foraging/feeding techniques, appropriate for certain prey or habitat (Hoelzel 2009) (e.g. cultural transmission of the use of marine sponges by bottlenose dolphins (Krützen *et al.* 2005), bottlenose dolphins acting as “drivers” in cooperative feeding formations (Gazda *et al.* 2005)). Specializations involve learned strategies for finding and feeding on prey with critical temporal and spatial components (Baird & Whitehead 2000). These specializations will result in different foraging strategies (Hoelzel 2009).

*S. guianensis* is an estuarine species (Chapter 1) and expresses strong patterns of habitat selection (Chapter 3), and high site fidelity especially to feeding habitats (Chapter 5). Only one study has previously been conducted in Colombia on this species’ cooperative feeding strategies (Avila 1995). The data analysed in this study represent the most extensive on Guiana dolphins in Colombia. This chapter describes the foraging and feeding strategies of the individuals of this species using the southern Gulf of Morrosquillo. In addition, this chapter explores the relationships between these strategies and eco-geographic characteristics of the feeding areas and prey species. It also explores the specialization of identified individuals (see Chapters 4 and 5) in specific feeding strategies. This study broadens the current knowledge of Guiana dolphin foraging and feeding strategies and their feeding habitats in the southern Gulf of Morrosquillo.

## **6.2. Aim and objectives of the Chapter**

### **6.2.1. General aim**

To explore coordinated surface foraging and feeding strategies of Guiana dolphins in the southern Gulf of Morrosquillo.

### **6.2.2. Objectives**

- Describe the main cooperative foraging and feeding surface strategies of the Guiana dolphins using the study area and its effects on the use of feeding habitat.
- Identify which combination of the measured eco-geographic variables influence the foraging and feeding behaviours of the Guiana dolphins in the study area.
- Explore individual specialization in specific foraging and/or feeding strategies.

## **6.3. Materials and Methods**

General survey and data collection methods are described in Chapter 2.

## **6.4. Foraging and feeding strategy data and analysis**

### **6.4.1. Data collection**

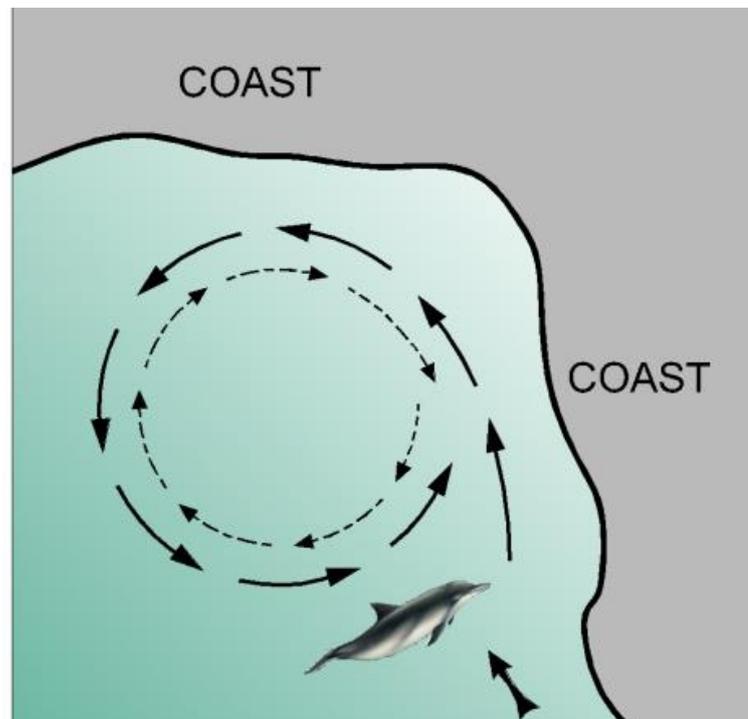
From 2002-2006 and 2009-2010, 395 boat surveys were conducted in the study area. This fieldwork yielded 318 dolphin sightings with foraging and feeding states observed during 120 of them (see Figure 3.16 in Chapter 3 and Figure 6.1). Data acquired from dolphin foraging and feeding sightings in 2002-2006 and 2009-2010 were used in analysis. The dolphins were followed for periods ranging from a few minutes up to three hours, sampling behavioural data every two minutes using the focal-group sampling methodology (Altmann 1974). Only one



indeterminate, (2) other (*Caranx crysos*, *Arius props*, *Pellona barroweri*, *Trichiurus lepturus*, or *Albula* sp.), and (3) *Mugil* sp. or *Sardinops* sp.

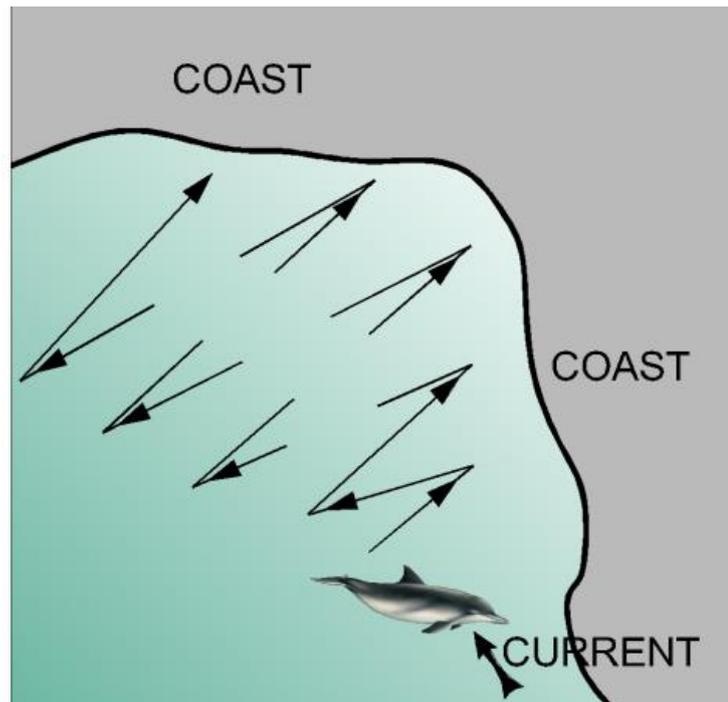
#### 6.4.2. Foraging strategies

- (1) None or dispersed: When the individuals did not express any pattern of aggregation.
- (2) Circle: Dolphins scanning the area making a wide circle. The circle was sometimes clockwise and at other times anti-clockwise. The individuals were not in a specific formation (Figure 6.2).



**Figure 6.2 - Foraging strategy Circle (2) schematic of Guiana dolphins in the Gulf of Morrosquillo.**

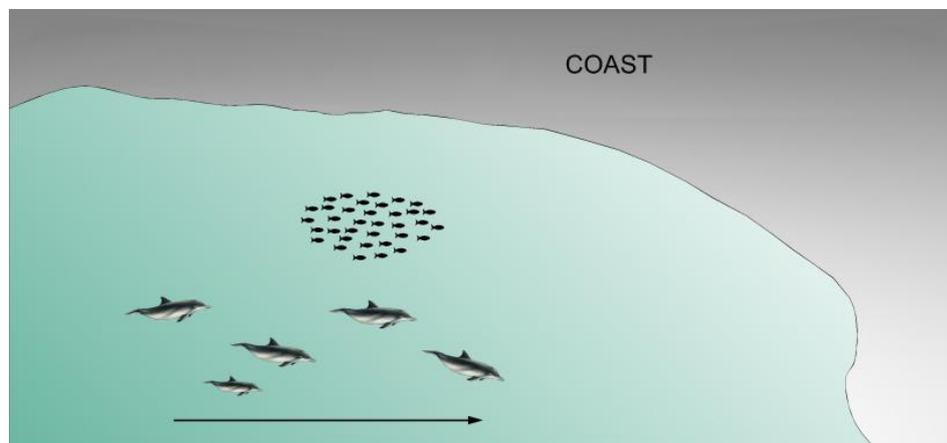
- (3) Zigzag: Dolphins scanning the area, moving towards and away from the coastline in a zigzag pattern. The individuals were not in a specific formation (Figure 6.3).



**Figure 6.3 - Foraging strategy Zigzag (3) schematic of Guiana dolphins in the Gulf of Morrosquillo.**

### 6.4.3 Feeding strategies

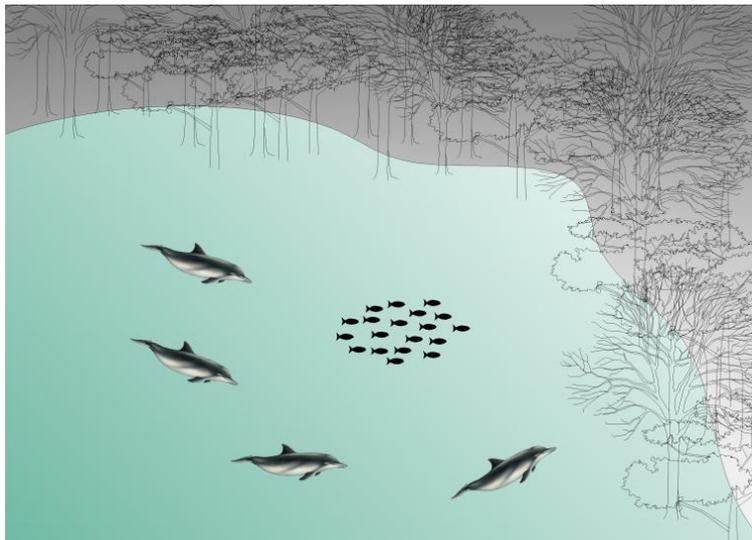
- (1) None or dispersed: When the individuals did not express any pattern of aggregation.
- (2) Against the shore, current or mangrove roots: Dolphins used topographic features of the environment to enhance feeding efficiency. The prey was driven into a tight aggregation and cornered between a physical barrier (e.g. shore, current or mangrove roots). The strategy could last from five minutes to an hour (Figures 6.4 – 6.8).



**Figure 6.4 - Feeding strategy against the shore (2) schematic of Guiana dolphins in the Gulf of Morrosquillo.**



**Figure 6.5 - Feeding strategy against the shore (2) of Guiana dolphins in the Gulf of Morrosquillo. Photograph by Salomé Dussán-Duque.**



**Figure 6.6 - Feeding strategy against mangroves (2) schematic of Guiana dolphins in the Gulf of Morrosquillo.**

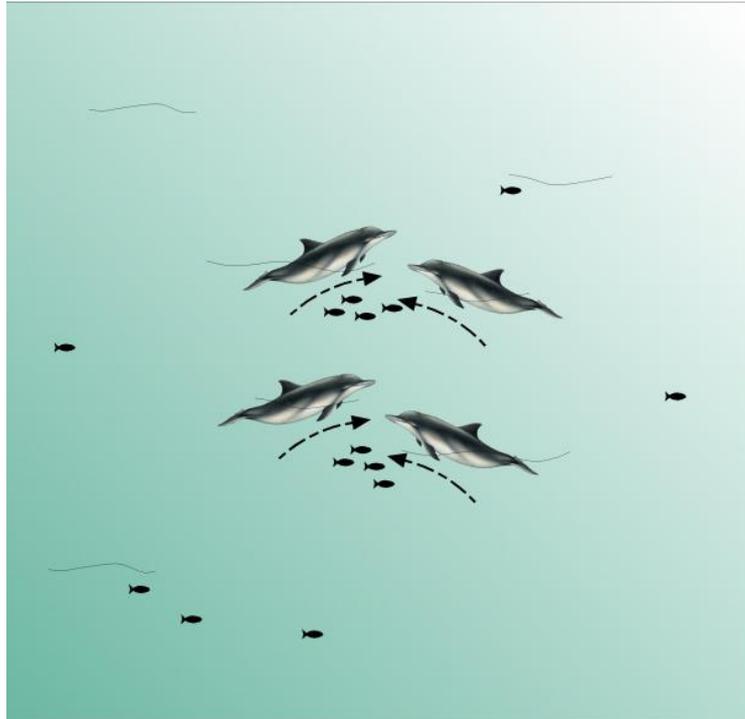


**Figure 6.7 - Feeding strategy against mangrove roots (2) of Guiana dolphins in the Gulf of Morrosquillo. Photograph by Salomé Dussán-Duque.**



**Figure 6.8 - Feeding strategy against the current (2) of Guiana dolphins in the Gulf of Morrosquillo. Photograph by Salomé Dussán-Duque.**

(3) Arch: Dolphins in pairs facing each other presenting synchronized immersions. If more than two pairs were present then they separated by less than a meter. Usually up to three pairs cooperatively engaged (Figures 6.9 and 6.10).



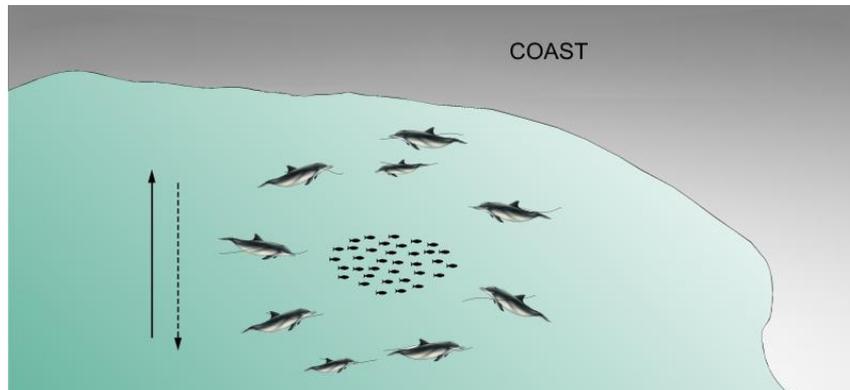
**Figure 6.9 - Feeding strategy arch (3) schematic of Guiana dolphins in the Gulf of Morrosquillo**



**Figure 6.10- Feeding strategy arch (3) of Guiana dolphins in the Gulf of Morrosquillo.**  
*Photograph by Salomé Dussán-Duque.*

(4) Surface circle: Dolphin (7-9) individuals formed a circle ~3m in diameter, with some individuals facing inward and some to the sides. Once the circle was formed the dolphins waited for a couple of seconds at the surface and then did a synchronized dive without exposure of the flukes. The group stayed submerged for ~1:30 minutes then emerged synchronized as well. The strategy was repeated from 30 minutes up to three hours.

There was no fission or fusion with the other sub-groups present in the area (Figures 6.11 and 6.12).



**Figure 6.11-** Feeding strategy surface circle (4) schematic of Guiana dolphins in the Gulf of Morrosquillo.



**Figure 6.12-** Feeding strategy surface circle (4) of Guiana dolphins in the Gulf of Morrosquillo. *Photograph by Salomé Dussán-Duque.*

#### **6.4.4 Model building and fitting**

A main aim of this study was to find out which environmental characteristics may explain best the observed surface foraging and feeding cooperative strategies of *S. guianensis* in the study area.

To determine the nature of the relationships between the foraging and feeding strategies and the eco-geographic variables, generalised linear models (GLMs) were used. A description of

GLMs is given in Chapter 3. All the modelling analysis was conducted in software R 2.15.2 (R Development Core Team 2012).

Binary levels of responses for the foraging and feeding strategies datasets were created in order to model each foraging and feeding strategy separately. Thus, three models were built for the foraging strategies: none, circle and zigzag and four models were built for the feeding strategies: none, against shore, arch and surface circle. Each model estimated the probability of occurrence of each different foraging or feeding strategy as a function of the environmental covariates: season, zone, depth, group size and type of prey. Data were pooled over years. Season (rainy, dry and semi-dry), zone, and type of prey: (1) indeterminate, (2) other (*Caranx crysos*, *Arius props*, *Pellona barroweri*, *Trichiurus lepturus* or *Albula* sp.), and (3) *Mugil* sp. or *Sardinops* sp., were included in the models as factors.

GLMs with binomial error structure and logit link function were run for each foraging strategy and each feeding strategy. The logit link function maps the response data onto linear space and ensures the model predictions are bounded by zero and one.

Over-dispersion in the residuals was investigated by running models with a quasi-binomial error structure. Over-dispersion was detected in two of the four of the feeding models: feeding model level 3 (arch) and feeding model level 4 (surface circle). For these two response variables, the over-dispersion in the residuals of the models was accounted for by using a quasi-binomial GLM. The residuals of the three foraging models and the other two feeding models did not show any over-dispersion so binomial GLMs were used for these models.

For each of the seven models an analysis of variance (ANOVA) was conducted to test for statistical significance of the covariates.

#### **6.4.5 Individual specialization**

As a detailed example, the sighting history of one individual (Luna-018, Figure 6.13) during foraging and feeding events was analysed to investigate intraspecific specialization of Guiana dolphins using the study area. Luna was presumed to be a male because he was never seen with a calf throughout the study period. Luna was the dolphin with the highest sighting frequency (see Chapters 4 and 5) and for this reason was chosen for this analysis. Out of 30 sightings during the study period, Luna was seen foraging and/or feeding 17 times in the study area. Lack of time prevented similar analysis of other frequently sighted dolphins.



**Figure 6.13-** Luna-018 feeding state in August 2005 in the Gulf of Morrosquillo. *Photograph by Salomé Dussán-Duque*

## 6.5 Results

Boat surveys were conducted on 395 days in the study area during the three climatic seasons, rainy, dry and semi-dry, in 2002-2006 and 2009-2010. Of 318 dolphin sightings, 120 included observation of foraging and feeding states (37.7%). The study area was divided into six zones, from the first mouth of the Sinú River (Boca Mireya) to Tolú (Figure 6.1). In Chapter 2, a detail description of the geo-morphological characteristics of each zone is given.

There were 65 foraging and feeding states observed during the rainy season, 50 foraging and feeding states observed during the dry season, and five feeding states observed during semi-dry season.

### 6.5.1 Foraging strategies

Table 6.2 shows the data for the different foraging strategies in relation to the eco-geographic variables measured in the study area, the group size and the prey species.

**Table 6.2 – Summary of the foraging strategies data in relation with environmental covariates, group size and prey type: (1) indeterminate, (2) other (*Caranx crysos*, *Arius props*, *Pellona barroweri*, *Trichiurus lepturus* or *Albula* sp.), and (3) *Mugil* sp. or *Sardinops* sp.**

Foraging strategy	Frequency	Season	Zones 1-6	Depth (m)	Depth (mean)	Group size	Group size (mean)	Prey type and (frequency)
1	26	Rainy and dry	1,2,3,5	1.4-20.4	8.8	2 - 18	7	1(13), 2(6), 3(7)
2	35	All	1,2,3	1.5-18.0	9.5	3 - 38	11	1(7), 2(16), 3(12)
3	59	All	All	2.1-22.2	9.7	2 - 60	10	1(24), 2(14), 3(21)

### 6.5.1.1 Foraging model level 1: none-dispersed

Table 6.3 shows the summary results for the model of foraging level 1: none-dispersed. None of the covariates were significant.

Table 6.4 shows the summary results for the analysis of variance for the foraging model level 1: none-dispersed. Group size had a marginally significant (negative) effect on the probability of this foraging strategy occurring, a result that is supported by the data (Table 6.2). None of the other covariates had a significant effect on this foraging strategy.

**Table 6.3 - Summary results for the foraging model level 1: none-dispersed. Prey, season and zone were modelled as factors.**

<b>Variable</b>	<b>coefficient</b>	<b>SE</b>	<b>p</b>
(Intercept)	-0.029	0.9096	0.975
Group size	-0.077	0.0473	0.104
Depth	-0.049	0.0629	0.434
Prey 2	-0.503	0.6333	0.427
Prey 3	-0.522	0.654	0.425
Dry season	0.278	0.530	0.601
Semi-dry season	-15.81	1970.6	0.994
Zone 2	-0.158	0.978	0.872
Zone 3	0.773	0.983	0.432
Zone 4	-16.58	1579.2	0.992
Zone 5	0.753	1.134	0.507
Zone 6	4.089	4419.8	0.999

**Table 6.4 - Summary of the ANOVA results for the foraging model level 1: none-dispersed. Significance code: · 0.1 < p < 0.1.**

<b>Variable</b>	<b>Chi-sq</b>	<b>p</b>	<b>Significance</b>
Group size	3.44	0.064	·
Depth	0.62	0.430	
Prey	0.99	0.611	
Season	1.69	0.430	
Zone	7.31	0.198	

### 6.5.1.2 Foraging model level 2: circle

Table 6.5 shows the summary results for the model of foraging level 2: circle (Figure 6.2). Table 6.6 shows the summary results for the analysis of deviance for the foraging model level 2: circle. The covariates group size, prey and zone had a significant effect on the probability of this foraging strategy occurring.

Group size had a slight positive effect on the probability of this foraging strategy (circle) occurring (Table 6.5). Type of prey had a strong effect as show by the variation in the coefficients. Prey type 2 (other) had a stronger effect than prey type 3 (*Mugil* sp. or *Sardinops* sp.); both effects were positive relative to prey type 1 (indeterminate), the effect of which is included in the intercept (Table 6.5). Zone had a strong effect on this foraging strategy. The effect of all zones was negative relative to zone 1 (included in the intercept). The effects of zones 2 and 3 were significant (Table 6.5).

**Table 6.5 - Summary results for the foraging model level 2: circle. Prey, season and zone were modelled as factors. Significance codes: \*  $0.01 < p < 0.05$ ; \*\*  $0.001 < p < 0.01$ .**

<b>Variable</b>	<b>coefficient</b>	<b>SE</b>	<b>p</b>	<b>Significance</b>
(Intercept)	-0.742	0.8600	0.388	
Group size	0.065	0.0321	0.041	*
Depth	0.027	0.0598	0.649	
Prey 2	1.793	0.6086	0.003	**
Prey 3	0.421	0.6393	0.510	
Dry season	0.282	0.5310	0.595	
Semi-dry season	1.412	1.141	0.216	
Zone 2	-2.177	0.8899	0.014	*
Zone 3	-3.114	1.1179	0.005	**
Zone 4	-18.426	1525	0.990	
Zone 5	-1.716	1.0717	0.109	
Zone 6	-22.954	3956	0.995	

**Table 6.6 - Summary of the ANOVA results for the foraging model level 2: circle. Significance codes: \*  $0.01 < p < 0.05$ ; \*\*  $0.001 < p < 0.01$ .**

Variable	Chi-sq	p	Significance
Group size	4.15	0.042	*
Depth	0.21	0.430	
Prey	9.96	0.006	**
Season	1.57	0.430	
Zone	17.84	0.002	**

### 6.5.1.3 Foraging model level 3: zigzag

Table 6.7 shows the summary results for the foraging model level 3: zigzag (Figure 6.3). Table 6.8 shows the summary results for the analysis of deviance for the foraging model level 3: zigzag. Zone had a highly significant effect on the probability of this foraging strategy occurring and prey type had a marginally significant effect.

All zones had a strong positive effect on this foraging strategy relative to zone 1 (effect included in the intercept). The effects of zones 2 and 3 were significant (Table 6.7). Prey type 2 (other) had a marginally significant negative effect relative to prey type 1 (included in the intercept) (Table 6.7).

**Table 6.7 - Summary results for the foraging model level 3: zigzag. Prey and zone were modelled as factors. Significance codes: ·  $0.1 < p < 0.1$ ; \*  $0.01 < p < 0.05$ .**

Variable	coefficient	SE	p	Significance
(Intercept)	-1.546	0.9286	0.096	·
Group size	-0.010	0.0283	0.710	
Depth	0.015	0.0509	0.757	
Prey 2	-0.982	0.5235	0.060	·
Prey 3	0.153	0.5287	0.771	
Dry season	-0.426	0.4573	0.351	
Semi-dry season	-0.508	1.0962	0.643	
Zone 2	2.147	0.9437	0.023	*
Zone 3	2.011	1.0004	0.044	*
Zone 4	19.59	1569.2	0.990	
Zone 5	1.056	1.1036	0.338	
Zone 6	19.88	3956.2	0.996	

**Table 6.8 - Summary of the ANOVA results for the foraging model level 3: zigzag. Significance codes: · 0.1 < p < 0.1; \*\*\* p < 0.001.**

Variable	Chi-sq	p	Significance
Group size	0.14	0.711	
Depth	0.09	0.757	
Prey	4.76	0.093	·
Season	0.96	0.620	
Zone	20.8	0.000	***

### 6.5.2 Feeding strategies

Table 6.9 shows the data for the different feeding strategies states in relation to the eco-geographic variables measured in the study area, the group size and the prey species.

**Table 6.9 – Summary of the feeding strategies data in relation to environmental covariates, group size and prey type: (1) indeterminate, (2) other (*Caranx crysos*, *Arius proops*, *Pellona barroweri*, *Trichiurus lepturus* or *Albula* sp.), and (3) *Mugil* sp. or *Sardinops* sp.**

Feeding strategy	Frequency	Season	Zones (1-6)	Depth (m)	Depth (mean)	Group size	Group size (mean)	Prey type and (frequency)
1	2	Rainy	2 and 5	2.4-22.2	9	2 - 3	3	1(2)
2	35	All	1 - 5	1.2 - 15.2	8	2 - 27	8	1(9), 2(12), 3(14)
3	47	All	1 - 5	1.4 - 20.4	9.3	2 - 28	10	1(16),2(15),3(16)
4	36	All	All	8.0-10.0	9	2 - 60	13	1(17), 2(8), 3(11)

#### 6.5.2.1 Feeding model level 1: none-dispersed

Table 6.10 shows the summary results for the model of feeding level 1: none-dispersed. None of the covariate terms were significant. Table 6.11 shows the summary results for the analysis of deviance for the model. Group size had a significant negative effect on the probability of occurrence of this feeding strategy.

**Table 6.10 - Summary results for the feeding model level 1: none-dispersed. Prey, season and zone were modelled as factors.**

<b>Variable</b>	<b>coefficient</b>	<b>SE</b>	<b>p</b>
(Intercept)	-15.46	28350	1
Group size	-0.721	0.5792	0.213
Depth	-0.658	1.1150	0.555
Prey 2	-20.270	17200	0.999
Prey 3	-21.160	13220	0.999
Dry season	-23.090	12510	0.999
Semi-dry season	-9.545	44120	1
Zone 2	23.430	28350	0.999
Zone 3	-1.941	35660	1
Zone 4	19.770	55870	1
Zone 5	22.650	28350	0.999
Zone 6	73.870	141700	1

**Table 6.11 - Summary of the ANOVA results for the feeding model level 1: none-dispersed. Significance codes: \* 0.01 < p < 0.05.**

<b>Variable</b>	<b>Chi-sq</b>	<b>p</b>	<b>Significance</b>
Group size	4.84	0.028	*
Depth	0.73	0.394	
Prey	1.19	0.552	
Season	3.69	0.158	
Zone	1.59	0.903	

### 6.5.2.2 Feeding model level 2: against (shore, current or mangrove roots)

Table 6.12 shows the summary results for the feeding model level 2: against. Table 6.13 shows the summary results for the analysis of deviance for the model. Group size had a marginally significant negative effect on the probability of this feeding strategy occurring. Overall, zone did not have a significant effect on this feeding strategy but two zones, 2 and 4, had a marginally significant negative effect relative to zone 1 (included in the intercept) (Table 6.12). Similarly, overall, prey type did not have a significant effect on this feeding strategy but prey type 2 had a significant effect relative to prey type 1 (included in the intercept) (Table 6.12).

**Table 6.12 - Summary results for the feeding model level 2: against. Prey, season and zone were modelled as factors. Significance codes: · 0.1 < p < 0.1; \* 0.01 < p < 0.05.**

<b>Variable</b>	<b>coefficient</b>	<b>SE</b>	<b>p</b>	<b>Significance</b>
(Intercept)	0.911	0.877	0.299	
Group size	-0.075	0.043	0.083	·
Depth	-0.079	0.064	0.212	
Prey 2	1.277	0.616	0.038	*
Prey 3	0.554	0.61	0.364	
Dry season	0.757	0.527	0.151	
Semi-dry season	1.498	1.186	0.206	
Zone 2	-1.563	0.89	0.079	·
Zone 3	-1.540	0.947	0.104	
Zone 4	-2.558	1.326	0.054	·
Zone 5	-1.402	1.074	0.192	
Zone 6	-12.926	1455	0.993	

**Table 6.13 - Summary of the ANOVA results for the feeding model level 2: against. Significance codes: · 0.1 < p < 0.1**

<b>Variable</b>	<b>chi-sq</b>	<b>p</b>	<b>Significance</b>
Group size	3.57	0.059	·
Depth	1.61	0.205	
Prey	4.58	0.101	
Season	3.06	0.217	
Zone	5.38	0.371	

### 6.5.2.3 Feeding model level 3: arch

Table 6.14 shows the summary results for the feeding binary model level 3: arch. None of the covariate terms were significant. Table 6.15 shows the summary results for the analysis of deviance for the model.

Zone had a highly significant effect on the probability of this feeding strategy occurring (Table 6.15). The effects of zones 2-5 were positive but the effect of zone 6 was negative

relative to zone 1 (effect included in the intercept) (Table 6.14). However, none of the terms for individual zones were significant. Type of prey had a marginally significant effect on this feeding strategy (Table 6.15). Prey type 3 (anchovies or sardines) had a stronger positive effect than prey type 2 (other) relative to prey type 1 (effect included in the intercept) but neither of these terms were significant (Table 6.14).

**Table 6.14 - Summary results for the feeding model level 3: arch. Prey, season and zone were modelled as factors.**

<b>Variable</b>	<b>coefficient</b>	<b>SE</b>	<b>p</b>
(Intercept)	-0.916	0.8321	0.271
Group size	-0.008	0.0283	0.776
Depth	-0.041	0.0513	0.423
Prey 2	0.083	0.5003	0.869
Prey 3	0.284	0.5113	0.578
Dry season	-0.530	0.4373	0.226
Semi-dry season	-1.272	1.2180	0.296
Zone 2	1.399	0.8577	0.103
Zone 3	1.070	0.9220	0.246
Zone 4	0.645	1.1440	0.573
Zone 5	0.672	1.0250	0.512
Zone 6	-12.620	1455.00	0.993

**Table 6.15 - Summary of the ANOVA results for the feeding model level 3: arch. Significance codes: · 0.1 < p < 0.1; \*\*\* p < 0.001.**

<b>Variable</b>	<b>chi-sq</b>	<b>p</b>	<b>Significance</b>
Group size	0.14	0.711	
Depth	0.09	0.757	
Prey	4.76	0.093	·
Season	0.96	0.620	
Zone	20.77	<0.001	***

### 6.5.2.3 Feeding model level 4: surface circle

Table 6.16 shows the summary results for the feeding model level 4: surface circle. Table 6.17 shows the summary results for the analysis of deviance for the model. Group size and depth had a significant positive effect on the probability of this feeding strategy occurring. Overall, zone did not have a significant effect on this feeding strategy but zone 4 had a marginally significant positive effect relative to zone 1 (included in the intercept) (Table 6.16).

**Table 6.16 - Summary results for the feeding model level 4: surface circle. Prey, season and zone were modelled as factors. Significance codes: · 0.1 < p < 0.1; \* 0.01 < p < 0.05.**

Variable	coefficient	SE	p	Significance
(Intercept)	-3.158	1.2621	0.012	*
Group size	0.064	0.0320	0.045	*
Depth	0.113	0.0572	0.048	*
Prey 2	-0.794	0.5786	0.170	
Prey 3	-0.622	0.5864	0.289	
Dry season	0.274	0.4964	0.581	
S-d season	0.052	1.3288	0.969	
Zone 2	0.619	1.2198	0.612	
Zone 3	0.965	1.2834	0.452	
Zone 4	2.392	1.4159	0.091	·
Zone 5	1.208	1.3362	0.366	
Zone 6	13.893	1455.40	0.992	

**Table 6.17 - Summary of the ANOVA results for the feeding model level 4: surface circle. . Prey, season and zone were modelled as factors. Significance codes: \* 0.01 < p < 0.05.**

Variable	chi-sq	p	Significance
Group size	4.34	0.037	*
Depth	4.13	0.042	*
Prey	2.33	0.313	
Season	0.31	0.856	
Zone	5.05	0.409	

### 6.5.2.4 Individual specialization: Luna-018

Table 6.18 shows the summary results from the foraging and feeding strategies expressed by Luna in the southern Gulf of Morrosquillo from 2003-2006 and 2009-2010. This individual dolphin had a sighting history of long term fidelity to the study site, being sighted 30 times (see Chapter 4) in the study area (see Figure 5.2 in Chapter 5). He was seen 17 times involved in foraging and feeding strategies (see Table 5.14 in Chapter 5) five in the dry season and 12 during the rainy season.

**Table 6.18 - The foraging and feeding history of individual Luna-018 from 2002-2006 and 2009-2010 in the southern Gulf of Morrosquillo. Season 1 - rainy season; season 2 - dry season.**

Foraging strategy	Frequency	Season (frequency)	Zone	Depth (m)	Group size	
1: None -dispersed	2	1 (1)	5	3	12	
		1 (1)	1	1.2	4	
2: Circle	10	1 (7)	2	1.5-2.3	6	
		2 (3)	1	2.5-18	10 to 38	
3: Zigzag	5	1 (4)	2	4.9-11	5 to 15	
		2 (1)	2	4.7	7	
Feeding strategy	Frequency	Season (frequency)	Zone	Depth (m)	Group size	Prey
1: None -dispersed						
2: Against	5	1 (2)	1	1.2-2.5	4 to 10	3
		2 (3)	1	1.5-2.3	6	3
3: Arch	8	1 (7)	2	4.9-15.5	7 to 28	1(3), 2(3), 3 (1)
		3 (1)	2	4.7	5	3
4: Surface circle	4	1 (4)	2(3)	2.4-18.0	24-38	1(1), 2(1), 3(1)
			5	3	12	1

As seen in Table 6.18 Luna seems to be a cooperative forager and hunter only during the rainy and dry seasons in zones 1, 2 and 5, but mostly in zone 2 (see Figure 5.2 and Table 5.14 in Chapter 5). This individual mostly engaged in the cooperative foraging strategy circle (Figure 6.2) in very shallow waters (< 2.5m depth) and an average group size of 6 individuals. During feeding events this dolphin joined cooperative groups using mainly the strategies of arch and against (Figures 6.4 and 6.9). Both of these strategies were used only in zones 1 (against strategy) and 2 (arch strategy) (see Figure 5.2 and Table in Chapter 5) during the rainy and dry seasons. The arch strategy was used in waters of >5m depth and by groups of 7 to 28 individuals. It was used mainly with prey type 2 (other: *Caranx crysos*,

*Arius proops*, *Pellona barroweri*, *Trichiurus lepturus* or *Albula* sp.). In contrast, the against feeding strategy was used in very shallow waters < 2.5m by groups of 4-10 individuals and it was used uniquely with prey type 3: *Mugil* sp. or *Sardinops* sp.

#### 6.5.2.5 Stomach contents

During the study years there were two individuals accidentally caught in artisanal gillnets that were set across channels inside Cispata Bay (Figure 6.1). Necropsies were conducted and the stomach contents were retrieved to be analyzed by Hector Saenz (Ichthyologist from the Instituto de Investigaciones Marinas y Costeras de Colombia, INVEMAR).

Food items retrieved, together with associated data on the specimens are listed in Table 6.19

**Table 6.19 – Food items retrieved from the stomachs of *S. guianensis* from the southern Gulf of Morrosquillo.**

Field code	Stomach contents	Sex	Body length (cm)	Weight (kg)	Collection date	Locality
GDMCB1	2 <i>Caranx crysos</i>	F	1.86	68.7	01-Dec-03	CB
GDMCB2	3 Engraulidae 1 Albulidae	M	1.65	45	13-Mar-04	CB

#### 6.5.2.6 Interspecific feeding associations

The feeding states of Guiana dolphins using the Gulf of Morrosquillo were accompanied 87% of the time by the sea birds of the species *Fregata magnificens* and *Sula leucogaster*. The birds were usually flying over the dolphins groups and feeding on the prey that the dolphins were bringing up to the surface (Figure 6.14).



**Figure 6.14-** *S. guianensis* in feeding associations with *F. magnificens* and *S. leucogaster* in the southern area of the Gulf of Morrosquillo. Photographs by Salomé Dussán-Duque.

## 6.6 Discussion

Understanding the foraging and feeding ecology of species demands knowledge of how the animals use their feeding habitats on a fine spatial scale (Dill 1987, Similä 1997, Nøttestad *et al.* 2002, Doniol-Valcroze *et al.* 2011).

Good descriptions of cetacean predatory behaviour remain elusive in natural settings, due to the technical difficulties involved in the long-term observations of foraging and feeding. Advances in technology in recent decades have improved our understanding of how cetaceans use their feeding habitats (Nøttestad *et al.* 2002, Nowacek 2002, Bernasconi *et al.* 2011) and much has been learned about the plasticity of their underwater behaviour. Notwithstanding this, delphinids are social mammals that exhibit a broad range of cooperative foraging and feeding techniques (Würsig 1986), some of which can be observed from the surface, at least in part (Torres & Read 2009).

As described in Chapters 1, 4 and 5, *S. guianensis* is characterized by long-term permanency in shallow waters of bays and gulfs (e.g. Avila 1995, Edwards & Schnell 2001, Dussán-Duque & Wells 2007). It also exhibits high site fidelity especially to feeding areas (Chapter 5), as also reported in Brazil (e.g. De O. Santos *et al.* 2001, De Freitas Azevedo *et al.* 2004, Rossi-Santos *et al.* 2007). These characteristics of the species make observation of surface behaviour less demanding than with other species of delphinids.

Social or cooperative hunting among the mammalian species is not as common as might be expected (Packer & Ruthan 1988). As the name implies, it requires a high degree of coordination and division of labour that can only be obtained through communication and

learning (Busse 1978, Chase 1980, Pulliam & Caraco 1984). At the individual level, cooperative feeding should maximize the energy return to the individual involved within the group (individual fitness) (Nudds 1978).

The results of this chapter have identified, for first time, those eco-geographic features that influence foraging and feeding strategies used by Guiana dolphins in the study site and described the adaptations and individual specializations related to foraging and feeding. These results should help inform ecological understanding and conservation management of this and similar species in other areas.

### **6.6.1 Observed data and models**

The models in this chapter were fitted to the observed data collected during the surveys conducted in the study area from 2002-2006 and 2009-2010 (see Chapter 2). Because the data were collected at a small spatial scale during a long-term study, this allowed foraging and feeding strategies of Guiana dolphins in the study area to be analysed at a fine scale. Guiana dolphins are characterized as a coastal, non-migratory species with a high site fidelity to specific areas throughout their distribution (Da Silva *et al.* 2010), so fine scale modelling of cooperative foraging and feeding strategies is highly appropriate. This work should also help identify core relationships for species with similar characteristics to *S. guianensis*.

### **6.6.2 Zone**

The effect of zone on the foraging and feeding strategies expressed by the Guiana dolphins in the study area was strong in several of the models, indicating that the particular site within the study area influenced the selection of their cooperative strategies. The results of Chapter 3 show that the dolphins were not observed feeding in all the zones, thus expressing a clear selection of the feeding habitats. Some strategies were present in some zones but absent in others. Zone had a significant effect on foraging levels 2 and 3: circle and zigzag. There was a significantly lower probability of circle foraging behaviour and a significantly higher probability of zigzag foraging behaviour in zones 2 and 3 (Tables 6.5 and 6.7). For feeding, zone had a significant overall effect on the arch strategy but the positive effect for zones 2-5 and the negative effect for zone 6 were not significant (Table 6.14).

The zones in the study area present different eco-geographical characteristics (Chapters 2 and 3) (e.g. depth, currents, sediments, primary productivity) that may influence the dolphins'

expression of certain techniques. For example, the waters in zone 2, due to the direction of the current, are highly productive estuarine waters in which prey species of Guiana dolphins are present year-round (Parra 1996, INVEMAR 2002, 2003). In addition, this zone has, in Punta Terraplén (Figure 2.3), a channel caused by the influence of the oceanic current flowing against the coast (Patiño-Corredor & Flórez-Amaya 1993). This channel may confer an advantage to the foraging and/or feeding strategies displayed by Guiana dolphins in the study site. This underwater channel, that is not visible from the surface, runs parallel to the coast in zone 2. The physical form of the channel may facilitate the zigzag strategy during foraging if the prey is moving inside the channel and making quick turns (e.g. prey type 3: anchovies or sardines). In addition, it may facilitate the capture of the prey due to the change in depth, basically “trapping” the prey and offering the dolphins a better control of their movements.

### 6.6.3 Group size

There were some significant effects of group size on the foraging and feeding strategies expressed by the Guiana dolphins in the study area. For foraging strategies, there was a marginally significant negative effect on none/dispersed foraging, but a positive effect on circle foraging. For feeding strategies, there were negative effects on none/dispersed and against feeding but a positive effect on surface circle feeding.

This highlights the importance of one of the key factors driving cooperative hunting in mammalian species: group size. The influence of group size has been widely studied in cooperative hunters including delphinids (e.g. Busse 1978, Nudds 1978, Chase 1980, Norris and Dohl 1980, Pulliam and Caraco 1984).

As the results of Chapter 3 show, the group size of Guiana dolphins varied from 1 to 60 individuals in the southern Gulf of Morrosquillo. The mean group size was nine individuals, which is typical for this species (Avila 1995, De O. Santos & Rosso, Dussán-Duque *et al.* 2003, 2006, Dussán-Duque & Wells 2007, 2007, Garcia 1998, Garcia & Trujillo 2004, Flores & Bazalo 2004, Rossi-Santos *et al.* 2010). For specific details of group sizes in the study area refer to Chapter 3.

The data presented here show (Tables 6.2 and 6.9) that both foraging and feeding strategies of the dolphins in this study area are highly influenced by group size. When smaller groups were foraging (range 2-18; mean 7) or feeding (range 2-3; mean 3), the strategies were absent

presenting no spatial aggregation or organization that may indicate a cooperative strategy. Special foraging and feeding strategies required a certain number of dolphins involved. For circle and zigzag foraging the mean group size was 11 and 10, respectively. For against, arch and surface circle feeding the mean group size was 8, 10 and 13, respectively. The more organized the strategy the higher the numbers of dolphins involved in it (Tables 6.2 and 6.9). As described by Nudds (1978), group size in social hunters is shaped by finding the balance between the cooperative effects among the individuals involved in the hunt and the competition for resources at the individual level.

The optimal group size in cooperative hunters has been reported for different predators and varies highly between the species. Larger groups are energetically more efficient when abundant or larger prey is hunted (Nudds 1978, Pulliam & Caraco 1984). However, per capita food availability attains a maximum at moderate group sizes (Pulliam & Caraco 1984). Packer & Ruthan (1988) described that the hunting ability of the individuals involved in a cooperative hunt must be equal in order for the predator to hunt in a truly cooperative manner. The advanced strategies shown by the dolphins in this study area may require a level of organization possible only for an optimal number of individuals in the group.

As part of this study, vocalisations of Guiana dolphins were sampled during 2009 in the study site. One of the results was that this species is highly vocal while cooperatively feeding (Bazúa-Durán *et al.* 2009). This suggests that communication between the individuals involved in the hunt is important. Group hunting success is expected to increase with group size (Busse 1978) but the individuals need to be able to coordinate their behaviour in response to each other's actions (Chase 1980).

Group size may also influence the rate at which patches of food are discovered in uncertain environments with a fast mobile prey (Pulliam & Caraco 1984). A food patch is a place where animals feed and in patch selection models (Krebs and McCleery 1984) finding these patches through efficient foraging strategies is energetically important. The higher the number of the individuals involved in the search, the higher the probability to find a patch. If the prey in the patch is abundant, and the group is big enough to organize the hunt, energy does not need to be expended moving between patches. Once a patch of food is located, the group may transform, sometimes breaking into smaller ones (fission). This may be due to prey dispersing and the dolphins having a better control over the prey if aggregated in smaller

groups. It may also be due to the need of every individual to maximize the return of energy during cooperative hunting (Nudds 1978).

Hence, group size is probably the most important factor in cooperative hunts. The different foraging and feeding strategies displayed by the Guiana dolphins in this study site are strongly linked with group size as shown by the results. The results are noteworthy for highlighting the complex social organization of this species required in organizing specific foraging and feeding strategies in response to a highly mobile prey species.

#### 6.6.4 Prey

Prey availability is a driving force in the distribution, movements, behaviour and habitat selection of predators (Halpin *et al.* 1988, Costa *et al.* 1989). It is to be expected that, over time, predators acquire knowledge about the location and quality of the prey and the travel distances between the patches in order to maximize the feeding states (Krebs & McCleery 1984). Different characteristics of the prey may cause predators to show different strategies in order to hunt the prey in an efficient manner (Packer & Ruthan 1998, Torres & Read 2009).

*S. guianensis* is a small dolphin (maximum length of males 2m (Rosas *et al.* 2010)) specialized in catching small prey species such as: *Mugil* sp. (De O. Santos 2010), *Caranx crysos*, Engrulidae and Albulidae (Dussán-Duque unpublished data). These species are estuarine but also inhabit coastal waters. The estuarine waters of Cispatá Bay represent a “nursery” for several species of fishes, molluscs and crustaceans in their larval and juvenile stages. Several of these species are known to be prey of Guiana dolphins.

The effect of prey type on the foraging and feeding strategies displayed by the Guiana dolphins in the study area was evident in some of the foraging and feeding models. For foraging, circle foraging had a higher probability of occurring and zigzag foraging had a lower probability of occurring when prey type 2 (other) was present, relative to other prey types. For feeding, the against strategy was more likely when prey type 2 was present but prey type was not a significant covariate in the model overall. For arch feeding, prey type was marginally significant overall but no specific prey type was significant.

Table 6.2 shows that the Guiana dolphins forage on different prey in the different zones of the study area. For example, when the prey type was 2: *Caranx crysos*, *Arius proops*, *Pellona barroweri*, *Trichiurus lepturus* or *Albula* sp., the dolphins used foraging strategy circle in zones 1, 2 and 3. When foraging on prey type 3 (anchovies or sardines) the dolphins used the

zigzag strategy in all the zones including zone 4 and 6, which were not used for the other foraging strategies. This may be because this strategy was more effective in capturing the fast moving and turning prey species like sardines or anchovies.

These results shows how the Guiana dolphins adapt, to some extent, their foraging and feeding techniques depending upon the prey species present in the feeding patches. In other studies, this species has been shown to exhibit long term high site fidelity to feeding areas in coastal estuarine waters (De O. Santos *et al.* 2001, De Freitas Azevedo *et al.* 2004, Rossi-Santos *et al.* 2007), indicating a feeding specialization for estuarine prey species.

For feeding strategies (Table 6.9) the pattern in the data between the prey and the strategy was not clear. This may have been because there were several times when the prey type was indeterminate.

#### **6.6.5 Water depth**

*S. guianensis* is characterised as having a costal distribution and being concentrated close to river mouths in estuarine and mangrove areas (M. Di Benedetto *et al.* 2004, Rossi-Santos 2006, Cremer *et al.* 2011) and apparently the species is limited to depths of less than 50m (Fernandes 2005). In Chapter 3, model results show a preference for waters greater than about 3m with a slightly increased preference for waters about 5m deep and between 15-25m.

Depth was significant only for the occurrence or the feeding strategy 4: surface circle, as it is support by the data (Table 6.9). This strategy only occurred when the water depth was between 8m-10m depth. The reason for this result may be that the dolphins may need of certain depth to organize this advance cooperative feeding strategy.

#### **6.6.6 Seasonality**

Guiana dolphins displayed all the different foraging and feeding strategies (except for none/dispersed) during all three climatic seasons as shown in Tables 6.2 and 6.9. The model results showed that season did not influence any of the foraging or feeding strategies. In a mostly stable environment like that present in tropical estuaries (Odum 1971), fluctuations in the distribution and abundance of prey species are almost non-existent. There is no seasonality in fisheries as there is in other areas and prey species are present almost year

round. Therefore, it was not unexpected that the Guiana dolphins using this study site did not express different strategies depending on the climatic seasons.

### **6.6.7 Individual specialization: Luna**

The dolphin named Luna seems to be a cooperative forager and hunter only during rainy and dry season in the feeding habitats of the southern gulf of Morrosquillo. The data show that this dolphin was specialized in the cooperative foraging strategy “circle” in very shallow waters of zones 1 and 2 (inside Cispata Bay) and in feeding strategies “against” and “arch” in groups of dolphins that used these strategies depending on the prey type.

These results are the first to describe foraging and feeding specializations at the individual level for this species. Individual foraging specializations in marine mammals have been reported previously for sea otters (Estes et al. 2003) and bottlenose dolphins (Torres & Read 2009) among others.

The specialization in foraging and feeding strategies will be explored in the future with other individuals in these population, which were seen multiple times but fewer times than Luna. The social and ecological reasons for the high specialization of this dolphin, and potentially others, remain to be explored.

## **6.7 Conclusions**

The principal goal of this chapter was to provide a consistent description of cooperative foraging and feeding strategies displayed in the study area by *S. guianensis* and to improve understanding of the eco-geographic relationships involved in the use of these strategies. The models developed in the chapter indicate that the observational behavioural methods applied in this study were appropriate in capturing some of the environmental features involved in the daily foraging and feeding decisions made by individual dolphins in the study site.

As expected, the data and model results indicated that the cooperative foraging and feeding strategies displayed by this species were influenced by both fixed and temporally varying environmental parameters in the study site. The most important of these covariates were zone, group size and prey type.

Through the results we can conclude that the use of foraging and feeding behavioural models can provide a fine scale description of the decisions made by the individuals of a population with respect to their environment. Through the modelling of feeding habitats in Chapter 3 it was highlighted that the distribution of Guiana dolphins in the southern area of the gulf may be driven by that of their prey species. Specialization in certain foraging and feeding strategies would maximize the use of the habitat of this species in this area.

The work presented in this chapter is the first attempt to explore the cooperative foraging and feeding strategies of Guiana dolphins in the study area, and the use of modelling as a tool to investigate the relationships between these strategies and eco-geographic variables. The results support the importance of transmission of knowledge, cooperative hunting, learning, and specialization in the highly complex societies of some species of cetaceans.

The results are noteworthy for highlighting the behavioural foraging and feeding plasticity of this species that should be important for informing the long-term conservation of this species and its habitats within the Gulf of Morrosquillo.

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**Chapter 7 – General discussion, conservation implications and future directions**



The Guiana dolphin (*Sotalia guianensis*) is found mainly in estuaries, bays and other protected shallow coastal waters (Edwards & Schnell 2001, M.C. de O. Santos *et al.* 2001, Dussán-Duque *et al.* 2003, Flores 2003, Da Silva *et al.* 2010). This species is listed as insufficiently known (Data Deficient) by the International Union for Conservation of Nature (IUCN 2013). Since 1997, Colombia, as many other countries, has its own national system for classifying species at risk of extinction. Based on informal reports of absence of the species where it was previously reported abundant and isolation due to habitat fragmentation and loss, it was classified as Vulnerable (Trujillo *et al.* 2006). In the Gulf of Morrosquillo in the Caribbean Sea of Colombia, only one previous study has been conducted on this species (Avila 1995). At present, this is the longest ongoing study on coastal dolphins in the country. Observed threats for the species in the southern area of the gulf are: regional changes in prey abundance (IVEMAR 2005), progressive loss of habitat (INVEMAR 2002, Sánchez-Páez *et al.* 2004), contaminants (REDCAM 2005) including sporadic oil spills, direct capture for national illegal marketing and display (Dussán-Duque *et al.* 2003), and incidental entanglement in gillnets (Avila 1995, Dussán-Duque 2003). Outside the boundaries of the southern Gulf of Morrosquillo there is no information the species' status.

The main goal of this study was to systematically advance understanding of the ecology of *Sotalia guianensis* and its habitats in the southern area of the Gulf of Morrosquillo to inform its conservation. The gulf is an open estuarine ecosystem that used to have the most extensive mangrove forest in Colombia. As for many of the other estuarine mangrove areas around the world, anthropogenic pressure has caused this ecosystem to be considered endangered.

In this chapter, the results of this study, its conservation implications and future directions are discussed.

### **7.1 Ecology of Guiana dolphins in the southern Gulf of Morrosquillo**

The most recent abundance estimate of Guiana dolphins using the southern Gulf of Morrosquillo (2010) for dry and rainy seasons respectively, are 225 (95% CI: 118-426) and 232 (95% CI: 127-246) (Chapter 4). Thus, there are an estimated approximately 230 (CV= 0.33) dolphins of this species using the southern area of the Gulf of Morrosquillo during all climatic seasons (Chapters 3 and 4). Unfortunately, it is not possible to compare this current

estimate of abundance with that estimated by Avila (1995) because different methodologies were used. Estimates of abundance of other populations of *S. guianensis* vary from 54 to 1067 individuals using Bays and Gulfs throughout the species range (De O. Santos *et al.* 2010).

The constant annual survival rate is estimated at 0.948 (95% CI = 0.876-0.980) (Chapter 4). A high survival rate was expected for Guiana dolphins using the study site, based on knowledge of longevity (30+ years) (Rosas *et al.* 2010). This estimated survival rate is consistent with those for other similarly long-lived cetacean species, including humpback whales (0.92-0.98) (Buckland 1990, Calambokidis & Barlow 2004, Larsen & Hammond 2004) and bottlenose dolphins (0.92-0.98) (Wells and Scott 1990, Gaspar 2003, Silva *et al.* 2009).

These results from the surveyed area (~310km<sup>2</sup>) show an overall density of 0.74 Guiana dolphins per km<sup>2</sup> (Chapter 4). Comparing this result with the results of density of this species in study areas from Brazil (0.18/km<sup>2</sup>, 0.17/km<sup>2</sup>, 0.70/km<sup>2</sup>, 2.88/km<sup>2</sup>, 7.36/km<sup>2</sup>, 19.0/km<sup>2</sup>) (De O. Santos *et al.* 2010, Cantor *et al.* 2012), the density of Guiana dolphins in this study site is at the low end of the range. Studies in Brazil have reported that Guiana dolphins have a tendency to remain in small areas for long periods of time when the resources are abundant (De O. Santos *et al.* 2010). The ecological reasons for the low density estimated in this study area are unknown. The only previous reports of density of Guiana dolphins in Cispatá Bay come from Bössenecker (1978), which reported that more than 400 individuals of this species use to be present daily in this zone. Traditional Ecological Knowledge of fishermen from this zone reports “so many dolphins that was sometimes difficult to paddle through the water” (*personal communication*). Avila (1995) reported an estimated density of 6.3/km<sup>2</sup> dolphins in Cispatá Bay and adjacent areas. Because of the differences in methodology and area studied, it is not possible to compare Avila’s (1995) results with those in this study. Thus, is not possible to report whether or there has been a real change in the density of Guiana dolphins using the southern Gulf of Morrosquillo. Even the number of dolphins using this area fluctuates from year to year, there is no evidence for either a seasonal difference in abundance or any directional trend in time (Chapter 4).

Guiana dolphins were encountered through the whole study area during all climatic seasons (rainy, dry and semi-dry) (Chapters 3, 4, 5 and 6). Through the fine scale analysis of habitat use and selection of this species in the study site, it is possible to conclude that this species is

present year-round (Chapter 3 and 4), as found in previous studies conducted in the study area (Avila 1995, Garcia 1998, Garcia & Trujillo 2004, Dussán-Duque *et al.* 2003, 2006, Dussán-Duque & Wells 2007) and studies conducted in other areas of their range (De Araujo *et al.* 2001, Edwards & Schnell 2001, Flores 2003, De Freitas *et al.* 2004, Rossi-Santos *et al.* 2010, Hardt *et al.* 2010).

The results also suggested that Guiana dolphins do not use the southern area of the gulf uniformly and that the use of particular zones is related to eco-geographic variables (Chapter 3). There was a clear preference for zones 2, 3, 5 and 6 during all seasons throughout all years (Chapter 3) as shown in previous studies conducted in the area (Bössenecker 1978, Avila 1995, Garcia 1998, Garcia & Trujillo 2004, Dussán-Duque *et al.* 2003, 2006, Dussán-Duque & Wells 2007). This habitat selection is likely to be driven mainly by the distribution of estuarine prey (Rosas 2010) and these zones may encompass the feeding habitat use by this population in the southern area of the gulf (Chapters 3 and 6). This highlights these zones as important habitat within the distribution of Guiana dolphins in the study site. The current distribution shows that there has been a shift from previous use of the zone closest to the river mouth (Zone 4) (Chapter 3), as reported previously by Dussán-Duque & Wells (2007). This change may be related to changes in the natural dynamics of the Sinú River water cycle after the construction of the Urrá I hydroelectric plant, as reported by INVEMAR (2002) and the local human communities (*personal communication*).

The Guiana dolphin individuals use the study area differently depending on the season (Chapters 3, 4 and 5). The southern and northern extremes of the study area are mostly used during the rainy season (Chapter 3). These are the zones closer to the Sinú River, Ciénaga de Mestizos and Ciénaga de la Caimanera the places with the greatest interchange of ocean water with coastal water. This may indicate a different distribution of estuarine prey patches (Rosas 2010) during the dry and rainy seasons.

Dolphins show a preference for waters greater than 3m in depth with a slightly increased preference for waters about 5m deep and 15-25m (Chapter 3) as described in previous studies conducted in other sites throughout their distribution (Flores & Bazalo 2004, De O. Santos & Rosso 2007, Rossi-Santos *et al.* 2010). This result agrees with the results of previous studies in Brazil, which report a distribution of this species within the 50m bathymetry contour (Fernandes 2006). Calves are also distributed inshore (Chapter 3) as reported in previous studies (Avila 1995, Garcia 1998, Garcia & Trujillo 2004, Dussán-Duque *et al.* 2003, 2006,

Dussán-Duque & Wells 2007, Wedekin *et al.* 2007, Cremer *et al.* 2009 and Rossi-Santos *et al.* 2010). Mother and calf pairs were found predominantly along the border between zones 2 and 1 (Cispatá Bay) during the rainy season (Chapter 3). Cispatá Bay used to be the delta of the Sinú River approximately 60 years ago (Chapter 2); this zone is the one within the study site that shows the most characteristics of a mangrove estuarine area. This zone is characterized by very shallow waters <5m and pairs of mothers and calves have been seen feeding in the mangrove roots (magla) (Chapter 6). The rainy season is the climatic season with a greater presence of calves in the study area (Chapter 3). Thus, it seems that even if there is no strong seasonality of births in the study area, as also reported by Avila (1995), there is a small increment in birth rates during the rainy season (Chapter 3). The average group size was nine individuals (Chapter 3), which is typical for this species (Avila 1995, Flores & Bazalo 2004, Rossi-Santos *et al.* 2010). Feeding aggregations were not very common, which may be influenced by the estuarine prey being distributed in small patches (Chapter 3).

Through the results it was possible to confirm that other unmeasured explanatory variables must have influenced the distribution and abundance of Guiana dolphins in the Gulf of Morrosquillo during the surveyed years. It is important to understand that the relationships among environmental variables in an ecosystem may not be direct but some may be proxies for other unmeasured variables (e.g. prey, currents) (Marcot *et al.* 2001, Stenseth *et al.* 2003). Proxy variables can be important because they can be measured more easily than other variables as in this study (Elser *et al.* 2007, Cañadas & Hammond 2008, and Torres *et al.* 2008).

Through the sighting histories of ten individuals with the highest sighting rates during the study period (Chapter 4), it was possible to determine that some Guiana dolphins show long-term high site fidelity for some zones within the study site boundaries (Chapter 5). All the ten individuals used for this analysis were re-sighted after the three year gap in research effort from 2006 to 2009 (Chapter 4). The data also show that some individuals use the study site regularly, remaining mainly within Zone 2 (Cispatá Bay) for up to five consecutive days (Chapter 5). This behaviour of the species has been observed widely in Brazil, where dolphins stay within very small areas for up to a week (e.g. Santos *et al.* 2001, De Freitas-Azevedo *et al.* 2004, Flores & Bazzalo 2004).

Foraging is among one of the most predominant behaviours observed in the study area, being surpassed only by travelling (Dussán-Duque unpublished data). Individuals came back to particular zones within the study site boundaries, especially to feed, showing localized patterns of preferential use of some zones for foraging and feeding (Chapter 5). Site fidelity has been documented for several coastal dolphin species (e.g. Wells 1991, Ballance 1992, Connor et al 2000). From these and other studies we know that areas of high site fidelity have two things in common: they are protected from predators and they have abundant food resources. In areas where prey species are abundant and risk of predation is low, dolphins do not have to move long distances for foraging and/or feeding (Karczmarski, 1999). This behaviour results in a high level of site fidelity. In a heterogeneous environment like the one in the Gulf of Morrosquillo, it may be possible that the Guiana dolphins remain closer to (or return to) areas where they know they can easily feed. As in any tropical estuarine area, its primary productivity is high and different prey species are abundant year-round (INVEMAR 2005). Due to the low risk of shark predation and high prey density, individuals may return regularly to Cispatá Bay and adjacent zones (Chapter 3 and 5).

However, Guiana dolphins do not stay after feeding in the same zones as has been reported for the majority of populations in Brazil (Chapter 5) (Santos *et al.* 2001, De Freitas-Azevedo *et al.* 2004, Flores & Bazzalo 2004). The individual movements show that some dolphins use the estuary waters and also waters outside the bay (Chapters 3, 4 and 5) as also reported by Rossi-Santos *et al.* (2007). This result provides evidence that this species uses a variety of habitats from the shallow waters inside the bays to the island waters in the northern Gulf. Site fidelity in Guiana dolphins in this study area varies among individuals (Chapter 5); this may lead to individual differences in foraging and feeding strategies (Chapter 6). For example, some Guiana dolphin individuals may be using the extremely shallow waters of Zone 1 to feed upon prey that hides under the mangrove roots. This behaviour was observed in mother and calf pairs, showing individual specializations and evidence of cultural transmission (Chapter 6). Some other individuals do not go inside Cispatá Bay, but instead concentrate the feeding at particular depths. Some of them moved longer distances between the feeding patches than the others. The site fidelity of Guiana dolphins to feeding areas varied individually, but all of the individuals focused mainly on one specific area: Zone 2. A similar result was also reported by Flores and Bazzalo (2004) for the same species in Brazil, where feeding occurred in one particular area.

Guiana dolphins in the study area show surface cooperative foraging and feeding strategies display (Chapter 6) as it has been reported previously for the species (Avila 1995, Rossi-Santos). These cooperative behaviours were influenced by both fixed and temporally varying environmental parameters. The most important of these parameters were zone, group size and prey type (Chapter 6). Individual foraging specializations in marine mammals have been reported previously for sea otters (Estes et al. 2003) and bottlenose dolphins (Torres & Read 2009) among others. The results indicated that particular sites within the study area influenced the selection of their cooperative strategies as reported with *T. truncatus* by Torres & Read (2009). Some strategies were present in some zones but absent in others. In addition, when small groups of dolphins were foraging or feeding the strategies were absent. Special strategies required a certain number of dolphins, the more organized the strategy, the higher the number of dolphins involved. Guiana dolphins seem to adapt to some extent their foraging and feeding techniques depending upon the prey species present in the feeding patches.

## **7.2. Conservation implications**

*Sotalia guianensis* is listed as Vulnerable in Colombia based on: absence in zones where it was previously reported abundant, isolation due to habitat fragmentation and loss, and declining prey species. (Trujillo *et al.* 2006). From a local perspective, the findings of this long-term study establish updated ecological information about *S. guianensis* and its habitats in the southern Gulf of Morrosquillo, Colombia. The study provides, for the first time, a scientific background that can be used as a basis for producing guidelines and recommendations for the long-term conservation of this coastal dolphin species and its habitats in Colombia.

Coastal dolphin populations, due to their restricted distribution and a fine-scale population genetic structure, are highly susceptible to environmental changes caused by anthropogenic pressure (Hoelzel 2009). Species with strong habitat use and selection and high levels of site fidelity, like the Guiana dolphin, are vulnerable to population declines due to the degradation and loss of coastal habitats. The loss of habitat may increase habitat fragmentation and therefore the distances needed to travel to find appropriate prey and mates. Returning to the same region may not lead to the discovery of suitable habitat resulting in a decrease in

survival probability (individual fitness) particularly among habitat specialists (Switzer 1993), like Guiana dolphins. The apparent intrinsic isolation of individuals due to the resources they follow may have important conservation and management implications (Block *et al.* 2007).

Clustering of the dolphins in some zones determines the importance of that specific habitat, thus informing the decisions to be made for the protection and conservation of this species and its core habitats in the southern area of the Gulf of Morrosquillo. Long-term site fidelity may cause feeding specializations that can reduce the gene flow in the species influencing the population structure especially of coastal dolphins (Hoelzel 2009). Evidence of strong site fidelity provides an opportunity to conservation and management agencies to monitor these populations (Shillinger *et al.* 2008).

Observed potential threats in the study area that require monitoring and assessment of impact include:

#### **Habitat degradation, loss and fragmentation**

Figure 7.1 shows that the loss of mangrove areas in the Gulf of Morrosquillo is extensive. The most preserved mangrove areas are in the southern gulf in Zones 1, 2, 3 and 4 of the study site. In the rest of the gulf including zones 5 and 6 of the study area, estuarine mangrove areas are almost non-existent. The mangrove deforestation has been under control in the south where research studies have been conducted for the last 20 years (Sanchez-Paez *et al.* 2004). Even these areas have recovered slowly; they do not present the characteristics of a mature mangrove forest anymore. Illegal deforestation still occurs in areas where continuous monitoring is difficult. Avila (1995) reported mangrove deforestation due to the construction of facilities for tourism. The illegal cutting of mangrove forest areas still continues at present (personal observation).

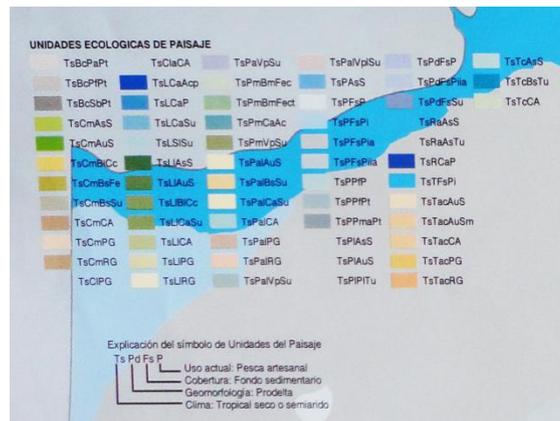
#### **Overlapping with artisanal fisheries activities**

As Figure 7.2 shows, the areas of artisanal fisheries overlap with the areas of high habitat use (Zone 2) of the Guiana dolphins. Even though education has been conducted in the area since almost two decades ago, the harsh life conditions of the human population have made it difficult to change some of the gillnets that the fishermen still use. Dolphin entanglements occur at a moderate rate especially caused by two artisanal fisheries techniques: “bolicheo” (Figure 7.3) and “trasmallo”. There is no information on how many animals die per year, since there is not report of the events by the majority of the fishermen. Bolicheo has been

prohibited in the area because it causes high rates of bycatch (INVEMAR 2002). Notwithstanding this, the technique is still used by some groups of fishermen.



**Figure 7.1- Coverage of vegetation in the Gulf of Morrosquillo. In: Formulación del Plan de Manejo Integrado de la Unidad Ambiental Costera Estuarina del Río Sinú- Golfo de Morrosquillo, Caribe Colombiano. Laboratorio SIG-INVEMAR 2001.**



**Figure 7.2- Ecological Units of Use in the Gulf of Morrosquillo. In: Formulación del Plan de Manejo Integrado de la Unidad Ambiental Costera Estuarina del Río Sinú- Golfo de Morrosquillo, Caribe Colombiano. Laboratorio SIG-INVEMAR 2001.**



**Figure 7.3-“Bolicheo”, artisanal fisheries technique, Cispatá Bay, Gulf of Morrosquillo. Photograph by Salomé Dussán-Duque.**

The “trasmallos”, gillnets approximate 2m long, are located sometimes at the entrance of channels inside Cispatá Bay. The trasmallos are left unattended for up to 10 hours causing entanglement and mortality of Guiana dolphins (Figure 7.4).



**Figure 7.4- Guiana dolphin lactating female entangled and dead in a “trasmallo” gillnet. Cispatá Bay, Gulf of Morrosquillo. Photograph by Salomé Dussán-Duque.**

## Overfishing

Depletion of fish stocks has caused serious problems for the local fishing communities in the southern area of the Gulf of Morrosquillo (personal communication) (INVEMAR 2002). The abundance of fisheries resources has decreased in the last decade, resulting in the displacement of artisanal fisherman to areas far away from the coast. It has caused an increment in the poverty in local communities because the resource is not enough to be sold in markets (personal communication). There is a high catch of under-sized fishes, because individuals cannot reach maturity due to anthropogenic pressure.

## Boat strikes

A high proportion of individuals of the population in the southern Gulf of Morrosquillo show evidence of malformations and mutilations of body and dorsal fins due to boat strikes (Figure 7.5). 52 individuals of the 98 identified, presented cuts or partial or complete mutilation of the dorsal fins and body injuries.



**Figure 7.5-** Guiana dolphin and bottlenose dolphin hit by boats, Gulf of Morrosquillo. *Photographs by Salomé Dussán-Duque.*

## Direct catch

Illegal direct catch of dolphins for display in tourist facilities still occurs, especially in unmonitored areas of the northern gulf of Morrosquillo. Individuals from the wild population have been taken continuously to replace the individuals that have died after being in captivity

or during capture. There is no information about the numbers of individuals that have been captured from the wild population (Figure 7.6).



**Figure 7.6- Liberation of an identified Guiana dolphin, after being illegally captured and held in captivity in an aquarium in Isla Múcura, northern gulf of Morrosquillo. Photographs Salomé Dussán-Duque personal collection.**

The work carried out through this long-term study has contributed to the conservation of the Guiana dolphins in the southern area of the Gulf of Morrosquillo. This study is the only one to date to provide long-term systematic information about the Guiana dolphins and its habitats in the southern Gulf of Morrosquillo, Colombia.

Through the results of this study a “Special Management Area” for the species has been approved by the Ministry of Environment of Colombia through the Corporación Autónoma Regional de los Valles del Sinú y del San Jorge (CVS) and the Instituto de Investigaciones Marinas y Costeras de Colombia (INVEMAR). This area and Management Plan will be included as part of the Plan de Manejo Integrado de la Unidad Ambiental Costera Estuarina del Río Sinú- Golfo de Morrosquillo, Caribe Colombiano.

From a wider perspective, the new information about the ecology of *S. guianensis* and its habitats in the southern Gulf of Morrosquillo, Colombia will contribute towards changing the IUCN Data Deficient listing for this species.

### 7.3. Applicability of methodology in other areas

The results of habitat use, selection and distribution of Guiana dolphins in the southern area of the Gulf of Morrosquillo (Chapter 3) highlighted the value of habitat modeling as an important tool to provide practical ecological understanding of this species and similar ones in other areas. In the case of this study, the use of habitat models and results had an explanatory purpose which is important for informing conservation policy and action. It can be apply to the same species populations and its sympatric one *T. truncatus* in Colombia, since we do not have at the moment any information of these species outside this study area.

The results of the mark-recapture analyses (Chapter 4) show that these techniques can be applied satisfactorily to a species living in highly coastal estuarine habitat, as much as to other cetacean species. These techniques provide accurate information about estimates of a population's survival and abundance and contribute to an understanding of its conservation status. These estimates of demographic parameters and abundance are necessary to inform conservation plans and to implement adequate management of human activities affecting the species and their ecosystems.

Studies about how cetacean species use heterogeneous complex environments enlarge our understanding of the importance of spatial structure in the ecology of these species. Long-term high sight fidelity in coastal dolphin species should not be overlooked, because it implies a fine scale population structure that may affect the demographic parameters of the species and its long-term conservation (Hoelzel 2009).

Through the results of the surface cooperative foraging and feeding strategies of Guiana dolphins we can conclude that the use of foraging and feeding behavioural models can provide a fine scale description of the decisions made by the individuals of a population with respect to their environment. The results highlighted the value of the use of modelling as a tool to investigate the relationships between these strategies and eco-geographic variables in cetacean species.

The overall results of the study highlight the importance of long-term studies towards the conservation of cetacean species and their habitats. This includes the importance of these studies for informing proposals for Marine Protect Areas or Areas of Special Management aimed at ensuring the long-term survival and conservation of the cetacean species and their

habitats. This work contributed to the creation of the first Special Management Area for dolphins in Colombia

The use of Traditional Ecological Knowledge (TEK) should not be overlooked by scientific researchers. It implies a level of knowledge of habitats and their species that a researcher may never be able to acquire even through years of scientific research. For example, the fishermen of the study area know where to sight dolphins every day. They use to inform the researcher where the dolphins were at specific moments of the day (Figure 7.7).



**Figure 7.6- Map of the study area design by the fishermen of the southern Gulf of Morrosquillo, whit the places where they sighted dolphins every day. Traditional Ecological Knowledge (TEK).**

#### **7.4. Future research**

Further research in the northern area of the Gulf of Morrosquillo and continued monitoring of the southern area needs to be conducted to be able to manage the Gulf of Morrosquillo as a whole. There is a need to improve our capacity to provide effective management actions towards the conservation of this species and its habitats in the whole Gulf of Morrosquillo.

Actions to maintain the population need to include management of anthropogenic pressures inside and outside the study site boundaries; we do not know anything about the populations of *S. guianensis* in Colombia outside the boundaries of this study site. Even though this species is protected by law in Colombia there is a lack of real management action to assure its

long term survival through the protection of its habitats. To this end, a Management Plan and a legal delimitation of the special management area for the species need to be accomplished.

Parallel to the data collection of *Sotalia guianensis* for this study, data were collected on the ecology of *Tursiops truncatus*. Preliminary data analysis shows a change in the abundance and distribution of this species in the southern area of the Gulf of Morrosquillo based in comparisons with the reports of Avila (1995) (Dussán-Duque unpublished data). Through these preliminary results, it is possible to say that the habitat loss and degradation has caused even bigger consequences for this species than to the ones reported here for *Sotalia guianensis*, and future work on *T. truncatus* is urgently needed.

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