UNIVERSIDADE do ALGARVE
Faculdade de Ciências e Tecnologia

Bioecology and Movement Patterns of Sharks off Recife, Brazil: Applications in the Mitigation of Shark Attack Hazard

Thesis for the degree in Doctor of Philosophy in Marine, Earth and Environmental Sciences, specialty in Marine Ecology

André Sucena Afonso

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Bioecologia e padrões de movimentação de tubarões na costa de Recife, Brasil: aplicações na mitigação do risco de ataque

Thesis for the degree in Doctor of Philosophy in Marine, Earth and Environmental Sciences, specialty in Marine Ecology

Tese de Doutoramento em Ciências do Mar, da Terra e do Ambiente, ramo de Ciências do Mar, especialidade de Ecologia Marinha

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Thesis supervised by: *Tese orientada por*:

Prof. Doutor **Fábio H. V. Hazin**

Prof. Doutor **Karim Erzini**

− 2013 −

Shark image in the cover by Anthony Kekona; Retrieved from www.kekonaart.com, with permission.

Dedico esta tese aos meus pais.

Nunca teria chegado até aqui
sem o vosso primeiro empurrão.

Abstract

An abnormally high rate of shark attacks on humans off Recife, Brazil prompted the development of a shark monitoring program aiming at mitigating shark peril. Bottom longlines and drumlines were used as fishing gears and optimized for increasing selectivity towards large sharks and reducing fishing mortality. The fishing methodology allowed to reduce the shark attack rate considerably and to generate important bioecological information on tiger and bull sharks, species which seem to be responsible for most of the attacks. Tiger sharks in this region move preferentially to the north through wide home ranges. The presence of a port complex to the south of Recife could be attracting tiger sharks shoreward, which would subsequently visit the littoral of Recife due to their natural movements. Other important, site-specific features such as the presence of an estuary and an alongshore channel close to the beach, together with high pollution and siltation levels, could further promote the high risk of shark attack in the area. Tiger sharks use the continental shelf off northeastern Brazil mostly during early juvenile stages, where they quickly grow between January and September before departing to oceanic waters. Larger tiger sharks use deep oceanic waters more often but they frequently visit nearshore waters, probably in search for prey. The depth distribution of tiger sharks seems to correlate with both diel and lunar cycles, and abundances off Recife were correlated with month, lunar phase, tidal amplitude, pluviosity and wind direction. This information could be useful in determining periods when tiger sharks are more likely to occur in the area of risk. Compared to traditional shark-meshing programs, which produce a considerable amount of bycatch and fishing mortality, the methodology herein reported provides an effective solution to increase user safety at local beaches with minimal ecological consequences.

Key-words: bycatch, coastal management, fishing mortality, longline, selectivity, shark attack mitigation, telemetry

Resumo

Um surto de ataques de tubarão verificado na costa de Recife, Brasil, levou à instauração de um programa de monitorização de tubarões com o intuíto de mitigar o risco de ataques. Os equipamentos de pesca utilizados corresponderam a palangres de fundo e linhas de pesca, os quais foram optimizados tendo em vista a maximização da selectividade dirigida a tubarões potencialmente agressivos e a minimização da mortalidade por pesca. A presente metodologia possibilitou uma considerável redução da taxa de ataques de tubarão, ao mesmo tempo que permitiu a recolha de dados importantes sobre a bioecologia das espécies envolvidas nos ataques. Os tubarões tigre e buldogue são aparentemente responsáveis pela maioria dos incidentes. Nesta região, os tubarões tigre deslocam-se preferencialmente para norte e alcançam consideráveis distâncias. A presença de um complexo portuário a sul de Recife parece contribuir para atrair tubarões para áreas costeiras, os quais se deslocariam, consequentemente, para o litoral de Recife. Algumas características do litoral de Recife, tais como a presença de um estuário e de um canal paralelo à linha de costa, juntamente com elevados níveis de poluição e turbidez da água, poderão potenciar o risco de ataque. O tubarão tigre utiliza a plataforma continental do nordeste brasileiro maioritariamente durante o início da fase juvenil, crescendo rapidamente entre os meses de Janeiro e Setembro e partindo em seguida para águas oceânicas. Os espécimes mais velhos utilizam águas profundas do ambiente oceânico mas visitam frequentemente a plataforma continental, provavelmente em busca de presas. A distribuição vertical do tubarão tigre parece correlacionar-se com ambos os ciclos circadiano e lunar, e a sua abundância no litoral de Recife foi correlacionada com o mês, a fase lunar, a amplitude da maré, a pluviosidade e a direcção do vento. Esta informação poderá ser útil para definir os períodos em que a presença de tubarões tigre na área de risco é mais provável. Em comparação com os programas de emalhamento de tubarões tradicionalmente conduzidos, esta metodologia apresenta-se como uma solução eficaz para aumentar a segurança balnear, simultaneamente assegurando a minimização do impacto ecológico local.

Palavras-chave: captura incidental, gestão costeira, mortalidade por pesca, palangre, selectividade, mitigação de ataques de tubarão, telemetria

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Preface on thesis style

Prefácio sobre o estilo da tese

This thesis comprises eight chapters, a general conclusion, a list of bibliographic references, and supplementary tables and figures. The first chapter includes a general introduction to the subject of the thesis, and provides background information on sharks, shark attacks, and the specific case-study of Recife. The second to seventh chapters correspond to roughly independent, but closely connected studies that were organized in a paper-style format, although they should not be interpreted as such because they are extensively discussed and may include nonessential information. Each of these chapters starts with an introduction including the state-of-the-art of that specific subject and the aims of the study, followed by a thorough description of the materials and methods used, the results obtained, including figures and tables, and the respective discussion. The eighth chapter is organized differently because it includes a theoretical reasoning of the shark attack problem and addresses mitigation strategies. All references were collated following the eighth chapter, and the acknowledgments were collated in the beginning of the thesis. The organization of the thesis does not require chapters to be read sequentially. Nevertheless, cross-references to other chapters have been used in order to avoid unnecessary repetitions. Some chapters or chapter sections have already been published, and references for those publications have been included along the text. Some chapters have not yet been submitted or accepted for publication, thus they are not included in the list of references. However, the scientific production resulting from this thesis is included in Annex I, namely all papers that have already been published and all papers that are currently in press or being prepared for submission, as well as all the presentations at scientific meetings.

Ethics and funding disclosure

Declaração de ética e financiamento

This study was conducted at the Department of Fisheries and Aquaculture of the Federal Rural University of Pernambuco (UFRPE). Every procedure carried out with sharks was conducted in accordance with the recommendations of the Commission of Ethics on the Usage of Animals from the UFRPE, and this study was ethically approved by license number 041/2009 (protocol number 23082.009679/2009 D18). In Brazil, this study was funded by the Financiadora de Estudos e Projetos of the Ministry of Science, Technology and Innovation (FINEP/MCT), by the State Government of Pernambuco and by the City Hall of Recife. In Portugal, this study was funded by Flying Sharks Lda. (http://www.flyingsharks.eu) and the Portuguese Association for the Study and Conservation of Elasmobranchs (APECE; http://www.apece.pt) through their Research Fund, and by the Fundação para a Ciência e Tecnologia (FCT; contract no. SFRH/BD/2007/37065).

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Chapter 1. General introduction

A sign warning of shark peril off the beaches of Recife.

1.1. An overview of shark exploitation as a fisheries resource

Sharks and batoids (i.e. rays and skates) together compose the subclass Elasmobranchii, a monophyletic group (Schaeffer and Williams, 1977) which is presently divided in two superorders: Galeomorphii, comprising four orders (Heterodontiformes, Orectolobiformes, Lamniformes, and Carcharhiniformes); and Squalomorphii, comprising four orders (Hexanchiformes, Squaliformes, Squatiniformes, Pristiophoriformes) and the group of batoids, whose phylogenetic positioning is yet unresolved (Kriwet et al, 2009 and references therein). Living sharks consist of at least 498 species (Compagno, 2005) whereas batoids include 574 extant species (Ebert and Compagno, 2007). Sharks correspond to a group of chondrychthyan fishes which may be distinguished from other fish *taxa* by possessing a cartilaginous endoskeleton, a palatoquadrate articulating with (instead of being fused to) the neurocranium, five to seven separate gill openings located laterally on the head, and pectoral fins not fused to the head (Compagno, 1999). Although fossil records evidenced chondrichthyans to exist since the Devonian period, about 400 million years ago (Mya), modern elasmobranchs arose during the Mesozoic era (250-65 Mya) after a major adaptive radiation − the *neoselachian revolution* (Compagno, 1999), which resulted in a sharp increase in species diversity (Underwood, 2006). As such, elasmobranchs successfully occupy a wide range of aquatic habitats, including limnetic systems such as rivers and lakes, inshore estuaries and lagoons, and both the neritic and oceanic provinces of the marine realm to depths as much as 2,000 m (Camhi et al., 1998).

Sharks have historically been regarded as a low-value fishing resource (Bonfil, 1994; Compagno, 1990) and so they have been mostly caught as by-catch in diverse fisheries (e.g. Coelho and Erzini, 2008; Mandelman et al., 2008; Megalofonou et al., 2005; Thorpe and Frierson, 2009), although some species, especially deep water sharks, were sought since 1940 for their livers as they were found to be rich in valuable organic compounds such as vitamin A, squalene, and diacyl glyceryl ether (Akhilesh et al., 2011; FAO, 2005; Figueiredo et al., 2005; Wetherbee and Nichols, 2000). The development of synthetic vitamin A in 1947, however, reduced the global interest of such fisheries (Kreuzer and Ahmed, 1978). All this scenario has changed in more recent years, as shark catches have increased considerably following an

intensification of global fishing effort (Barker and Schluessel, 2005) which was motivated by a growing demand for shark fins and, to a lesser extent, meat (Cahmi et al., 1998). The higher market value of shark fins compared to shark meat resulted in tens of millions of specimens taken in fisheries each year having their fins removed and their carcasses discarded overboard (Fowler and Musick, 2002). Such practice, known as finning, represents a substantial waste as fins correspond to only about 5% of the total weight of a shark (Vannuccini, 1999), hence it has recently been prohibited by many countries and Regional Fisheries Management Organizations (RFMOs).

The world elasmobranch yearly catches reported for the period between 1947 and 1991 grew relatively steadily until a maximum of 704,000 t, but Bonfil (1994) considered 1,350,000 t to be a more realistic estimate. According to the Food and Agriculture Organization of the United Nations (FAO, 2010), the global shark catch peaked at about 900,000 t in 2003 but it has been declining ever since. However, the flow of shark fins through the Hong Kong fish markets suggests that somewhere between 1.21-2.29 million tons of sharks are killed each year for the fin trade (Lack and Sant, 2009), indicating that FAO statistics underestimate global catches of sharks to a great extent. In accordance, an analysis of the fin trade data combined with genetic analysis for species identification estimated the shark biomass in the fin trade to be three to four times higher than shark catch reported by fisheries databases (Clarke et al., 2006). Facing such an extreme fishing pressure, once abundant elasmobranch populations are now quickly declining throughout the globe (Baum et al, 2003), although the rate of decline is not consensual (Burgess et al., 2005). In any case, it is now widely accepted that most elasmobranch species do require a considerable amount of protection from fisheries in order to warrant the conservation of their populations.

Except for a few large-bodied, planktophagous species, sharks are typically apex or high-level predators (Cortés, 1999). Such positioning in the trophic chain tends to benefit *K*-selected life-history strategies, which balance populations with the carrying capacity of the environment, in detriment of *r*-selected strategies, which balance populations with the maximal intrinsic rate of natural increase (Pianka, 1970). In accordance, the life cycles of elasmobranchs are generally characterized by slow growth, late maturity, and low fecundity, resulting in low reproductive potential and reduced capacity for population increase (Pratt and

Casey, 1990; Garcia et al., 2008). Furthermore, as top predators, their abundance is considerably lower than the abundance of other *taxa* belonging to lower trophic levels (Odum, 1971). All these reasons make elasmobranch populations particularly sensitive to anthropogenic-derived disturbance, either directly through overfishing (Stevens et al. 2000), or indirectly through environmental pollution (Seitz and Poulakis, 2006) or habitat degradation (Jennings et al., 2008).

The low population resilience of sharks is readily verified as most fisheries targeting sharks begin with promising catch rates but subsequently experience rapid declines in production which eventually lead to the collapse of the fishery (Stevens et al., 2000). This is particularly true for coastal species as their populations are much more accessible to harvest and their habitats much more exposed to environmental damage. Indeed, the human pressure historically inflicted on coastal areas induced many changes to the environment and to the communities and ultimately resulted in the general collapse of coastal ecosystems, as described by Jackson et al. (2001). In nearshore waters, local symptoms of overfishing have been documented even in small-scale, artisanal fisheries targeting sharks with 6-8 m sailing "pirogues" crewed by two persons (McVean et al., 2006). The sustainable exploitation of elasmobranch resources is therefore quite challenging. However, it appears to be achievable at least for species with higher productivity such as *Mustelus antarcticus*, *Rhizoprionodon terraenovae*, *Sphyrna tiburo* and *Prionace glauca* (Walker, 1998). In effect, the spiny dogfish, *Squalus suckleyi*, fishery in the North Pacific recently became the first elasmobranch fishery in the world certified as sustainable by the independent, non-profit Marine Stewardship Council (MSC, 2011), although such certification has been highly criticized (Jacquet et al., 2010).

The widespread concern over the increase of shark fishing and the respective impact on shark species prompted international institutions to actively address the situation. In 1991, the Species Survival Commission (SSC) of the International Union for the Conservation of Nature (IUCN) established the Shark Specialist Group (SSG), an assemblage of about 160 authorities from 90 countries whose mission consists on providing leadership and expertise for the long-term conservation and effective management of chondrichthyan fishes. The ultimate output of the SSG is the IUCN Red List of Threatened Species, and until May 2012 the SSG had listed 584 chondrichthyan species under the prevailing classification system (IUCN,

2011). More precisely, 25 species were considered as critically endangered (CR), 41 as endangered (EN), 115 as vulnerable (VU), 132 as Near-Threatened (NT), and 271 as of Least-Concern (LC). The SSG assessments have also been valuable for sustaining proposals for the inclusion of chondrichthyans in the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). Until May 2012, four chondrichthyan species, namely the basking shark, *Cethorhinus maximus*, the great white shark, *Carcharodon carcharias*, the whale shark, *Rhincodon typus*, and the largetooth sawfish, *Pristis microdon*, were listed in Appendix II of that treaty, while all the remaining pristid sawfishes were listed in Appendix I (CITES, 2012). Another important initiative from an international organization was the establishment of the International Plan of Action for the Conservation and Management of Sharks (IPOA Sharks) by FAO, as part of the Code of Conduct for Responsible Fisheries, which occurred in 1999. The goal of the IPOA Sharks was to provide a framework for the promotion of adequate management of shark fisheries to ensure the conservation of their populations worldwide, although not many countries have yet implemented their National Plans of Action (NPOA) effectively and little progress has been verified at a global level. According to Lack and Sant (2011), seven out of the twenty major elasmobranch-fishing countries still do not possess a NPOA. Moreover, information suggesting that sharks are effectively being managed by NPOAs is yet to be found (Lack and Sant, 2011). Altogether, the amount of measures in use for mitigating threats to chondrichthyan species seem to be insufficient as population declines have generally persisted (Baum and Blanchard, 2010).

Not only are the reductions in elasmobranch abundance and diversity, by themselves, a regrettable loss, but they also imply further consequences for the marine ecossystem, which draw additional concerns. The fact that sharks are typically high-level predators (Cortés, 1999) grants them a great ecological significance as top-down regulators of marine food webs. The effect of the predatory pressure of elasmobranchs is visible on their direct preys and also indirectly on non-prey species through trophic linkages up to the third degree (Schindler et al., 2002). Thus, the removal of sharks by fisheries equals the subtraction of a very important component of the ecosystem, which is responsible for maintaining a wide variety of mesopredators in balanced numbers. Without such a component, the trophic chain is expected to experience a top-down forcing resulting from the increase in large-prey populations following the reduction in predatory pressure (Sandin et al., 2010), which will subsequently

increase predation on smaller prey. Such an effect may eventually trigger a cascade effect over lower trophic levels and potentially change the structural properties of the food web and compromise its stability (Heithaus et al., 2008; Rezende et al., 2009). Sudden increases in the abundance of mesopredators following the removal of large sharks (i.e., mesopredator releases) have been observed (Shepherds and Meyers, 2005, Ferretti et al., 2010) and might affect all trophic levels. Consequences of such phenomena may include reductions in primary and secondary productivity (Mann, 1977; Reisewitz et al., 2006, Ferretti et al., 2010), invasion by alien species and demographic outbreaks of native species (Baum and Worm, 2009), and increased threat to more vulnerable prey species (Polis and Holt, 1992; Courchamp et al., 1999; Ritchie and Johnson, 2009). It is therefore urgent to ensure the conservation of elasmobranch populations and the health of marine ecosystems (Ward-Paige et al., 2012).

1.2. Shark-human interactions and mitigation programs

1.2.1. Historical perspective

Except when directly targeted in fisheries or in some countries from the Pacific Ocean where they are deified, sharks are popularly considered as a nuisance. In fisheries targeting other species, sharks are frequently responsible for damaging fishing gears (Bigelow and Schroeder, 1953) and for depredating bait and catch (Mandelman et al., 2008; MacNeil et al, 2009), resulting in substantial ecological, economic and social losses (Gilman et al., 2008), not to mention the risk they pose to the fishermen who handle them. Sharks are also responsible for damaging oceanographic equipment and submarine communication cables (Johnson, 1978; Marra, 1989). However, no other circumstance provokes more anxiety and antagonism towards sharks than when they attack humans.

The first representation of a shark attack may have been found on a vase dated from 725 BC and uncovered at Ischia, Italy, which shows a man seized by a fish possibly reminiscent of a shark (www.sharkattacks.com/historical.htm; Accessed on May 28th 2012). Although Herodotus had already referred to attacks by marine monsters in 492 BC (Rawlison, 1996), the first written evidence of a shark attack seems to come from the third century BC, when the Greek lyric poet Leonidas of Tarentum evoked the tragic fate of a sponge-fisher

when he was attacked by a sea monster, probably a shark, which tore the lower section of his body apart while being hoisted aboard by his two companions (Clack, 1999). More recently, one of the first published allusions to shark attacks came from Rome, in 1555, in the book *Historia de Gentibus Septentrionalibus* by the Swedish writer and cartographer Olaus Magnus, which depicts a man being seized by three sharks (Fig. 1.1).

Figure 1.1. The first published representation of a man being attacked by sharks, dated from 1555 and included in *Historia de Gentibus Septentrionalibus*, by Olaus Magnus (www.sharkattacks.com/historical.htm; Accessed May 28th 2012).

Early in the past century, during a heat wave in the summer of 1916, the coast of New Jersey witnessed a series of shark attacks in which four people were killed and one injured (Fernicola, 2001). According to the same author, these incidents had great repercussion in the media and contributed to the inclusion of sharks in American popular culture as a symbol of danger. Also, they compelled researchers and ichthyologists to deepen their work on these species, as scientific knowledge about sharks was hitherto based mostly on conjecture and speculation. Nonetheless, sharks were of little concern to common people before World War II, and bathers generally ignored the possibility of shark attack, with the possible exception of South Africa and Australia (Gilbert, 1963). After the war began, however, direct contacts with sharks were frequently reported following air or sea disasters, which raised concerns regarding the peril represented by them. The most dramatic episode was undoubtedly the one of the USS *Indianapolis*, on July 30th 1945. While on a secret mission to deliver some components for the atomic bomb in the Marianas, the USS *Indianapolis* was hit by two torpedoes launched by a Japanese submarine and sank. A surviving crew of about 880 men was forced into the water

with nothing but their life jackets, being rescued four days later. During that time lag they had to endure dehydration, starvation, exposure, and terrifying shark attacks. By the time they were found, only 321 men remained alive, with four of those later dying from their wounds (http://militaryhistory.about.com/od/shipprofiles/p/ussindiana-polis.htm; Accessed May 28th 2012). Such testimonies prompted the development of a shark repellent for military use, which was named *Shark Chaser* and was composed of copper acetate combined with a nigrosine-type dye (Gilbert, 1963). In spite of all these impressive reports, the event which brought most popularity to sharks was probably the 1974 novel entitled *Jaws*, by Peter Benchley, which was based on the New Jersey's shark attack episode and turned into a blockbuster by Steven Spielberg in the following year. *Jaws* quickly became the most influential film about sharks ever, popularizing the belief that sharks were vicious animals capable of hunting for humans and, therefore, impossible to coexist with.

1.2.2. The shark hazard concern

A great proportion of incidents with sharks are derived from interactions motivated by humans. Frequently, sharks react to disturbance by biting at their opponents (Martin, 2007), and therefore many accidents have happened when fishermen remove live sharks from their fishing gears or when incautious divers startle otherwise unresponsive sharks, or even during recreational shark diving or scientific research operations. All these human-derived interactions are considered as provoked attacks, disregarding of the consequences to the victim, since such interaction would most probably not happen if the human had not provoked it. While the causes which trigger provoked attacks are sufficiently clear, the motives which lead unprovoked sharks to attack humans are yet to be understood.

It is generally consensual that sharks are rather shy animals and difficult to observe in the wild, as they tend to avoid contact with humans. Currently, most unprovoked shark attacks on humans are believed to be cases of prey misidentification (Burgess, 1990) resulting from humans producing stimuli that sharks interpret as being from natural prey. For example, the silhouettes of floating surfboards and swimmers easily resemble animals such as marine turtles, dugongs, or fish swimming near the surface, and the low-frequency sounds emitted by

stroking legs and arms on the sea surface are comparable to the sound produced by a stressed, wounded fish (Nelson and Gruber, 1963; Myrber, 1978). The acoustic sensory system of sharks is extremely well developed (Myrberg, 2001) and enables them to get aroused by such sounds and pursue its source, even from considerable distances (Nelson, 1967, Myrberg et al., 1972). Likewise, the rod-rich retina of sharks allows them to sharply distinguish the shadow of an object against a contrasting background (Gruber, 1977; Hueter, 1991), even though they may possess low visual acuity and be eventually color blind due to cone monochromacy (Hart et al., 2011). Sharks still enjoy other specialized sensory mechanisms which grant them additional abilities to sense the surrounding environment and locate potential prey, such as a mechanosensory lateral line system (Maruska, 2001), an electrosensory system (Tricas, 2001), and an extremely sensitive olfactory system (Tricas et al., 2009). In particular environmental conditions, e.g. in low visibility waters, the stimuli other than visual produced by a person and perceived by a shark could be quite similar to those of natural preys.

Other possible explanation for unprovoked shark attacks could be related to territoriality and competition. Shark agonistic displays towards humans have been frequently elicited (Martin, 2007). One of the most common threat displays among sharks is the strong bilateral depression of both pectoral fins, which can be observed in different *taxa* with distinct sizes and feeding habits (Martin, 2007). In the grey reef shark, *Carcharhinus amblyrhynchos*, a distinctive, highly stereotyped "hunch display", which combines a raised snout-arched back posture with laterally exaggerated swimming motion or rolling/spiral looping movements, is usually performed in response to crowding or pursuit by divers or submersibles (Johnson and Nelson, 1973; Nelson et al., 1986). Against persistent pursuing, the agonistic display quickly evolves to either a withdrawal or a slashing attack, leading to the conclusion that such displays are an accurate predictor of defensive behaviours with further hostility (Fellows and Murchison, 1967). Such evidence strongly denotes a lack of initiative from the shark to confront the divers and indicates that, in some circumstances, agonistic behaviour towards humans should be interpreted as a warning response, e.g. to the insisting presence of a possible competitor.

A strong indication that shark attacks are not triggered by predatory behaviours directed toward humans is that, in many cases, sharks release the victim after the first bite and

appear to lose their interest henceforth (Baldridge, 1974; Martini and Welch, 1981; Burgess and Callahan, 1996). This hit-and-run behavior agrees with the hypothesis of prey misidentification, although it could derive from a non-predatory state as well. The term *exploratory bite* has been previously used to describe single, more superficial shark bites which seem to have an intention other than actually seizing a prey (Collier et al., 1996, Ritter and Levine, 2004), and it is believed that such bites do not represent an aggressive behaviour but rather a way of sharks getting acquainted with a novelty, although this bite pattern would be hard to distinguish from agonistic displays such as the ones described in Martin (2007) if the pre-attack behaviour of sharks is not assessed. In any case, it is unquestionable that shark bites do cause extensive trauma to the victim even in optimistic scenarios (Caldicott et al., 2001; Ritter and Levine, 2005), and even relatively minor shark bites may lead to lethal hemorrhages if inflicted on main blood vessels. Furthermore, many shark attack victims were repeatedly and powerfully bitten (Ihama et al., 2009), and human remains have been found in shark stomachs (Lowe et al., 1996; Rathbun and Rathbun, 1984), which demonstrates that some shark attacks on humans do happen due to predatory behaviour and that the awareness of prey being nonstandard not always results in the shark giving up the attack after the first bite.

On the other hand, the behaviour of an individual shark could reveal higher aggressiveness than its conspecifics. Gilbert (1963) introduced the term *accessory population* to describe the portion of individuals from a migratory *principal population* (i.e., the main breeding population that maintains its numbers and follows regular patterns of distribution and habitat) which is lost either through wandering from the usual geographic range of the species or through disorientation in seasonal movements, resulting in individuals turning out of phase in the reproductive cycle. According to the same author, individuals from the accessory population may exhibit distinct, more aggressive behaviors compared to individuals from the principal population. Similarly, Coppleson (1958) recognized that some sharks behave differently enough to be categorized as *rogue sharks* to distinguish them from regular individuals, although his theory that these sharks could potentially be man-hunters has been generally refuted. In conclusion, it is clear that shark attacks do exhibit great variability in causes and patterns, which could be regulated by the interactions between shark species-specific behavior, environmental conditions, and human behavior.

1.2.3. Trends in shark attacks

The International Shark Attack File (ISAF) has been operating since 1958 and is internationally recognized as the most accurate source of shark attack data to date, housing more than 5,000 investigations which cover the period from the 16th century until the present. Although much of the available ISAF information requires caution when analyzed, as many confounding factors not directly related to sharks have changed through time, it has been used to assess trends in shark attacks which could assist mitigation efforts (e.g. Baldridge, 1974; Burgess et al., 2010). According to ISAF (http://www.flmnh.ufl.edu/fish/sharks/statistics/Trends2.htm; Updated Feb 7th 2012; Accessed June 1st 2012), the number of shark attacks reported has been globally increasing since 1960. Although such a trend is partially an artifact produced by factors such as ISAF logistic improvements (in 1987) and an increase in reporting rate and media coverage, particularly of minor attacks which had previously gone unreported (since 1993), it is clear that incidents involving sharks have become more common in the last couple of decades than ever before. One of the main factors driving this trend, however, is certainly the rate of beach use. Since the number of shark-human interactions directly correlates with the number of humans in the water and with the amount of time they spent there, it is to be expected that shark attacks would increase following human population growth and the rising demand for aquatic recreation in recent decades. Consequently, not only shark attacks but also other incidents related to the use of the sea by humans have increased in frequency, such as drowning events which have always been much more frequent than shark attacks (ISAF; http://www.flmnh.ufl.edu/fish/sharks/isaf/isaf.htm, Accessed May 31st 2012).

Some human activities, however, may lead to higher abundances of sharks close to shore and modify their typical behavior. Water chumming, for instance, is a practice regularly conducted by the shark diving industry and it has been perceived as being responsible for attracting sharks to an area and for conditioning them to associate vessels with easy food (Presser and Allen, 1995). Pollution and coastal development may also contribute to attract sharks shoreward (Baldridge, 1974, Hazin et al., 2008). The implications of human interference over the environment are frequently complex and unpredictable, thus the role of anthropogenic pressure on the shark attack problem should not be underrated.

On the other hand, the number of shark-human interactions in Florida, which historically presents the highest shark attack rates in the world, has been decreasing steadily over the last decade, with 2011 exhibiting the lowest number since 1993, a trend which is not observed at a global scale (Fig. 1.2). Possible causes for this reduction include less sharks in US waters due to fishing, less people going in traditional high shark-human contact areas, and better, more efficient behaviors from aquatic recreationists and beach safety personnel in avoiding times, sites, and activities which increase the likelihood of encounters between sharks and humans (ISAF; http://www.flmnh.ufl.edu/fish/sharks/isaf/ 2011summary.html; Accessed May 31st 2012). Indeed, the type of aquatic activity has shown an effect on the number of shark attacks, with surface recreationists surpassing swimmers in the number of victims since 1980 (Fig. 1.3). This could be explained by the outbreak of surf and other similar water sports, which resulted in more people further away from shore producing new, distinct stimuli which were not produced by humans before.

According to ISAF (http://www.flmnh.ufl.edu/fish/sharks/statistics/species2.htm; Accessed May 31st 2012), the three species responsible for most of the unprovoked attacks are the great white, *C. carcharias*, the tiger, *Galeocerdo cuvier*, and the bull, *C. leucas*, sharks (Fig. 1.4), the first one being a lamnid and the last two being carcharhinids. All these species are circumglobal in tropical and warm-temperate waters, are regular visitors of coastal areas, and attain considerable large sizes (Compagno, 2001). The bull shark, which in Africa has been named after the Zambezi river, is even found in lakes and rivers as far as 4,000 km from the ocean (Thorson, 1972) due to an efficient osmoregulatory capacity (Pillans, 2005). The distribution of these species naturally corroborates their importance for the shark attack concern. Nevertheless, a vast number of shark species is known to have attacked humans, with ISAF identifying at least 32 species responsible for inflicting unprovoked attacks (http://www.flmnh.ufl.edu/ fish/sharks/statistics/species2.htm; Accessed May 31st 2012) and even the cookiecutter shark, *Isistius* sp., which is one of the smallest shark species growing to a maximum size of 40−50 cm, being implicated in such incidents (Honebrink et al., 2011).

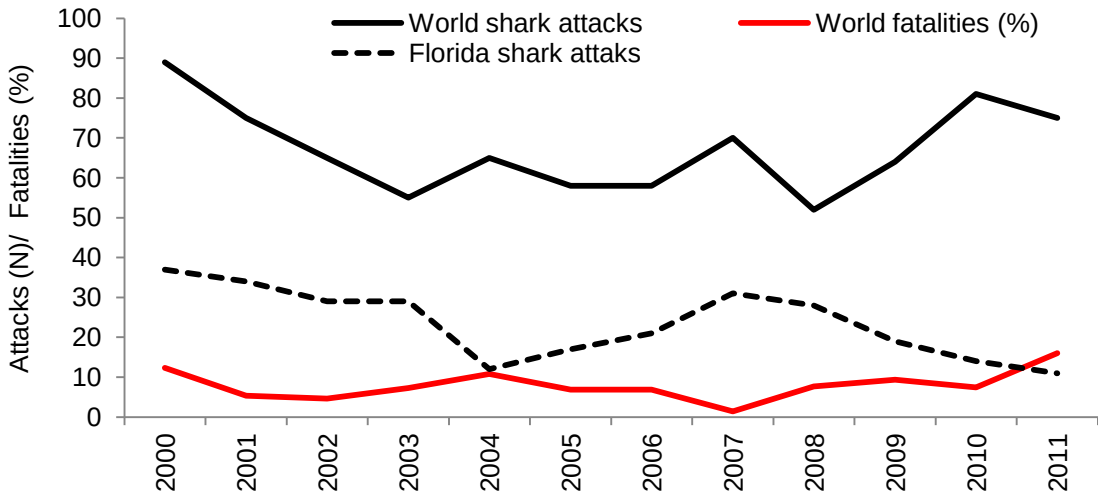


Figure 1.2. Variation in the yearly number of reported shark attacks worldwide and in Florida only, and the respective proportion of fatalities between 2000 and 2011. Note that the vertical axis represents both counts and percentages (Source: http://www.flmnh.ufl.edu/fish/sharks/statistics/statsw.htm, updated January 30th 2012, accessed May 31st 2012).

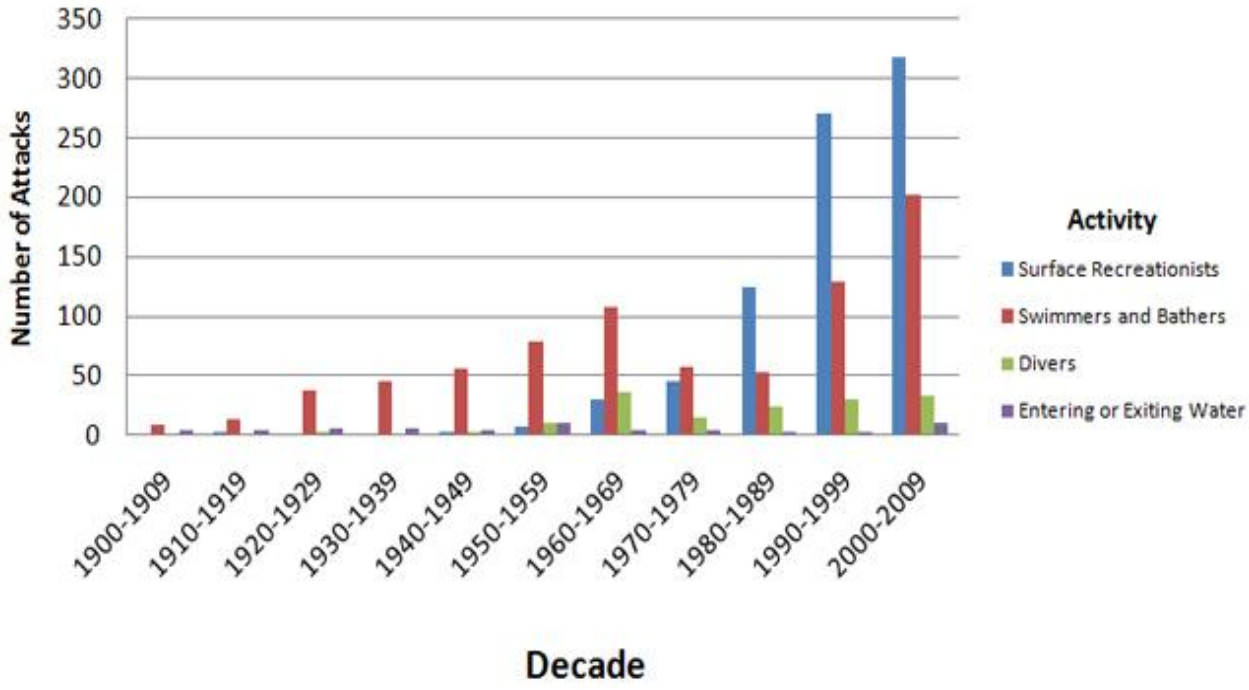


Figure 1.3. Decadal variation in the number of shark attacks between 1900−2009 (*N* = 1,826) categorized by the activity of the victim before the attack. Retrieved from ISAF (http://www.flmnh.ufl.edu/fish/sharks/statistics/Act.htm; Accessed May 20th 2012), with permission.

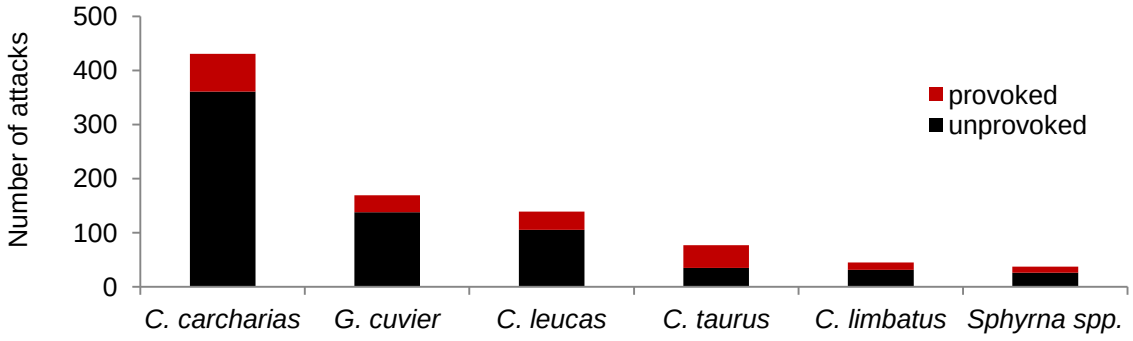


Figure 1.4. Number of provoked and unprovoked shark attacks worldwide inflicted by the most attacking species (source: ISAF; http://www.flmnh.ufl.edu/fish/sharks/statistics/species2.htm; Updated January 30th 2012; Accessed May 31st 2012).

1.2.4. Shark attack mitigation programs and strategies

Even though shark attacks on humans are extremely rare events, averaging 64 attacks per year worldwide (Burgess et al., 2010), they may produce severe deleterious impacts on local communities and economy (Bullion, 1976; Dudley, 1997, Wallet, 1983). The psychological impact of a shark attack has been known to outweigh that of other, more frequent forms of danger (Davies, 1961). This is particularly true in regions where the risk of attack is consistently present (Cliff, 1991; Maillaud et al., 2009; McCosker and Lea, 2006; Nacaya, 1993; Rtshiladze et al., 2011; Schultz, 1967). To face such hazard, some local governments have adopted measures aiming at mitigating the risk of shark attack. One of the earliest examples dates back to 1937, off the beaches of Sydney, Australia (Dudley, 1997), when the Shark Menace Advisory Committee of New South Wales was set up to develop methods for reducing shark hazard (Coppleson and Goadby, 1988). The proposed strategy for shark attack mitigation consisted in reducing the numbers of large sharks in the region by installing anchored gillnets permanently in nearshore waters. Contrary to some popular beliefs, these shark-meshing programs do not provide a shark-safe environment but instead they were projected to passively fish for sharks which approach the protected shores, consequently reducing the probability of shark-human encounters. In fact, a considerable proportion (35%) of sharks are caught in the shoreward side of the mesh (Cliff and Dudley, 1992), presumably while moving seaward.

There are three major shark meshing programs currently operating in the world, namely in New South Wales and Queensland, Australia, and in KwaZulu-Natal, South Africa (Dudley and Cliff, 2010), which started in 1937, 1962, and 1952, respectively (Dudley, 1997). In addition, some shark meshing has been also conducted off Dunedin, New Zealand, during the summer (Francis, 1998), and there are references to shark meshing off Qingdao, China, in 1982, although it is unknown if that program continues and if there are other places in China using shark nets (Dudley and Gribble, 1999). In Hawaii, shark control was attempted with baited, bottom longlines instead of gillnets. Between 1959 and 1976, six different shark control programs with varying fishing effort were conducted there, leading to the capture of a large number of sharks, but the operations were discontinued as they showed no visible effect on the rate of shark attacks (Wetherbee et al., 1994). In contrast, the three main shark-meshing programs have shown to have a significant effect on the reduction of attacks at protected sites, although at variable rates (Dudley, 1997).

In spite of their effectiveness in mitigating the shark attack problem, shark meshing programs have been associated with high mortalities not only of potentially aggressive sharks but also of harmless *taxa* including several threatened species such as turtles, dugongs and cetaceans (Gribble et al., 1998a; Krogh and Reid, 1996; Dudley, 2006; Paterson, 1990). Declining catch rates and lengths of some species caught in protective gillnets in Australia (Reid et al., 2011) and South Africa (Dudley and Simpfendorfer, 2006) have raised serious concerns regarding the ecological impact of shark meshing programs (Paterson, 1990; Sumpton et al., 2010), particularly under a scenario of global depletion of marine top predators (Jackson et al., 2001, Myers et al., 2007).

Other methods to reduce the risk of shark attack have been used, each with its own limitations. Shark exclusion devices offer a promising concept since they provide full protection by imposing a physical barrier to sharks, thus creating a shark-free area without capturing the sharks. However, they are only suited to sheltered shores with no or little surf (Dudley and Cliff, 2010). These barriers have been repeatedly installed in several places since the beginning of the 20th century but, unfortunately, they proved to be prohibitively expensive for maintenance as they were generally subjected to continual damage by wave action and so most of them were eventually dismantled (Coppleson and Goadby, 1988). Currently, only a

few places have barrier nets installed for shark avoidance, namely the Sidney harbor, Queensland's Gold Coast marinas, and Hong Kong (Dudley and Gribble, 1999). Another strategy for shark avoidance relies on the development of shark deterrents, either chemical or electrical. However, despite the apparent success of an electrical deterrent in reducing the probability of a white shark biting the bait (Smit and Peddemors, 2003), no practical use for protecting bathing beaches with such equipment has yet been achieved (Cliff and Dudley, 1992). Finally, surveillance schemes in which spotters positioned in strategic, high places next to the water monitor the presence of sharks in the area and alert bathers in case of peril have been used in Australia (Whitley,1963) and South Africa (Oelofse and Kamp, 2006). However, their efficacy is greatly dependent on atmospheric conditions and water visibility, which restricts the time and places where they can be employed.

1.3. The Case-Study of Recife

The Metropolitan Region of Recife (MRR), Brazil has been experiencing an abnormally high shark attack rate during the past 20 years. Since 1992, a total of 55 shark attacks occurred in these waters, resulting in 20 fatalities. Most attacks occurred within a 15 km, densely populated shoreline which comprises the Barra de Jangadas estuary. Hence, the area of higher risk is very small, resulting in Recife exhibiting one of the highest shark attack rates per unit of area in the world. Surprisingly, despite intense recreational use of these beaches since the early 1950s, there had been no records of shark attacks in this region before 1992, except for a few anecdotal reports (Hazin et al., 2008).

Recife is the capital of the State of Pernambuco and one of the biggest urban centers in northeastern Brazil, with a population of about 1.5 million people (nearly 4 million in the whole MRR) (Instituto Brasileiro de Geografia e Estatística; www.ibge.gov.br; Accessed October 10th 2012). The shoreline of Recife comprises a stretch of sandy beaches with warm seawater that fosters year-round use. The tourism industry has historically been an important component of local economy and, as the shark peril off Recife was highly publicized by local, national and international media, this sector suffered severe losses whith negative impacts on

social welfare, although the full dimension of the socioeconomic damages caused by shark attacks is always difficult to quantify (Gaiser, 1976).

The shark attack outbreak happened after the construction of a large port complex about 25 km to the south of Recife, the port of Suape, which was built on a wide, pristine estuarine system to which four rivers converged, namely the Massangana, Tatuoca, Ipojuca, and Merepe (Fig. 5). The development required deep modifications to a substantial area of the estuary, including damming, dredging, and the embankment of two rivers which had their courses diverted (Neumann-Leitão and Matsumura-Tundisi, 1998), resulting in significant environmental degradation (Hazin et al., 2008; Koening et al., 2003).

To contain the sudden increase in shark attacks, and given that a large proportion of the victims were surfers, the Government decreed the prohibition of all board-riding activities in the area on January 1st 1995 and reinforced it in May 1999 with a new, stricter decree. This resulted in a higher proportion of bathers being attacked compared to surfers in the following years (Hazin et al., 2008). Also, warning signs with information on shark peril were abundantly installed across the area. In May 2004, the State Government created the State Council for Shark Hazard Monitoring (CEMIT) with the purpose of adopting and coordinating measures to reduce the shark attack rate and the proportion of fatalities associated to it, which equaled about 35%, being thus considerably higher than those of other regions (ISAF, http://www.flmnh.ufl.edu/fish/sharks/isaf/ isaf.htm; Accessed June 3rd 2012). The CEMIT is composed of five permanent members that synergistically intervene on the several components of the shark attack problem: the Firemen Department, responsible for beach surveillance, law enforcement, and rescue; the Legal Medicine Institute, responsible for the coroner examination of fatal victims; the State Agency for the Environment and Aquatic Resources, responsible for the environmental recovery of this region; the Instituto Oceanário de Pernambuco, responsible for providing environmental education and further information to the beach users and general community; and the Universidade Federal Rural de Pernambuco (UFRPE), responsible for developing measures to reduce the risk of shark attack and to increase the scientific knowledge on this situation, since virtually nothing was previously known about the coastal ecosystem off Recife and the species responsible for the attacks.

Figure 1.5. Map depicting the littoral of Recife with a tentative projection of the nearshore relief and the location of the port of Suape, to the south. Most shark attacks occurred off the gray area. Retrieved from Hazin et al. (2008), with permission.

Hazin et al. (2008) assessed trends in shark attacks off Recife in relation to attack location, day of the week, time of the day, moon phase, and distance from shore. The beaches of Boa Viagem and Piedade exhibited disproportionally higher rates of shark attacks, although the data were not standardized by unit of area. Regarding the day of the week, most attacks occurred between Friday and Tuesday, while no attacks were verified on Wednesdays. The most hazardous times of the day were early in the morning (between 6:00 and 8:00 a.m.) and late in the afternoon (between 16:00 and 18:00), while the full and new moon phases corresponded to the periods in which more attacks occurred (Hazin et al., 2008). The analysis of trends in shark attacks is an important step towards the adequate understanding of subjacent causes and the generation of mitigation measures.

Several causes have been implicated in the shark attack outbreak off Recife. Yet, the construction of the port of Suape and the subsequent increase in maritime traffic are believed to have triggered the situation (Hazin et al., 2008). Sharks are known to be attracted by ships (Baldridge, 1974; Schultz, 1975) and even small boats (McCord and Lamberth, 2009), and frequently enter port areas (Coppleson, 1958). Attraction of sharks by low-frequency sounds (Myrberg, 2001), which are emitted by transiting vessels (Arveson and Vendittis, 2000), could partially explain such behavior. Thus, it is likely that the port of Suape may promote the approximation of sharks to this region. Additionally, habitat degradation during the construction of the port may have driven sharks that use estuarine and fluvial waters for foraging or reproduction, such as the bull shark, away from Suape (Hazin et al., 2008). Since northward coastal currents prevail during most of the year (Lira et al., 2010), those sharks could have moved to the nearest estuary northward from Suape, i.e., the Jaboatão estuary. Moreover, the presence of the Jaboatão estuary within the area of risk raised additional concerns because the local public slaughterhouse was, since 1982, dumping its untreated effluents, including blood and entrails, directly into Jaboatão river at an average volume of 345 cubic meters per day, and untreated liquid waste flowed from the Muribeca Waste Landfill into Jaboatão river at an average of at least 60 liters per minute (Hazin et al., 2008). According to FAO (1991), this type of waste has a great potential for attracting predators and, if discharged into the ocean, it may increase the numbers of sharks in the affected area. Yet, closure of the slaughterhouse in 2005 did not reduce the shark attack rate, thus it alone could not be responsible for the situation. Finally, the existence of a deep channel adjacent to the

beach has been also pointed out as a probable cause for high shark-human interaction off Recife as it would facilitate the approach of sharks to the shoreline (Hazin et al., 2008).

1.4. General objectives

Given that *i)* shark attacks off Recife produce serious damage to local economy and social welfare, *ii)* the populations of large, coastal sharks are strongly depleted worldwide, *iii)* knowledge of the dynamics and ecology of large predators in nearshore waters off the northeastern coast of Brazil is still scarce, and *iv)* shark attack mitigation techniques that have been published so far are either unsuitable to the case-study of Recife or do not provide the desired performance, this study aimed at the following objectives:

1) Description of the inner continental shelf off Recife with regard to some environmental parameters relevant to the ecology and behavior of sharks − Chapter 2.

2) Design and optimization of a fishing methodology with high selectivity for sharks and low fishing mortality − Chapter 3.

3) Characterization of the Shark Monitoring Program of Recife with respect to the fishing operations and catches − Chapter 4.

4) Assessment of spatiotemporal trends in elasmobranch abundance off Recife and investigation of environmental predictors − Chapter 5.

5) Description of some biological aspects of sharks caught off Recife − Chapter 6.

6) Assessment of movement patterns of potentially aggressive sharks caught off Recife − Chapter 7.

7) Development and evaluation of shark attack mitigation measures − Chapter 8.

Chapter 2. The nearshore environment off Recife

Aerial view of the beaches of Recife. Photo by Carlos Bayma, available at http://recife-night-day.blogspot.com.br/2010/03/zona-sul-boa-viagem-vista-aerea.html

2.1. Introduction

Recife is located in the northeastern coast of Brazil, around 8º10'S and 34º54'W. According to Peel et al. (2007), Recife is included in a thin littoral fringe with a tropical monsoon climate, corresponding to type *Am* under the Koppen climate classification, although it has been previously associated to drier weather (Schwerdtfeger, 1976). This region experiences a clear seasonality composed by a rainy season from May to July, with monthly precipitation varying between 100-400 mm, and a dry season from September to March with monthly rainfall below 100 mm (Rolnicc et al., 2011). This seasonality is mostly shaped by the prevailing southeastern trade winds, whose velocities average 4.0 $m \cdot s^{-1}$ and are higher during winter months but lower during the dry season, eventually getting to a minimum between December-January, when Northeast and East winds may occur (Rolnicc et al., 2011).

The area off Recife where most attacks occurred (hereafter referred to as the area of risk) is approximately 20 km long and includes five contiguous beaches: Paiva, Candeias, Piedade, Boa Viagem, and Pina (Fig 1.5). The stretch between Candeias and Pina is densely urbanized and has the highest density of beach users in the region (Silva et al., 2008), while Paiva is a comparatively undeveloped area frequented by few people. All these beaches are under the influence of the Barra de Jangadas estuary, formed by the Pirapama and Jaboatão rivers which together drain an area of about 1,000 km^2 into the Atlantic Ocean (Carneiro and Coelho, 1960). The local tidal regime is semi-diurnal and exhibits an average amplitude of 1.67 m, with neap tides averaging 0.97 m and spring tides averaging 2.07 m of amplitude (Rollnic, 2002). Sea water temperature shows little variation, ranging from 24ºC during winter to 30ºC during summer (Hazin et al., 2000). Salinity is typically high, oscillating between 36-37 ups in the first 80 m of the water column and further reducing to about 35 ups at deeper water layers (Macêdo et al., 2004). Northward coastal currents driven by the southeastern trade winds predominate almost all year-round (Bittencourt et al., 2005), but southward coastal currents may occur during the dry season (Lira et al., 2010; Rollnic et al., 2011), when the southeast trade winds are weaker and the northeastern winds trades become more frequent.

The continental margin off the northeastern Brazil consists of a narrow shelf (63 km average width; Souza, 2007) bordered by one of the longest, consistently steep (4 to 20º) continental slopes in the world (Fainstein and Milliman, 1979). Off Recife, the continental shelf slants smoothly for about 40 km down to the 60 m isobath, where the slope abruptly starts. Such a relatively narrow shelf results in this region being strongly influenced by the South Equatorial Current (SEC), whose oligotrophic waters usually stimulate long trophic webs, while more coastal waters are exposed to nutrient input from estuarine plumes and may exhibit trophic webs with fewer links (Neumann-Leitão et al., 2004). Resurreição et al. (1996) suggested that the influence of estuarine plumes off Recife was visible until the 30 m isobath, whilst Medeiros et al. (1999) measured the concentration of Chlorophyll-a in coastal waters to be 4 times higher than in oceanic waters. Calcareous algae such as *Halimeda* spp. and *Udotea* spp. (order Bryiopsidales), and *Lithothamnium* spp. (order Coralinalles) dominate the substratum and are responsible for the high proportion of biogenic carbonate in the sediment (Coutinho, 1976; Manso et al., 2003). Based on geomorphic and sedimentological aspects, Coutinho (1976) divided the continental shelf off northeastern Brazil in three distinct segments, namely *i)* the inner platform, extending to the 20 m isobath with a smooth topography and dominated by terrigenous sediments such as silicates and silts, which contain a considerable amount of organic detritus and a percentage of biogenic carbonate generally inferior to 25%; *ii)* the middle platform, extending between 20-40 m isobaths with a more irregular topography and predominance of biogenic carbonates; and *iii)* the outer platform, extending from the 40 m isobath until the slope and being dominated by biogenic carbonate in a proportion generally higher than 75%, and by a bluish calcareous mud in a proportion between 10-15%. Another characteristic of this continental shelf is the low abundance of corals compared to algae. Presently, the distribution of corals is generally restricted to the seaward side of beachrocks and reefs which border the shoreline and that represent the only hard substrate available (Manso et al., 2003), except for several ship wrecks (Fischer, 2009).

Beachrocks can play an important role in nearshore waters, particularly when the seafloor is dominated by soft substrate. The mesolittoral of Pina, Boa Viagem, and Piedade exhibits an intermittent line of reefs which form tidal pools during low tide. Further offshore, a second, submerged line of beachrocks disturbs the infralittoral topography and creates a channel-like, alongshore structure about 6.4 m in average depth (Gregório et al., 2010; Hazin

et al., 2008). This second line of beachrocks acts as a barrier against hydrodynamic surge and so it provides mechanical protection to local benthic communities. Also, beachrocks add complexity to the nearshore habitat and provide a suitable substrate for incrusting and sessile organisms. Off Recife, beachrocks may additionally be a factor contributing to the high shark attack rate verified in this shore. In fact, the channel-like structure that they generate could restrict the movements of large, potentially aggressive sharks that enter the channel by imposing an obstacle to the seaward motion. As such, sharks may be confined to the area between the beach and the beachrock when foraging through this shore, which would certainly increase the likelihood of a shark-human encounter.

The objective of this chapter is to describe the spatiotemporal variation of some environmental parameters in the study area which could be relevant to the occurrence and distribution of elasmobranchs, and to increase previous knowledge on the environmental dynamics in this region. This chapter also aims at assessing the bathymetry of the area of risk in finer detail and relating it with shark-human encounters off Recife.

2.2. Materials and methods

Local atmospheric data concerning pluviosity (in mm), wind direction (in degrees), wind maximum speed (in knots), and atmospheric pressure (in kPa) for the period between January 2004 and December 2011 were obtained from the Sistema Nacional de Dados Ambientais, managed by the Centro de Previsão de Tempo e Estudos Climáticos (CPTEC) from the Instituto Nacional de Pesquisas Espaciais (INPE) of the Brazilian Ministry of Science and Technology (http://sinda.crn2.inpe.br/PCD/historico/consulta_pcdms.jsp; Accessed January 16th 2012). The environmental monitoring of the study area was conducted in parallel with fishing operations (see chapter 4) at two sampling sites, hereafter referred to as Boa Viagem (BV) and Paiva (PA). Between May 2004 and December 2011, the sea surface temperature (±0.2ºC) was measured at both sites with a FURUNO FCV-5821 echosounder installed in the R/V Sinuelo. In order to assess variations in the water column, the temperature and salinity were sampled at 2 m-depth intervals between the sea surface and the sea floor, thus generating 8 samples at depths 0, 2, 4, 6, 8, 10, 12 and 14 m at each site. Temperature

(±0.15ºC) and salinity (±0.1 ups) were measured with a YSI 556 handheld multiparameter system between July 2009 and April 2011. Additionally, sea water transparency was measured with a Secchi disk at both sites between May 2004 and December 2011. Measurements of water transparency were taken to the nearest 1.0 m except in the first meter of water, which was divided in 0.5 m, and sampling was systematically taken around the same period in the morning. Differences in water transparency between sampling sites were assessed with a 1-way factorial ANOVA. Differences in temperature and salinity between sampling sites and between the different depth strata were assessed with a 2-way factorial ANOVA, followed by Tukey's post-hoc multicomparison procedure when significant differences were found. The significance level of all statistical tests was 0.05. Normality and homocedasticity of the data were previously assessed with normal Q-Q plots and Levene tests, respectively. All statistical analyses were performed in *R* version 2.14.0 (*R* Development Core Team, 2011).

The bathymetric profile of the area of risk was surveyed with a FURUNO FCV-5821 echosounder, a GPS and a digital camera. Depth measurements were taken by photographing the echosounder and the GPS simultaneously aboard the R/V Sinuelo. The area extending between the shoreline and longitude 34º50'00"W, and between latitudes 8º5'0"S and 8º13'0"S, was thoroughly surveyed following an intensive zigzag motion pattern, and every time a sudden change in depth was observed the boat would drive around that area and sampling was intensified, especially when surveying the submerged beachrocks. The time of each sampling was recorded and depths were corrected to the nearest 0.1 m for tidal variation in relation to the hydrographic zero, based on data for the Port of Recife provided by the Hydrographic and Navigation Directory of the Brazilian Navy (data available at http://www.mar.mil.br/ dhn/chm/tabuas/ index.htm). A bathymetric map of the study area was then generated using Surfer 8 (Golden Software, Golden, CO) using the Kriging algorithm as a gridding method. Finally, the bathymetric map was exported to ArcMap 9.3 (ESRI Inc., Redlands, CA) for including tentative estimates of the locations of shark attacks on humans off Recife. Such estimates were based on records and testimonies available in the media and in the database managed by CEMIT.

2.3. Results

All atmospheric variables exhibited a clear seasonality. Pluviosity was highest (>100 mm) between April and August, peaking in June at maximum values of more than 500 mm, while the period between October and December had lowest rainfall (Fig. 2.1). The atmospheric pressure revealed little variation throughout the year, with an amplitude of only about 12 kPa, but it was highest between July and September and lowest between February and April (Fig. 2.2). The wind direction and speed also evidenced variations throughout the year. Between November and February, winds blowing from the east and the northeast were more frequent, but from April through October southeastern winds were generally most common (Fig. 2.3). A frequent, ~25-knot wind blowing from about 280º, i.e. almost west, was observed in nearly every month. In general, wind speed was lower than 25 knots but occasional strong wind, as high as 55 knots, was present during most of the year.

The seawater temperature in the study area ranged between 24.4 and 31.0 ºC, whereas salinity ranged between 30.3 and 39.9 ups and water transparency ranged between 0.5 and 13 m, the latter corresponding roughly to the whole water column at both sampling sites. The spatial variability in seawater temperature, salinity, and transparency was generally insignificant. Differences in water transparency between sampling sites were not detected by the 1-way factorial ANOVA ($F = 0.672$, $df = 1$, $p = 0.412$). Likewise, the 2-way factorial ANOVA performed to compare temperature and salinity between sampling sites and sampling depths did not detect differences in temperature for either sampling sites ($F = 0.444$, $df = 1$, $p = 0.505$) or the interaction term ($F = 0.119$, $df = 6$, $p = 0.994$). Similarly, no differences in salinity were found for either sites ($F = 0.779$, $df = 1$, $p = 0.378$) or the interaction term ($F = 0.128$, $df = 6$, $p = 0.993$). As such, those terms were removed from the model and 1-way ANOVAs detected significant differences in temperature ($F = 5.899$, $df = 7$, $p < 0.001$) and salinity ($F = 6.032$, $df = 7$, $p < 0.001$) between sampling depths. Temperature tended to decrease with depth, while salinity tended to increase (Table 2.1). The Tukey's post-hoc procedure further identified significant differences in temperature between depths 0 and 6 m ($p = 0.035$), 0 and 8 m ($p < 0.001$), 0 and 10 m ($p < 0.001$), and also between depths 2 and 8 m ($p = 0.002$) and 2 and 10 m ($p = 0.001$). Regarding salinity, the same procedure identified differences between depths 0 and 8 m ($p = 0.004$), 0 and 10 m ($p = 0.001$), 0 and 12 m ($p <$

0.001), and also between depths 2 and 12 m ($p < 0.001$), 4 and 12 m ($p = 0.007$), and 6 and 12 m ($p = 0.020$).

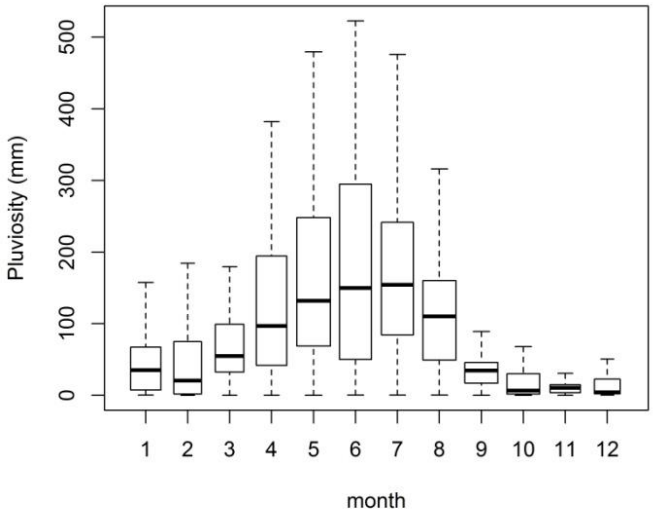


Figure 2.1. Monthly variation of pluviosity, measured in mm, in the region of Recife between January 2004 and November 2011.

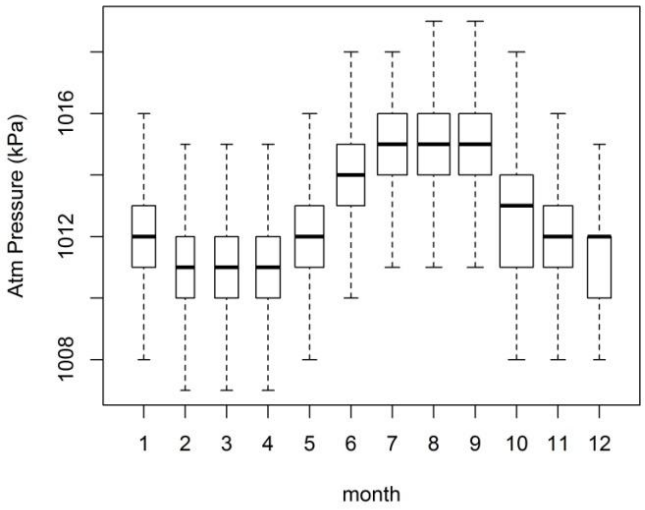


Figure 2.2. Monthly variation of atmospheric pressure, measured in kPa, in the region of Recife between January 2004 and November 2011.

Table 2.1. ANOVA coefficients for two models incorporating water temperature and depth, and water salinity and depth.

Factor	intercept	2 m	4 m	6 m	8 m	10 m	12 m	14 m
Temperature	28.403	−0.016	−0.077	−0.149	−0.205	−0.216	−0.272	−0.235
Salinity	36.521	0.092	0.158	0.199	0.263	0.295	0.645	1.105

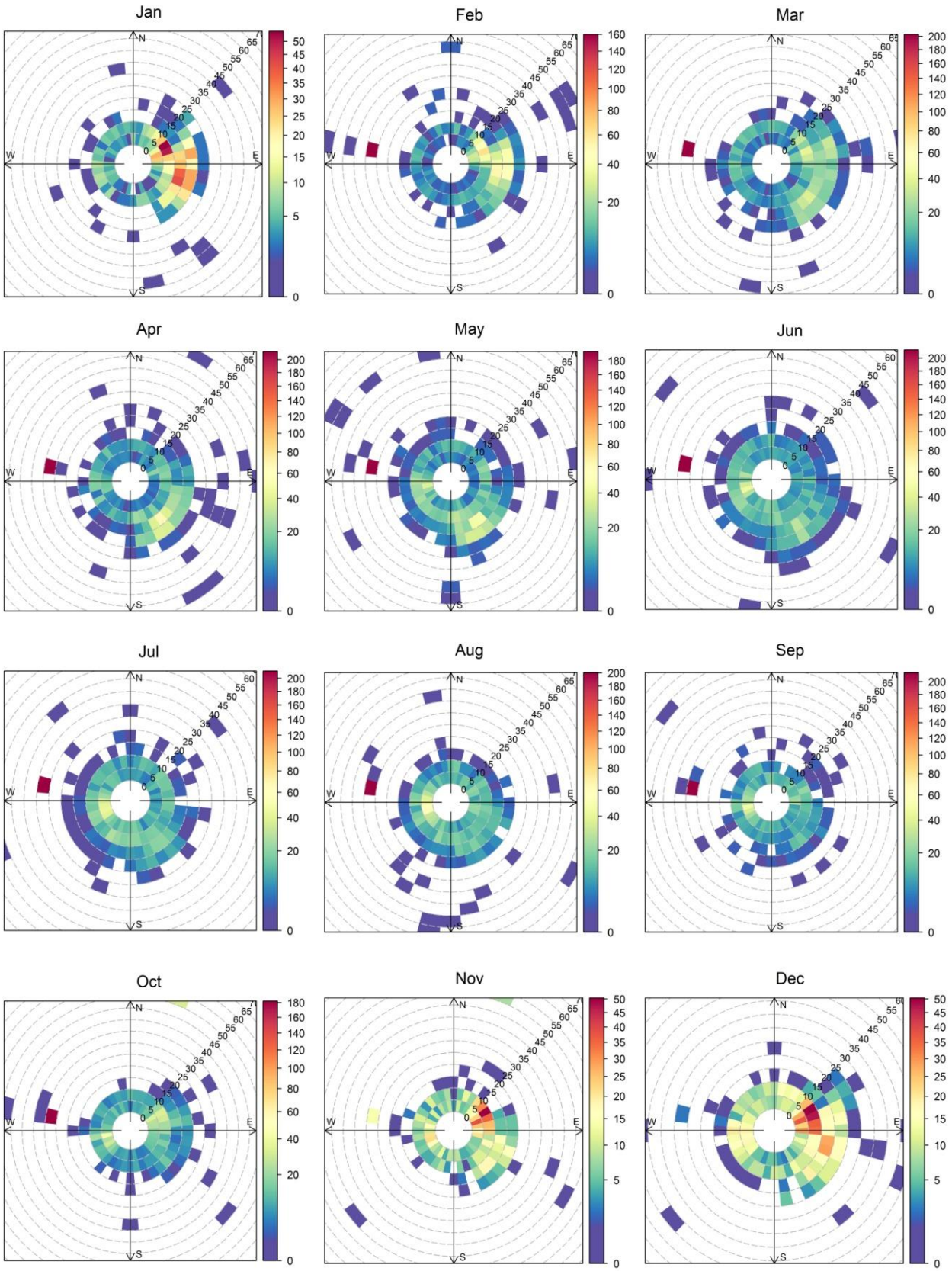


Figure 2.3. Polar plots depicting monthly variation of wind direction and wind maximum speed, in 5-knot intervals. Colors represent the absolute frequency. Plots created in *R* with the function *polarFreq* (Carslaw and Ropkins, 2011).

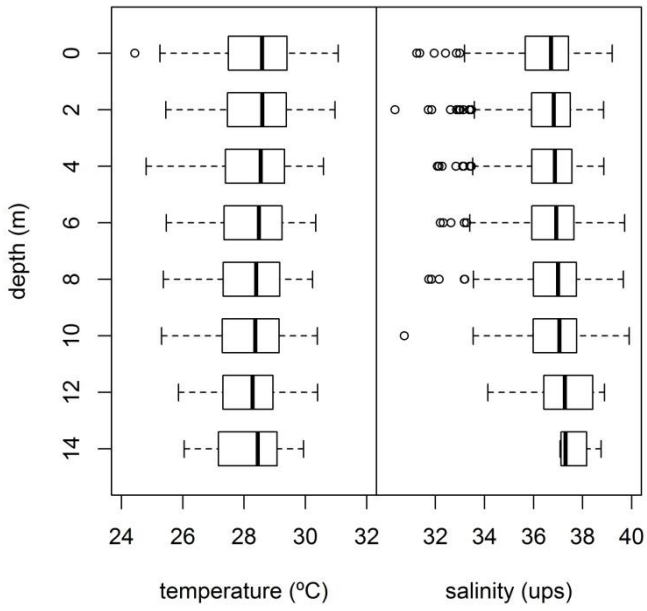


Figure 2.4. Distribution of temperature (left panel) and salinity (right panel) along the water column off Recife.

No major deviations from normality were evidenced by normal Q-Q plots, and Levene tests did not detected differences in the variance of temperature between sampling sites (F = 2.623, df = 1, p = 0.105) and sampling depths (F = 1.160, df = 7, p = 0.323), neither in the variance of salinity between sampling sites (F = 0.932, df = 1, p = 0.334) and sampling depths (F = 0.800, df = 7, p = 0.587) or in the variance of water transparency between sampling sites (F = 1.063, df = 1, p = 0.303). Despite statistical significance, the variation of temperature and salinity along the water column was rather small, being less than one unit of measurement in both cases (Fig. 2.4).

The temporal variation of sea surface temperature assessed after pooling data from both sampling sites was markedly seasonal, peaking between February and April and being lowest between July and September (Fig. 2.5). On the other hand, the variation of salinity showed a less obvious trend, but lower values and narrower ranges were observed between May and September, while the period between October and February generally showed higher salinity values distributed along a broader range (Fig. 2.6). Regarding water transparency, most months exhibited high variability in this parameter, particularly between August and September, when the range of values was highest (Fig. 2.7). The period between April and July, however, had generally lower values of water transparency and narrower distributions.

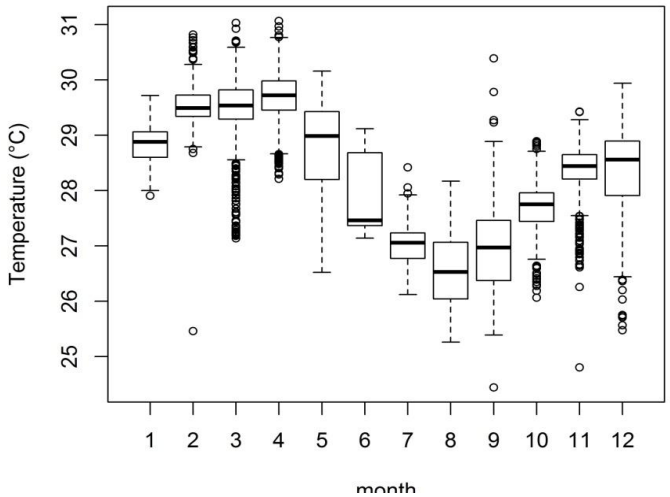


Figure 2.5. Sea surface temperature in the littoral of Recife between May 2004 and December 2011.

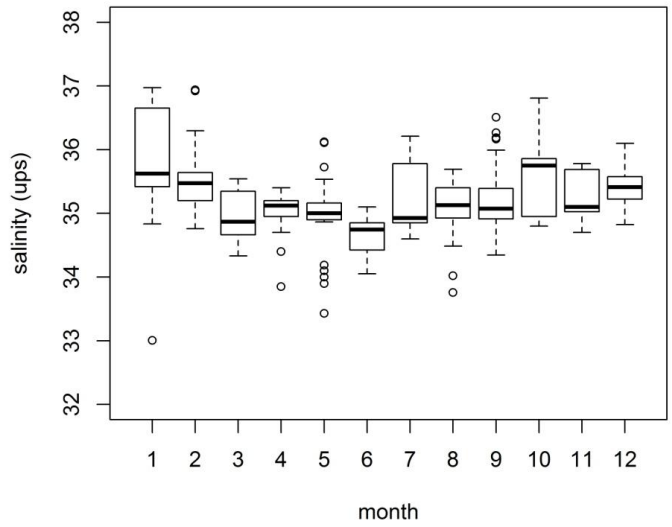


Figure 2.6. Seawater salinity measured at the subsurface in the littoral of Recife between May 2004 and December 2011.

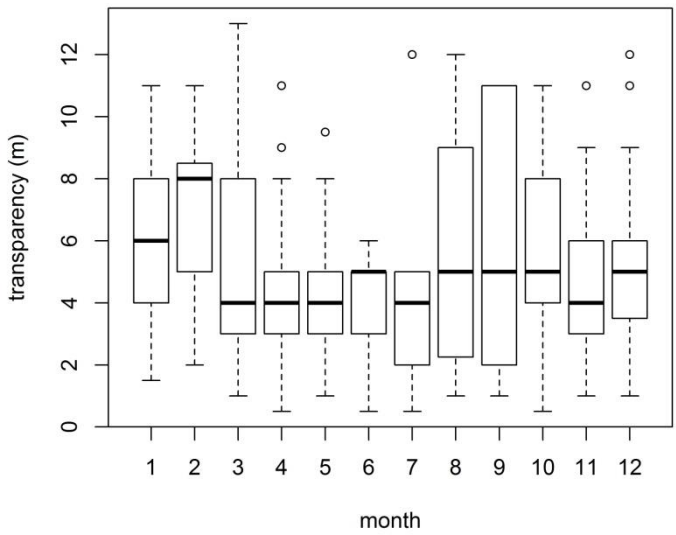


Figure 2.7. Seawater transparency measured with a disc of Secchi in the littoral of Recife between May 2004 and December 2011.

A bathymetric survey of the area of risk off Recife, between Pina and Candeias beaches, was also conducted, with a total of 2,394 depth measurements being taken and corrected for tidal variation. The survey evidenced a well-defined channel, with 6−7 m at its deepest point and about 650 m in average width, limited seaward by a submerged line of beachrocks about 2 m deep (Fig. 2.8). The shape of the channel resembles an 8 km long half-pipe running parallel to the coastline between Pina and Piedade beaches. The main entrances to the channel are in its northernmost and southernmost sections. Although fairly uniform, the ridge formed by the beachrocks exhibits three deeper passageways throughout its extent, around latitudes 8º9'20"S, 8º8'0"S, and 8º6'50"S. The locations of the shark attacks that occurred in this shore are also depicted, and areas with higher densities of attacks were generally close to the two northernmost passageways (Fig. 2.8), although these sites correspond to estimates based on different testimonies whose accuracy could vary.

2.4. Discussion

The study area showed a remarkable spatial homogeneity in the parameters monitored. Vertical stratification of the water column regarding temperature and salinity was minimal, with significant differences occurring between the uppermost and lowermost layers only. Furthermore, such differences were considered negligible compared to overall variability of these parameters. The two sampling sites showed no significant differences in water temperature, salinity, and transparency, and no interaction was detected between sampling depths and sites for temperature and salinity. The Barra de Jangadas estuary seems to have little effect on the spatial distribution of these parameters within the study area, which could be explained by its shallow depth (< 15 m) and local hydrodynamics (Rollnic et al., 2011), resulting in the effective mixing of the water column. Nevertheless, variability in some environmental parameters should be expected across a gradient perpendicular to the coastline, as verified by Ressurreição et al. (1996) and Medeiros et al. (1999).

The observed seasonality in the parameters monitored generally agrees with the environmental dynamics previously described for this region (Macêdo et al., 2004; Rollnic et al., 2011). During the study period, the rainy season occurred between April and August and

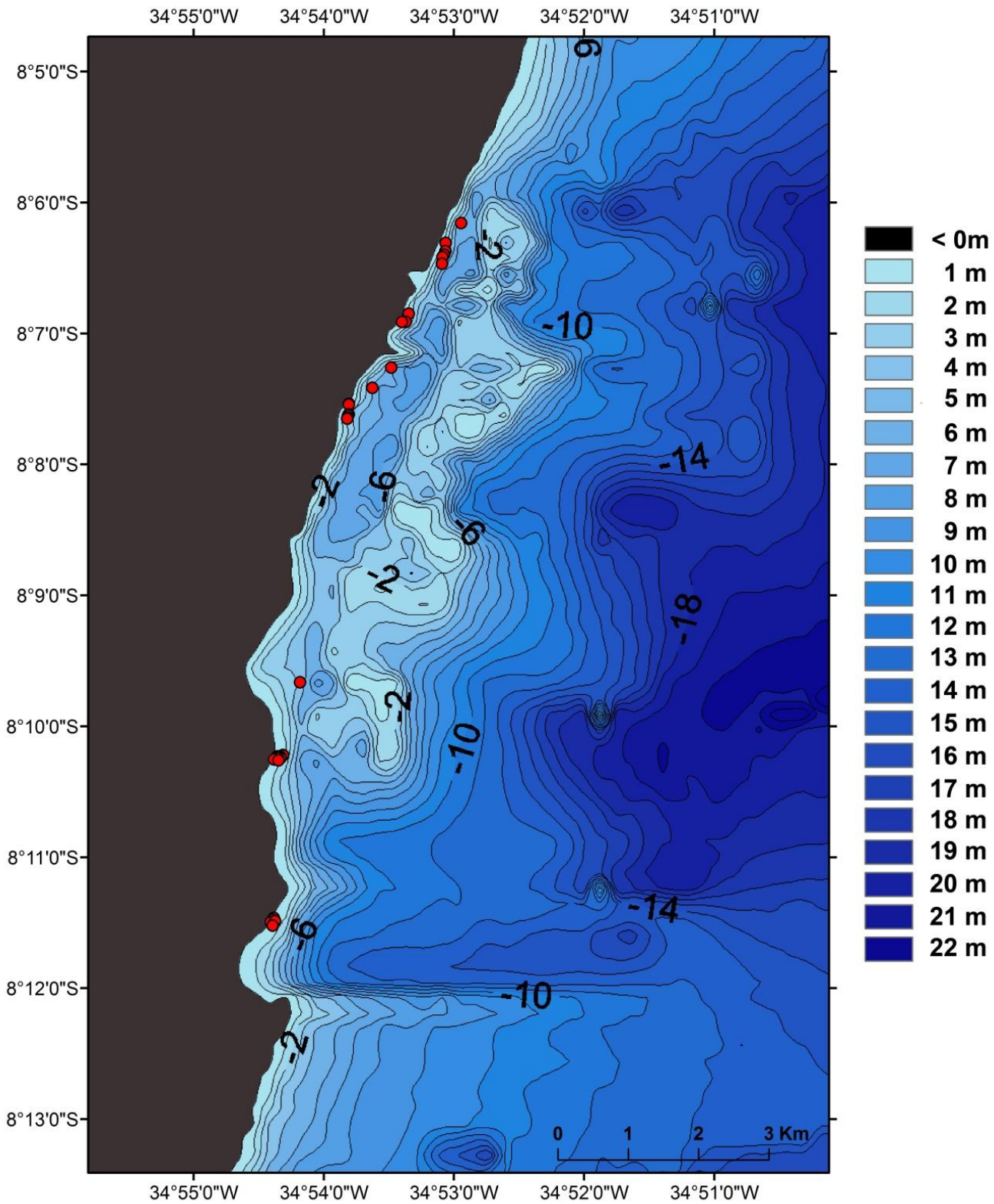


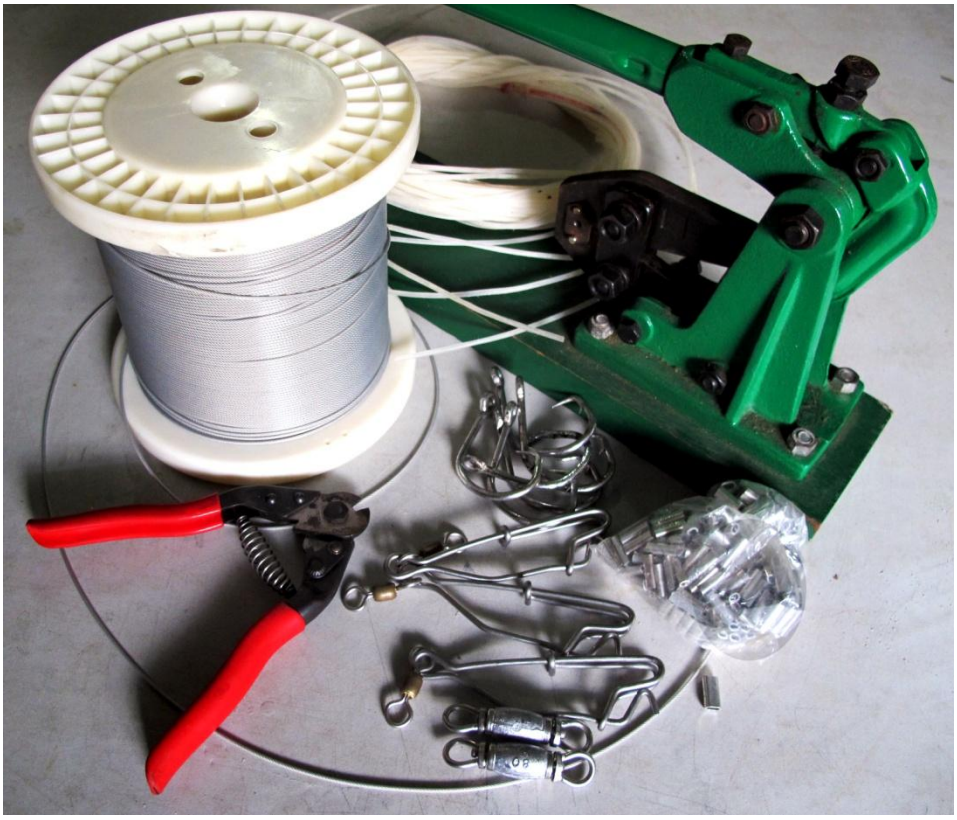
Figure 2.8. Bathymetric chart of the nearshore area off Recife, between Pina and Candeias beaches, depicting an alongshore, submarine channel next to the beach. The red dots represent tentative estimates of the location of shark attacks on humans in this region.

peaked in June−July, while the sea surface temperature was lowest by the end of the rainy season, between July and September. Salinity also followed a similar but less conspicuous trend, probably due to high variability in pluviosity and solar irradiation between years and within months, both of which strongly influence sea water salinity in coastal areas. A Principal Component Analysis indicated that tidal variation and pluviosity were the main factors influencing coastal waters off Maracaípe (Bastos et al., 2001). Water transparency was lowest in July, during highest rainfall, but it also showed substantial variability which could result from the tidal cycle, wind-driven hydrodynamics and trends in freshwater discharge from the Barra de Jangadas estuary. The wind regime verified off Recife followed the pattern already known in this region, with a clear dominance of southeastern trades during the rainy season and with east-northeastern winds emerging during the dry season. The persisting existence of winds coming from the West should be related to the local geography, as the westward continental landmass has a different thermal behavior than the oceanic waters, thus producing predictable daily winds due to land heating and cooling.

The morphology of the seafloor at the northern section of the study area is rather irregular due to the presence of a shallow, submerged line of beachrocks, a broad structure which spans from Pina trough Piedade and which is absent in Paiva. These beachrocks shape an alongshore channel next to the beach which is believed to be related to the high numbers of shark attacks in this region (Hazin et al., 2008). The bathymetric survey showed that the main openings to the channel are located in its extremes, but the northern entrance is considerably narrower and steeper than the southern one. Also, the southern entrance is associated with a deeper basin whose morphology could direct sharks towards the channel more easily. Based on such bathymetric features, it is likely that most sharks access to the channel by its southern entrance. Once inside, depth constraints would possibly compel sharks to swim along the channel, thus increasing the likelihood of a shark-human encounter. Despite the uniformity and shallowness of the ridge of beachrocks, three lesser, slightly deeper passageways were detected along the crest of the reef. Two of these passageways are located near from sites with high densities of shark attacks which resemble shark attack density close to the main entrance of the channel. Such passageways could be considered, therefore, as hot-spots because they may facilitate shoreward movements of large, potentially aggressive sharks across the reef of

beachrocks, especially during higher tides, thus adding important information to a better comprehension of the shark attack problem off Recife.

Chapter 3. Definition and optimization of the fishing gear



Setting up longline gear.

3.1. Introduction

Many types of fishing activities have a significant effect on non-target populations, habitats, and communities (Hall, 1996; Kaiser et al., 2002; Pauly et al., 2001; Sainsbury, 1987), therefore one of the most decisive guidelines when developing the fishing methodology to be used off Recife was to reduce the environmental impact to a minimum. Despite its apparent efficacy on shark attack mitigation (Dudley and Cliff, 2010), shark-meshing was immediately excluded as an option because it would not provide the desired selectivity for sharks and it would probably inflict high mortalities to sharks and other large-sized *taxa* such as turtles, dolphins, and manatees (Dudley and Cliff, 1993a; Gribble et al., 1998a), all of which occur in this region. A hook-based fishing strategy was thus elected. Baited longlines could unravel concerns regarding gear selectivity and fishing mortality because different parameters, such as the type of hook and bait, can be adjusted in order to optimize the performance of the longline towards the required purpose. Such optimization is essential, since incidental mortality of cetaceans, seabirds, sea turtles, sharks, rays, and teleosts in longline fisheries is recognized as a key threat for many of these species (Musick, 1999).

Although pelagic sharks are caught with a variety of fishing gears in the Atlantic Ocean, longline fisheries targeting tunas and swordfish account for the majority of catches (Anonymous, 2007). In Brazil, the pelagic longlining for tunas was started more than 50 years ago, in the northeastern region (Paiva and Le Gall, 1975), with sharks always representing an important part of the bycatch (Hazin et al., 1998). In the tuna fleet operating in the south of Brazil, the landings of sharks have also been historically important, increasing throughout time (Anuska-Pereira et al., 2005).

Global concerns regarding the unsustainable exploitation of fishery resources, particularly of elasmobranchs, have led to several legislations aiming at ensuring the conservation of their populations. Accordingly, international, national, and regional legal frameworks have been developed to reduce the incidental catch of sharks for stock management purposes. However, management tools such as quotas or catch prohibition are based on the assumption that individuals of regulated species are returned to the sea alive, which could be misleading in case such species exhibit high at-vessel fishing mortality

(Morgan and Burgess, 2007). To be effective, therefore, conservation measures generally need to be accompanied by complementary tools that can promote the achievement of their objectives. In that respect, gear modifications are expected to be one of the most effective and inexpensive tools in reducing incidental fishing mortality (Brewer et al., 1996; Fonteyne and Mrabet, 1992; Madsen et al., 2006).

Modifications to pelagic longline gear have often included changes in terminal tackle from J-hooks to circle hooks. Circle hooks are distinct because their point is aligned perpendicular to their shank rather than parallel to it, which is the case of traditional hook types such as J-hooks (Cooke and Suski, 2004). Due to their design, circle hooks tend to minimize deep hooking in potentially lethal internal regions and instead typically hook fish in the upper jaw (Montrey, 1999). Also, the catch rate of target species appears not to be significantly affected by the use of circle hooks in the case of tuna and billfishes, and it has been reported to even increase in comparison with J-style hooks, in some cases (Falterman and Graves, 2002; Kerstetter et al., 2007; Kerstetter and Graves, 2006; but see Read, 2007). Because of its performance, fishery managers have focused considerable attention on circle hooks as a way to reduce bycatch mortality. This type of hook is currently being tested in different types of fisheries and has been shown to be a practical and economical measure to reduce mortality in pelagic longline fisheries. Despite previous studies on the mortality rate (Falterman and Graves, 2002), catch rate (Prince et al., 2002), hooking efficiency (Skomal et al., 2002), and hook location on teleost fishes (Bacheler and Buckel, 2004; Beckwith and Rand, 2005), there is little published information on the influence of hook type in the catches and mortality of elasmobranchs, with a few exceptions (e.g., Kerstetter and Graves, 2006). In the South Atlantic fisheries, such information is yet non-existent.

The vertical position of the hook within the water column is likely to be another important factor influencing catch composition. Coelho et al. (2003) described the effect of the depth of hooks on elasmobranch catches by attaching floats to bottom longline branch lines in oceanic fishing grounds at depths between 200 and 550 m. However, no previous study to date has evaluated the influence of the vertical position of the hooks on the catch rates of coastal elasmobranchs.

The overall goal of this chapter, therefore, was to examine the influence of gear modifications on the bycatch and mortality rate of elasmobranchs caught in Brazilian longline fisheries. These gear modifications included a comparison of conventional J-style *versus* circle hooks, and mid-water deployment *versus* demersal deployment of hooks. Since the catch rate of coastal elasmobranchs off Recife is generally low (Hazin et al., 2000), additional experiments were conducted in a pelagic, oceanic longline in order to increase the numbers and species of individuals caught, and thus the robustness of gear comparisons. This approach allowed the results to be addressed also under a commercial fisheries perspective.

3.2. Materials and Methods

Between August 2004 and April 2007, two experiments were conducted to test the influence of hook type and physical position of the hook in catch composition, catch rates, and mortality at haulback of elasmobranchs caught with longline fishing gear, using both pelagic longlines (section 3.2.1) and bottom longlines (section 3.2.2).

3.2.1. Pelagic longlining experiment

In the first experiment, 12 pelagic longline sets were deployed from a chartered commercial longline vessel (~25 m in length) off the coast of Natal, Northeast Brazil. The pelagic longline sets targeted tuna and were concentrated between 30º−35ºW longitude and 0º−5ºS latitude (Fig. 3.1). This area is an oceanic region characterized by the presence of several seamounts, some of which as shallow as 40−70 m, around which carcharhinid sharks tend to aggregate (Hazin et al., 1998). A total of 650 hooks were deployed per set, of which 325 were circle hooks and 325 were J-style hooks. Circle hooks used were size 18/0 with a 0° offset (Lindgren-Pitman model LPCIR18SS), whereas J-style hooks were identical to the hooks most commonly used by Brazilian pelagic longliners targeting tuna and were size 9/0, with a 10° offset (Mustad model #7698) (Fig. SUP.3.1). The longline was subdivided in 130 baskets with 5 hooks each, and the two hook types were alternated throughout the set to ensure equal representation of hooks across the gear (Fig. 3.2). The gear configuration used for these sets was similar to that traditionally used by the pelagic longline fishery off northeast Brazil,

which targets tuna with a 3.5 mm monofilament mainline, 18 m buoy floatlines, and 18 m branch lines with 3.6 m monofilament leaders. Bait was composed of skipjack tuna, *Katsuwonus pelamis*.

Species composition, catch rate, and the condition of caught individuals (alive or dead) at the time of haulback were recorded in relation to hook type. Although the sets encompassed only 650 hooks, catch rates were expressed as catch-per-unit-effort (CPUE) in number of individuals caught per 1000 hooks for clarity sake. Hooking location was also recorded for each fish caught during the pelagic experiment, following Kerstetter and Graves (2006), and were characterized into three types: 1) *external*, if the hook lodged in the edge of the jaw, the corner of the mouth, or the snout/ bill area; 2) *internal*, if the hook was swallowed (non-visible) or lodged in the roof of the mouth or throat; and 3) *entangled*, if the fish was entangled in the leader or hooked on body parts other than the mouth region.

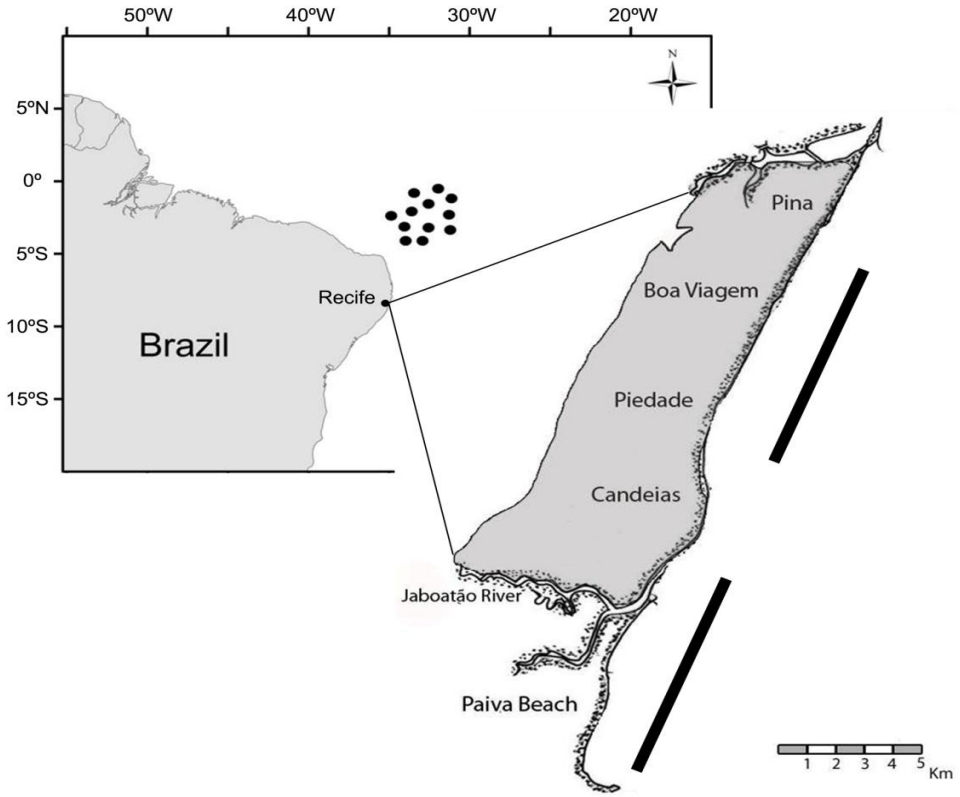


Figure 3.1. Location of the 12 longline sets (black circles) of the pelagic experiment in the Equatorial Atlantic Ocean, and of the 608 coastal longline sets (black rectangles) conducted off Recife.

3.2.2 Bottom longlining experiment

In the second experiment, 608 bottom longline sets were monitored off the coast of Recife. Fishing was conducted in a 20 km nearshore area stretching between Pina and Paiva beaches which included the Barra de Jangadas estuary (Fig. 3.1). The fishing gear was set at depths ranging between 8 and 14 m, corresponding to a distance of about 1-3 km from the coastline. The bottom longline consisted of one main, 8-mm multifilament polyamide line with 4 km in length, subdivided into four sections with 25 hooks each, thus totaling 100 hooks per set. The branch lines were composed of an 8-m long monofilament line that was 3.0 mm in diameter, which was followed by a stainless steel leader with 2 m in length (Fig. 3.3). Bait was composed of moray-eel (*Gymnothorax* sp.). This experiment was conducted in two distinct phases. During the first phase, spanning from September 2004 to August 2005, 384 sets were conducted using only J-hooks. During this phase, the influence of the vertical position of the hook on the catch composition and catch rate of elasmobranchs was determined by deploying half of the hooks demersally (i.e., sitting on the bottom) and suspending the other half in mid-water by attaching one 200 cm^3, cylindrical Styrofoam buoy (about 200 g flotation) to the proximal end of the leader of each secondary line with a snap, about 2 m from the hook. The latter configuration assured that hooks would fish in the upper half of the water column independently of tidal height or current speed. In the second phase, extending from May 2006 to April 2007, the influence of hook type on catch rate and mortality at haulback was compared during 224 sets by alternating circle and J-style hooks along a mainline with all hooks suspended in mid-water (Fig. 3.3). Both circle and J-style hooks used in the bottom longlining experiment were identical to the hooks used in the pelagic longlining experiment (section 2.1).

Data on species composition, cath-per-unit-effort (CPUE), and condition of caught individuals (alive or dead) at the time of haulback were recorded in relation to fishing depth of the hook (phase 1) and hook type (phase 2) during the bottom longline experiment. CPUE was expressed as number of individuals caught per 1,000 hooks to allow for comparisons. For both experiments, CPUE of dead specimens, hereafter referred to as mortality-per-unit-effort (MPUE), was calculated for all elasmobranch species as a way to combine the catch rate with

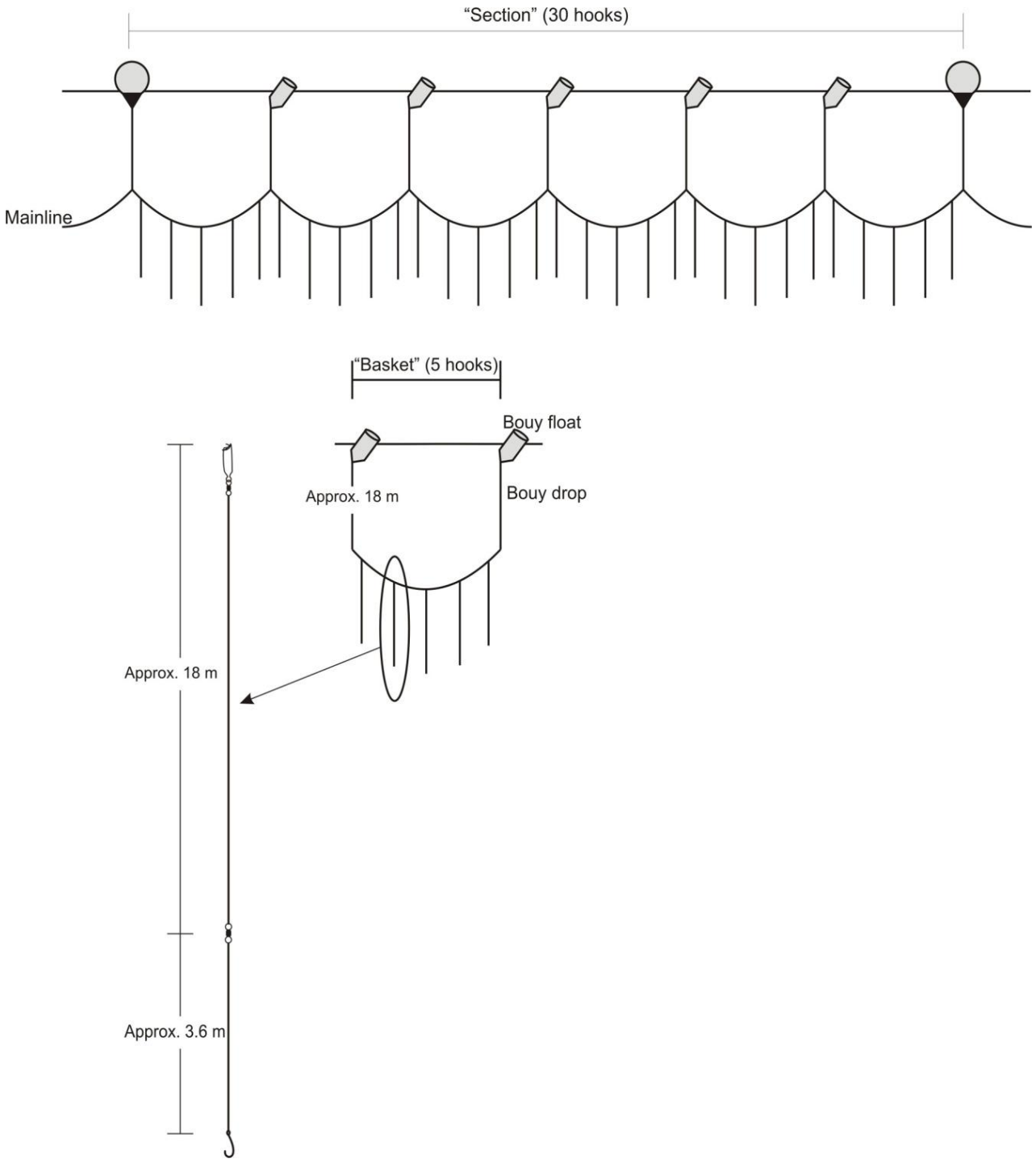


Figure 3.2. Schematic drawing of the longline gear used in the pelagic experiment off northeastern Brazil to compare the performance of circle hooks and traditional J-hooks.

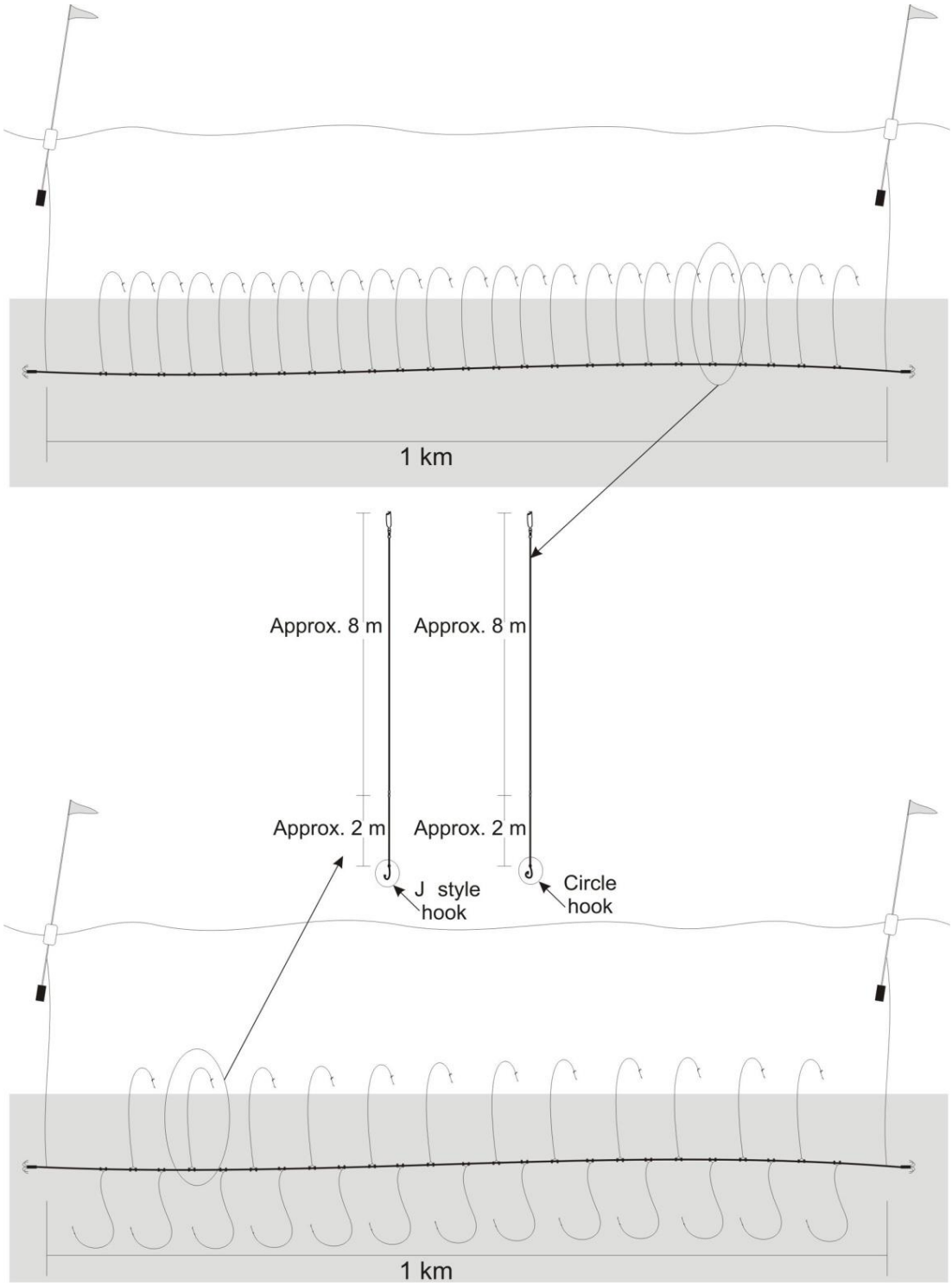


Figure 3.3. Schematic drawing of the coastal longline used off Recife, Brazil; bottom: first phase, using only J-hooks either suspended in the water column or laying on the bottom; middle: details of the branch lines utilized in both phases; top: second phase, using alternating J-hooks and circle hooks both suspended in the water column.

the at-vessel mortality rate. Fish that did not actively move in the water or on deck were conservatively considered "dead". Differences in CPUE between circle and J-style hooks and between hooks suspending in the water column and hooks deployed on the sea floor were tested for species with > 10 individuals caught. Paired t-tests were conducted after assessing homoscedasticity with a Levene's test and performing the X = log (X + 1) transformation to conform to the assumption of normality (Zar, 1996). As in Kerstetter and Graves (2006), the Cochran-Mantel-Haenszel chi-square test (CMHχ2) was used to compare species differences in mortality at haulback and differences in hooking location between the two hook types, since the robustness of the test allows relatively low sample sizes. SAS/STAT (SAS Institute Inc., 2006) was used for all statistical analyses.

3.3. Results

3.3.1. Pelagic Longlining experiment

Overall, the pelagic longline sets (7,800 hooks) caught 134 sharks corresponding to 10 species (Table 3.1). The night shark, *Carcharhinus signatus*, and the blue shark, *Prionace glauca*, were the most common shark species, comprising 48.5% of the total shark bycatch, followed by the silky shark, *Carcharhinus falciformis* (10.4%), the oceanic whitetip, *Carcharhinus longimanus* (9.0%), the scalloped hammerhead, *Sphyrna lewini* (8.2%), the dusky shark, *Carcharhinus obscurus* (7.4%), the tiger shark, *Galeocerdo cuvier* (6.0%), the nurse shark, *Ginglymostoma cirratum* and the shortfin mako, *Isurus oxyrinchus* (both with 4.4%), and the bull shark, *Carchahinus leucas* (1.5%). Total CPUE for sharks caught using circle or J-hooks was 25.8 and 10.7 sharks per 1,000 hooks, respectively. Except for the scalloped hammerhead and the bull shark, circle hooks exhibited higher CPUE for every species (Table 3.1). The Levene's test showed no differences between the variances of the CPUE of both types of hook (F = 0.543, p = 0.731). CPUE for the night (t = 4.011, p = 0.002), blue (t = 3.652, p = 0.001), silky (t = 2.461, p = 0.013), and oceanic whitetip (t = 1.249, p = 0.031) sharks were significantly greater with circle hooks as opposed to J-hooks. Despite low overall catch ($\leq$ 10 individuals), dusky, tiger, shortfin mako, and nurse sharks also tended to be caught more with circle hooks (Table 3.1).

Table 3.1. Catch composition, capture per unit of effort (CPUE), relative fishing mortality at haulback (in percentage), and mortality per unit of effort (MPUE) for selected species caught in pelagic longline fishery with circle hooks (CH) and J-style hooks (JH). Asterisks (*) indicate significant differences between hook types regarding fishing mortality.

Species	*N*	CPUE		Mortality (%)		MPUE		
		CH	JH	CH	JH	CH	JH	
Carcharhinus signatus	33	6.41	2.05	100	100	6.41	2.05	
Prionace glauca	32	5.64	2.56	27.2	70	1.54	1.79	*
Carcharhinus falciformis	14	2.31	1.28	22.2	80	0.51	1.03	*
Carcharhinus longimanus	12	2.31	0.77	22.2	66.6	0.51	0.51	*
Sphyrna lewini	11	0.77	2.05	33.3	87.5	0.26	1.79	
Carcharhinus obscurus	10	1.79	0.77	28.5	100	0.51	0.77	
Galeocerdo cuvier	8	1.54	0.51	16.6	50	0.26	0.26	
Isurus oxyrinchus	6	1.28	0.26	20	100	0.26	0.26	
Ginglymostoma cirratum	6	1.28	0.26	0	0	0.00	0.00	
Carcharhinus leucas	2	0.26	0.26	0	100	0.00	0.26	

Elasmobranch mortality rate at haulback varied considerably among species and hook types (Table 3.1). The night shark had 100% relative mortality on both hook types, in contrast to the nurse shark that had 0% mortality on both types of hook. The blue ($CMH\chi^2 = 2.132$, $p < 0.001$), silky ($CMH\chi^2 = 1.442$, $p = 0.006$), and oceanic whitetip ($CMH\chi^2 = 1.003$, $p = 0.002$) sharks had significantly higher relative mortality at haulback with J-hooks than with circle hooks, with scalloped hammerhead, dusky, tiger, shortfin mako, and bull sharks following this trend but not tested statistically due to small sample sizes. In spite of both types of hook presenting equal relative fishing mortality for the night shark, the associated MPUE was considerably higher with circle hooks, due to the higher CPUE of this species with this hook type. In contrast, the MPUE of J-hooks was higher for blue, silky, scalloped hammerhead, dusky, and bull sharks (Table 3.1).

Hooking locations varied between hook types and among species. All species were hooked externally more often with circle hooks than with J-hooks, which tended to lodge mostly internally in the throat or gut (Figure 3.4). Significant differences on hooking location between the two types of hook were found for night ($CMH\chi^2 = 1.349$, $p < 0.001$), blue

(CMHχ^2 = 2.142, p = 0.013), silky (CMHχ^2 = 2.001, p = 0.002), and oceanic whitetip (CMHχ^2 = 0.112, p = 0.013) sharks.

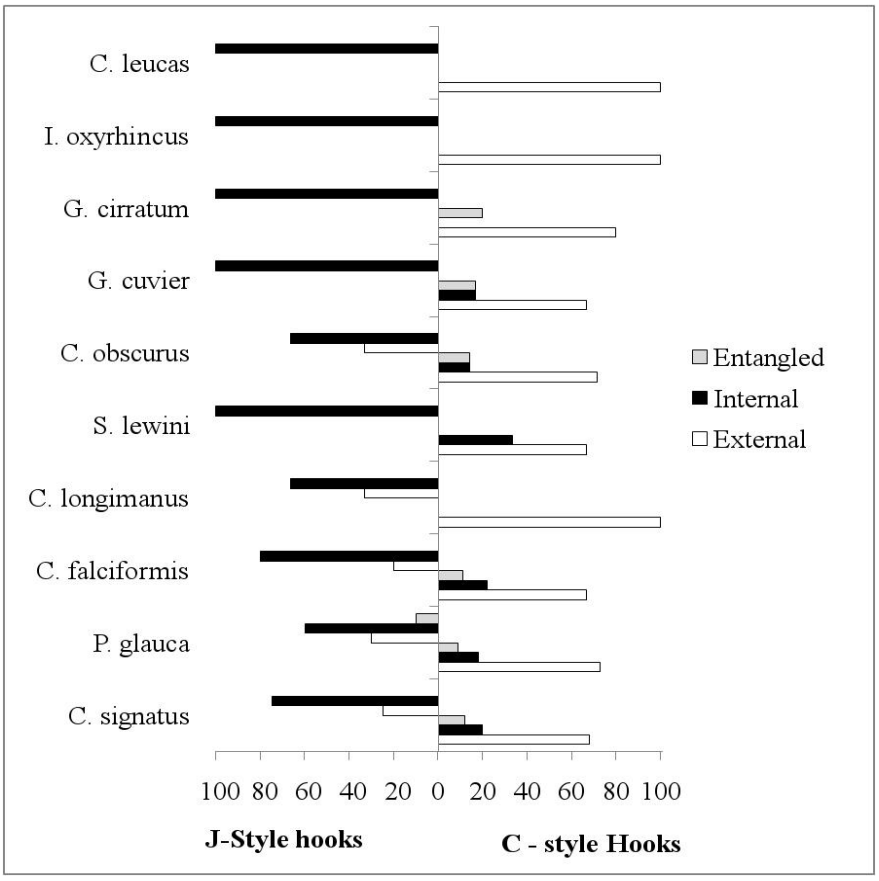


Figure 3.4. Pelagic longline experiment. Percentage (%) of capture by external (white) and internal (black) hooking and by entangling (gray) of selected species observed at the moment of the haulback for J-style (left) and circle (C-style, right) hooks.

3.3.2. Bottom longlining experiment

During the first phase of the research using bottom longline to test for the influence of fishing depth on CPUE, 109 elasmobranchs were caught on a total of 11,200 hooks, including 46 rays and 63 sharks represented by nine species (Table 3.2). Demersal hooks showed significantly higher CPUE than hooks suspended in the water column for blacknose (t = 2.341, p = 0.002) and nurse (t = 3.001, p < 0.001) sharks, as well as for southern stingray (t = 1.038, p = 0.013). The Levene's test showed no significant differences between CPUE variances of

hooks suspending in the water column and hooks deployed on the sea floor (F = 1.778, p = 0.207). Shark species considered potentially aggressive, including the tiger, the bull, the blacktip, and the scalloped hammerhead sharks (ISAF, 2008), were caught infrequently but always on the suspended hooks (Table 3.2).

Table 3.2. Catch composition and CPUE (individuals per 1000 hooks) based on position of the hook in the water column (demersal vs suspended) for the species caught during the first year of the bottom longline experiment off the coast of Recife, Brazil. Asterisks indicate significant differences ($p < 0.05$) in CPUE between hook positions.

Species	Percent composition (*N*)	CPUE		
		Demersal	Suspended	
Dasyatis americana	39.5% (43)	3.30	0.54	*
Carcharhinus acronotus	37.6% (41)	2.86	0.80	*
Ginglymostoma cirratum	12.8% (14)	1.16	0.09	*
Galeocerdo cuvier	3.7% (4)	0.00	0.36	
Manta birostris	2.7% (3)	0.00	0.27	
Carcharhinus leucas	1.8% (2)	0.00	0.18	
Sphyrna lewini	0.9% (1)	0.00	0.09	
Carcharhinus limbatus	0.9% (1)	0.00	0.09	

In the second phase of the bottom longlining experiment comparing hook types, 38 specimens were caught on a total of 11,097 hooks. Comparison between circle and J-hooks showed no significant differences in CPUE for the species analyzed. Levene's test found no significant differences between CPUE variances of both types of hook (F = 3.87, p = 0.347). Southern stingray, nurse shark, and manta ray suffered no mortality from either hook type. The number of tiger ($CMH\chi^2$ = 4.330, $p < 0.001$) and blacknose ($CMH\chi^2$ = 2.221, $p < 0.001$) sharks alive at haulback, however, was significantly higher using circle hooks (Figure 3.5). Since both hook types showed similar catch rates, MPUE was not assessed in this experiment.

Because of insufficient catch numbers, it was not possible to statistically test the data for the other species (scalloped hammerhead, bull and blacktip sharks).

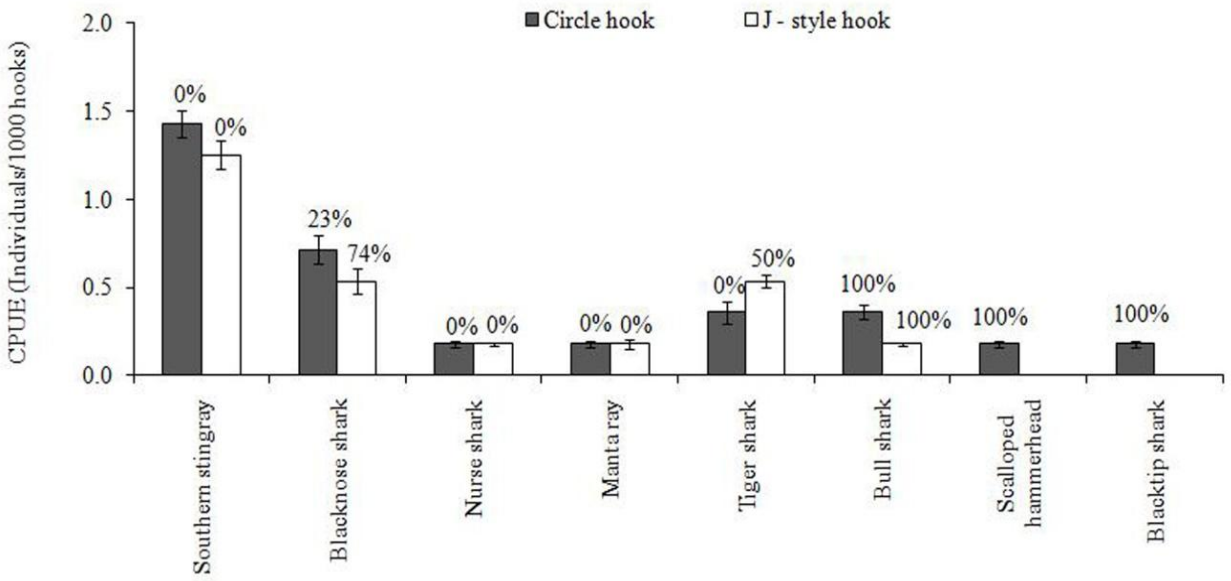


Figure 3.5. Average CPUE (individuals per 1000 hooks) of elasmobranchs caught with circle and J-style hooks off the coast of Recife, Brazil. Error bars represent standard error, while numbers above bars correspond to the percentage of at-vessel mortality.

3.4. Discussion

Results of the pelagic longline sets operating off northeastern Brazil showed that the night shark was the most abundant species in the elasmobranch catch, followed by the blue shark. The high abundance of night sharks was most likely due to fishing being concentrated in areas close to seamounts, where this species tends to aggregate (Hazin et al., 1998). This should also explain the presence of the nurse shark in the catch composition, since this species has been noted to occur off Brazil at depths between 40−130 m (Compagno, 2002).

Compared to J-hooks, circle hooks significantly increased the catch rates of blue, night, silky, and oceanic whitetip sharks in pelagic sets operating off Natal. However, Watson et al. (2005) suggested that the increase in the catch rates of blue sharks using circle hooks

could be misleading because sharks that were gut-hooked by J-hooks were more likely to bite off monofilament leaders and thus escape detection. The use of circle hooks has been known to reduce the rate of deep hooking and to increase mouth hooking in some pelagic fish such as the Atlantic bluefin tuna, *Thunnus thynnus*, yellowfin tuna, *T. albacares*, and istiophorid billfishes (e.g. Falterman and Graves, 2002; Prince et al., 2002; Skomal et al., 2002). The present study follows the assumption that the difference in the catch rate between circle and J-hooks only results from an interaction after the shark biting the bait, i.e. different hooks will not exhibit different attractiveness or elicit distinct behaviors and catch differences are only ascribed to distinct gear capacities to hook and to retain the animal until retrieval of the gear. Therefore, the significantly higher catch rates found for circle hooks could only be attributed either to a lower probability of a shark to avoid being hooked after biting the bait or to escape the hook after being caught. Unfortunately, the absence of hooks in the secondary lines was not tracked at haul-back, making it impossible to investigate these possibilities. Evidences that the interaction between hook types and leader materials has a significant influence on the catchability of sharks in longline gear have been recently reported (Afonso et al., 2012a). It is thus advisable that future experiments include missing hooks (i.e., the so-called *bite-offs*) at gear retrieval within their data collection protocols.

The type of hook in the bottom longline experiment did not present any significant effect on the catch rates of elasmobranchs, a pattern that might be related to the fact that stainless steel leaders were used in this fishing gear, thus reducing the probability of sharks escaping after biting off the monofilaments in case of deep hooking (Gilman et al., 2008).

In the pelagic longline sets, the circle hooks showed significantly lower mortality rates at haulback for three of the species caught, most likely due to the lower rate of internal hooking. This is consistent with the findings of prior studies in teleosts (Domeier et al., 2003; Horodysky and Graves, 2005), yet Yokota et al. (2006) found no significant differences in blue shark mortality rates using tuna hooks and two sizes of circle hooks. In the present study, the mortality per unit of effort (MPUE) was calculated in order to compare fishing impacts of both hooks used. Circle hooks resulted in a higher MPUE of *Carcharhinus signatus*, but only due to its higher CPUE with this hook type, since in both hooks all specimens of this species were dead at haulback. Such severe mortality could be associated to a particularly low resilience of

this species. The MPUE for five other species, however, was considerably lower with the circle hooks, in spite of a generally higher CPUE. Besides, if the absence of stainless steel leaders indeed influenced the CPUE of specimens caught with J-hooks, then a significant portion of the individuals that escaped detection might have not survived due to the injuries inflicted by the fishing gear, and this ultimately may have resulted in an underestimation of the mortality induced by J-hooks (Afonso et al., 2012b). Further studies will be required to analyze the effect of the interactions between leader materials and hook type on shark CPUE and mortality before reaching any definitive conclusion.

In the present study, circle hooks decreased relative mortality at haulback of most species caught. Externally-hooked individuals most likely have higher survival rates, and therefore such animals are expected to die not from direct injuries inflicted by the fishing gear but presumably from the physiological stress caused by the capture and, in some species, from insufficient oxygenation caused by swimming constraints (Brill et al., 2008; Manire et al., 2001; Skomal, 2007a; Young et al., 2002). This was corroborated to some extent by MPUE results, which provided potentially useful information for management purposes, like the eventual adoption of a mandatory release of live elasmobranchs, which has precedence for other species in Brazilian waters (e.g. both white and blue marlins alive at haul-back are currently required to be released). Thus, at least for some species of sharks, the fishing mortality of externally-hooked individuals appears to be ultimately shaped by gear soak time. Conservation measures aiming at reducing bycatch post-release mortality by requiring the reduction of soak time coupled with the mandatory release of sharks and rays that are alive at the time of haulback could, therefore, be much more effective with the use of circle hooks.

The shark and ray species caught using bottom longline in the coastal sets off Pernambuco are the same species as those identified in previous surveys in that area. This included potentially aggressive species recognized as being involved in shark attack incidents in the beaches of Pernambuco, such as tiger and bull sharks (Hazin et al., 2000), and several other rather inoffensive species, such as the southern stingray, and the blacknose and nurse sharks. The high relative abundances of the three latter species could be attributed to their distribution, since they are known to typically inhabit shallow, nearshore areas in the western Atlantic Ocean (Bigelow and Schroeder, 1948).

The influence of the vertical position of the hook on catch rates is probably a consequence of the feeding depth distribution of the species caught, as previously proposed by other authors; e.g., Bigelow and Schroeder (1948) and Compagno (2002) described the blacknose and nurse sharks, as well as the southern stingray, as species highly associated with demersal habitats, whereas the tiger, bull, and blacktip sharks and scalloped hammerhead would more commonly swim and feed in the middle depths of the water column. The suspension of the hooks in midwater depths, therefore, significantly increased the selectivity of the longline by sharply reducing the catch rates of demersal species, such as blacknose and nurse sharks and the southern stingray, while increasing the CPUE of species that swim in the water column, such as the tiger and bull sharks. Similarly to the pelagic longline, the use of circle hooks in the bottom longline also significantly decreased the mortality rate at haulback of two of the species caught, thereby increasing the number of successful post-capture releases.

Overall, the present results indicate that rather simple, non-expensive gear modifications, such as changing the type of hook and the relative hook position within the water column, may be an efficient way to increase longline selectivity and to reduce bycatch, while decreasing significantly the fishing mortality of unwanted species. While there could be a concern regarding the impact of such modifications on the catch rate of valuable target species, such as tunas and billfishes, growing evidence has been demonstrating that some of those strategies have no negative effects on harvest, and so they would not necessarily pose any economical loss to fisheries. In spite of the catch rate of tunas and billfishes was not herein addressed, a recent study conducted in the same region verified that the circle hook utilized in this experiment did not result in any reduction in the CPUE of that target group when compared to the commonly used J-hook (Pacheco et al., 2011). Thus, it seems advisable to consider such potentially effective measures for integrating more efficient management plans of oceanic fisheries, especially given the fact that they are comparably inexpensive and quick to implement.

Chapter 4. The Shark Monitoring Program of Recife

The R/V Sinuelo during monitoring operations off Recife.

4.1. Introduction

The high incidence of shark attacks on humans off Recife prompted the development of the Shark Monitoring Program of Recife (SMPR), which has been operated by the Universidade Federal Rural de Pernambuco (UFRPE) since its creation, in May 2004. The main goal of the SMPR is the mitigation of the shark attack rate in the monitored region. Shark attack mitigation can be ultimately achieved by removing potentially aggressive sharks from the area of risk and/or by imposing behavioral changes to beach users. Both strategies may reduce the occurrence of shark-human interactions considerably. However, the effectiveness of mitigation measures strongly depends on detailed knowledge on the bioecology of the species involved in the attacks. Understanding the patterns in occurrence and abundance of sharks in nearshore waters is a key-component of risk management and can be accomplished with standardized, long-term fishing surveys, which not only allow the removal of sharks from the area of risk but also provide essential bioecological information pertaining to shark hazard management. Extreme caution is nonetheless required to avoid damage to the local environment, since such surveys typically employ intensive fishing effort in a relatively small area through long periods of time.

Traditional programs to reduce shark attacks generally do cause significant impacts on the marine ecosystem. As previously referred, shark control programs historically conducted with gillnets in South Africa and Australia have been associated with high catch rates and fishing mortality not only of potentially aggressive sharks but also of a myriad of inoffensive *taxa* (Dudley, 1997). Dudley and Simpfendorfer (2006) reported significant declines in the catch rates of four shark species (*Carcharhinus leucas*, *C. limbatus*, *Sphyrna lewini*, and *S. mokarran*) and in the mean length of three shark species (*Carcharhinus amboinensis*, *C. limbatus*, and female *Carcharodon carcharias*) caught in protective gillnets off KwaZulu-Natal, South Africa, during a 26-year period. The catch rates of grey nurse, *Carcharias taurus*, and Australian angel, *Squatina australis*, sharks declined by over 90% from the initial catch rates in protective gillnets off New South Wales (Reid et al., 2011), accompanied by a reduction in mean length (Reid et al., 2011, Green et al., 2009). However, distinct trends in catch rate of various shark species between neighboring meshed areas

suggest that, for some sharks, stock depletion may occur only at a local scale and not at the population level (Holden, 1977), which could result from species-specific philopatric behavior (Dudley and Cliff, 2010). Rapid declines in bull shark catch rates following the installation of protective gillnets (Cliff and Dudley, 1991; Davies, 1963), together with high bull shark catches at unprotected shores not distant from meshed areas (Cliff and Dudley, 1991), support the localized stock depletion hypothesis. Whether localized depletions in the abundance of sharks could significantly impact their populations should depend on several biological and demographic factors, albeit the generalized exhaustion of the populations of coastal elasmobranchs (Jackson, 2001) demands extreme caution as minimum interferences upon already damaged populations could have increased deleterious consequences.

Catches of *taxa* other than sharks in shark meshing programs include whales, dolphins, seals, dugongs, marine birds, sea turtles, batoids, and teleosts (Dudley and Cliff, 1993a; Gribble et al., 1998a; Krogh, 1996; Patterson, 1990). Mortality rates are considerably high, totaling 95−100% for dolphins and teleosts, 62−66% for turtles, and 30−39% for batoids in South Africa (Dudley and Cliff, 1993a) and New South Wales (Green et al., 2009). Between 1992−95, the relative mortality of dugongs, *Dugong dugong*, and dolphins in the Queensland shark meshing program was about 3.8 and 10.3 individuals per year, respectively (Gribble et al., 1998a). The same authors claim that the impact of shark meshing upon populations of susceptible species is mild, but shark meshing in Australia has been listed as a key threatening process by the Fisheries Scientific Committee (http://www.dpi.nsw.gov.au/fisheries/species-protection/conservation/what-current/key/shark-meshing; Accessed July 4th 2012) due to significant declines in the catch rates of vulnerable and endangered species such as the giant guitarfish, *Rhynchobatus djiddensis* (Dudley and Cliff, 2010), and among sharks, the scalloped, *Sphyrna lewini*, and great, *S. mokarran*, hammerhead sharks (Dudley and Simpfendorfer, 2006), and the grey nurse shark (Reid et al., 2011). Moreover, the entanglement of baleen whales, particularly the humpback whale, *Megaptera novaeanglidae*, and the southern right whale, *Eubalaena australis*, has been pointed out as an increasing problem in South Africa and Australia during the last decade, especially concerning young individuals as they do not have enough strength to break their way out of the gillnets and quickly die (Dudley and Cliff, 2010).

Altogether, it is unquestionable that the fishing methodologies used by shark control programs should be carefully selected in order to prevent deleterious environmental impacts, which could, above all, depend on adequate gear selectivity towards the most aggressive species of sharks. The protective gillnets used in Australia and South Africa are characterized by reduced selectivity and substantial fishing mortality, and so they have been widely criticized (Paterson, 1990; Sumpton et al., 2010). Hook-based fishing methodologies could provide better results, but selectivity towards potentially aggressive sharks and incidental mortality should nevertheless be optimized. Understanding the relationship between fishing methodologies and catch rate is essential to effectively enhance fisheries performance while minimizing unavoidable, potentially harmful effects on the marine ecosystem.

This chapter introduces and characterizes the Shark Monitoring Program of Recife (SMPR), and investigates several aspects of the fishing performance.

4.2. Materials and Methods

Fishing operations in the study area off Recife were conducted aboard the R/V Sinuelo and R/V Pedrinho and spanned from May 2004 through December 2011, with interruptions in August 2004, March−April 2006, May−September 2007, September−November 2008, February−June 2009, and June 2011 due to discontinuity of funding. Until August 2005, fishing cruises generally consisted of seven fishing sets and were conducted during the new and full moon-phases. After September 2005, the methodology was modified in order to perform four sets per fishing cruise scheduled on a weekly basis so that fishing operations were continuous from Fridays through Tuesdays. This modification was due to the necessity of synchronizing fishing operations with the weekly distribution of both balneal use (Silva et al., 2008) and shark attacks (Hazin et al., 2008).

Taking the local topography into account (see chapter 2), a combination of bottom longlines and drumlines was selected as a fishing strategy. Longlines were composed of a 4-km long, 8-mm diameter, multifilament, polyamide mainline with 5 moorings which subdivided the mainline in 4 similar sections. Each section comprised 25 branch lines which were composed of a snap followed by an 8-m long, 3.2-mm diameter, monofilament,

polyamide line crimped to a 2-m long, 2-mm diameter, stainless steel leader, a 60-g swivel, and a hook. Thus, each longline had 100 hooks. During the first two years of fishing, different longline gears were compared for optimization purposes (see chapter 3). Until August 2005, a Styrofoam float (200 g in flotation) was attached to the proximal extremity of the leader (i.e. about 2 m from the hook) of half of the secondary lines for selectivity assessment (Afonso et al., 2011). After September 2005, however, all secondary lines were equipped with such floats in order to suspend all hooks in the water column. Similarly, both J-style (9/0) and circle (17/0, 10% offset) hooks were used until May 2006 for fishing mortality assessment, after which only circle hooks were used. Drumlines consisted of a 18-m long, 6-mm diameter, multifilament, polyamide mainline which was vertically stretched by an anchor and a float, being equipped with two 4-m long, 3.2-mm diameter, branch lines. Moray eels, *Gymnothorax* spp., were generally used as bait (~300 g), since they were low-priced and readily accessible, but occasionally the oilfish, *Ruvettus pretiosus*, was also used, especially during the full and new moon phases. Both bait types yielded high catch rates of target species in preliminary field testing (Hazin et al., 2000).

The survey area was divided in two nearshore, contiguous fishing sites: Boa Viagem/ Piedade (BV), to the north, corresponding to a widely urbanized coastline off which most attacks occurred (Hazin et al., 2008); and Paiva (PA), to the south, a comparatively undeveloped region which includes the Barra de Jangadas estuary (Fig. 4.1). Two longlines were deployed ~1.5−3 km from shore at each site, corresponding to mean depths of 13.5 (±1.0) m at BV and 13.2 (±0.8) m at PA. Drumlines were deployed ~0.5−1 km from shore, at depths averaging 6.4 (± 1.5) m in BV and 10.2 (± 2.5) m in PA. In BV, 13 drumlines were positioned inside an alongshore channel (see chapter 2), preferentially off beach sections where shallower, inshore reefs are absent, while 10 drumlines were deployed in PA where no channel exists (Fig. 4.1). Such spatial configuration aimed at establishing a first barrier (longlines) designed not only to intercept approaching sharks before they accessed the area of risk but also to lure sharks away from the shore to the baited longline, instead of entering into the channel. The second barrier (drumlines), placed inside the channel, was designed to capture any shark that would bypass the first shield although using a much lower fishing effort to avoid attracting sharks into the area of risk by the effect of bait.

A total of 246 hooks (200 in two longlines and 46 in drumlines) were usually deployed each fishing day. Soak time averaged 15.04 (±1.86) h at BV and 14.05 (±2.07) h at PA. The longlines were routinely deployed in the afternoon and hauled back at dawn. At BV, such schedules averaged 15:58 (±1:16) and 07:05 (±1:24), respectively, while they averaged16:13 (±1:28) and 06:22 (±1:32) at PA. Drumlines were allowed to fish continuously and were hauled daily at dawn for bait replacement. Sea surface temperature, salinity, and water transparency were monitored each fishing day at both sites (see chapter 2).

A total of 2,247 longlines were deployed just evenly in BV and PA, totaling 221,694 hooks (Table 4.1). Analogously, 2,247 drumline settings totaling 51,796 hooks were deployed in both sites but the number of hooks was ~30% higher in BV (Table 4.1). Thus, a total of 273,490 hooks were deployed in the study area and longlines accounted for 81% of total effort.

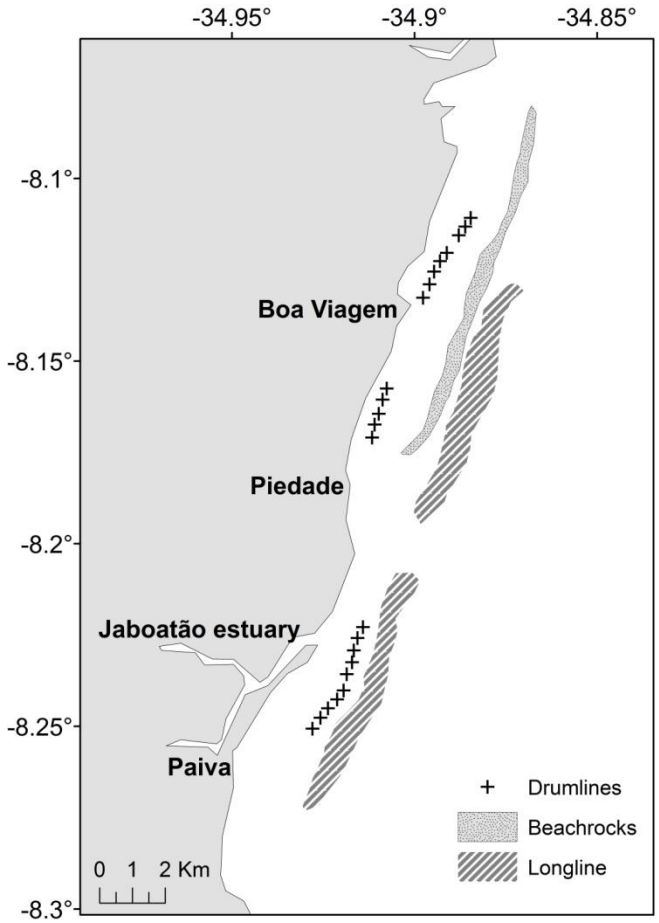


Figure 4.1. Map of the study area off Recife depicting the location of submerged beachrocks and the location of longline and drumline deployments at two surveyed sites.

Thirty eight additional longline sets (200 hooks per set) were conducted offshore at the middle continental shelf (CS), usually in the last set of some fishing cruises, and accounted for 6,589 hooks, raising the overall total effort to 280,079 deployed hooks. However, the low sampling effort in CS precluded the inclusion of this site in the analyses. Sampling effort was highest in 2006, 2010, and 2011, and lowest in 2004 (Table 4.1). Some seasonality in sampling effort was noted since it was higher during summer, between November−January, and lower during winter, especially between June−July.

Table 4.1. Distribution of fishing effort, in number of sets performed and number of hooks deployed, in a longline and drumline survey off Recife, between 2004−2011.

	Longline		Drumline	
	Sets	Hooks	Sets	Hooks
Year				
2004	120	11,911	120	2,760
2005	310	30,852	310	7,130
2006	356	35,374	356	8,625
2007	297	29,456	297	6,417
2008	236	23,561	236	5,175
2009	211	20,659	211	4,830
2010	396	40,760	396	8,809
2011	359	35,900	359	8,050
Month				
Jan	228	22,728	228	5,175
Feb	180	18,249	180	4,048
Mar	182	18,863	182	5,106
Apr	187	18,668	187	4,232
May	177	17,796	177	2,921
Jun	116	11,536	116	2,530
Jul	152	14,939	152	3,412
Aug	197	19,519	197	4,469
Sep	181	17,771	181	4,194
Oct	204	20,212	204	4,608
Nov	234	23,258	234	5,413
Dec	247	24,934	247	5,688
Site				
BV	1,130	111,480	1,130	29,331
PA	1,117	110,214	1,117	22,465
TL	38	6,589		
Total	2,285	228,283	2,247	51,796

Target species are herein considered as potentially aggressive sharks (PAS) and comprise tiger, bull, silky, blacktip, Caribbean reef, scalloped and great hammerhead sharks, whilst bycatch is interpreted as all the remaining species. The fishing mortality at gear retrieval of every species was monitored. All live bycatch was measured and promptly released. Until September 2007, all PAS were collected and brought to the laboratory regardless of their survival, but since then all PAS caught alive were accommodated in a water-filled, wooden tank which was assembled on the deck of R/V Sinuelo (Fig. SUP.7.1), and transported towards the continental slope in order to remove them away from the area of risk. The distance and duration of the transport depended on the size and health of the shark, and some primary vital signs such as the contraction periodicity of gill openings and the maintenance of body equilibrium were continuously monitored to assure that the shark was released in good condition. All sharks were measured, sexed, and tagged with both a numbered, stainless steel dart tag and a telemetry tag, including both acoustic and satellite transmitters, before being released. Further information on tagging and transport of sharks can be found in chapter 7.

Catch rates were analyzed as catch-per-unit-effort (CPUE), defined by the number of individuals caught per 100 hooks. Statistical analyses were conducted only on the most significant species ($N > 30$) and pertain to longlines only. Drumlines were excluded from the analyses because distinct spatial arrangements and effort densities prevented a direct comparison with longlines. All analyses were interpreted at a significance level of 0.05 and refer to the period between September 2005 and December 2011 unless stated otherwise. The period between May 2004 and August 2005 was not considered due to distinct fishing gear configurations which significantly influenced longline catch rate (Afonso et al., 2011). The number of individuals caught in each of the four fishing sets of each cruise after October 2007 was compared with a Chi-squared test for given probabilities with simulated *p*-value (based on 20,000 replicates). The Pearson's Chi-squared test with simulated *p*-value (based on 20,000 replicates) was used to compare the yearly proportions of the most significant species caught in 2006, 2008, 2010, and 2011. The years 2005, 2007 and 2009 were not included in this analysis because they comprised only ~4−7 months of valid sampling. The catch rates of tiger, blacknose and nurse sharks, stingrays, and ariid catfish were compared between months and between years (the latter for 2006, 2008, 2010, and 2011 only) with Kruskal-Wallis rank sum tests, and between fishing sites with Wilcoxon rank sum tests with continuity correction.

Previously, differences in soak time between fishing sites were assessed with a Welch´s *t*-test. Water parameters were compared between sites with unpaired t-tests. All statistical analyses were conducted in *R* version 2.14.0 (*R* Development Core Team, 2011).

4.3. Results

A total of 1,121 individuals were caught in both fishing gears between May 2004 and December 2011, yet the longline was responsible for the vast majority of the catch (92.6%). Teleosts corresponded to 59.1% of the overall catch, while elasmobranchs and marine turtles represented 40.1% and 0.8%, respectively (Table 4.2). Ariid catfishes were by far the most caught group (45.9% of the overall catch) and comprised three identified species: *Bagre bagre*, *B. marinus* and *Sciades proops*. *Gymnothorax* moray-eels and *Lutjanus* snappers were commonly represented amongst teleosts, accounting together for 10.7% of the overall catch. In this region, a recently described lutjanid species, *Lutjanus alexandrei*, has been often misidentified as the gray snapper, *L. griseus*, or the schoolmaster, *L. apodus*, (Moura and Lindeman, 2007), and so these three species were grouped as *Lutjanus* spp., while the mutton snapper, *L. analis*¸ and the dog snapper, *L. jocu*, were discriminated. The goliath grouper, *Epinephelus itajara*, was the largest teleost caught but it was seldom observed. Other infrequently caught teleosts included barred grunts, *Conodon nobilis*, tarpons, *Megalops atlanticus*, angelfishes, *Pomacanthus paru*, spadefishes, *Chaetodipterus faber*, sphyraenid barracudas, echeneid shark suckers, and tetraodontid pufferfish (Table 4.2).

Amongst elasmobranchs, carcharhinid sharks were the most abundant (18.0% of the overall catch). The blacknose shark, *Carcharhinus acronotus*, was the most frequent carcharhinid, followed by the tiger shark, *Galeocerdo cuvier*, which equaled about 5% of the overall catch. Less frequently caught carcharhinids included bull, *C. leucas*, blacktip, *C. limbatus*, silky, *C. falciformis*, Caribbean reef, *C. perezi*, and Brazilian sharpnose, *Rhizoprionodon lalandii*, sharks (Table 4.2). Sphyrnids were represented by both scalloped and great hammerheads (*Sphyrna lewini* and *S. mokarran*, respectively), which were only caught once. The nurse shark, *Ginglymostoma cirratum*, was the most abundant elasmobranch and represented 13.3% of the overall catch. Seven potentially aggressive shark species were

identified (bull, silky, blacktip, Caribbean reef, tiger, scalloped and great hammerheads), accounting for 7.0% of the overall catch.

Table 4.2. Catch composition, number of individuals caught (*N*) and catch-per-unit-effort (CPUE), as the number of individuals caught per 100 hooks, in a longline (LL) and drumline (DL) survey off Recife, between 2004−2011.

Family	Species	N_{LL}	$CPUE_{LL}$	N_{DL}	$CPUE_{DL}$
Teleostei					
Ariidae		476	0.214 (± 0.67)	38	0.208 (± 0.95)
Lutjanidae		37	0.018 (± 0.16)	1	0.007 (± 0.18)
	Lutjanus analis	4	0.002 (± 0.04)		
	Lutjanus jocu	8	0.003 (± 0.09)		
	Lutjanus spp.	25	0.012 (± 0.12)	1	0.007 (± 0.18)
Haemulidae	*Conodon nobilis*	3	0.001 (± 0.04)		
Echeneidae		3	0.001 (± 0.05)		
Muraenidae	*Gymnothorax* spp.	74	0.033 (± 0.27)	8	0.047 (± 0.48)
Serranidae	*Epinephelus itajara*	9	0.004 (± 0.06)	3	0.018 (± 0.28)
Megalopidae	*Megalops atlanticus*	5	0.002 (± 0.06)		
Pomacanthidae	*Pomacanthus paru*	1	0.000 (± 0.02)		
Ephippidae	*Chaetodipterus faber*	1	0.000 (± 0.02)		
Sphyraenidae		1	0.000 (± 0.02)		
Tetraodontidae		1	0.000 (± 0.02)		
n. id.		2	0.001 (± 0.04)		
Elasmobranchii					
Carcharhinidae		192	0.082 (± 0.41)	10	0.065 (± 0.56)
	Carcharhinus acronotus	118	0.051 (± 0.32)	7	0.047 (± 0.48)
	Carcharhinus falciformis	2	0.001 (± 0.04)		
	Carcharhinus leucas	9	0.004 (± 0.06)	2	0.011 (± 0.23)
	Carcharhinus limbatus	6	0.003 (± 0.05)		
	Carcharhinus perezi	1	0.000 (± 0.02)		
	Galeocerdo cuvier	55	0.023 (± 0.20)	1	0.007 (± 0.18)
	Rhizoprionodon lalandii	1	0.000 (± 0.02)		
Ginglymostomatidae	*Ginglymostoma cirratum*	141	0.062 (± 0.28)	8	0.049 (± 0.47)
Sphyrnidae		2	0.001 (± 0.04)		
	Sphyrna mokarran	1	0.000 (± 0.02)		
	Sphyrna lewini	1	0.000 (± 0.02)		
Dasyatidae	*Dasyatis* spp.	71	0.031 (± 0.25)	5	0.032 (± 0.39)
Myliobatidae	*Aetobatus narinari*	4	0.002 (± 0.04)		
Mobulidae	*Mobula* spp.	16	0.007 (± 0.10)		
Turtles					
Cheloniidae		8	0.004 (±0.07)	1	0.007 (± 0.18)

Sting rays (*Dasyatis* spp.) were also relatively common (7.0%), while devil (*Mobula* spp.) and eagle (*Aetobatus narinari*) rays were present in lower numbers. Marine turtles were episodically caught and comprised two identified chelonids: the green turtle, *Chelonia mydas*, and the hawksbill turtle, *Eretmochelys imbricata*. Overall, longlines caught at least 30 different species and drumlines caught 12 species. Blacktip and tiger sharks, devil and eagle rays, snappers, tarpons, and turtles were almost exclusively caught in the longlines. Longline average catch-per-unit-effort (CPUE) by fishing set per species ranged between 0.0002−0.214 individuals per 100 hooks for the whole study period. Drumline CPUE showed similar values to longline CPUE for most mutual species, but goliath groupers and bull sharks had considerably higher catch rates in the drumlines while both lutjanids and tiger sharks had higher catch rates in the longlines (Table 4.2).

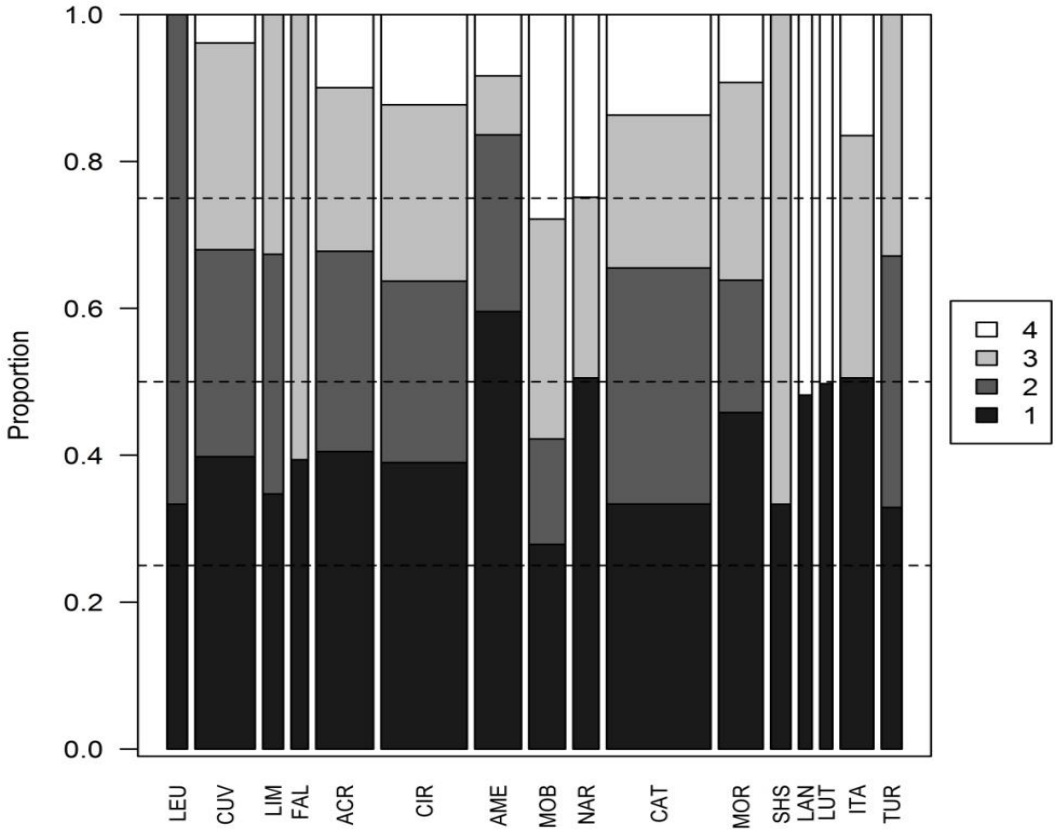


Figure 4.2. Proportion of captures per each of the four longline sets of all cruises between October 2007 and December 2011. Bar widths are logarithmically proportional to the number of individuals caught. Horizontal dashed lines represent the 25%, 50% and 75% quartiles. LEU: bull shark; CUV: tiger shark; LIM: blacktip shark; ACR: blacknose shark; CIR: nurse shark; AME:southern stingray; MOB: devil rays; NAR: eagle ray; CAT: ariid catfishes; MOR: moray eels; LAN: mutton snapper; LUT: other lutjanids; ITA: goliath grouper; TUR: turtles.

Species occurrence followed distinct temporal patterns. Within fishing cruises conducted between October 2007 and December 2011, virtually all species were more frequently caught in the first of the four longline sets, with sting and eagle rays, moray eels, goliath groupers, and snappers exhibiting a frequency close to or higher than 50% in the first set (Fig. 4.2). About 66% of catfish, moray eels, turtles, tiger, blacktip, blacknose, and nurse sharks, about 80% of stingrays, and all bull sharks were caught in the first two fishing sets. Nurse, blacknose, and tiger sharks were also caught in the fourth set, but blacktip sharks and marine turtles were uniformly caught in the first three sets only. Significant differences between the number of individuals caught in the four fishing sets were found for nurse sharks ($\chi^2 = 13.168$, $p = 0.004$), stingrays ($\chi^2 = 8.00$, $p = 0.049$), and catfish ($\chi^2 = 11.994$, $p = 0.009$). Data from all eight years of survey by Julian day to assess the occurrence of every species throughout the year show that catfish were continuously caught year-round (Fig. 4.3). Nurse shark catches were also relatively invariable, but they presented lower occurrence between May-July and in December. Blacknose sharks and snappers were hardly caught between January-March, while stingrays, mobulids, and marine turtles were virtually absent before April. Moray eels were always present but showed several gaps in occurrence. Tiger sharks were mainly caught in temporal clusters, with long periods of absence followed by periods of high catch rates during which more than one individual per set were repeatedly observed, especially between January−March and late June through mid-September. Bull sharks presented a more solitary pattern and occurred mostly between June−August and December−January. The total number of hooks deployed by Julian day during eight years of sampling was always ≥ 100 and generally oscillated between 400−800 (Fig. 4.3). Monthly catch rates were assessed for the most caught species. Tiger sharks exhibited some seasonality, peaking at 0.04 and ~0.06 ind·100 hooks^{-1} in both March and July, respectively, and being lowest in October (Fig. 4.4). All potentially aggressive sharks (PAS) combined followed the same pattern but March showed a considerably higher catch rate (~0.08 ind·100 hooks^{-1}). The catch rate of blacknose sharks was lowest in January and peaked in March and November at ~0.12 and ~0.06 ind·100 hooks^{-1}, respectively, while nurse sharks were always caught in relatively high numbers, especially during the first semester, although their catch rate decreased suddenly in May, July, and December. Stingrays were most caught in April and most absent in January, June, and October. The catch rate of catfish showed a distinct seasonality, being lowest

between December−February and peaking at nearly 0.8 ind·100 hooks^{-1} in June (Fig. 4.5). Significant differences between months were found for the catch rates of both tiger (Kruskal-Wallis χ^2 = 20.311, df = 11, p = 0.041) and nurse (Kruskal-Wallis χ^2 = 20.727, df = 11, p = 0.036) sharks, and catfish (Kruskal-Wallis χ^2 = 21.822, df = 11, p = 0.026).

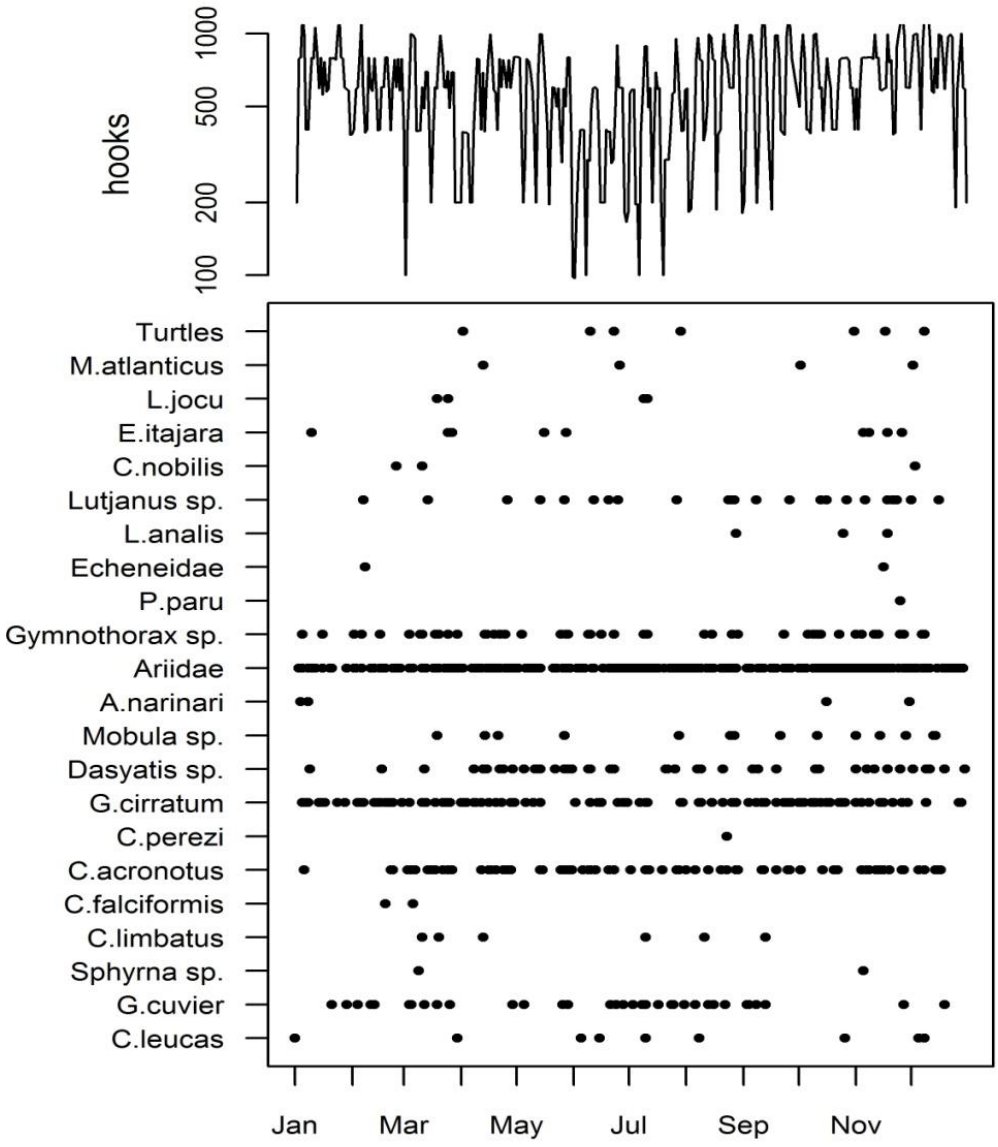


Figure 4.3. Dates with positive capture (lower panel) and corresponding total effort, as the number of hooks deployed per Julian day (upper panel), for all species and groups caught in a longline survey off Recife. Data correspond to combined years (2004−2011). Note the logarithmic scale of the *y*-axis in the upper panel.

The methodological modifications implemented in September 2005 influenced the catch rate of some species, but the two hook types used until May 2006 showed no effect on the catch rate of the species caught (Afonso et al., 2011; see chapter 3), thus the fishing period between September 2005 and December 2011 is comparable. However, shorter sampling periods (~4−7 months) during 2005, 2007, and 2009 could result in biased yearly catch rate estimates if species abundance reveal seasonality. Therefore, yearly catch rates should be truly comparable only between 2006, 2008, 2010, and 2011. Tiger sharks decreased slightly down to <0.02 ind·100 hooks^{-1} from September−December 2005 through 2010, but then peaked up to ~0.05 ind·100 hooks^{-1} in 2011 (Fig. 4.4). Such trend was also observed for all PAS combined. The catch rates of blacknose sharks and stingrays were highest in 2006 and further decreased to minimal numbers through 2011. In contrast, nurse sharks were less caught in the beginning of the study and then increased monotonically up to ~0.1 ind·100 hooks^{-1} through 2010−2011. The catch rate of catfish oscillated steadily around 0.1-0.3 ind·100 hooks^{-1} between 2006−2011, being highest in 2008 (Fig. 4.5). Significant differences in catch rates between the years 2006, 2008, 2010, and 2011 were found for tiger (Kruskal-Wallis χ^2 = 18.516, df = 3, p < 0.001), blacknose (Kruskal-Wallis χ^2 = 31.297, df = 3, p < 0.001), and nurse (Kruskal-Wallis χ^2 = 18.229, df = 3, p < 0.001) sharks, and stingrays (Kruskal-Wallis χ^2 = 11.710, df = 3, p = 0.008). Regarding the relative frequencies of the catch composition, some yearly variation was observed. Catfishes were always most represented, accounting for ~0.4−0.7 of yearly catches (Fig. 4.6). Nurse sharks presented an increasing importance in catch composition which was concomitant with an apparent decrease in the relative frequency of blacknose sharks, stingrays, and moray eels. Tiger sharks were always caught in lower proportions (< 0.03) but their relative frequency increased suddenly to > 0.1 in 2011. The Pearson's Chi-squared test with simulated p-value evidenced significant differences between the proportions of the most caught species (N > 30) across 2006, 2008, 2010, and 2011 (χ^2 = 142.806, p < 0.001).

Although longline soak time was significantly different between fishing sites (t=8.543, df=1134, p<0.001), the average magnitude of such difference (~1 h) was small (~7%) compared to average soak times at each site (14−15 h). Also, since the most caught species are typically nocturnal foragers (Bruton, 1996; Compagno, 2001), the difference in soak times between fishing sites should have had a negligible effect on the catch rate.

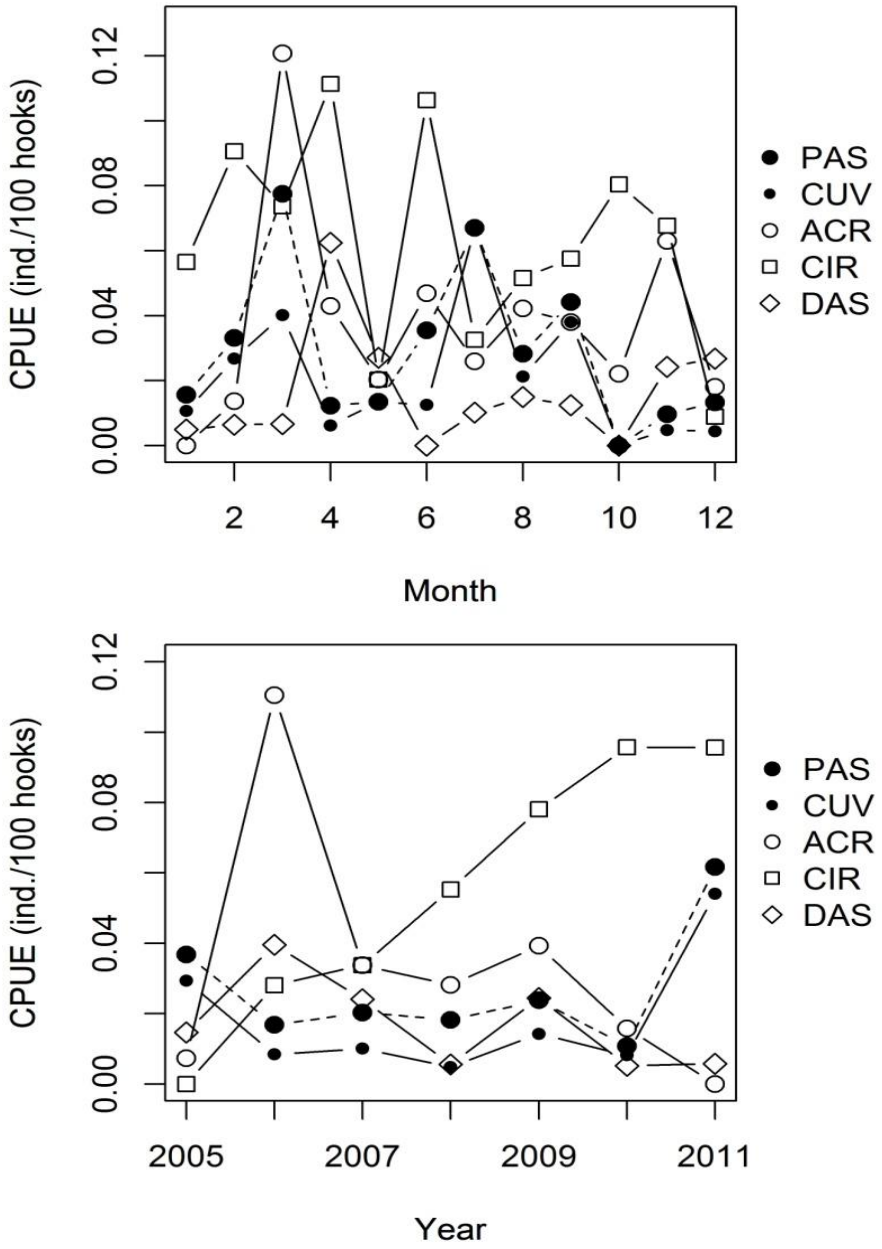


Figure 4.4. Temporal variability of the catch-per-unit-effort (CPUE), as the number of individuals caught per 100 hooks, of all potentially aggressive sharks combined (PAS; big solid circles), tiger (CUV; small solid circles), blacknose (ACR; empty circles), and nurse (CIR; empty squares) sharks, and sting rays (DAS; empty diamonds) between months (upper panel) and years (lower panel). Data before September 2005 was not considered in the monthly time series (upper panel) due to differences in fishing methodology which did not allow monthly comparisons of the catch rate. Note that during 2005, 2007, and 2009 only ~4−7 months were sampled.

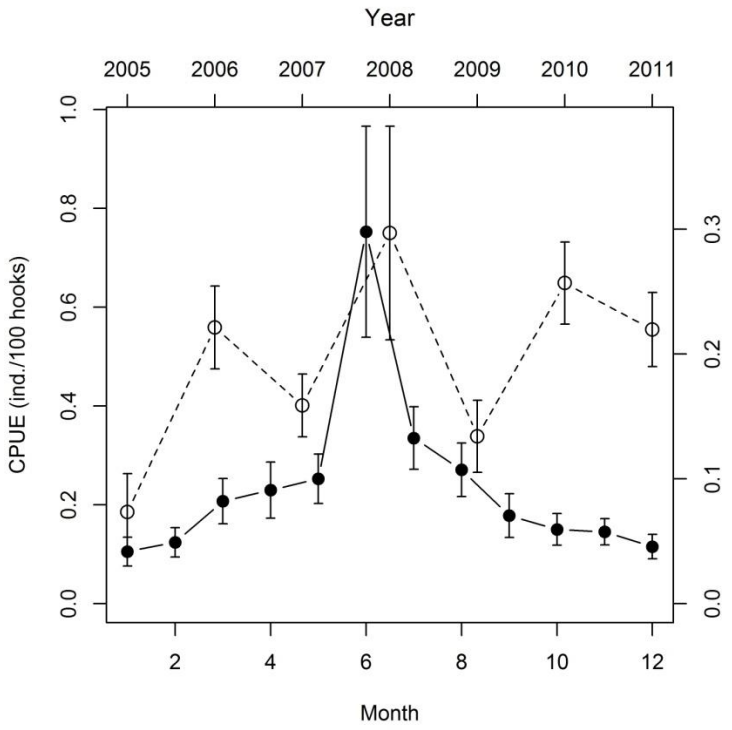


Figure 4.5. Temporal variability of the catch-per-unit-effort (CPUE), as the number of individuals caught per 100 hooks, of catfish between months (solid line with solid circles) and years (dashed line with blank circles). Left axis corresponds to monthly CPUE (mean±SE) and right axis corresponds to yearly CPUE (mean±SE). Note that only ~4−7 months were sampled during 2005, 2007, and 2009.

The catch rates of the most caught species between fishing sites evidenced distinct trends (Fig. 4.7). BV exhibited significantly higher CPUE of blacknose sharks (W = 44891.5, p = 0.048), and moray eels (W = 46087.5, p < 0.001). Tiger sharks, nurse sharks, and sting rays were also more abundant at BV, but the differences were not statistically significant. In contrast, the catch rate of catfish was significantly higher in PA (W = 35740, p < 0.001).

Fishing mortality was assessed in 506 individuals caught after September 2007. Among commonly caught species, only moray eels and blacknose sharks experienced high (> 80%) relative mortality (Table 4.3). The remainder, such as catfish, tiger and nurse sharks, and stingrays presented low (≤ 25%) or zero relative mortality. The relative mortality of all PAS combined was 0.28 since October 2007, thus 72% of the individuals were released alive. Protected species such as marine turtles, goliath groupers, and nurse sharks had virtually zero mortality. The global fishing mortality was 22.7%. Hooking location was additionally assessed in 375 of those individuals. Most species were hooked exclusively in the mouth (externally). Internal hooking in the gut or gills was verified only in ~3.2% of catfishes and ~4.7% of nurse sharks (Table 4.3). Eagle rays and turtles exhibited high proportions of hooks lodge externally

in other regions of the body other than mouth. Overall, only ~2.7% of the catch was hooked internally in potentially lethal anatomical regions of the body.

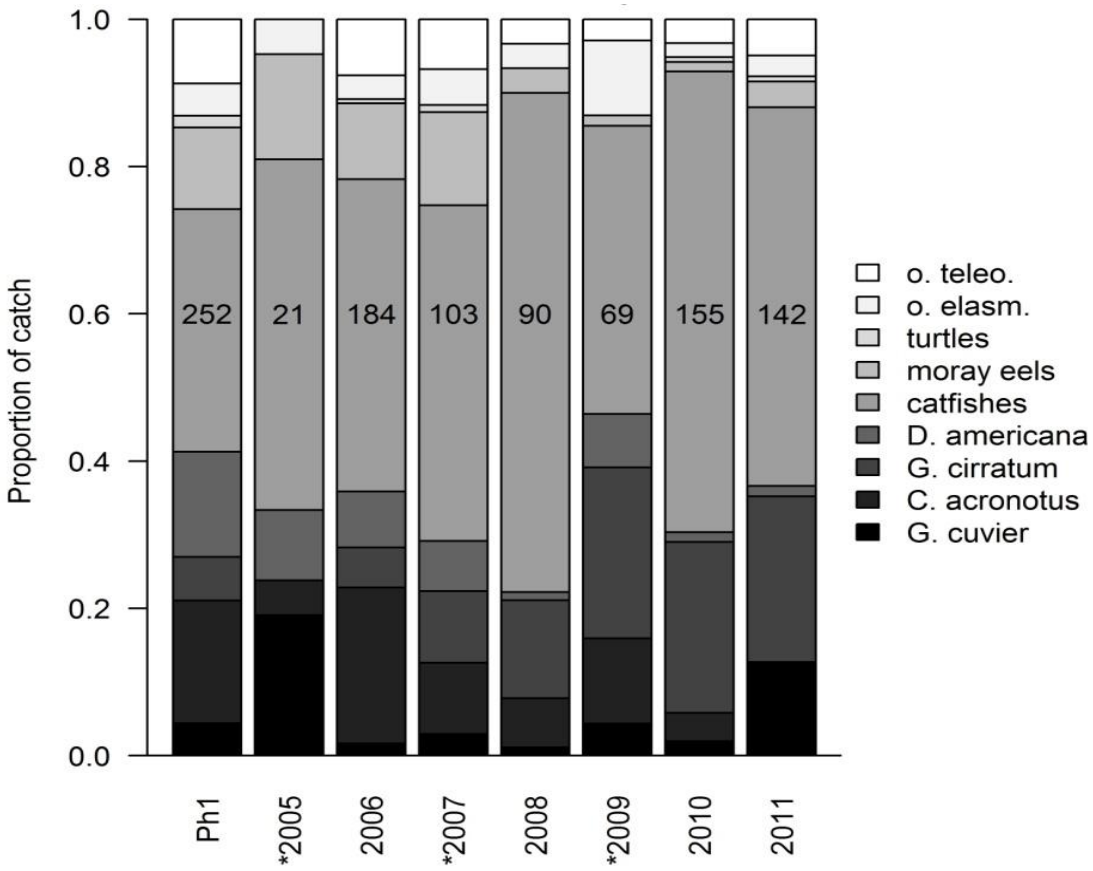


Figure 4.6. Yearly variation of relative frequencies for *taxa* caught in a longline survey off Recife between 2004−2011. O. elasm. and o. teleo. comprise all less frequently caught elasmobranchs and teleosts, respectively. Numbers in bars correspond to the number of individuals caught in the respective period. Ph1 corresponds to the period between May 2004 and August 2005 using a different fishing methodology. Years with asterisk (*) correspond to years with lower sampling effort (~4−7 months) and thus are not strictly comparable.

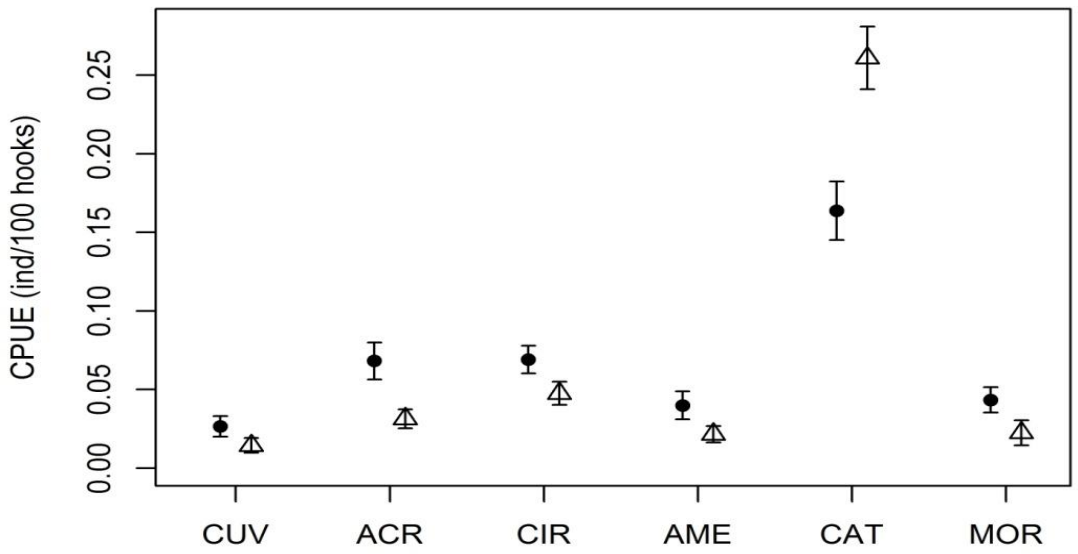


Figure 4.7. Comparison of the average catch-per-unit-effort (CPUE ± SE), as the number of individuals caught per 100 hooks, of most abundant species (N > 30) between fishing sites. Solid circles correspond to Boa Viagem/Piedade and blank triangles correspond to Paiva.

4.4. Discussion

The species caught in this study correspond mostly to known inhabitants of coastal waters off northeastern Brazil. Target species, defined as potentially aggressive shark species which may be implicated in the shark attacks off Recife, included 5 carcharhinids and 2 sphyrnids; however, observed catch rates indicate that tiger, bull, and blacktip sharks should be responsible, in decreasing order, for most of the incidents. Accordingly, both tiger and bull sharks have been previously identified as aggressors in some occasions (Gadig and Sazima, 2003; Hazin et al., 2008).

The catch composition was clearly dominated by ariid catfishes, which are most abundant in coastal lagoons and estuaries in tropical America (Yáñez-Arancibia and Lara-Domínguez, 1988). Nevertheless, carcharhinids and ginglymostomids were highly represented in catch composition, suggesting that the fishing methodology was fairly optimized for sharks. The selectivity of the fishing gear is a key-component for fisheries management since it allows reducing the bycatch while improving the catch rate of target species. Other medium/large, coastal species such as moray eels, stingrays, and snappers were also relatively frequent but in

Table 4.3. Number of specimens monitored (*N*), relative fishing mortality (RelMor) and hooking location as gut-hooked (internal), mouth-hooked (external), and hooked in other anatomical regions other than gut or mouth (other), in a longline and drumline survey off Recife between 2007−2011.

	Fishing mortality		Hooking location			
	N	RelMor	*N*	internal	external	other
Catfish	244	0.250	190	0.032	0.911	0.058
Lutjanus analis	4	0.500	3	0.000	1.000	0.000
Lutjanus spp.	2	0.000	2	0.000	1.000	0.000
C. nobilis	3	0.333	2	0.000	1.000	0.000
Gymnothorax spp.	11	0.818	7	0.000	1.000	0.000
E. itajara	13	0.000	10	0.000	1.000	0.000
C. acronotus	26	0.885	18	0.000	1.000	0.000
C. falciformis	2	0.500	1	0.000	1.000	0.000
C. leucas	4	0.750	1	0.000	1.000	0.000
C. limbatus	3	0.667	1	0.000	1.000	0.000
C. perezi	1	1.000	1	0.000	1.000	0.000
G. cuvier	34	0.176	32	0.000	1.000	0.000
R. lalandii	1	1.000				
G. cirratum	130	0.008	85	0.047	0.953	0.000
Dasyatis spp.	14	0.071	11	0.000	1.000	0.000
A. narinari	4	0.000	4	0.000	0.250	0.750
Mobula spp.	6	0.500	3	0.000	0.667	0.333
Turtles	4	0.000	3	0.000	0.333	1.000
Total	506	0.227	375	0.027	0.928	0.045

lower numbers. The longlines exhibited higher species diversity than drumlines, which could be ascribed to heterogeneity in the species-specific distribution within the study area or to the fact that longlines are seaward in relation to drumlines, thus resulting in the formers being eventually favored regarding species which perform shoreward movements. Higher catch rates of tiger sharks on longlines sustain such hypothesis, since this species moves within large home ranges in both coastal and oceanic realms (Holland et al., 1999). In contrast, bull sharks and goliath groupers are common in inshore waters (Eklund and Schull, 2001; Snelson, 1984) and showed higher catch rates on drumlines. Despite being operationally similar, however, longline and drumline catch rates in this study should not be fully comparable because both

gears had very distinct spatial arrangements and fishing efforts, which may have led to different interactions with the species caught.

Species-specific trends regarding the temporal variation of catch rates were described in various ways. Within fishing cruises, the catch rates in the first longline set held highest values for virtually all species. The schedule of the fishing operations involved ~3 days of rest between consecutive cruises, which may have contributed to increase abundances in the fishing area due to immigration from adjacent areas. Nevertheless, the most abundant species were represented in the four longline sets, but tiger sharks were barely caught in the fourth set. Differences in the catch rate of consecutive, standardized fishing sets may be useful to understand species-specific foraging dynamics and eventually to distinguish between common, resident species and less frequent, visiting species. Furthermore, such differences suggest that longline sets within a fishing cruise should not be considered independent and that fishing cruises, not longline sets, would probably be the most adequate sampling unit.

Catfish were continuously caught throughout the year. Other relatively abundant coastal species such as moray eels, snappers, stingrays, and both blacknose and nurse sharks followed the same trend but with varying densities of occurrence. Species with oceanic habits such as mobulids and marine turtles were caught interspersedly, while tiger sharks occurred in higher densities mostly in the first and third trimesters of the year. Seasonality of catch rate was verified for tiger sharks and all potentially aggressive sharks combined, with October presenting lowest catch rate and March and July presenting highest catch rates, which coincide with months when highest shark attack rates off Recife were verified (Hazin et al., 2008). Nurse sharks evidenced no seasonality as they were frequently caught year-round, although attaining highest catch rates during the first semester. Similarly, blacknose sharks were reasonably caught all months except January and showed peaks of abundance in March and November. Regarding catfish, a strong seasonality was observed with considerably higher catch rates in June. The higher outflow of the Barra de Jangadas estuary during the rainy season (May−August) could partially explain such pattern since catfish are usually associated with estuarine environments (Yáñez-Arancibia and Lara-Domínguez, 1988).

Regarding yearly variation of the catch composition, a decline in the relative frequency of blacknose sharks and stingrays since 2006 was accompanied by a significant rise

of nurse shark catches, suggesting that the community structure sampled by this study may be shifting. All the referred species are demersal or bottom-associated (Compagno, 2001) and so they are expected to be ecologically linked to a certain extent. The relative frequency of tiger sharks was highest in 2011 when their catch rate peaked. Variability in yearly catch rates of tiger sharks could be ascribed to biological factors which regulate reproductive rhythmicity. Catfish showed distinct yearly catch rates but no tendency for increasing or decreasing was observed. The yearly comparison of catch rates needs caution, however, since 2005, 2007, and 2009, each represent only about 4−7 sampled months, which could induce significant biases if species present some seasonality, and so a continuity in yearly sampling could not be considered. Nevertheless, the rapid initial decline in the catch rates of some species recorded in this study has been also observed elsewhere (e.g. Reid et al., 2011) and it could be explained by the harvest of resident communities (Stevens et al., 2000), and by the suspension of all hooks in the water column after September 2005, which significantly reduced the catch rate of some bycatch (Afonso et al., 2011).

Some species showed different catch rates between fishing sites. Catfish were more abundant at PA, which could be associated to the presence of the Barra de Jangadas estuary within this site. On the other hand, blacknose sharks and moray eels were more abundant at BV, where higher habitat complexity is found due to the presence of an alongshore reef of beachrocks. Increased habitat complexity could explain higher catch rates of these species because moray eels tend to occupy crevices and holes (Gilbert et al., 2005) and blacknose sharks prey mostly on reef-associated species (Compagno, 2001) whose abundance may be proportional to habitat complexity (Gratwicke and Speight, 2005). Another possible explanation would be that BV is exposed to the outflow of the Barra de Jangadas estuary to a greater extent, since coastal currents run predominantly to the north (Bittencourt et al., 2002) and thus only the northernmost section of PA is influenced by it. However, t-tests failed to detect significant differences in the monitored water parameters between sites (see chapter 2).

Overall fishing mortality was reasonably low (~20%) and endangered species with protection status in Brazil, such as goliath groupers, nurse sharks, and marine turtles (Brazilian Ministry of the Environment, Normative Instruction #5, May 21st 2004), suffered negligible or zero at-vessel mortality and so they are believed to have not experienced any negative effects produced by this study. However, some less resilient species such as blacknose sharks and

moray eels experienced significant relative mortalities. Previous gear modifications based on circle hooks have contributed to increase the percentage of live releases (Afonso et al., 2011; see chapter 3) and further methodological improvements focusing on soak time reduction are currently being explored to minimize the mortality of the referred species. So far, the exclusive use of circle hooks has evidenced a remarkable dominance of mouth-hooked individuals, resulting in most of the catch being in good health by the time of gear retrieval. While inoffensive species are promptly released at the site of capture, potentially aggressive sharks must be removed from the area of risk in order to reduce the likelihood of a shark-human encounter. The seaward transport of live sharks is performed aboard the R/V Sinuelo and, although it may inflict additional stress to the animals, it has been proven successful since virtually all sharks survived to this procedure, as evidenced by the tagging and telemetry data (see chapter 7).

Shark attack mitigation programs conducted in Australia and South Africa use mostly gillnets (Dudley, 1997) which inflict undesirable fishing mortality (Gribble et al., 1998a; Reid et al., 2011). In Recife, given the high precision of the area where most attacks occurred, the combination of longlines and drumlines seems a more adequate fishing strategy than shark meshing in respect to the selectivity towards potentially aggressive sharks and mortality of caught species. The fishing methodology herein described has proven to be highly selective towards sharks since it caught a reduced diversity of other *taxa* compared to shark meshing programs (Dudley and Cliff, 2010). Organisms other than fish were limited to a negligible number of marine turtles, despite the occurrence of large vertebrates such as dolphins, whales and manatees in this region. The fishing mortality produced by the Shark Monitoring Program of Recife was also considerably lower than those produced by shark meshing programs and is considered to be negligible for most species caught. In South Africa and New South Wales, the relative mortality of turtles and batoids equaled 62−66% and 30−39%, respectively (Dudley and Cliff, 1993a; Green et al., 2009), while both these *taxa* had little or zero mortality in Recife, except for mobulid rays which were rarely caught but still experienced 50% mortality. The stress of capture is milder on longlines compared to gillnets (Hyatt et al., 2011), thus longlines are expected to enhance survival rates. In South Africa, longlining was abandoned after a few years of use (Cliff and Dudley, 1992) but Cliff and Dudley (2011) examined several methodological improvements for reducing the environmental impacts of shark

meshing, including the introduction of drumlines for replacing some gillnetting effort. Drumlines are also used in Queensland in combination with gillnets (Gribble et al., 1998b). However, the percentages of releases reported there are yet much lower than the ones obtained in this study, which again demonstrates the better performance of longlining in the reduction of fishing mortality compared to gillnetting. Some discontinued shark control programs in Hawaii also used longlines for reducing local populations of large sharks and mitigating shark attack rates, but information on at-vessel mortality was not available as there was no intention of releasing the sharks caught (Wetherbee et al., 1994).

Altogether, the Shark Monitoring Program of Recife allowed to efficiently survey the dynamics of large, coastal predators in nearshore waters with minimum disturbance to the local environment. The information so far collected has been crucial for managing the conflicts triggered by the shark attack outbreak verified in this region and it could be useful for addressing similar concerns elsewhere. Additionally, the fishing methodology herein presented contributed to effectively mitigate the shark attack rate off Recife (see chapter 8), indicating that longlining is an adequate alternative to gillnetting. The efficacy of this methodology could, however, depend on several factors such as the shape and extent of the area of risk and the species responsible for the attacks. Thus, management initiatives resulting from shark attack outbreaks should carefully analyze all relevant, site-specific aspects before endorsing mitigation strategies.

Chapter 5. Structure and dynamics of the elasmobranch assemblage off Recife

A tiger shark caught by the Shark Monitoring Program of Recife.

5.1. Introduction

Nearshore areas generally comprise highly productive habitats supporting great abundance and diversity of fish and invertebrates (Beck et al., 2001), therefore they provide ideal foraging grounds where elasmobranchs may optimize growth (Simpfendorfer and Milward, 1993). Additionally, nearshore waters could enhance elasmobranch survival because young juveniles may shelter in shallow or low salinity environments in order to decrease predation risk (Heupel and Simpfendorfer, 2011; Wetherbee et al., 2007). Thus, several species use coastal waters as primary and/or secondary nursery grounds (Heupel et al., 2007; Skomal, 2007b). Adults of these species may also exploit coastal habitats to target high quality prey items which are unavailable in oceanic waters (Heithaus et al., 2002) or, in case of females, to give birth or lay eggs (e.g. Castro, 1996; Snelson et al., 1984). Yet, other species do not use discrete areas during early life-stages (Ulrich et al., 2007) and instead perform wide-ranging movements with little time being spent at any specific location (Carlson et al., 2008), resulting in immature and mature individuals frequently sharing the same habitats (Heupel et al., 2006; Parsons and Hoffmayer, 2005; Ulrich et al., 2007). A combination of life-stages may thus compose elasmobranch assemblages in nearshore areas, with different species expectedly using distinct strategies to enhance population success (Knip et al., 2010).

On the other hand, nearshore waters typically comprise highly dynamic ecosystems (Mann, 2000) to which inhabitants must adapt in order to remain in these regions. Highly vagile species such as sharks may cope with environmental variability by accessing coastal waters only when favorable conditions are met and moving away otherwise. Habitat use in coastal sharks has been associated to the tidal cycle (Ackerman et al., 2000), water salinity (Heupel and Simpfendorfer, 2008; Ubeda et al., 2009) and temperature (Grubbs et al., 2007), and storm events (Heupel et al., 2003). Sharks can thus increase survival by moving away from preferred habitats when facing adverse environmental conditions, and failing to do so may result in severe mortality (Smith and Abramson, 1990; Snelson and Bradley, 1978; Stoner, 2004). Moreover, coastal elasmobranchs are also generally exposed to high anthropogenic pressure due to habitat degradation and loss (Jennings et al., 2008; Suchanek,

1994; Vitousek et al., 1997; Ward-Paige et al., 2010), and fishing. The historical decline and eventual collapse of coastal ecosystems have been previously inferred (Jackson, 2001), so has the impoverishment of marine trophic webs as a consequence of overfishing (Pauly et al., 1998), inclusively in Brazilian waters (Freire and Pauly, 2010). Also, species that reside in nearshore areas throughout their ontogenetic development are more vulnerable to varying coastal processes, habitat degradation, and fishing pressure than are species that use nearshore areas for only a small part of their life-span (Knip et al., 2010). As such, several coastal elasmobranchs are nowadays critically endangered and may incur in a considerable risk of extinction (Musick et al., 2000).

Elasmobranchs are a key-component of coastal ecosystems because they act as high-level predators and consume a large portion of available energy (Cortés, 1999). Thus, the depletion of their populations may have striking consequences, such as mesopredator releases and trophic cascades (Ferretti et al., 2010; Shepherds and Meyers, 2005) which may potentially change the structural properties of the ecosystem (Heithaus et al., 2008; Rezende et al., 2009). Such phenomena have also been associated to regions where protective shark meshing takes place (van der Elst, 1979). Understanding how species and communities use nearshore areas is of utmost importance so that effective conservation and management can be implemented. On that account, assessing the spatiotemporal variability in community structure is a first step to acquaint ecological processes in elasmobranchs (Vaudo and Heithaus, 2009). The strategy a species utilizes to maximize survival is shaped by both its life-history characteristics (Branstetter, 1990; Cortés, 2000) and the surrounding environment (Sims, 2003), frequently resulting in high interspecific variability in distribution (Knip et al., 2010) and behavior (Berthea et al., 2004). Distribution and habitat use of elasmobranchs within nearshore areas are likely influenced by a combination of ecological factors including environmental features, resource abundance and distribution, and presence of predators and/or competing species (Belcher and Jennings, 2010; Hopkins and Cech, 2003; Knip et al., 2010; Wiley and Simpfendorfer, 2007). Identifying the factors which regulate the dynamics of the elasmobranch community should improve the efficiency of conservation measures. Additionally, such information is crucial for addressing socioeconomic issues in regions with high incidence of shark attacks on humans, as is the case of Recife (Hazin et al., 2008). The ability to predict the occurrence of potentially dangerous sharks at hazardous areas could

improve the efficacy of risk management strategies and reduce the environmental impacts of bather protection programs (Reid et al., 2011).

However, the nature of this sort of research and the high intensity of sampling, which are characteristic of shark monitoring programs, usually originate an analytical constraint due to large proportions of zero-valued observations which may yield zero-inflated distributions, a common situation in longline surveys (Maunder and Punt, 2004). Models that explicitly relate covariates to the occurrence of excess zeros (i.e., more than expected from a Poisson process) have been recently developed to fit zero-inflated data because traditional statistical methodologies cannot be reliably used in such circumstances (Barry and Welsh, 2002). A general approach to nonparametric regression analysis with zero-inflated data consists on modeling the response distribution as a probabilistic mixture of zero (the so-called 0-atom) and a regular component (i.e., the non-zero-inflated variate), whose distribution belongs to the exponential family (Liu et al., 2011). Generalized Additive Models (GAM) are widely used for modeling nonlinear effects of covariates in quantitative studies (Hastie and Tibshirani,1990; Wood, 2006) and can be extended for such data, resulting in Zero-inflated Generalized Additive Models (ZIGAM) (Welsh et al., 1996; Cunningham and Lindenmayer, 2005). Generalized regression models can be estimated by maximizing the penalized likelihood, which generally equals $L(\eta) - \lambda^2 \cdot J^2(\eta)$, where η is the unknown regression function on the link scale, $L(\eta)$ is the log-likelihood functional, J^2 is some roughness penalty, and λ^2 is the smoothing parameter that controls the trade-off between the goodness-of-fit and the smoothness of the function (Liu and Chan, 2010). Under GAM-derived approaches, the unknown regression function η is additive in the number m of covariates t, such that $\eta(t_i) = \beta_0 + s(t_{1i}) + s(t_{2i}) + ... + s(t_{mi})$, where each s is a centered, unknown smoothing spline function, and β_0 is the intercept, all of which constitute the estimated regression parameters (Liu and Chan, 2010). However, the ZIGAM approach implicitly assumes that the zero-inflation process is completely uncoupled from the underlying population abundance process, which may not always be true. In that account, a Constrained Zero-inflated Generalized Additive Model approach (COZIGAM), which assumes that the probability of non-zero inflation and the mean non-zero-inflated population abundance are linearly related on some link scales, has been developed (Liu and Chan, 2010).

This study aims at characterizing the structure of the elasmobranch assemblage off the Metropolitan Region of Recife and assessing its spatiotemporal dynamics together with the environmental factors that regulate species abundance.

5.2. Materials and Methods

This study used data between May 2004 and December 2011 obtained from the Shark Monitoring Program of Recife. The study area comprised two adjacent, nearshore fishing sites, hereafter referred to as Boa Viagem (BV) and Paiva (PA), and is described in chapter 2. Additionally, fishing sets conducted in deeper waters at the middle continental shelf (CS) were also included in the analyses. The fishing methodology and effort, and further details on sampling procedure are thoroughly described in chapter 4. While both longlines and drumlines were used as a fishing strategy, drumline data were considered for biological analysis only because both fishing gears had distinct efforts and spatial arrangements, and only a few elasmobranchs were caught in drumlines compared to longlines (Table 4.2), which precludes a direct comparison between the two gears. Catch per unit of effort (CPUE), as the number of individuals caught per 100 hooks, was calculated for assessing the relative abundance of all species. Analyzes involving catch rates pertain to the period between September 2005 and December 2011 due to gear modifications implemented in September 2005 which significantly influenced catchability (Afonso et al., 2011).

All sharks caught were identified, sexed, and measured to the nearest centimeter. Dead sharks were collected and brought to the laboratory for biological analyzes, while live sharks were tagged and returned to the water. Rays caught alive were generally not measured or sexed to avoid further stress from handling, but they were identified to the lowest possible *taxon* while in the hook and then quickly released. Several environmental parameters, namely sea surface temperature, salinity, and water transparency, were monitored along the fishing cruises (see chapter 2). Tidal amplitude (±0.1 m) for the Port of Recife was obtained from the Hydrographic and Navigation Directory of the Brazilian Navy (http://www.mar.mil.br/dhn/chm/tabuas/index.htm). The day of the lunar cycle was obtained from http://kalender-365.de/calendario-lunar-pt.php, with the new-moon day corresponding to the first day of the

cycle. Meteorological variables such as pluviosity (mm), wind direction (0−360º) and speed ($m \cdot s^{-1}$), and cumulative solar radiation ($kW \cdot h \cdot m^{-2}$) were obtained from the Center for Weather Forecasting and Climate Studies (CPTEC) of the National Institute for Space Research (INPE) (http://sinda.crn2.inpe.br/PCD/historico/consulta_pcdm.jsp) for the region of Recife between January 2004 and December 2011.

Size and sex compositions were assessed for each shark species, and statistical tests were performed on the most abundant species ($N > 50$). Differences in total length between males and females were verified with 2-sample t-tests. Kruskal-Wallis rank sum tests were used to compare total lengths between years and between quarters. Whenever significant differences between quarters were detected, a post-hoc, multiple comparison procedure available in *pgirmess R*-library (Giraudoux, 2011) was used to investigate which quarters were different. This procedure generates an observed difference ($Diff._{Obs}$) for each pair of levels, which can be compared with a critical difference ($Diff._{Cri}$) to assess its significance (Siegel and Castellan, 1988). Pearson's chi-square tests were used to detect significant shifts in sex ratio across years and quarters for each species.

Because fishing sets within fishing cruises could not be considered independent samples (see chapter 4), catch and effort data were aggregated by fishing cruise and environmental variables were averaged by fishing cruise for abundance analyses. Each fishing cruise usually comprised four continuous longline sets with 100 hooks each, thus the fishing effort equaled to about 400 deployed hooks per fishing cruise at each site. Elasmobranchs numbering more than 50 individuals caught were considered for abundance analysis, which corresponded to blacknose, nurse, and tiger sharks, and stingrays (Table 4.2). On the other hand, a total of 12 candidate predictors of species abundance were considered, namely: *Year*, *Month*, *Fishing site*, *Lunar day*, *Sea surface temperature*, *Salinity*, *Visibility*, *Pluviosity*, *Tidal amplitude*, *Wind direction*, *Wind speed*, and *Cumulative solar radiation*. All predictors were interpreted as continuous variables except for the nominal variable *Fishing site*. Further details on predictor variables, including the abbreviations hereafter used, can be found in Table 5.1.

Possible correlations between predictors were investigated in order to avoid including correlated variables in the same model, which could interfere in the data fitting process. Because some environmental variables could be directly or indirectly linked due to e.g.,

seasonality in major forcing processes such as weather, a certain amount of correlation between covariates should be expected when using high numbers of predictor variables in the same model. Both Pearson's product-moment correlation coefficient, r, and Spearman's rank correlation coefficient, ρ, were assessed for those pairwise combinations of continuous predictors which could theoretically demonstrate significant correlations. Additionally, the significance of Pearson's product-moment correlation coefficient was assessed using Student's t distribution with $n - 2$ degrees of freedom, as the bivariate normal distribution of r follows the t distribution when the null hypothesis, $r \approx 0$, is verified (Rahman, 1968). Also, 95% confidence intervals for r were calculated using Fisher's Z transformation (Fisher, 1915). Both procedures were conducted using the *cor.test* function in *stats R*-library (*R* Development Core Team, 2011). Correlation coefficients lower than 0.3 are generally considered small (Cohen, 1988). Before the trade-off between excluding potentially useful predictors from the analysis and the reduction in model accuracy due to the inclusion of significantly correlated predictors, it was defined that conflictive correlations between predictors would require the meeting of

Table 5.1. Description of the predictive variables as used in the models for elasmobranch relative abundance off Recife.

Predictor	Abbreviation	Type	Description
Site	*Site*	Categorical	Boa Viagem (BV), Paiva (PA)
Year	*Year*	Continuous	2005−2011
Month	*Month*	Continuous	1−12
Lunar day	*LunDay*	Continuous	The day number of the lunar cycle, starting in new-moon day
Temperature	*Temp*	Continuous	Sea surface temperature, in degrees
Salinity	*Salin*	Continuous	Practical salinity units
Visibility	*Visib*	Continuous	Water visibility, in meters
Tidal amplitude	*TidAmp*	Continuous	Difference between highest and lowest tidal height per day
Pluviosity	*Pluvio*	Continuous	Rainfall in milimeters
Wind direction	*WindDir*	Continuous	Direction in 0−360 degrees, clockwise
Wind speed	*WindSpe*	Continuous	Velocity in meters per second
Cumulative solar radiation	*SolarRad*	Continuous	Total solar radiation per day, in kiloWatts·hour per square meter

three criteria, nominally *i*) *r* being significantly different from zero ($p < 0.05$), *ii*) the highest absolute value in the confidence interval for *r* being greater or equal than 0.3, and *iii*) either the absolute value of ρ or the lowest absolute value in the confidence interval for *r* being greater or equal than 0.3. Whenever a problematic correlation was detected, the responsible covariates were not used simultaneously in any model.

Catch data for each species were fitted against each of the predictive variables individually, using two different types of models: the non-inflated GAM and the zero-inflated ZIGAM. This comparison allowed to assess if the distribution of the data was zero-inflated. While zero-inflated models proved to be the best alternative, the constrained, zero-inflated COZIGAM was also fitted to the data in order to make comparisons with the larger (more parameters) ZIGAM, which would allow to verify the independency of the non-zero-inflated data generation process relatively to the zero-inflated process. The type of model which generally exhibited best performance was selected for the analysis.

Modeling was conducted with *COZIGAM R*-package (Liu and Chan, 2010). The non-zero-inflated process was defined to follow a Poisson distribution, while the zero-inflated process followed a binomial distribution. The thin-plate regression spline was used as a penalized smoothing basis, and the *k* dimensions of the basis used to represent the smooth terms, which simplistically indicate the amount of degrees of freedom in the smoothing function, were optimized for each predictor variable. Optimization was accomplished by running several univariate models (i.e. models containing only one predictor variable) with increasing *k* values and comparing their output. Parameter estimates were obtained with the EM algorithm (Dempster et al., 1977) because typical procedures to obtain parameter estimates for Generalized Additive Models cannot be used when the state (i.e., the zero-inflated or the non-zero-inflated processes) which the zero-valued observations belong to is unknown (Minami et al., 2011). A maximum of 250 interactions were allowed to occur for the algorithm to converge. The approximated logarithmic marginal likelihood by Laplace method, *logE*, was used for model comparison and selection, as suggested by Liu and Chan (2010). Model fitness was evaluated with the adjusted coefficient of determination, R^2_{adj}, which is a modification of R^2 that adjusts for the number of explanatory terms in a model. The logarithm

of fishing effort was included in the model as an offset covariate for standardization of the catch rate. Missing values were replaced by the mean value of the non-missing observations.

Given the particular nature of the covariate *Month*, which contains complex interactions with environmental variables most notably when seasonality is present, modeling was approached in two separate forms: the spatiotemporal model (*SPT*), which includes the covariates *Year*, *Month*, and *Site*; and the environmental model (*ENV*), which includes the remaining covariates that are not correlated. Regarding *SPT* modeling, two different approaches, only differing in the interaction between terms, were conducted, more precisely: *i) SPT1*, comprising *Site* as a factorial covariate and covariates *Year* and *Month* as independent smooth functions, and *ii) SPT2*, comprising *Site* as a factorial covariate and covariates *Year* and *Month* linked by the same smoothing spline, thus interacting while being adjusted. Regarding *ENV* modeling, *Site* was also included as a factor because the catch rates of some species were found to be significantly different between fishing sites (see chapter 4). Predictive variables with higher effect on abundance were selected to be included in the *ENV* model with a forward stepwise approach (Ortiz and Arocha, 2004). Forward selection starts by adding the most significant variable to the model, which can be assessed by generating models with single predictor variables and comparing their fitness. At each subsequent step, the procedure adds the next most significant variable of those not in the model until there are no further variables to be included or the inclusion of new variables do not improve model fitness, which leads the selection procedure to stop. In case the inclusion of a new variable improved model fitness but the resulting fitting process generated a smooth function with only one efficient degree of freedom (edf), or if statistical significance of the new variable was not achieved, such solution was eliminated and the next valid variable was introduced in the model. Backward selection was also attempted but it did not allow the fitting algorithm to converge, thus preventing model-building with such an approach. Despite some authors discouraging the use of step-by-step model-building (Flom et al., 2009; Mundry and Nunn, 2009), this approach was selected because it is widely disseminated (Khan et al., 2007) and is computationally easy to implement. In addition to multivariate models assessed with forward selection, species abundance was also described using univariate models for all environmental variables with *Site* as a factorial covariate, as a way to investigate the exclusive relationship between each predictive variable and the response in elasmobranch abundance. All statistical

analyses were conducted in *R* statistical software, version 2.14.0 (*R* development core team, 2011).

5.3. Results

As already described in chapter 4, the elasmobranch assemblage surveyed by the present study was clearly dominated by three shark species, namely the nurse shark, *Ginglymostoma cirratum*, the blacknose shark, *Carcharhinus acronotus*, and the tiger shark, *Galeocerdo cuvier* (Table 4.2), thus the following analyses will focus mostly on these *taxa*. Among elasmobranchs, dasyatid stingrays were also frequently caught and they will be included in the modeling of abundance. Less frequent sharks and rays are identified in Table 4.2 and will be approached from a descriptive perspective only.

5.3.1. Size composition

The three most represented shark species included 149 nurse sharks measuring 189.0 (±43.5) cm TL, 125 blacknose sharks measuring 111.8 (±16.1) cm TL, and 56 tiger sharks measuring 158.2 (±58.4) cm TL (Table 5.2). Tiger sharks exhibited highest abundance and largest size among potentially dangerous species, but the bull shark, *Carcharhinus leucas*, exhibited highest mean total length, with the smallest individual caught measuring 144 cm TL. Smaller blacktip, *C. limbatus*, and silky, *C. falciformis*, sharks averaging 125.7 (±53.3) and 109 (±18.5) cm in length, respectively, were sporadically caught, although the maximum length of blacktip sharks exceeded 200 cm TL. Caribbean reef, *C. perezi*, smooth hammerhead, *Sphyrna lewini*, and great hammerhead, *S. mokarran*, sharks were caught in single events, with sphyrnids presenting large sizes (> 200 cm TL).

The frequency of blacknose shark size-classes exhibited a distinct modal distribution, with 68% of the individuals measuring between 100 and 120 cm TL, and 92% measuring between 90 and 130 cm TL (Fig. 5.1a), although specimens as small as 39 cm TL and as large as 180 cm TL were caught. Since blacknose sharks mature at about 100 cm TL in this region (Hazin et al., 2002), most individuals were adults or late juveniles. The size distributions of both males and females were identical, but the largest individual caught was a female (Fig.

5.1a). Nurse sharks measuring between 120−240 cm TL were uniformly abundant and totaled 91% of the nurse sharks caught, but total lengths ranged between 92 and 300 cm TL (Table 5.2), although extreme size-classes were little represented (Fig. 5.1b). Sizes > 220 cm TL were clearly dominated by females, but both sexes were abundant in smaller size classes. Regarding tiger sharks, the length frequency distribution evidenced a clear prevalence of juveniles of both sexes measuring between 82 and 200 cm TL, which totaled 88% of the tiger sharks caught. Larger individuals were mostly females measuring between 220 and 360 cm TL (Fig. 5.1c). Similarly, the largest, 250 cm TL bull shark was a female, but ten other bull sharks measuring between 140 and 220 cm TL were equally represented between sexes. The two largest blacktip sharks caught measured > 160 cm TL and were both females, while all three male blacktip sharks measured < 100 cm TL. Nevertheless, no statistically significant differences in total length between sexes were verified for blacknose ($t = -0.0933$, $p = 0.9258$), nurse ($t = -1.3663$, $p = 0.1749$), and tiger ($t = -0.4525$, $p = 0.6527$) sharks, thus both sexes were pooled together for length analyses.

Table 5.2. Summary of total lengths (minimum, maximum, mean, and standard deviation) and sex ratio, as the proportion of males to one female, of sharks caught off Recife, Brazil between 2004 and 2011. N_t and N_s denote the number of individuals caught and sexed, respectively.

Species	N_t	Total length (cm)				Sex ratio
		Min	Max	Mean	S.D.	M:F (N_s)
Ginglymostoma cirratum	149	92	300	189.0	43.5	0.78:1 (116)
Carcharhinus acronotus	125	39	180	111.8	16.1	0.77:1 (122)
Galeocerdo cuvier	56	82	355	158.2	58.4	0.69:1 (56)
Carcharhinus leucas	11	144	250	193.7	32.5	0.67:1 (11)
Carcharhinus limbatus	6	80	209	125.7	53.3	1:1 (6)
Carcharhinus falciformis	2	83	126	104.5	30.4	1:1 (2)
Carcharhinus perezi	1	107	107	−	−	0:1 (1)
Rhizoprionodon lalandii	1	51	51	−	−	0:1 (1)
Sphyrna mokarran	1	346	346	−	−	1:0 (1)
Sphyrna lewini	1	222	222	−	−	1:0 (1)

Blacknose sharks showed little variation in total length across years and quarters (Fig. 5.2a), although a significant reduction in the catch rate of this species (Fig. 4.4) constrained the size-structure assessment in more recent years. Nonetheless, blacknose sharks measuring between 100−125 cm TL were predominant throughout the sampling period, with the largest and smallest sharks being caught during the first four years of surveying (Fig. 5.3A). The seasonal distribution of lengths showed some amount of temporal segregation, with sharks < 100 cm TL occurring only between January and September and sharks > 125 cm TL occurring mostly between July and December, but always in low numbers (Fig. 5.3B). Kruskal-Wallis tests, however, failed to detect differences in blacknose shark total length between years or quarters (Table 5.3).

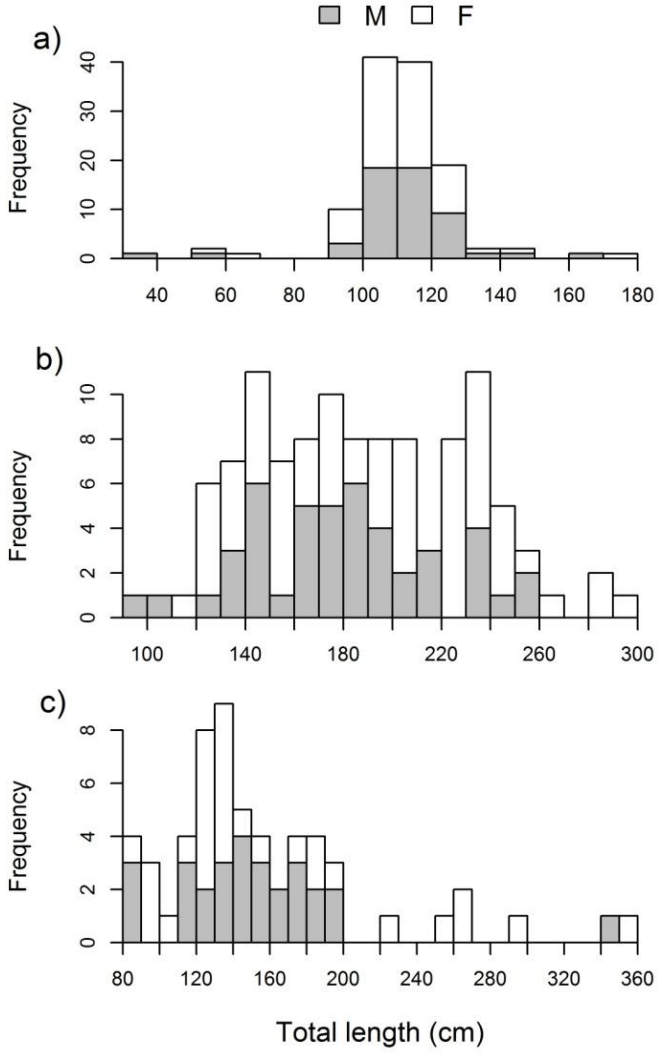


Figure 5.1. Absolute frequencies of 10-cm total length-classes for male (gray) and female (white) a) blacknose sharks, b) nurse sharks, and c) tiger sharks caught off Recife from 2004 to 2011.

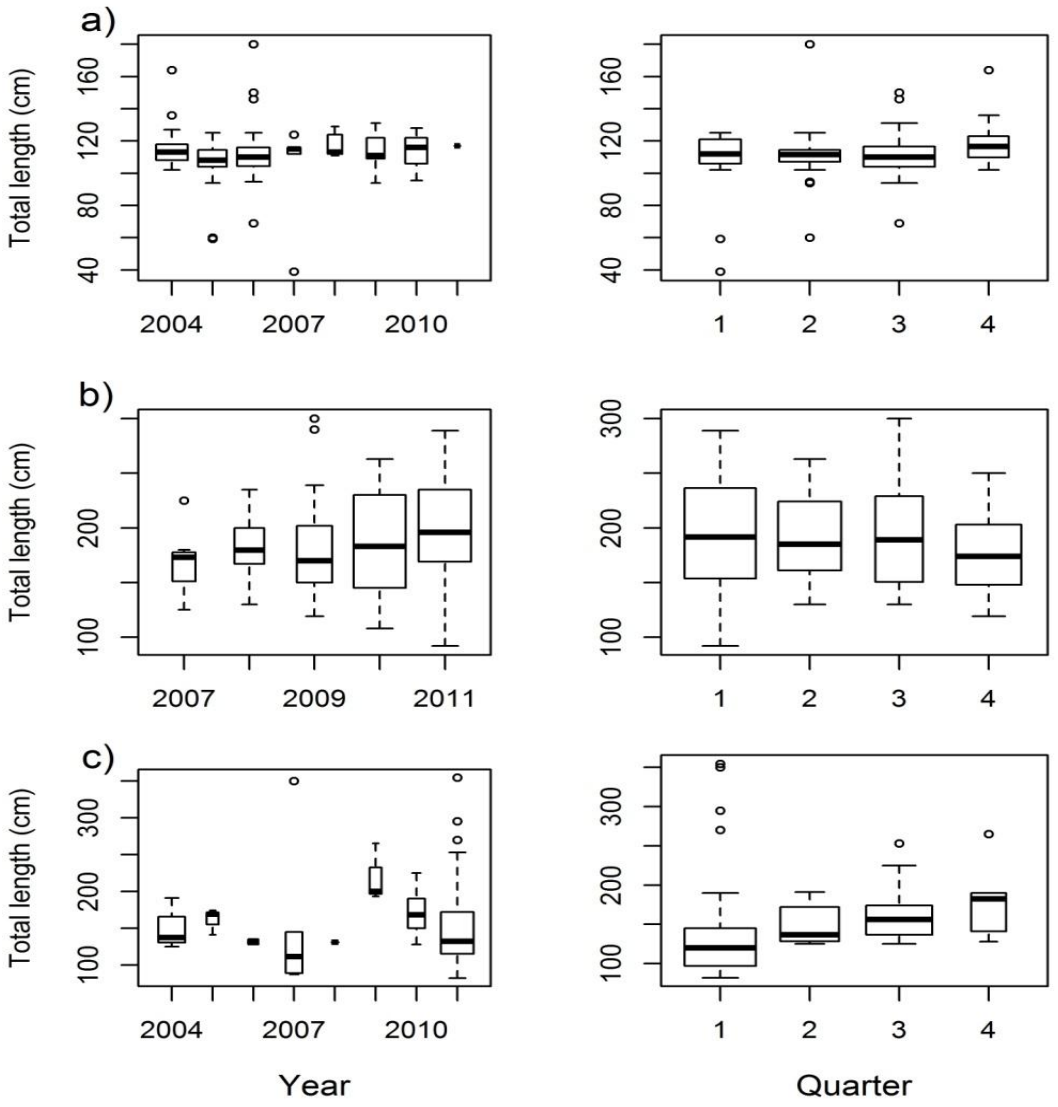


Figure 5.2. Distribution of total lengths per quarter and per year for a) blacknose shark, b) nurse shark, and c) tiger shark. In each plot, box width is proportional to the square root of the number of individuals measured.

Contrasting with blacknose sharks, nurse shark total length exhibited a tendency for increasing and widening the range of its values from 2007 through 2011, although such trend in size was accompanied by an increase in the number of nurse sharks sampled (Fig. 5.2b). Indeed, during the final years of this study the length-frequency distribution assumed a sort of bimodal structure, with expansion of the most extreme size-classes (Fig. 5.4A). Sizes between 125−200 cm TL were most represented between 2007 and 2009, while sizes between 200−250

cm TL became most frequent between 2010 and 2011, together with sizes > 250 cm TL which were absent in 2007 and 2008. Nurse sharks < 100 cm TL were present in 2011 only. No clear seasonality in total length was observed, but the first quarter showed highest variability in shark size (Fig. 5.2b), which was associated to the occurrence of sharks < 125 cm TL exclusively between October and March and to the prevalence of large sharks, particularly sharks > 250 cm TL, between January and March, while in the remainder of the year the most frequent size-classes were between 125−200 cm TL (Fig. 5.4B). However, no significant differences in total length between quarters or years were found for nurse sharks (Table 5.3).

Tiger shark abundance showed strong variability across years (Fig. 4.4), resulting in small sample sizes in most years. As such, variations in the yearly distribution of total lengths were impossible to assess due to strong fluctuations particularly in years with low abundance of tiger sharks (Fig. 5.2c). Nevertheless, only sharks < 200 cm TL were caught between 2004 and 2006, whereas sharks > 250 cm TL were caught only in 2007, 2009, and 2011 (Fig. 5.5A). On the other hand, a clear seasonality in total length was observed, with tiger sharks increasing in size from January through December (Fig. 5.2c). A Kruskal-Wallis test detected significant differences in total length between quarters but not between years (Table 5.3), and a post-hoc procedure indicated that the first and the third quarters were significantly different ($Diff._{Obs}$=14.8770; $Diff._{Cri}$=14.3104). The quarterly distribution of 10-cm size classes shows a

Table 5.3. Summary of Kruskal-Wallis rank sum tests for comparing total lengths between quarters and years for three shark species. Table includes degrees of freedom (d.f.), χ^2 statistics, and associated *p*-value.

Species	Factor	d.f.	χ^2	*p*-value
Carcharinus acronotus	Quarter	3	4.6007	0.2035
	Year	7	8.1028	0.3236
Ginglymostoma cirratum	Quarter	3	1.5272	0.6760
	Year	4	5.1879	0.2686
Galeocerdo cuvier	Quarter	3	9.1307	0.0276
	Year	7	10.919	0.1422

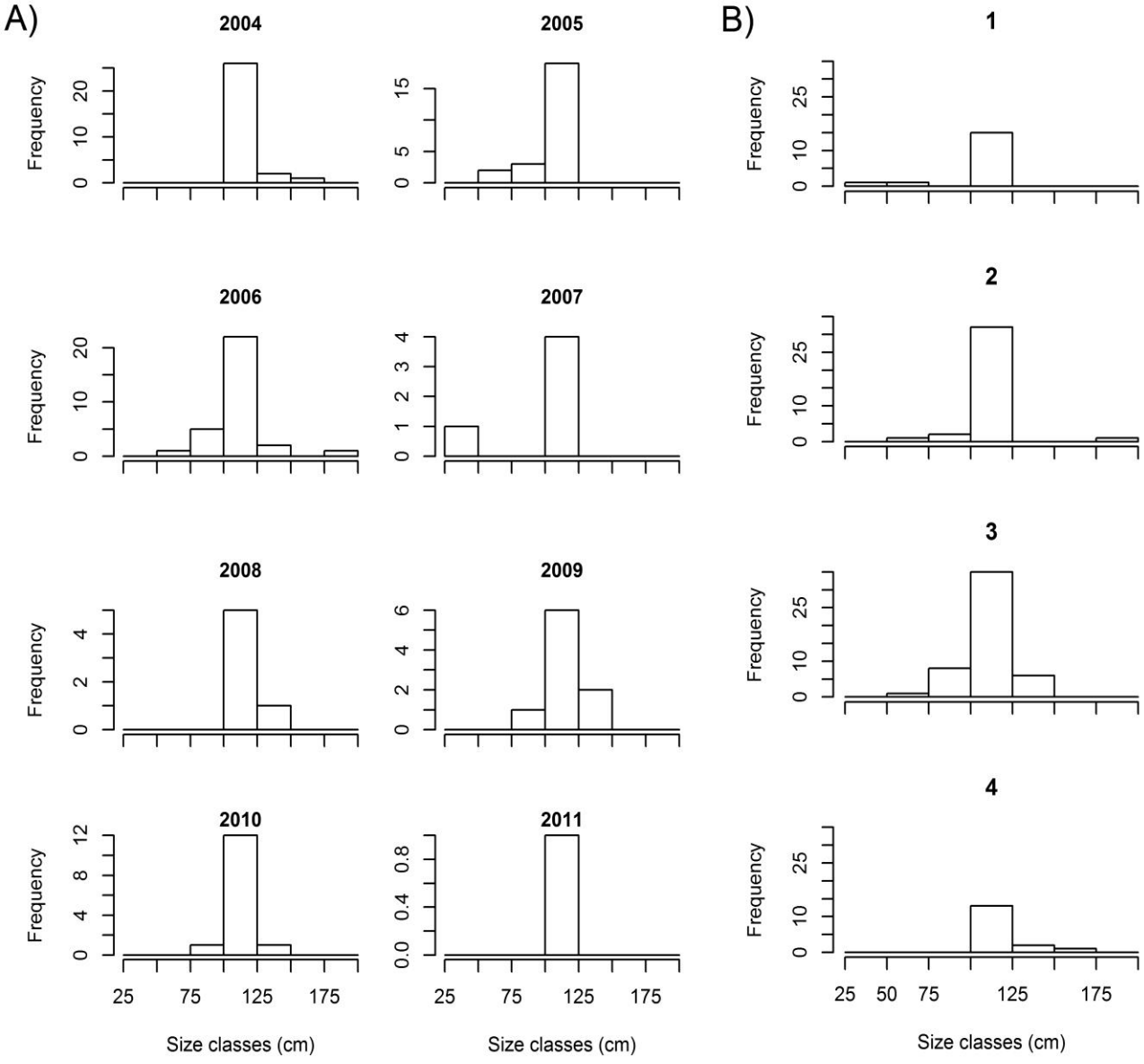


Figure 5.3. Distribution of blacknose shark total lengths in 25-cm size classes across A) years, and B) quarters.

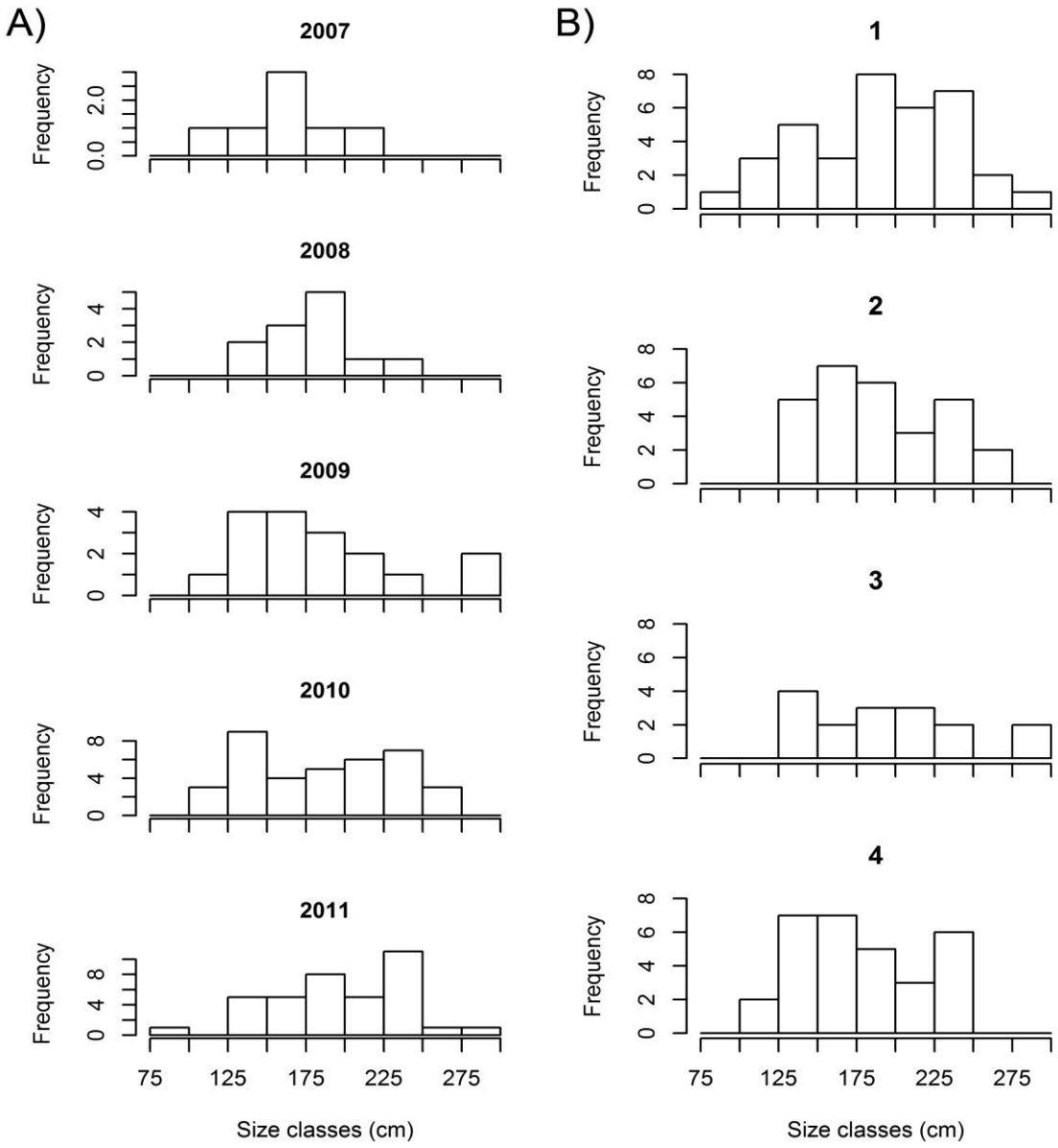


Figure 5.4. Distribution of nurse shark total lengths in 25-cm size classes across A) years, and B) quarters.

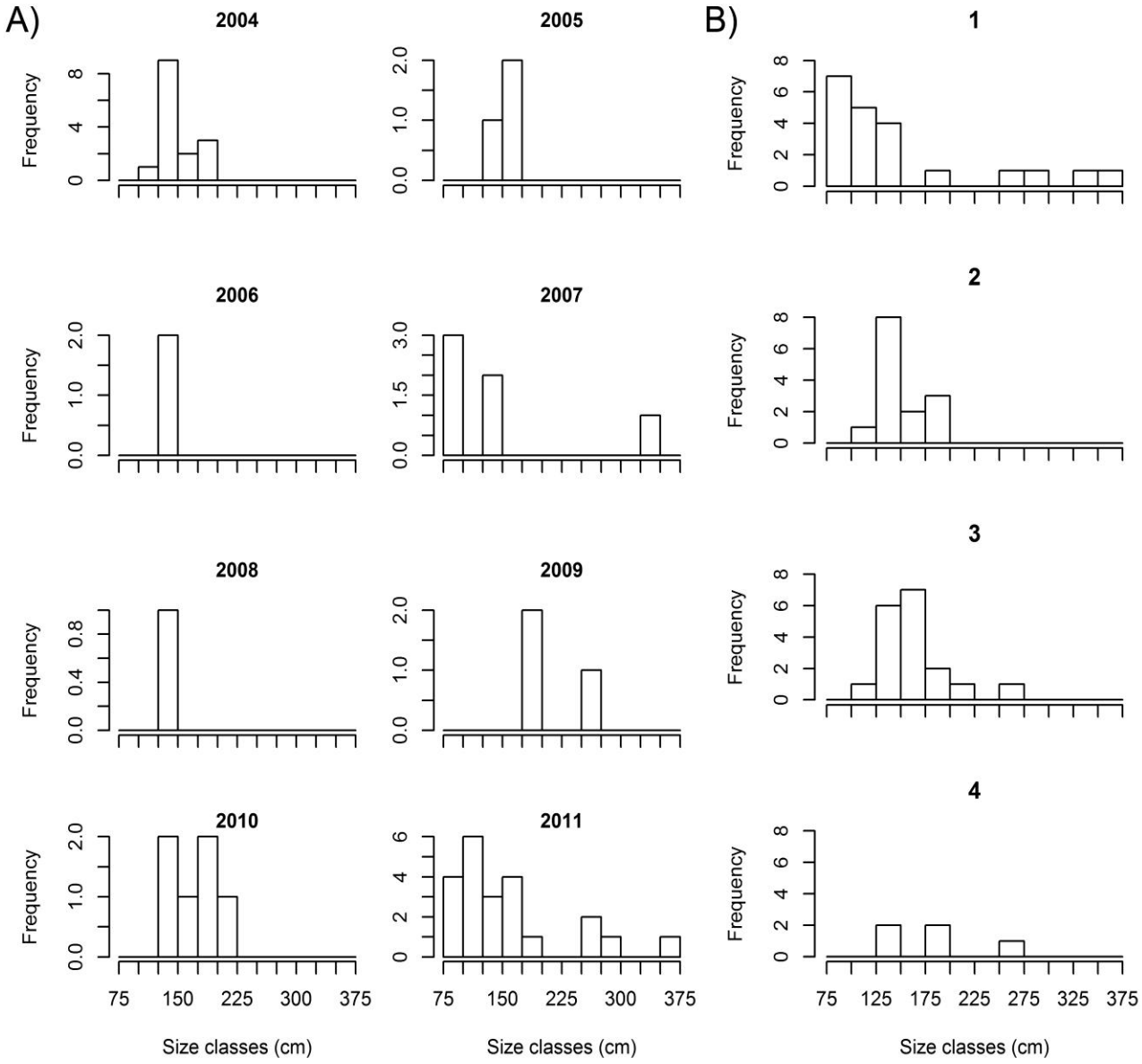


Figure 5.5. Distribution of tiger shark total lengths in 25-cm size classes across A) years, and B) quarters.

distinct modal progression across a relatively narrow range of sizes (Fig. 5.5B). Juveniles < 100 cm TL occurred exclusively between January and March, when 76% of the tiger sharks measured less than 150 cm TL. However, this period also showed highest occurrence of larger, frequently > 250 cm TL, specimens. During the second quarter, sharks measuring 125−150 cm TL were most abundant, whereas the 150−175 cm TL size-class was most frequent during the third quarter (Fig. 5.5B). The period between October and December showed comparably lower tiger shark abundances and a diffuse, amodal distribution of lengths which included just a few medium-sized juveniles.

5.3.2. Sex ratio

The male to female ratio in 122 sexed blacknose sharks equaled 0.77:1 (Table 5.1) and did not deviate significantly from 1:1 (χ^2=2.0984, df =1, p=0.1475). However, males exhibited significantly higher relative frequency in the first quarter and females had higher relative frequencies in the second and third quarters (χ^2=11.1203, df=3, p=0.00131) (Fig. 5.6a). The sex ratio of blacknose sharks was not different across years (χ^2=8.8482, df=7, p=0.2637). The nurse shark sex ratio in 116 sexed individuals was 0.78:1 (Table 5.1), which was not significantly different from 1:1 (χ^2 = 1.6897, df = 1, p = 0.1936). Yet, individuals larger than 220 cm TL were mostly female (Fig. 5.1b) . Seasonality in the sex ratio was detected as males predominated during the first quarter and females predominated during the second and third quarters (Fig. 5.6b), with significant differences between quarters being detected (χ^2 = 18.1207, df = 3, p < 0.001). No differences in nurse shark sex ratio between years were found (χ^2 = 4.5667, df = 4, p = 0.3347). Regarding tiger sharks, the sex ratio in 56 sexed individuals equaled 0.69:1 but it was not significantly different from 1:1 (χ^2 = 0.1525, df = 1, p = 0.6961). However, individuals larger than 200 cm TL were mostly female (Fig. 5.1c). No trend was discernible in yearly or quarterly variation in sex ratio (Fig. 5.6c), and no significant differences were found between years (χ^2 = 8.9808, df = 7, p = 0.254) or quarters (χ^2 = 2.1205, df = 3, p = 0.5478).

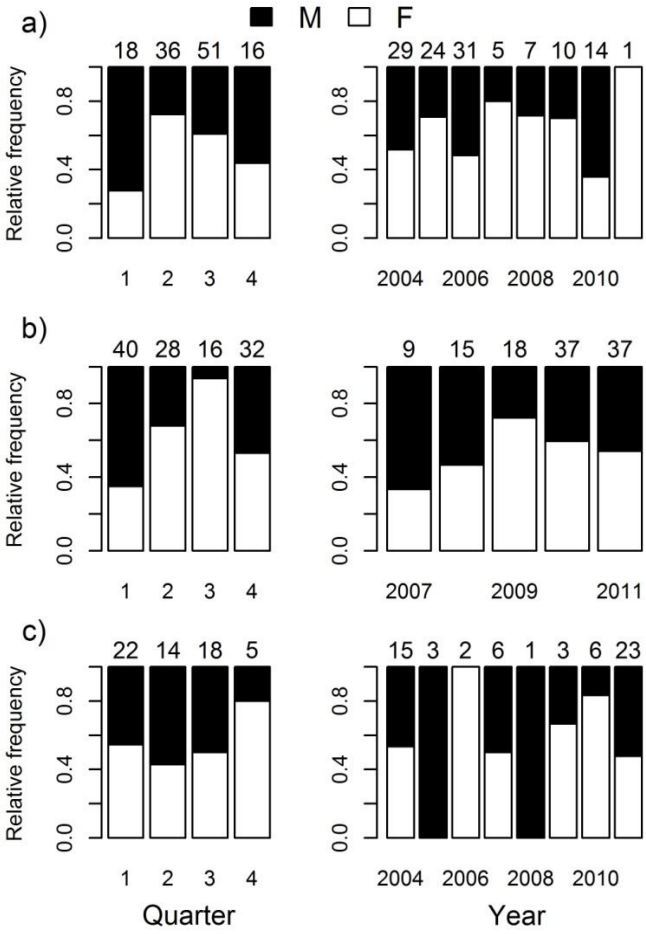


Figure 5.6. Variation of the relative frequency of male (solid bars) and female (blank bars) a) blacknose sharks, b) nurse sharks, and c) tiger sharks, between quarters (left) and years (right). Numbers above bars correspond to the number of sharks caught in the respective period. Note that nurse sharks were not sexed before 2007.

5.3.3. Patterns and dynamics in abundance

After discarding inadequate longline data due to different fishing methodologies (see section 5.2) and aggregating fishing sets by fishing cruise, a total of 518 samples equally distributed between two fishing sites, Boa Viagem/Piedade (BV) and Paiva (PA), plus 38 samples concerning the middle continental shelf (CS) were considered for abundance analysis. The amount of fishing sets with no catch was considerably high for all species. Positive catch equaled 9% for blacknose sharks, 16% for nurse sharks, 6% for tiger sharks, and 5% for stingrays. Single models with only one predictor variable were tested for all variables and for each species with a GAM and a ZIGAM, and the approximated logarithmic marginal likelihoods, *logE*, were compared. Altogether, ZIGAM always exhibited higher *logE*'s than GAM (Table SUP.5.1), thus confirming zero-inflation in data distribution. Further

comparisons between ZIGAM and COZIGAM revealed that ZIGAM exhibited higher *logE*'s for virtually all variables (Table SUP.5.1), thus the non-constrained version of the zero-inflated model was chosen to model elasmobranch abundance off Recife.

Although time-consuming, the iterative procedure for assessing the optimal number of dimensions for each penalized smoothing spline basis allowed for a better control of the parameters involved in regression splining. Inclusively, the iteration evidenced that some solutions for the number of dimensions frequently did not allow the fitting algorithm to converge and successfully maximize the penalized log-likelihood function, resulting in failure of the regression procedure. These results are however not included in this document as they would require an exhaustive amount of space.

Correlation analyses between environmental variables detected significant correlations between covariate *Visib* and covariates *Temp*, *WindSpe*, and *WindDir*, and between covariate *Pluvio* and covariate *WindDir* (Table SUP.5.2). As such, these variables were not included simultaneously in the same multivariate model. No problematic correlations involving nominal variables from the spatiotemporal model were detected. For clarity sake, the modelling results will be sectioned by species.

5.3.3.1. The blacknose shark, *Carcharhinus acronotus*

The *SPT1* model evidenced significant variations in blacknose shark relative abundance, which decreased considerably throughout the survey span, although the year 2009 hampered an otherwise monotonous depletion (Fig. 5.7a). The negative effect of the year 2005 could be misleading because only data between September and December were considered (see chapter 4), and the abundance of blacknose sharks exhibited a clear seasonality, being higher between January and May and lower from June onwards (Fig. 5.7b). However, if the interaction between *Year* and *Month* in *STP2* model is considered, higher abundances of blacknose sharks spanning from September through May are evidenced during the first years of surveying, but from 2008 onwards the period between September and December showed an increasingly negative effect on abundance, with the same tendency being verified for the

period between January and May although with milder effects (Fig. 5.7c). Both predictors *Year* and *Month*, as well as the interaction between the two terms, were significantly correlated with blacknose shark catch (Table 5.4). Regarding spatial distribution, the catch rate was highest in the middle continental shelf (CS) and lowest in PA (Fig. 5.7d). BV showed significantly higher catch rates than PA ($Z = -2.141$; $p = 0.0323$) but no differences were found between BV and CS ($Z = -1.517$; $p = 0.1294$). Overall, *SPT1* model seems to fit the data better than *SPT2* because it presented higher adjusted coefficient of determination, R^2_{adj}, and it explained a higher percentage of null deviance (Table 5.4).

Table 5.4. Summary of spatiotemporal (*SPT*) mutivariate and univariate modelling of the abundance of blacknose, nurse, and tiger sharks and stingrays off Recife with zero-inflated, generalized additive models (ZIGAM). *SPT1* models approach the additive effects of *Year* and *Month* with independent smooth functions, whereas *SPT2* models approach the interacting effects of *Year* and *Month* with the same smooth function. Included are the amount of efficient degrees of freedom (edf) and reference degrees of freedom (Ref.df), the χ^2-statistics value (χ^2), the *p*-value, the adjusted coefficient of determination ($R^2_{adj.}$) and the percentage of null deviance explained by the model (Dev.exp.).

Species	Model	Predictor	edf	Ref.df	χ^2	*p*-value	$R^2_{adj.}$	Dev.exp.
C. acronotus								
	SPT1						0.558	40.3%
		Year	4.519	4.887	25.82	<0.001		
		Month	1.888	1.987	44.74	<0.001		
	SPT2		5.874	5.994	81.84	<0.001	0.464	33.4%
G. cirratum								
	SPT1						0.233	13.7%
		Year	1.748	2.113	16.11	<0.001		
		Month	5.654	6.821	13.74	0.0512		
	SPT2		5.734	5.973	25.01	<0.001	0.236	12.1%
G.cuvier								
	SPT1						0.415	38.5%
		Year	1.951	1.996	32.55	<0.001		
		Month	6.320	7.607	22.54	0.0031		
	SPT2		10.46	10.92	61.04	<0.001	0.544	47.5%
Dasyatis spp.								
	SPT1						0.358	29.1%
		Year	1.000	1.000	22.55	<0.001		
		Month	2.851	2.983	7.889	0.0477		
	SPT2		3.360	4.230	31.30	<0.001	0.378	31.9%

Table 5.5. Summary of environmental (*ENV*) mutivariate and univariate modelling of the abundance of blacknose, nurse, and tiger sharks and stingrays off Recife with zero-inflated, generalized additive models (ZIGAM). Included are the species names, the final *ENV* models assessed by forward selection, the predictor variables composing the *ENV* model or the most significant univariate models, the amount of efficient degrees of freedom (edf) and reference degrees of freedom (Ref.df), the χ^2-statistics value (χ^2), the *p*-value, the adjusted coefficient of determination ($R^2_{adj.}$) and the percentage of null deviance explained by the model (Dev.exp.).

Species	Model	Predictor	edf	Ref.df	χ^2	*p*-value	$R^2_{adj.}$	Dev.exp.
C. acronotus								
	Temp + WindDir						0.478	44.6%
		Temp	10.66	12.15	36.71	<0.001		
		WindDir	2.682	3.43	18.89	<0.001		
	Univariate							
		LunDay	10.32	12.35	23.24	0.0299	0.716	31.3%
G. cirratum								
	Visib	*Visib*	2.428	2.97	16.46	<0.001	0.269	13.8%
	Univariate							
		WindDir	4.792	4.98	21.04	<0.001	0.277	10.3%
		Temp	3.568	4.23	16.87	0.0030	0.272	8.86%
G.cuvier								
	TidalAmp + Pluvio						0.215	28.5%
		TidalAmp	3.856	3.99	20.85	<0.001		
		Pluvio	3.153	3.90	10.86	0.0261		
	Univariate							
		LunDay	1.574	1.91	14.76	<0.001	0.129	14.3%
		WindDir	1.716	1.92	5.991	0.0462	0.255	23.1%
Dasyatis spp.								
	TidalAmp + Temp						0.362	32.6%
		TidalAmp	2.621	3.25	18.68	<0.001		
		Temp	2.093	2.63	12.19	0.0047		
	Univariate							
		Pluvio	2.928	3.44	10.05	0.0262	0.086	6.56%

The *ENV* modeling resulted in two candidate variables being selected to predict blacknose shark abundance, given that the addition of any other term did not increase the penalized logarithmic likelihood of the model. Therefore, the abundance of blaknose sharks were best predicted by the additive effects of sea surface temperature and wind direction, with the resulting model showing a R^2_{adj} value of 0.478 and explaining 44.6% of the data null

deviance (Table 5.5). Blacknose shark abundance was positively affected by temperatures lower than 27.5ºC, whislt higher temperatures until 29.5ºC had a negative effect on abundance (Fig. 5.8). A strong positive effect was visible in temperatures higher than 29.5ºC, but this interpretation requires caution due to small sampling size at extreme temperatures. On the other hand, blacknose sharks were most abundant when wind direction was between 0−110º, corresponding to northern and eastern winds, while wind directions greater than 130º exerted a negative effect on their abundance (Fig. 5.8). Although not included in the model by the variable selection process, the lunar day showed a significant effect (p = 0.0299) on blacknose shark abundance (Table 5.5), with higher abundances being generally observed during the week following the new moon (Fig. 5.9).

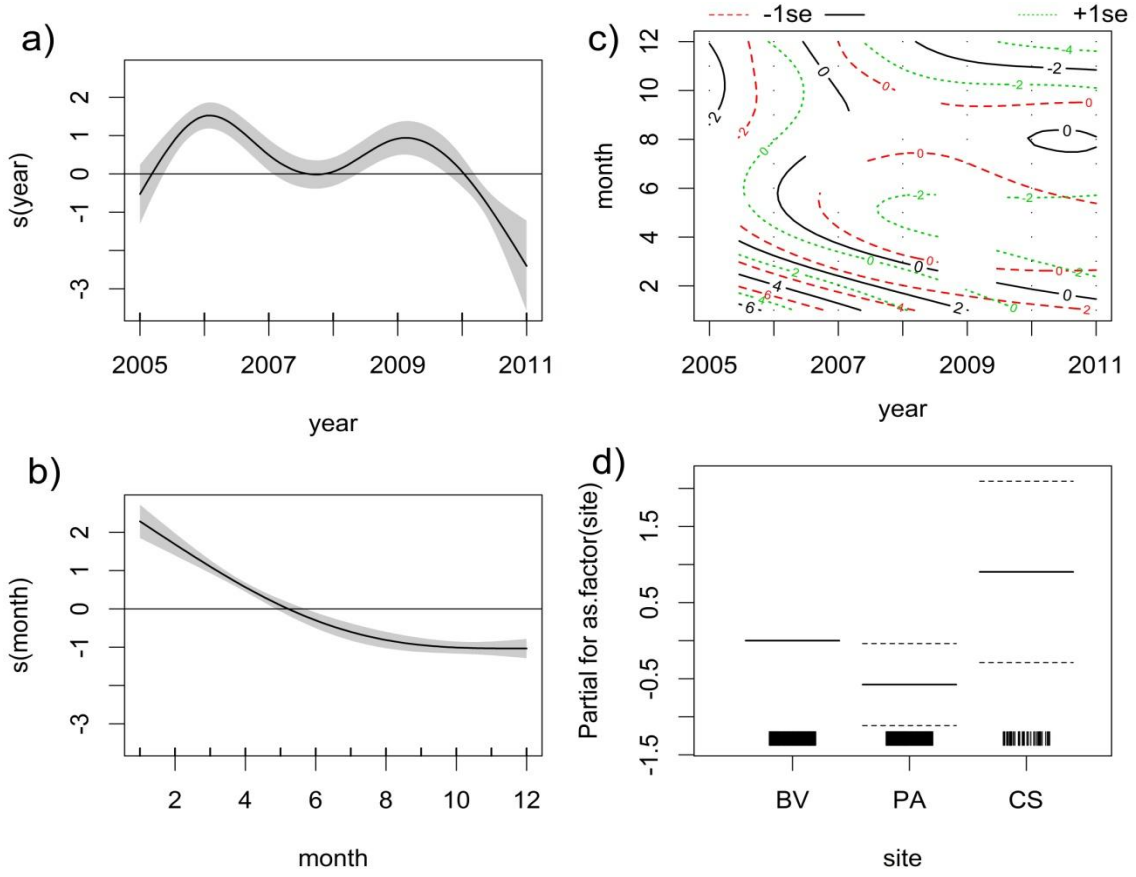


Figure 5.7. Spatiotemporal modeling of blacknose shark, *Carcharhinus acronotus*, abundance off Recife, comprising the *STP1* model of the additive effects of a) year and b) month fitted with independent smooth funcions, c) the *STP2* model of the interacting effects of year and month fitted with the same smooth function, and d) the spatial effects of the three sampling sites, namely Boa Viagem (BV) and Paiva (PA), both nearshore, and the middle continental shelf (CS). The solid, horizontal lines in a), b) and c) depict null effects, while the solid and dashed horizontal lines in d) depict effect coeficients and standard errors, respectively.

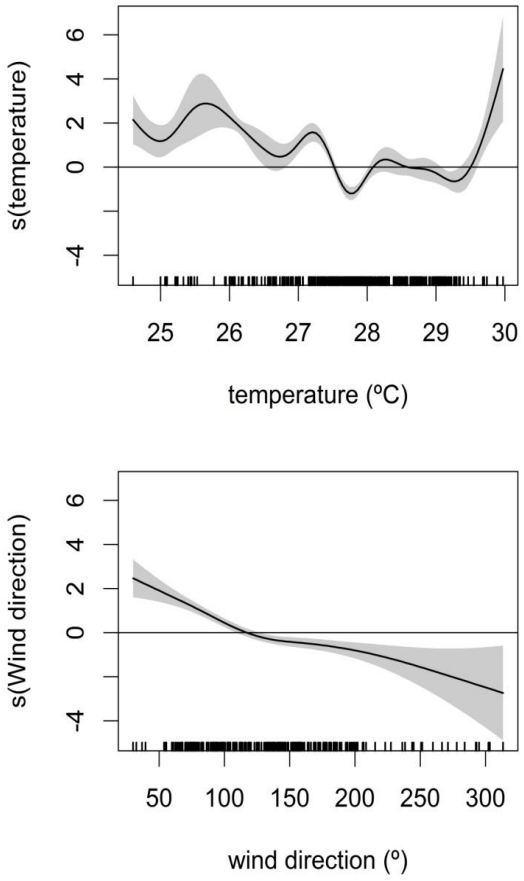


Figure 5.8. Environmental modeling of blacknose shark, *Carcharhinus acronotus*, abundance off Recife, depicting the smooth functions that measure the effects of sea surface temperature (top) and wind direction (bottom) on catch rates. The horizontal lines depict the null effect.

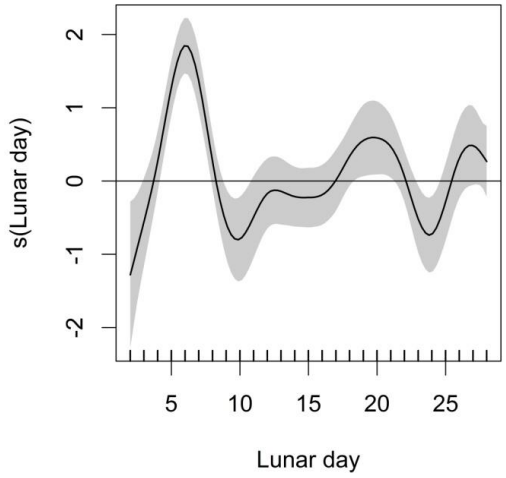


Figure 5.9. Univariate modeling of blacknose shark, *Carcharhinus acronotus*, abundance off Recife, depicting the smooth function that measure the effect of lunar day on catch rates. The horizontal line depicts the null effect.

5.3.3.2. The nurse shark, *Ginglymostoma cirratum*

The *SPT1* model revealed that nurse shark yearly abundance increased monotonically from 2005 through 2011, with *Year* significantly inducing a strong, negative effect on nurse shark abundance at the beginning of the time series, and a positive effect posteriorly to 2008 (Fig. 5.10a). Seasonality in abundance was not much clear, but *Month* produced positive effects between February and April and around October, whereas December showed a strong, negative effect on nurse shark abundance (Fig. 5.10b). The interaction of *Year* and *Month* showed that nurse sharks were most absent between October and May in the beginning of the survey and that the increase in abundance reinforced this seasonal pattern, with highest abundances being observed between June and October during 2008 and 2009 (Fig. 5.10c). However, after 2009 such seasonality shifted to earlier months, with the period between January and May exhibiting highest nurse shark abundance. The predictor *Year* and the interaction between *Year* and *Month* produced significant effects on nurse shark abundance, but no significant effect was detected for the predictor *Month* (Table 5.4). Regarding spatial distribution, BV showed significantly higher numbers of nurse sharks compared to PA ($Z = -2.377$; $p = 0.0174$), while no differences in abundance were observed between BV and CS ($Z = -0.061$; $p = 0.9517$) (Fig. 5.10.d). The data-fitting performance of both *SPT1* and *SPT2* models was fairly similar, but the resulting R^2_{adj} values were low, as were the amount of null deviance explained by the models (Table 5.4).

The *ENV* modeling resulted in only one candidate variable being selected to predict nurse shark abundance, more precisely *Visib*, but this model yielded a low R^2_{adj} value and explained a little amount of the data null deviance (Table 5.5). Nevertheless, low (< 6 m) visibility had a positive effect on nurse shark abundance, whereas higher water visibility had an increasingly negative effect (Fig. 5.11). On the other hand, univariate modeling showed that *WindDir* and *Temp* also exhibited significant effects on nurse shark abundance when considered independently (Table 5.5). Generally, wind blowing from northeastern to southeastern quadrants, between 0−160º, had a positive effect on catch rates, whereas wind blowing from southern and western quadrants had negative effects (Fig. 5.12). Regarding sea surface temperature, higher nurse shark abundances were verified at temperatures lower than

27ºC, while higher temperatures showed lower abundances (Fig. 5.13). However, the resulting R^2_{adj} values and amount of null deviance explained were globally low (Table 5.5).

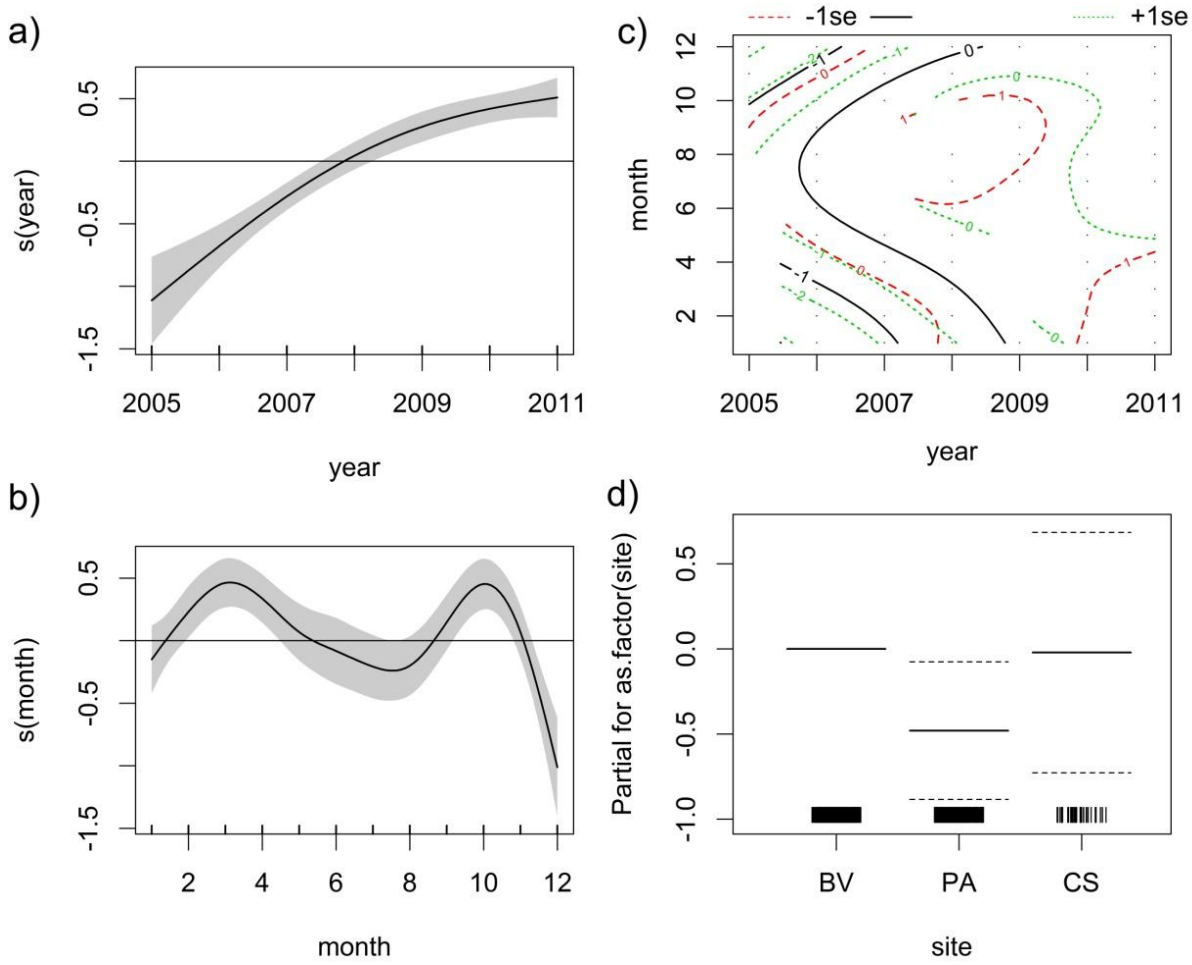


Figure 5.10. Spatiotemporal modeling of nurse shark, *Ginglymostoma cirratum*, abundance off Recife, comprising the *STP1* model of the additive effects of a) year and b) month fitted with independent smooth funcions, c) the *STP2* model of the interacting effects of year and month fitted with the same smooth function, and d) the spatial effects of the three sampling sites, namely Boa Viagem (BV) and Paiva (PA), both nearshore, and the middle continental shelf (CS). The solid, horizontal lines in a), b) and c) depict null effects, while the solid and dashed horizontal lines in d) depict effect coeficients and standard errors, respectively.

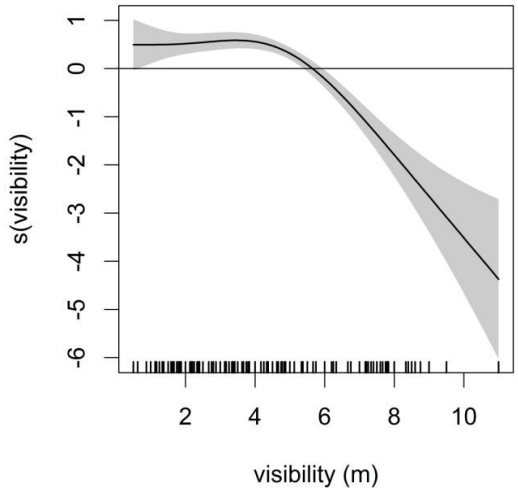


Figure 5.11. Environmental modeling of nurse shark, *Ginglymostoma cirratum*, abundance off Recife, depicting the smooth function that measure the effect of visibility on catch rates. The horizontal line depicts the null effect.

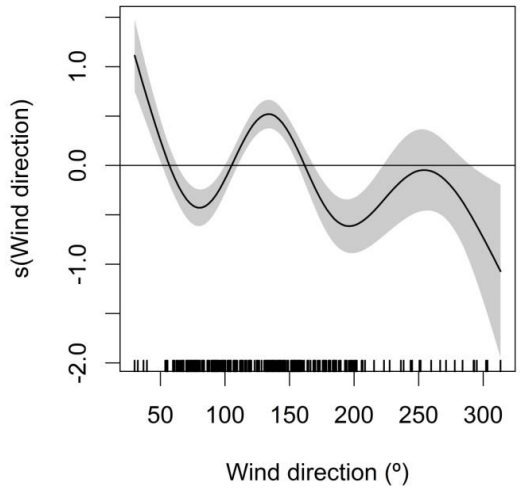


Figure 5.12. Univariate modeling of nurse shark, *Ginglymostoma cirratum*, abundance off Recife, depicting the smooth function that measure the effect of wind direction on catch rates. The horizontal line depicts the null effect.

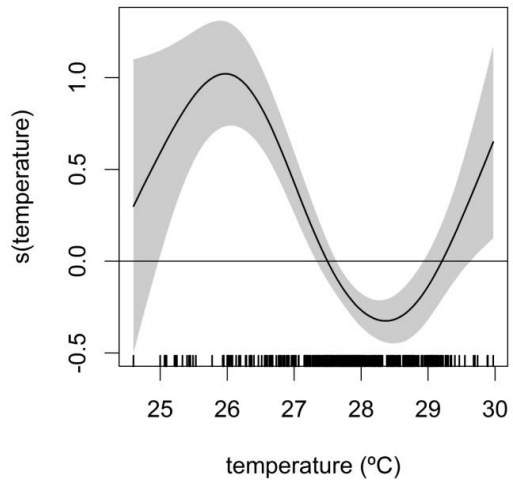


Figure 5.13. Univariate modeling of nurse shark, *Ginglymostoma cirratum*, abundance off Recife, depicting the smooth function that measure the effect of sea surface temperature on catch rates. The horizontal line depicts the null effect.

5.3.3.3. The tiger shark, *Galeocerdo cuvier*

The *STP1* model of tiger shark abundance showed a strong decrease in yearly catches from 2005 through 2009, with *Year* producing positive effects only before 2007 (Fig. 5.14a). Around 2009 this tendency inverted and tiger shark abundance increased through 2011. Regarding seasonal variation, the effect of *Month* on tiger shark abundance followed a sinusoidal curve, with positive effects spanning from January through March and from June through September, and negative effects occurring mostly during April, October and November (Fig. 5.14b). However, the interaction of both temporal variables in the *STP2* model evidenced that seasonal peaks of abundance occurred between April and August and between October and December during the first three years of surveying, but in the subsequent years a great absence of tiger sharks was verified, particularly between September and May (Fig. 5.14c). This period of absence was temporally well defined, and is depicted as a roughly elliptical array of negative isolines centered at about February 2008 and spanning from 2006 through 2010, although negative effects were still present in the last quarter of 2011. The orientation of the ellipse also indicates a delay of the negative effects along the years, from January towards May, whereas the last quarter showed a similar tendency but later in time, starting around 2008 (Fig. 5.14c). On the other hand, the period between June and August always showed a positive effect on tiger shark abundance. Both predictors *Year* and *Month*, and the interaction between the two terms, produced significant effects on tiger shark abundance (Table 5.4). Regarding spatial distribution, tiger sharks were most abundant in CS and least abundant in PA (Fig. 5.14d). Significant differences were found between BV and CS ($Z = 3.499$; $p < 0.001$), but not between BV and PA ($Z = -0.378$; $p = 0.7057$). Overall, the *SPT2* model fitted the data better than *SPT1* due to greater R^2_{adj} and percentage of null deviance explained (Table 5.4).

The *ENV* modelling of tiger shark abundance achieved highest penalized log-likelihood with two candidate variables, more precisely *TidAmp* and *Pluvio*. Positive effects on tiger shark abundance were verified when tidal amplitude was low, < 1.4 m, or high, between 2−2.4 m, and pluviosity was low, < 50 mm, whereas negative effects were observed at intermediate, between 1.4−1.9 m, tidal amplitudes, and high, between ~60−300 mm, pluviosity (Fig. 5.15). It should be noted that the tendencies observed at the upper limits of the

variable ranges could be misleading due to lower amounts of sampling (Fig. 5.15). Despite statistical significance showed by both variables, the resulting R^2_{adj} value was low and only 28.5% of the data null deviance was explained by this model (Table 5.5). Additionally, independent, univariate modelling of tiger shark abundance showed that *LunDay* and *WindDir* had significant effects which were however superseded by the effect of other variables, thus being ignored during model selection. Tiger sharks were more abundant during the period until ten days after the new moon, whereas the full moon and last quarter showed a negative effect on tiger shark abundance (Fig. 5.16). Regarding wind direction, tiger sharks were most absent during northern and eastern winds, between 0−120º, while winds blowing from southern quadrants, especially between 130−220º, had a positive effect on tiger shark abundance (Fig. 5.17). Nonetheless, the value of R^2_{adj} and the amount of explained null deviance were yet low for both univariate models (Table 5.5).

5.3.3.4. The stingray, *Dasyatis* spp.

The *SPT1* model of stingray abundance revealed a significant decrease from 2005 through 2011, with negative effects being visible since 2009 (Fig. 5.18a). However, interpreting this result requires caution because the number of efficient degrees of freedom (edf) were reduced to 1 by the end of the algorithm iteration process (Table 5.4), thus indicating that the smoothing function was not able to effectively fit a spline to the data. Seasonal fluctuations in stingray abundance were observed, with significantly more individuals being caught between April and June and between November and December, whereas the period between January and February showed a negative effect on stingray abundance (Fig. 5.18b). The interaction between terms in the *SPT2* model showed that stingray abundance decreased uniformly throughout the survey span, but in the last semester this effect was visible about 3 years earlier than in the first semester (Fig. 5.18c). Both predictors *Year* and *Month*, and the interaction between terms, produced significant effects on stingray abundance (Table 5.4). Regarding spatial distribution, BV showed slightly higher abundances of stingrays than PA, while CS showed the lowest abundance. However, no statistical significance was detected neither between BV and PA ($Z = -1.161$, $p = 0.246$) or between BV and CS ($Z = -0.569$; $p = 0.569$). The data-fitting performance of *SPT1* and *SPT2*

models was fairly similar, but the resulting R^2_{adj} values and percentage of explained null deviance were relatively low (Table 5.4).

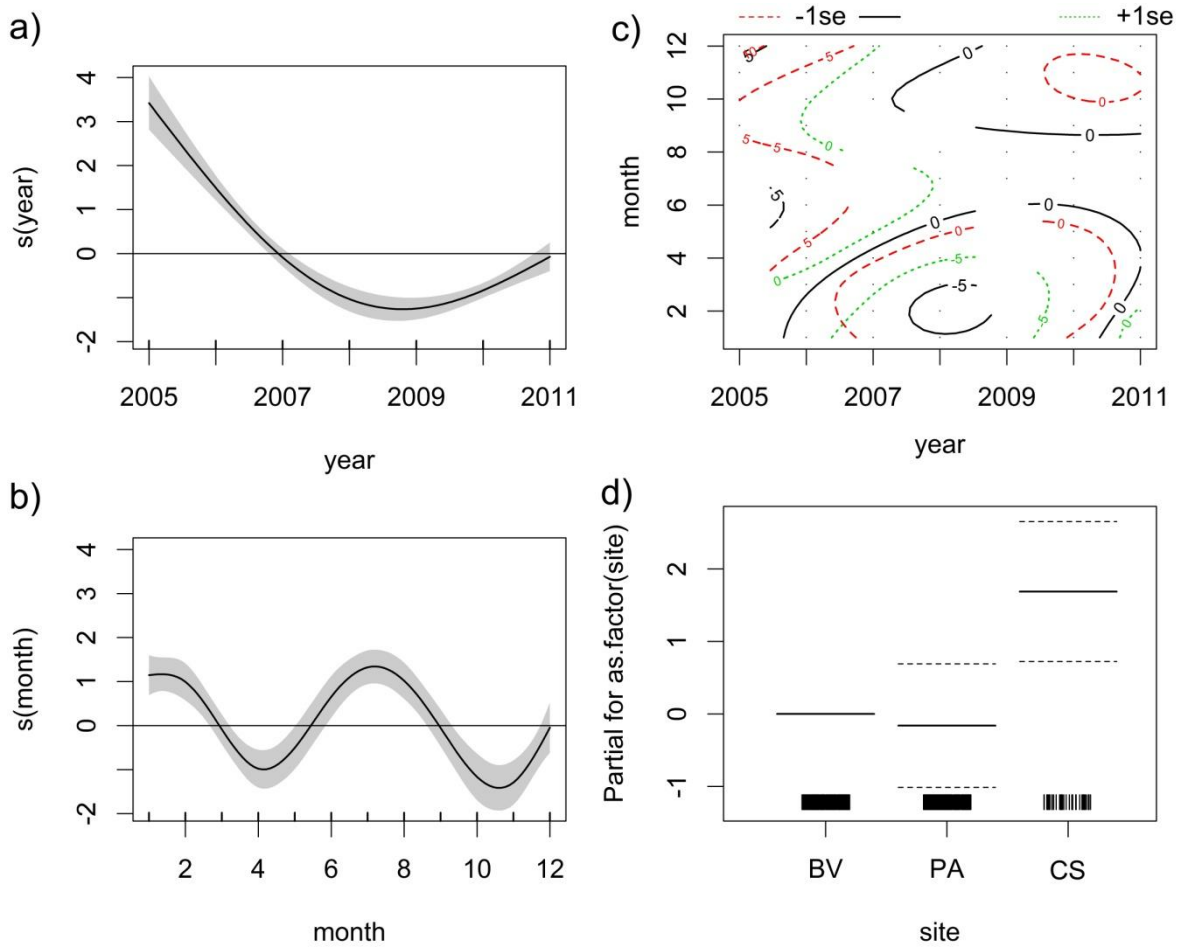


Figure 5.14. Spatiotemporal modeling of tiger shark, *Galeocerdo cuvier*, abundance off Recife, comprising the *STP1* model of the additive effects of a) year and b) month fitted with independent smooth funcions, c) the *STP2* model of the interacting effects of year and month fitted with the same smooth function, and d) the spatial effects of the three sampling sites, namely Boa Viagem (BV) and Paiva (PA), both nearshore, and the middle continental shelf (CS). The solid, horizontal lines in a), b) and c) depict null effects, while the solid and dashed horizontal lines in d) depict effect coeficients and standard errors, respectively.

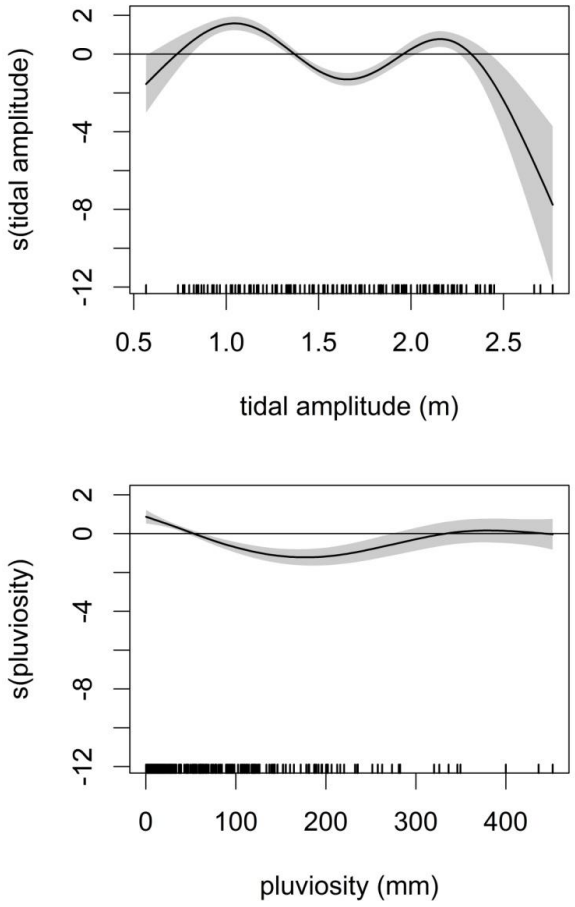


Figure 5.15. Environmental modeling of tiger shark, *Galeocerdo cuvier*, abundance off Recife, depicting the smooth functions that measure the effects of tidal amplitude (top) and pluviosity (bottom) on catch rates. The horizontal lines depict the null effect.

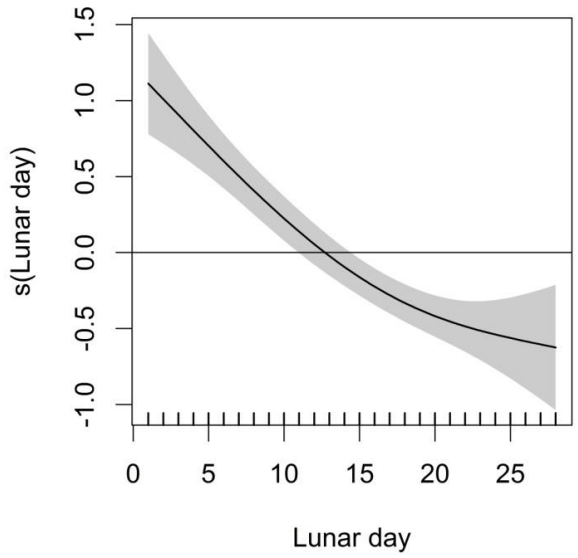


Figure 5.16. Univariate modeling of tiger shark, *Galeocerdo cuvier*, abundance off Recife, depicting the smooth function that measure the effect of lunar day on catch rates. The horizontal line depicts the null effect.

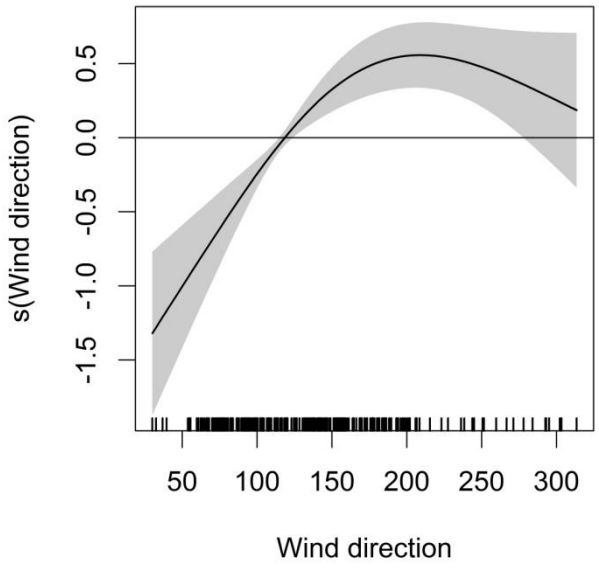


Figure 5.17. Univariate modeling of tiger shark, *Galeocerdo cuvier*, abundance off Recife, depicting the smooth function that measure the effect of wind direction on catch rates. The horizontal line depicts the null effect.

The *ENV* modelling of stingray abundance included two candidate variables, *TidalAmp* and *Temp*, in the final model. Tidal amplitudes lower than 1.5 m generally showed a positive effect on stingray abundance, while abundances were lower at tidal amplitudes higher than 1.6 m (Fig. 5.19). Regarding sea surface temperature, abundances were higher when temperature was lower than ~28ºC, with temperatures > 28ºC producing negative effects on stingray catch rates (Fig. 5.19). The stingray *ENV* model provided a moderate R^2_{adj} value, equalling 0.36, with about one third of the data null deviance being explained by this model (Table 5.5). Further univariate modeling resulted in *Pluvio* exhibiting significant effects on stingray abundance (Table 5.5),with higher abundances being associated with higher, between 130−350 mm, pluviosity, and lower abundances occurring when pluviosity was < 100 mm (Fig. 5.20). However, the resulting R^2_{adj} value and the percentage of explained null deviance were extremely low (Table 5.4).

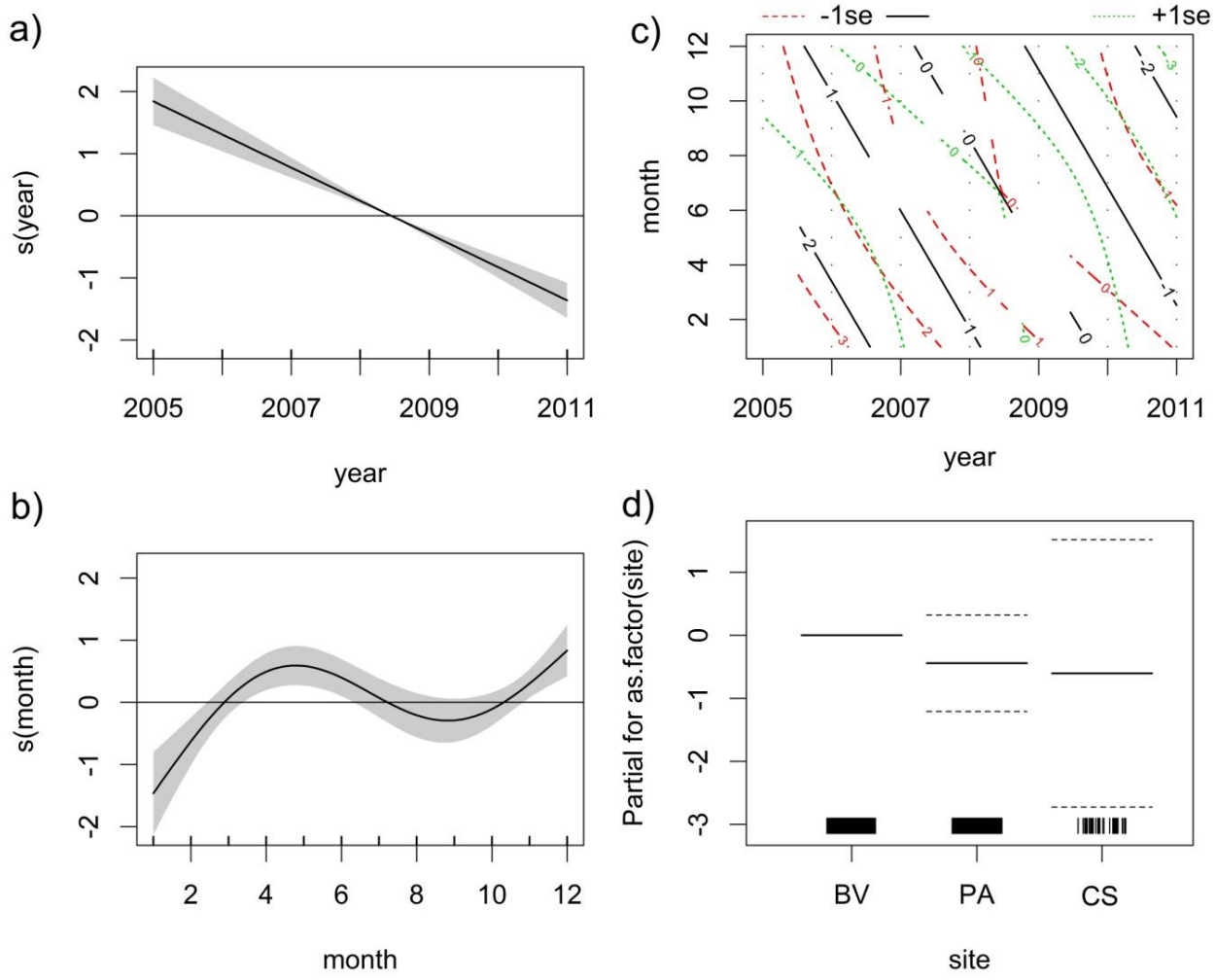


Figure 5.18. Spatiotemporal modeling of stingray, *Dasyatis* spp., abundance off Recife, comprising the *STP1* model of the additive effects of a) year and b) month fitted with independent smooth funcions, c) the *STP2* model of the interacting effects of year and month fitted with the same smooth function, and d) the spatial effects of the three sampling sites, namely Boa Viagem (BV) and Paiva (PA), both nearshore, and the middle continental shelf (CS). The solid, horizontal lines in a), b) and c) depict null effects, while the solid and dashed horizontal lines in d) depict effect coeficients and standard errors, respectively.

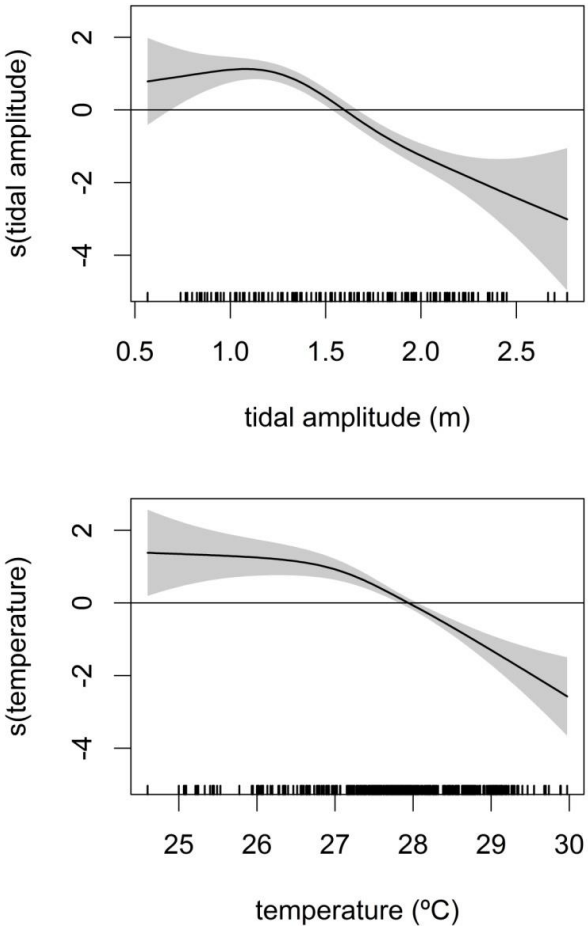


Figure 5.19. Environmental modeling of stingray, *Dasyatis* spp., abundance off Recife, depicting the smooth functions that measure the effects of tidal amplitude (top) and sea surface temperature (bottom) on catch rates. The horizontal lines depict the null effect.

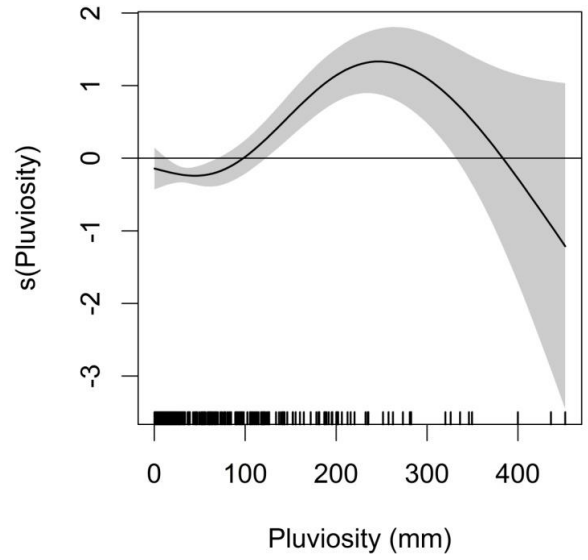


Figure 5.20. Univariate modeling of stingray, *Dasyatis* spp., abundance off Recife, depicting the smooth function that measure the effect of pluviosity on catch rates. The horizontal line depicts the null effect.

5.4. Discussion

The ecological significance of elasmobranchs in nearshore waters warrants the sustainable management of their populations, which can only be achieved with adequate knowledge on their bioecology. Likewise, such knowledge is essential to address serious socioeconomic concerns deriving from situations on which shark attacks on humans persistently occur within the same region. Perceiving the structure of the elasmobranch assemblage off Recife and the species-specific factors which regulate their spatiotemporal distribution will thus benefit species conservation and contribute to a better understanding of the circumstances behind the shark attack outbreak in this region.

The elasmobranch assemblage surveyed in this study comprised a considerable diversity of carcharhinid, ginglymostomatid and sphyrnid sharks which are known to occur in tropical region (Bigelow and Schroeder, 1948; Compagno, 1984; Last and Stevens, 2009). It is important to identify the diversity of elasmobranchs in coastal environments because habitat use and functioning may vary for different species or life-stages (DiBattista et al., 2008; Feldheim et al., 2004; Grubbs et al., 2007; Hueter et al., 2005; Keeney et al., 2005; Kinney and Simpfendorfer, 2009; Mucientes et al., 2009; Yokota and Lessa, 2006). The most abundant sharks off Recife were the nurse, *Ginglymostoma cirratum*, the blacknose, *Carcharhinus acronotus*, and the tiger, *Galeocerdo cuvier*. Dasyatid stingrays are also common inhabitants of coastal, tropical waters (Bigelow and Schroeder, 1953) and were frequently caught in the present survey, being mostly represented by the Southern stingray, *Dasyatis americana*. However, other dasyatids such as *D. marianae* and *D. centroura* have been punctually identified in the catch composition and should compose a small portion of this group. Uncertainties regarding the accuracy in stingray species identification during the eight years of sampling resulted in this *taxon* being analyzed at genus, rather than species, level. Nurse sharks and stingrays are typical bottom-dwellers, exhibiting a sluggish behaviour and spending most time in association with the benthos (Bigelow and Schroeder, 1953; Compagno, 1984). In contrast, blacknose sharks rely exclusively on RAM ventilation to breathe (Carlson and Parsons, 2001) and thus are most associated to the water column, as is the case of tiger sharks. Tiger sharks are circumglobal at tropical latitudes and nurse sharks occur in the tropical

Atlantic and eastern Pacific oceans, whereas blacknose sharks and the stingrays caught occur exclusively in the tropical western Atlantic ocean (Compagno, 1984; Robins and Ray, 1986).

The blacknose shark size distribution in the present survey spanned from about the size at birth (38−50 cm TL) through near the maximum length of possibly 200 cm TL (Compagno, 1984). Castro (1983) reported a maximum size of only 140 cm TL for this species, suggesting that blacknose sharks from the South Atlantic grow larger than conspecifics from the North Atlantic. The prevalence of individuals of both sexes measuring 100−130 cm TL was evident. In this region, blacknose sharks mature at about 100 cm TL (Hazin et al., 2002), thus most sharks were mature. Juveniles smaller than 90 cm TL were scarce, suggesting that either fishing gear selectivity or segregation by size could be occurring. Hook selectivity may have not had a deterministic effect on blacknose shark size-specific catchability because catch composition comprised a few small specimens. However, this region bears a small artisanal fleet dedicated to nearshore gillnetting which frequently captures small juvenile blacknose sharks (Barreto et al., 2011), hence younger life stages are definitely present in the study area. In agreement, conspecifics from the North Atlantic use nearshore waters during their whole life-cycle (Castro, 1993; Schwartz, 1984; Ulrich et al., 2007), but juveniles seem to use waters < 10 m in depth (Compagno, 1984; Schwartz, 1984). Some spatial segregation by size could also occur off Recife, eventually resulting in the distribution of smaller sharks not overlapping with the fishing area. Moreover, a seemingly progression in blacknose shark size distribution throughout the year was observed, which could be indicative of a certain amount of temporal segregation by size, as blacknose sharks grow slowly (Barreto et al., 2011; Driggers et al., 2004) and thus the observed progression in shark length should not reflect growth. Schwartz (1984) reports males to dominate catches during the first semester and females being more common from August to early fall, which differs slightly from the pattern verified in the present study, possibly due to study areas being located at different latitudes and hemispheres.

The nurse shark size-structure off Recife was wide-ranging, with roughly uniform prevalence of individuals measuring between 120−260 cm TL. Nurse sharks are born with 27−30 cm TL (Rosa et al., 2006) but the smallest nurse shark caught measured 92 cm TL, thus younger juveniles were absent from the survey area. This could be related to either fishing

gear selectivity, e.g. hooks too large for being taken by smaller individuals, or spatial segregation of early juveniles, which may reside in other habitats before recruitment into the study area. Castro (2000) reported juveniles 50−120 cm TL inhabiting shallow coral reefs and grass flats in waters 1−3 m deep, but those biocenoses are missing off Recife. The lack of suitable habitat could thus explain the absence of young nurse sharks from the study area. Nurse shark size at first maturity is about 214−227 cm TL for males and females, respectively (Castro, 2000), which implies that most individuals caught were juveniles and that most mature individuals caught were female. Nurse shark abundance and size range increased throughout the survey span, suggesting that the nurse shark population could be expanding. Both larger and smaller individuals were more common by the last years of surveying, when the annual size structure exhibited a somewhat bimodal distribution. No seasonal pattern in nurse shark size distribution was visible except that sharks smaller than 120 cm TL were caught exclusively between October and March. Despite no overall difference in nurse shark sex ratio, a significant seasonal pattern was detected with males being most abundant during the summer months, between October and March, and least abundant between April and September. Indeed, while the monthly catch rate of female nurse sharks fluctuates around steady values along the year, male catch rates drop considerably during winter months (Ferreira et al., 2012), suggesting that male nurse sharks tend to leave the study area between April and September. Such pattern has been approached in an acoustic telemetry study (Ferreira et al., 2012) and will be addressed no further.

Regarding tiger sharks, the size-structure of the population occurring off Recife followed an unimodal distribution with positive skeweness. Individuals of both sexes measuring between 80−200 cm TL and exhibiting frequency mode at 120−140 cm TL comprised the bulk of the tiger shark catch. Tiger shark size at birth lies between 51−90 cm TL (Randall, 1992; Simpfendorfer, 1992), so early juveniles were present in the survey area. On the other hand, larger individuals were infrequently caught and were mostly females. Tiger sharks mature at about 310−320 cm TL (Branstetter, 1987), thus only two adult sharks were caught throughout the survey. Significant temporal trends in tiger shark size were detected only between quarters, with smaller sharks being most abundant during the first trimester and larger sizes being gradually more represented during the second and third trimesters. During the last trimester, tiger shark abundance dropped considerably and the observed trend was no

longer visible. Such result suggests that juvenile tiger sharks use coastal habitats off Recife mostly between January and September, eventually leaving the study area from October onwards. The greater occurrence of large sharks during the first trimester is also noteworthy as it coincides with the period when the smallest sharks were caught. Likewise, juveniles < 100 cm TL and mature sharks were caught in 2007 and 2011 only.

Modeling species relative abundance with longline catch data is not always feasible. The use of catch rates as an index of abundance conventionally assumes that catch rate is proportional to abundance and that catchability does not change over time (Harley et al., 2001). However, long-term longline data is mostly available from commercial fisheries, which raises concerns regarding significant variability in fishing gear, effort, and strategy with probable influence on catchability (Bigelow et al., 2002; Polacheck, 2006; Walters, 2003). Long-term, rigorously standardized, fishery-independent longline surveys conducted at fixed locations should provide optimal CPUE standardization and expectedly reflect species abundance within the surveyed areas, although they will still depend on several unavoidable assumptions (e.g. factors such as prey availability will not influence catchability).

Several approaches are currently available to model catch rate series (e.g. Baum and Blanchard, 2010; Maunder and Punt, 2004; Myers et al., 2007). Due to distinctive large proportions of zero observations in some longline fisheries, zero-inflated distributions seem to provide a more adequate solution to model the abundance of infrequently caught species, particularly within the scope of a shark monitoring program which presumes high sampling intensity in the same fishing area. Yet, despite zero-inflated models have been widely employed in other areas of research (e.g. Agarwal et al., 2002; Hall, 2000; Lambert, 1992), their use in the analysis of fisheries data has been sparse (Arab et al., 2008; Carlson et al., 2009; Minami et al., 2007). In the present study, a recently developed extension of the zero-inflated approach, the constrained generalized additive model (COZIGAM) (Liu and Chan, 2010) was compared with the un-constrained ZIGAM. The COZIGAM incorporates a proportionality constraint between the mean of the regular component and the probability of non-zero-inflation, which reflects the mechanistic nature of the zero-inflation process and promotes estimation efficiency by reducing the number of parameters in the model (Liu and Chan, 2010). However, the bayesian *logE* indicated a better performance of ZIGAM in

modeling the catch rates of the four most abundant *taxa* in this survey, suggesting that the zero-inflated and the non-zero-inflated processes were generally independent. Partially-constrained ZIGAM with relaxed proportionality constraints could further improve the predicitive accuracy of the models estimated because they assume proportionality constraints to some, not all, covariates (Liu and Chan, 2011), but they were recently developed and have not yet been implemented in standard statistical software (Hai Liu, University of Iowa, pers. comm.).

The spatiotemporal modeling of species abundance showed some interesting trends. Blacknose shark annual abundance declined considerably throughout the survey, whereas nurse shark abundance increased. The blacknose shark has been identified as one of the most abundant shark species in this region, and previous surveys reported a catch rate of 0.29 individuals per 100 hooks in a total of 10,072 hooks deployed off Recife between September 1994 and March 1995 (Hazin et al., 2000). In agreement, blacknose sharks were the most abundant species and nurse sharks were less important during the first years of sampling, but this pattern inverted as nurse shark catch rates increased monotonically up to one order of magnitude along the years and blacknose sharks became infrequent in the catch composition (Fig. 4.4). Stingray abundance also decreased in a similar fashion to blacknose sharks. Stock assessments relying on multiple sources of bioecological data are the most robust analyses to determine the status of harvested species (Carlson et al., 2012), but abundance trends can be used as a proxy of species status when adequately approached (Carlson et al., 2009). Blacknose sharks were one of the species in this survey which experienced higher fishing mortality, contrasting with nurse sharks and stingrays which exhibited virtually zero mortality (Table 4.3). Therefore, the impact of this survey on the local population of blacknose sharks should have been considerably greater than that on nurse sharks and stingrays. Although only about 120 blacknose sharks were removed by this 8-year survey, the extremely localized fishing effort could have significantly reduced the number of individuals using the study area. An upublished assessment of the blacknose shark population based on artisanal gillnetting landings across the State of Pernambuco found evidence that it was overexploited, with an estimated reduction rate of 13.6% for every ~8 years (R. Barreto, Universidade Federal Rural de Pernambuco, pers. comm.). Thus, the replenishment of the removed blacknose sharks with immigrants arriving into the study area should be occurring at lowest capacity. The high

fishing mortality along with a presumably low immigration rate of blacknose sharks could have contributed to the expansion of nurse sharks, as they were not affected by the survey. Tag-and-recapture and acoustic telemetry data showed that nurse sharks are residents in this region (Ferreira et al., 2012). Both nurse and blacknose sharks are common, mostly nocturnal, coastal sharks off northeastern Brazil using roughly the same habitats, such as rocky reefs and sand flats (Compagno, 1984). Additionally, diet overlap between these two species exists to some extent (Compagno, 1984; Cortés, 1999). It seems thus plausible that these two sharks could directly compete for space and prey within the study area.

Evidence of interspecific competition affecting the distribution of sympatric sharks has been previously reported (Papastamatiou et al., 2006). The distinct fishing effects inflicted by this survey upon possible competing species could have disturbed the ecological balance between those species and endowed the nurse shark with a competitive advantage, ultimately allowing it to occupy the niche previously taken by the blacknose shark and quickly expand its population. This suggests that interspecific mechanisms such as competitive exclusion could exacerbate the effects of fishing pressure on the abundance of less resilient species. On the other hand, the reduction in stingray abundance could be linked to the increase in nurse shark abundance. Similarly to nurse sharks, stingrays are bottom dwellers and feed mostly on benthic invertebrates and demersal teleosts (Grubs et al., 2006), thus the increase in nurse shark abundance could have increased the competitive pressure on stingrays, resulting in reduced available space and prey for their subsistence. If this interpretation is true, then the reduction in stingray abundance would correspond to a second-level, non-trophic consequence of blacknose shark removal. Similarly to trophic interactions (Ferretti et al., 2010; Shepherds and Meyers, 2005), non-trophic linkages may be important regulators of species abundance because many organisms modulate the availability of resources to other species, eventually conditioning the niche they occupy (Kéfi et al., 2012; Laland and Boogert, 2010). The disturbance of such mechanisms could be notorious in that it may result in one species being quickly placed in a disadvantageous position before another and being locally removed by ecological phenomena such as competitive exclusion (Hardin, 1960). The apparent sensitiveness of these ecological processes could contribute for explaining local extinction scenarios and the presumed collapse of nearshore ecosystems (Jackson et al., 2001), since

deleterious impacts on elasmobranch populations have been observed even under mild fishing pressure (McVean et al., 2006).

Tiger shark abundance was particularly low during a 4-year period centered around 2008, but there was no evidence that it could be decreasing. Tiger shark catch rates in the North Atlantic seem to be stable (Baum and Blanchard, 2012) or even increasing (Carlson et al., 2012; Ingram et al., 2005), contrasting with tiger sharks off Australia which seem to be declining (Holmes et al., 2012). Previous long-term studies report fluctuating annual catch rates for tiger sharks (Holmes et al., 2012; Dudley and Cliff, 1993b; Green et al., 2009), with peaks of abundance occurring in periods of several years (Reid et al., 2011). Tiger sharks have long gestation periods of 15−16 months and seem to give birth only once every three years (Whitney and Crow, 2007). Also, they experience high mortality as neonates and early juveniles (Driggers et al., 2008). The maximization of neonate survival and growth could thus depend on parturition occurring at optimal environmental conditions, when prey is more available. Since female tiger sharks may store spermatozoa in their oviducal glands for extended periods of time before fecundation (Pratt, 1993), they could be able to synchronize gestation and parturition with oceanographic cycles, which typically have long periods. Yet, a longer time series is required to evaluate large-scale trends in tiger shark abundance off Recife.

Blacknose shark abundance evidenced some seasonality, similarly to conspecifics from the North Atlantic (Compagno, 1984; Schwartz, 1984), suggesting that they could move to other regions or depths between December and February. Since most blacknose sharks caught were mature it is plausible that such migrations could be driven by reproductive behavior. Reproduction in blacknose sharks off Brazil could be completed within 10 to 11 months and parturition occurs from December to January (Hazin et al., 2002), thus mating should take place from January to February, which coincides with the period of lower catch rates off Recife. Since the sex ratio in the first trimester was male-biased, it is possible that such migratory process comprises more females than males. Further research on blacknose shark movements is required to clarify behavioral shifts in this species.

Seasonality was also observed in tiger shark abundance, with higher catch rates being associated to the first and third trimesters. The size-frequency distribution by trimester shows a population of juvenile tiger sharks using nearshore waters off Recife from January to

September and leaving the area from October onwards. The modal progression in size observed between the first and third trimesters is probably growth-related due to fast growth rate of tiger sharks in this region (Afonso et al., 2012b), thus suggesting that juvenile tiger sharks use nearshore waters for enhancing growth before moving to oceanic waters in the fourth trimester. In the pelagic longline fishery around the Hawaiian islands most tiger sharks were caught during the first and fourth trimesters (Polovina and Lau, 1993), but tiger sharks may behave differently off oceanic islands compared to continental land masses. In western Australia, tiger shark abundance in coastal waters was lowest during the cold season, from June to August (Wirsing et al., 2006), which could be ascribed to low water temperatures (Heithaus, 2001). Tiger shark abundance was highest when water temperature was > 19ºC (Heithaus, 2001), but the minimum temperature measured in this study was 24.4ºC, thus habitats off Recife should provide suitable thermal conditions for tiger sharks to subsist year round. Since tiger sharks from the northwestern Atlantic reside year round off Florida and seasonally migrate as north as Nova Scotia (Kohler et al., 1995), a symmetrical trend could perhaps be verified in the southern hemisphere.

Regarding spatial effects, blacknose and nurse sharks were more abundant in Boa Viagem than in Paiva, which could be ascribed to some sort of habitat preference, possibly related to the positioning of the Barra de Jangadas estuary within the study area. However, environmental variables other than the ones herein monitored may be responsible for such heterogeneity in the spatial distribution of these species because no significant differences between the two nearshore sites were detected for sea surface temperature, salinity, or visibility (see chapter 2). Tiger shark catch, on the other hand, did not differ between those nearshore sites but it was significantly higher in the middle continental shelf. The tiger shark is not a typical coastal species in that it frequently performs extensive excursions in oceanic waters (Compagno, 1984). This species is found across the continental shelf (Stevens and McLoughlin, 1991), where catch rates are positively influenced by depth (Carlson et al., 2012), but it also moves regularly to shallow, inshore waters to forage (Heithaus et al., 2002). Tiger sharks off Recife also seem to spend more time at deeper waters and eventually move shoreward to forage. Stingrays showed no differences in abundance between all sampling sites, suggesting that this group uses a large portion of the continental shelf uniformly.

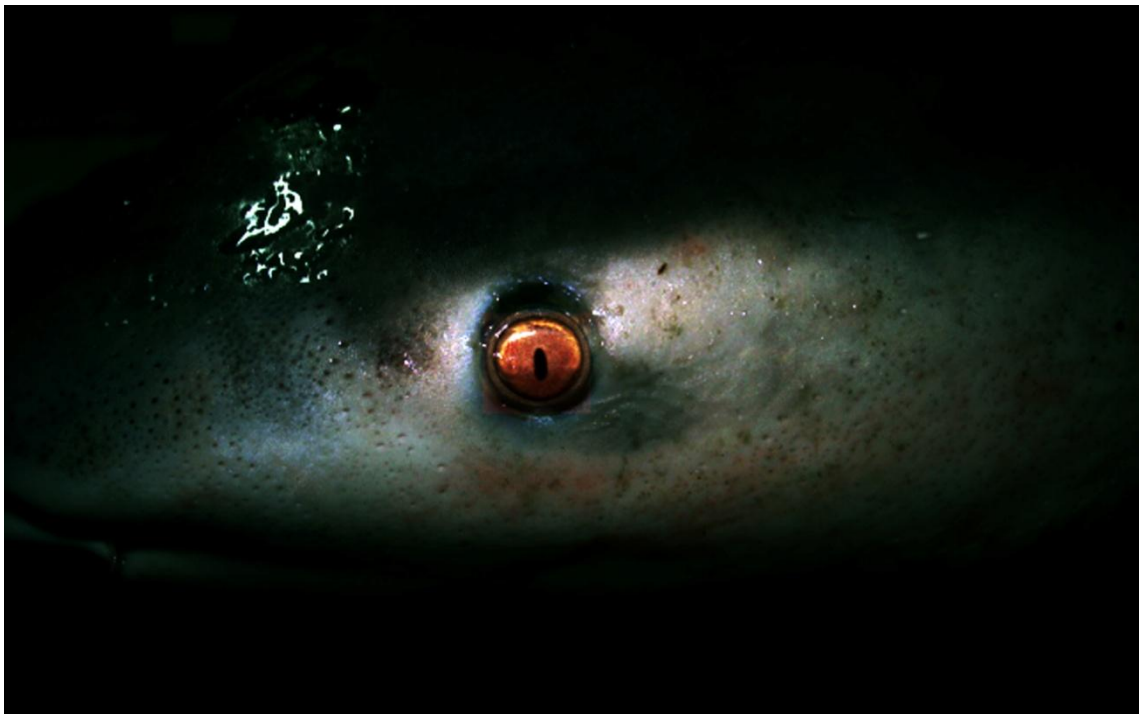
The environmental modeling resulted in both sea surface temperature and tidal amplitude being selected twice for predicting species abundance, while wind direction, visibility, and pluviosity were selected a single time. Additionally, some variables such as lunar day, wind direction, temperature, and pluviosity provided significant results in univariate modeling. The wind direction showed some interesting influence on species abundance because blacknose sharks were more abundant when wind was blowing from northern quadrants, whereas univariate modeling showed tiger sharks to be more abundant when wind was blowing from southern quadrants. The wind direction has a strong influence on local coastal hydrodynamics, with northeastern winds being usually associated with clearer waters. Nurse shark abundance showed positive responses to wind coming from several directions and thus is difficult to relate to the previous species. Yet, nurse sharks seem to prefer low visibility waters, which are more common during winter months when the southeastern trades prevail. Tidal amplitude and pluviosity were selected as predictors of tiger shark abundance. Intermediate and great tidal amplitudes and low pluviosities showed a positive effect on tiger shark catchability. Tidal amplitude has been reported to influence the distribution of sharks in coastal habitats (Ackerman et al., 2000), and tiger sharks could take advantage of high tides to forage shallow, productive inshore waters. On the other hand, high pluviosity would expectedly have a positive effect on tiger shark abundance due to increased freshwater runoff from the Barra de Jangadas estuary. Sharks can be attracted to estuarine environments because they hold considerable amounts of organic matter and have high prey densities, particularly following heavy rainfall (Gilbert, 1963). A possible lag between rainfall events and increased estuarine discharge could possibly explain the association of tiger shark abundance with low pluviosity values. On the other hand, univariate modeling showed that tiger sharks were more likely to be caught between the new and full moon phases. In Australia game-fish tournament fishing, no association between tiger shark catch rate and lunar phase was detected (Lowry et al., 2007), but foraging efficacy in coastal waters could be higher in dim light conditions. Contrasting with tiger sharks, stingrays showed avoidance for great tidal amplitudes and low pluviosities, and affinity for high pluviosities. This could be related to predator-avoidance behaviour, as stingrays compose part of the diet of large sharks (Cortés, 1999).

Understanding the relationship between environmental variables and elasmobranch abundance is crucial for the development of optimal shark attack mitigation measures off

Recife. The present approach allowed to identify some of the variables which most likely influence tiger shark abundance in the study area and to estimate the ranges of those variables at which this species is more probable to occur. Simultaneously, univariate modeling was conducted because the variables selected by the *ENV* model may not always be monitored or be readily available for incorporation in mitigation strategies. The peculiarity of this study encourages the assessment of every possible correlation in order to create the most comprehensive set of information within the limits of the data collected. Despite univariate models, in this analysis, being presumably worse predictors of species abundance than models subjected to the variable selection procedure, they are believed to still hold some valued information which may contribute to mitigate the shark attack problem.

Overall, the *SPT* and *ENV* models showed a reasonably good fit and explained a fair amount of null deviance, particularly regarding blacknose and tiger sharks and stingrays. Nurse shark models performed poorer which could be ascribed to nurse shark data distribution exhibiting great variance or requiring a different modeling approach, such as the partially-constrained solution for zero-inflated generalized additive models (Liu and Chan, 2011). Nevertheless, other similar studies showed lower explained deviances (e.g. Carlson et al., 2012). Caution is however required as the deviance explained should be interpreted only as an indicator of the goodness of fit between the observed data and the final model and cannot be compared among error distributions because it is, as a matter of fact, a function of the error distribution (McCullagh and Nelder, 1989).

Chapter 6. Bioecological aspects of potentially aggressive sharks



Details on the head of a shark caught off Recife.

6.1. Introduction

Coastal waters constitute essential habitats for many elasmobranch species which use them for a multitude of purposes. The bull shark, *Carcharhinus leucas*, possesses an efficient osmoregulatory mechanism (Pillans et al., 2005) which enables it to enter in low-salinity environments and even to swim upstream rivers and lakes (Thorson, 1972), and usually delivers its offspring in estuaries and river-mouths (Jensen, 1976) where neonates and early juveniles remain for some years (Heupel and Simpfendorfer, 2008). Such strategy presumably reduces the predatory pressure upon young individuals as most large sharks are stenohalines and do not tolerate low salinity values. Evidence of female reproductive phylopatry has been reported recently (Tillett et al., 2012), corroborating the evolutionary importance of this strategy. Similar solutions have been adopted by other exclusively marine sharks, which use shallow, coastal habitats as primary and/or secondary nurseries where neonates and/or juveniles take advantage of abundant prey and sheltering from large predators and thus increase growth and survival. This is the case of numerous tropical carcharhinids and sphyrnids such as the lemon, *Negaprion brevirostris* (Feldheim et al., 2002), the dusky, *Carcharhinus obscurus* (Hussey et al., 2009), the sandbar, *C. plumbeus* (Rechisky and Wetherbee, 2003), the Caribbean reef, *C. perezi* (Garla et al., 2006), and the scalloped hammerhead, *Sphyrna lewini* (Baum et al., 2007) sharks, among others. Coastal waters may also be used for mating, as is the case of whitetip reef sharks, *Triaenodon obesus*, off Hawaii (Tricas and Le Feuvre, 1985).

Nearshore habitats may also be important foraging grounds for older juveniles and adult sharks. Coastal waters are among the most productive ecosystems in the world and generally harbor a high abundance and diversity of fish (Gray, 1997) and other large *taxa* such as marine mammals and turtles (Lanyon, 2003; López-Castro et al., 2010). Such productivity provides an excellent feeding resource for roaming sharks which visit those habitats. Sharks feed on a great variety of prey (Cortés, 1999) and thus can efficiently use the large amount of energy available at coastal systems. In conclusion, coastal waters generally benefit the life-cycles of the species which use them.

On the other hand, elasmobranchs are typically slow growing species with late maturity and low fecundity, therefore correct estimation of life-history parameters is crucial for the effective conservation of their populations, which is only achievable with biological data. For all these reasons, knowledge on the bioecological traits of sharks at coastal waters is of utmost importance for clearly understanding the species-specific processes of habitat utilization and, ultimately, promoting species conservation.

Bioecological data on large sharks is also crucial for effectively addressing mitigation measures in regions experiencing high shark attack rates, such as Recife (Hazin et al., 2008). The patterns of occurrence and behavior of potentially aggressive sharks in coastal areas should be directly linked to both biological and ecological features that first determine species' abilities and constraints within those areas. Prenatal gravid females in nearshore waters will probably exhibit different distribution and behavior compared to foraging adults, and the same would be expected regarding competing juveniles and neonates. Likewise, a species feeding on large prey such as turtles and dugongs will expectedly pose a higher threat than a species feeding on small teleosts. Therefore, assessing basic aspects of the bioecology of a shark such as the reproductive status, diet, age and growth may provide inestimable assistance for understanding trends and motivations behind shark attack episodes (Miller and Collier, 1980).

This chapter aims at approaching some aspects of the bioecology of potentially aggressive sharks off Recife focusing mainly on reproduction, diet, age and growth.

6.2. Materials and Methods

All the individuals sampled were caught under the scope of the Shark Monitoring Program of Recife (SMPR; see chapter 4) except for six tiger sharks and one bull shark which were obtained from local fishermen or sampled by observers onboard commercial longline fishing vessels operating off northeastern Brazil. Seven potentially aggressive species were considered, namely the tiger shark, *Galeocerdo cuvier*, the bull shark, *Carcharhinus leucas*, the blacktip shark, *C. limbatus*, the silky shark, *C. falciformis*, the Caribbean reef shark, *C. perezi*, the great hammerhead, *Sphyrna mokarran*, and the scalloped hammerhead, *S. lewini*.

The tiger shark was the most abundant of such species (see chapter 4) and will be the main focus of this study.

The relationships between total length (TL) and other measurements such as fork length (FL), precaudal length (PCL), interdorsal length (IDL), and total weight (W) in the tiger and the bull sharks were investigated with linear regression models and power regression models using the *stats* library in *R* statistical software (*R* Development Core Team, 2011). The coefficient of determination, R^2, was used to evaluate the predictive efficacy of the model.

Until September 2007, all potentially aggressive sharks caught in the SMPR were collected and dissected regardless of their condition at gear retrieval. However, since that date, every shark caught alive begun to be returned to the water for telemetry studies, and thus most reproductive tract samples were collected before 2008. Every specimen brought to the laboratory was carefully inspected for assessing maturity stages according to Stehmann (2002). In males, clasper length was measured and other features such as clasper calcification and rotation and riphidion maturation were examined. In sequence, the testis were weighted and measured for length and width, the epididymis was measured for width and described according to the degree of coiling, and the presence and amount of sperm in the ampulla ductus deferens were assessed. In females, the size and weight of the ovary were recorded and the presence of corpora lutea and vitellogenic follicles was assessed. Both oviducal glands were measured and weighted and the uteri were measured. Uteri were further dissected and assessed for the presence of embryos. When present, embryos were sexed, weighted and measured. Linear regression models were used to assess the relationship between shark size and several reproductive traits such as ovary width and weight, oviducal gland width and weight, clasper length, and testis width and length.

The stomach contents of dissected sharks were analyzed and identified to the lowest possible *taxon*. The repletion index (RI) was evaluated as a proxy of the proportion of food volume related to stomach volume and was visually classified into five classes, namely 0% (empty stomach), 25%, 50%, 75%, and 100% (full stomach). Additionally, the drained weight of the stomach contents was measured to the nearest gram.

Age and growth in tiger sharks were assessed with tag-and-recapture and vertebrae analysis. At each capture, sharks were brought onboard, sexed and measured in their natural position (Garrick, 1982). Depending on size, sharks were restrained on the deck or inside a water filled, 1000 L capacity tank, and eye-covered with a soaked tissue during the sampling procedure. Prior to release, a numbered, stainless steel, dart tag (FH-69; Floytag, Seattle WA) containing owner`s contact and reward information was inserted into the left dorsal musculature, just beneath the first dorsal fin. In one circumstance, a tagged shark returned by a fishermen allowed to analyze growth annuli in vertebral centra. A section of the vertebral column below the first dorsal fin was excised from the shark and vertebrae were cleaned, fixed in 4% formaldehyde for 24 h and further stored in 70% alcohol. One vertebrae was then embedded in polyester resin, sectioned to a thickness of approximately 2 mm, and polished with wet, fine-grit sand paper according to Caillet and Goldman (2004). The growth annuli, consisting of one opaque band followed by one translucent band, were then examined and counted using a stereomicroscope with transmitted light, and the vertebrae radius, corresponding to the distance from the vertebrae focus to its edge across the corpus calcareum, was measured. When missing, fork length and weight were derived from total length following Kohler et al. (1995). As in Natanson et al. (1999), published von Bertalanffy's growth parameters based on fork length were converted to total length for comparison purposes. Shark age was estimated based on an average size at birth of 70 cm (Branstetter et al., 1987), on observed growth during time at-liberty and, in one case, on vertebrae growth annuli.

6.3. Results

6.3.1. Morphometric relationships

Length−length and length−weight regressions were assessed for tiger and bull sharks as these were the only species providing sufficient data for model fitting. The tiger shark showed isometric growth between total length (TL) and all the remaining lengths monitored, i.e. fork (FL), precaudal (PCL), and interdorsal (IDL). Both FL and PCL regressions had similar slopes slightly lower than the unit, but IDL showed a considerably smaller slope, indicating slower relative growth (Fig. 6.1). Regarding weight, relatively smooth increases in

tiger shark mass with increasing lengths were observed until size ~250 cm TL, at which tiger sharks weight less than 100 kg, but after that size the mass increment rate inflates greatly and tiger sharks attain up to 400 kg in weight around size 350 cm TL (Fig. 6.2). In general, all models had high coefficients of determination, R^2, thus demonstrating an acceptable fit to the data. Bull shark lengths showed similar relationships to tiger sharks, although the slopes for FL and IDL were a little smaller (Fig. 6.3). Bull sharks were generally heavier than tiger sharks of the same length, and their weight increased geometrically until about 150 kg, which was the weight of the largest bull shark sampled measuring 250 cm TL (Fig. 6.4). The R^2 values resulting from bull shark models were lower than the ones obtained in tiger shark models, but they were still higher than 0.9.

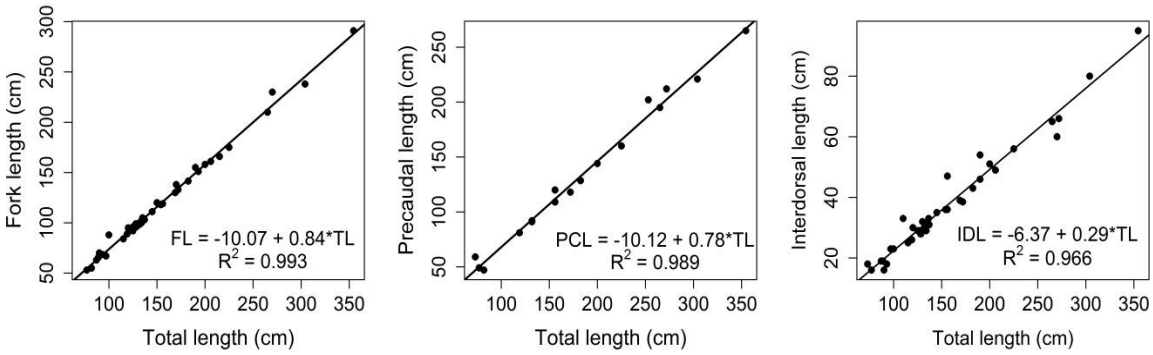


Figure 6.1. Linear regression models between total length (TL) and fork length (FL; left panel), precaudal length (PCL; middle panel), and interdorsal length (IDL; right panel) in tiger sharks caught off northearstern Brazil. The equations of the estimated linear models and the respective coefficients of determination, R^2, are also shown.

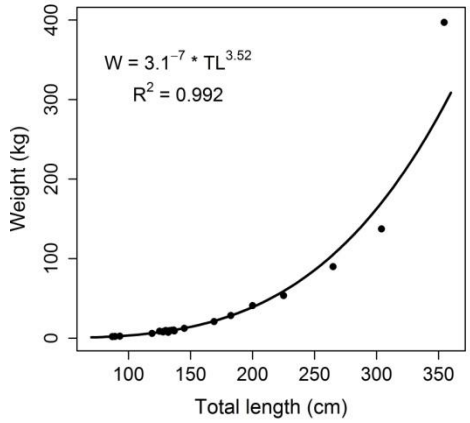


Figure 6.2. Power regression model between total length (TL) and total weight (W) in tiger sharks caught off northearstern Brazil. The model equation and the respective coefficient of determination, R^2, are also shown.

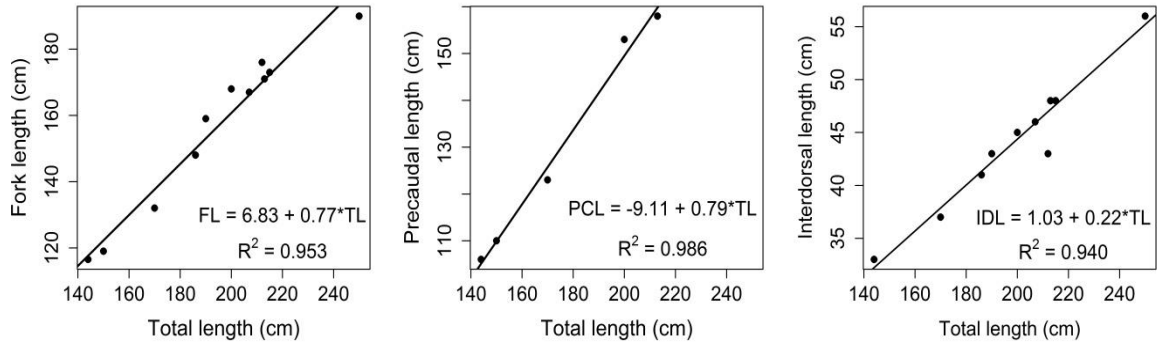


Figure 6.3. Linear regression models between total length (TL) and fork length (FL; left panel), precaudal length (PCL; middle panel), and interdorsal length (IDL; right panel) in bull sharks caught off Recife. The equations of the estimated linear models and the respective coefficients of determination, R^2, are also shown.

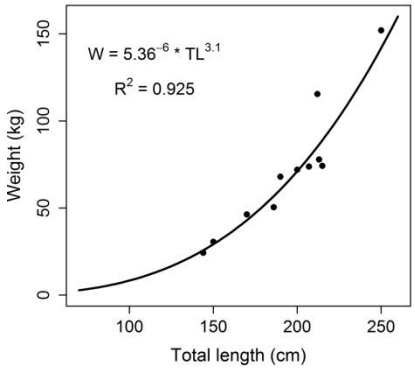


Figure 6.4. Power regression model between total length (TL) and total weight (W) in bull sharks caught off Recife. The model equation and the coefficient of determination, R^2, are also shown.

6.3.2. Reproduction

Concerning potentially aggressive sharks, a total of 33 females and 19 males were dissected and their reproductive tracts examined. Tiger sharks accounted for 56% of the specimens analyzed. Among 19 female tiger sharks, all but one were juveniles measuring less than 270 cm TL and weighting 90 kg at the most (Table 6.2). These juvenile females generally had incipient reproductive organs across a variety of sizes. The ovaries increased little in width with shark total lengths from 120 to 260 cm TL, but they doubled in width at ~350 cm TL

(Fig. 6.8). While this behavior may indicate that a power regression could better fit the data distribution, insufficient sampling at larger shark sizes and a resulting R^2 value of nearly 0.8 suggests that the linear model could be preferable in this case. The ovary weight also showed little variation from size 120 through 260 cm TL, with values incomparably lower than the weight of the ovary of a 354 cm TL specimen (Fig. 6.8). Given such discrepancy, the largest female was not included in the linear regression model, which nevertheless held a low R^2 value and thus was not able to successfully predict ovary weight from juvenile female shark length. This same approach was used to verify the relationship between total length and the width and weight of both left and right oviducal glands. The oviducal gland width showed little variation across the juvenile stage, attaining less than 2 cm in its largest size, while the adult specimen had oviducal glands measuring > 12 cm in width (Fig. 6.9). On the other hand, the oviducal gland weight was not significantly correlated with shark size during the juvenile stage, as verified by the presence of negligible slopes and negative adjusted R^2 values (Fig. 6.9), implying that the oviducal gland does not grow in mass significantly until tiger sharks attain at least 260 cm TL. Moreover, the one adult female tiger shark, which was caught in January 2011, was found to be gravid. The shark was holding 12 embryos, all but one concealed in the right uterus. Also, the left uterus contained 25 unfertilized eggs, whereas the right uterus had only 9. The embryos were equally sized, measuring in average 69.2 ($\pm$1.9) cm TL and weighing in average 0.858 ($\pm$0.052) kg. The sex ratio of embryos equaled 1.4 females per each male.

Ten male tiger sharks were also examined, all but two being juveniles measuring 272 cm TL at the most (Table 6.3). The clasper length presented a seemingly isometric growth with shark length (Fig. 6.10), although little sampling at larger sizes and an R^2 value of ~0.9 do not exclude the possibility that claspers could grow in a non-linear relationship with shark length. Likewise, testis length and width showed isometric growth with shark length, with high adjusted R^2 values suggesting that the resulting models fitted the data properly (Fig. 6.11). Large gaps on the sizes of the sharks sampled do however warrant caution on the interpretation of this morphometric relationship. Large juvenile males were mostly absent from the survey, the exception being a 272 cm TL specimen. Two male sharks measuring > 300 cm TL were considered to be adults, although the 304-cm TL shark was probably not fully mature because,

Table 6.2. Reproductive aspects of potentially aggressive female sharks caught off Recife, including the number of sampled specimens (*N*), the maturation stage (Matur. stage), and the range in total length (TL), total weight (W), ovary width (OvaWi) and weight (OvaW), oviducal gland width (OviGlWi) and weight (OviGlW), and uterus width (UterWi) and length (UterLe).

Species	*N*	Matur. stage	TL (cm)	W (kg)	OvaWi (cm)	OvaW (g)	OviGlWi (cm)	OviGlW (g)	UterWi (cm)	UterLe (cm)
Tiger shark	18	juvenile	73−265	2.32−90	0−5.1	0−35.6	0.3−1.5	0.1−2.7	0−1.7	0−34
	1	mature	354.5	397	16	588	13−14	196−206	25−45	89−116
Bull shark	3	juvenile	144−190	24.3−68	0−2.5		0.67−1.4	1.1−1.3	0.4−0.57	
	4	mature	207−250	73.6−115.5	8.7−14.5	89.5−751	3.8−7.7	26.5−65	2.2−11.3	44−59
Blacktip shark	1	juvenile	65	2.12	0	0			0	0
	2	mature	176−190	37.4−57	4−6.3	22.3	3.2−4	8.9	3.3−4.5	29
Silky shark	3	juvenile	123−126	10.6−12.9	1.9−4.4	9.6−32.4	2.1−3.9	3.5−5.5	2−3.3	26−33
Caribbean reef shark	1	juvenile	107	7.8	0	0	0.5	0.2	0	0

Table 6.3. Reproductive aspects of potentially aggressive male sharks caught off Recife, including the number of sampled specimens (*N*), the maturation stage (Matur. stage), and the range in total length (TL), weight (W), clasper length, testis weight (Testis W), width (TestisWi) and length (TestisLe), and epididymis length (EpididLe).

Species	*N*	Matur. stage	TL (cm)	W (kg)	Clasper (cm)	TestisW (g)	TestisWi (cm)	TestisLe (cm)	EpididLe (cm)
Tiger shark	8	juvenile	87−272	2−21*	1.2−6*	1.6−66.3	0.7−3	7.5−30	0.5−1.4
	2	mature	304−320	137.4*	22−30	267−272	3.5−4.5	31−39.5	1.5−2.4
Bull shark	2	juvenile	150−186	30.6−50.5	6.2−8	18−22.5	0.7−3.2	10.3−11	0.1−1.1
	2	mature	213−215	74.2−77.9	23−27.5	49−67.5	5.3−5.5	18−22	3−3.5
Blacktip shark	3	juvenile	80−100	3.34−6.9	3.5−6		0.6−0.7	7.6−7.8	
Scalloped hammerhead	1	juvenile	222		6				
Great hammerhead	1	mature	346		23.5	329−373	7.2−9.2	37−44.5	3.3−4

*does not include samples from the largest specimens; blanks correspond to data not collected

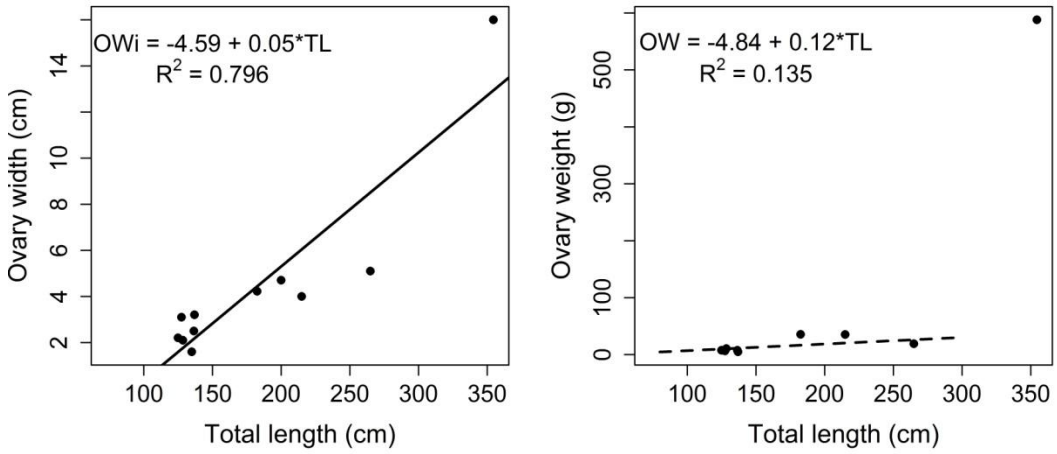


Figure 6.8. Linear regression models between total length (TL) and ovary width (OWi; left panel) and between TL and ovary weight (OW; right panel) in female tiger sharks caught off Recife. The equations of the estimated linear models and the respective adjusted coefficients of determination, R^2, are also shown. Note that the OW regression model does not include the largest specimen sampled.

in spite it presented a convoluted epididymis and the ampulla ductus deferens contained abundant sperm, the 22-cm claspers appeared not to be functional as they were not totally calcified and did not exhibit full rotation. Nevertheless, this evidence indicates that sexual maturation was nearly complete. A collection of pictures depicting some aspects of the reproductive tract of tiger sharks can be found in figure SUP.6.1.

Less abundant species such as the bull, blacktip, silky, Caribbean reef, smooth hammerhead, and great hammerhead sharks showed diverse trends regarding reproductive traits. The maximum observed length for juvenile bull sharks was 190 cm TL for females and 186 cm TL for males, whereas the minimum length for mature female and male bull sharks was 207 and 213 cm TL, respectively (Tables 6.2 and 6.3). Most blacktip sharks were juveniles and the two mature individuals were relatively small, measuring < 200 cm TL. Both silky and Caribbean reef sharks were small juveniles but the reproductive tract of silky sharks was already in a more conspicuous stage and thus could be sampled. Regarding hammerheads, they were both large males but only the great hammerhead was mature, as evidenced by clasper calcification and rotation and by the presence of abundant sperm in the ductus deferens. The small sample sizes of less abundant species precluded the assessment of morphometric relationships, but the range of the monitored measurements can be found in tables 6.2 and 6.3.

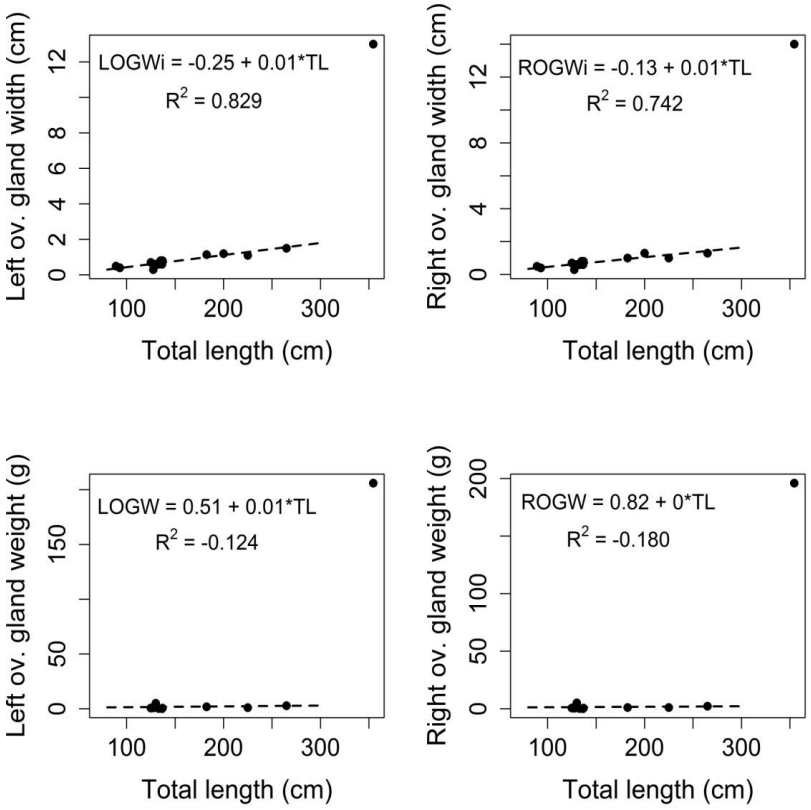


Figure 6.9. Linear regression models between total length (TL) and the left and the right oviducal glands width (LOGWi and ROGWi; left and right upper panels, respectively) and the left and the right oviducal glands weight (LOGW and ROGW; left and right lower panels, respectively) in female tiger sharks caught off Recife. The equations of the estimated linear models and the respective adjusted coefficients of determination, R^2, are also shown. Note that models do not include the largest specimen sampled.

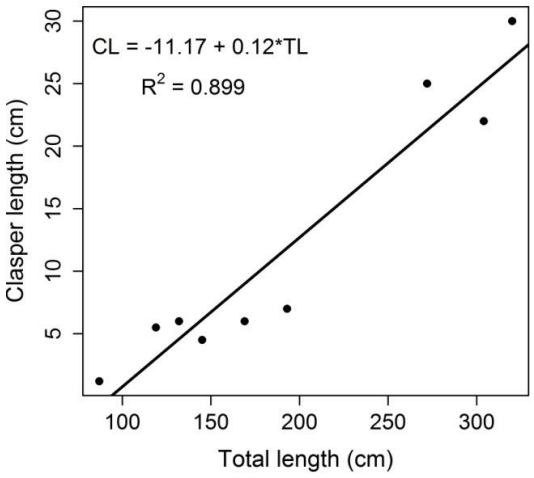


Figure 6.10. Linear regression model between total length (TL) and clasper length (CL) in male tiger sharks caught off Recife. The model equation and adjusted coefficient of determination, R^2, are also shown.

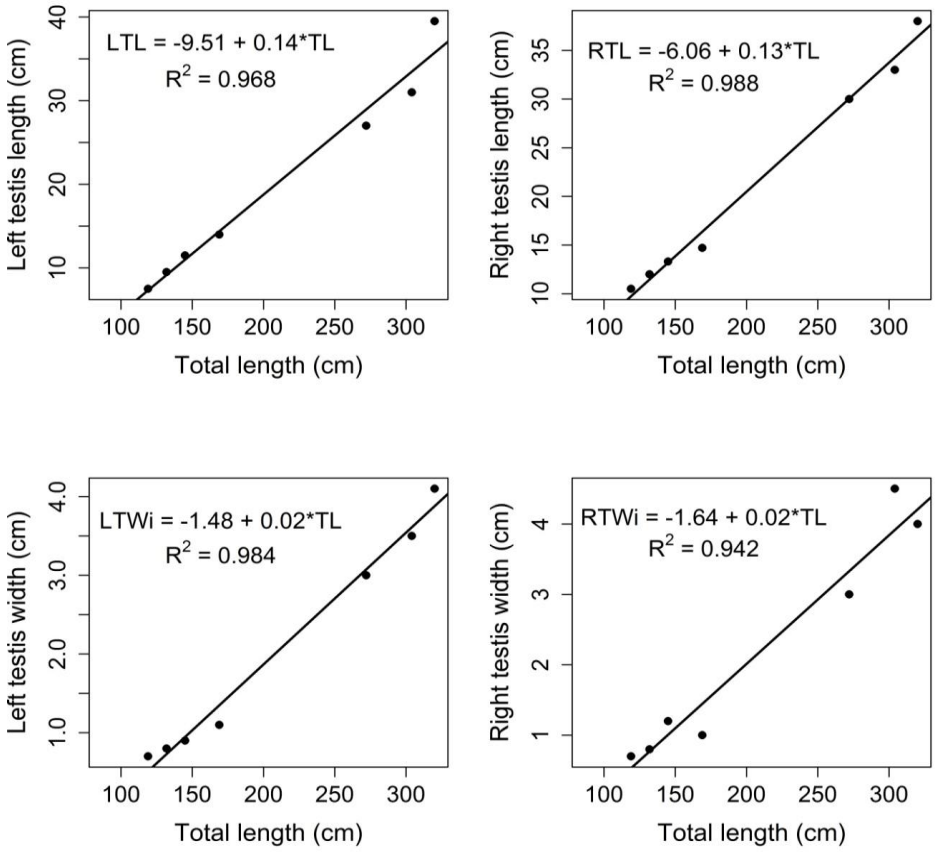


Figure 6.11. Linear regression models between total length (TL) and left and right testis length (LTL and RTL, respectively; upper panels) and width (LTWi and LTWi, in the same order; lower panels) in male tiger sharks caught off Recife. The model equations and adjusted coefficients of determination, R^2, are also shown.

6.3.3. Diet

The stomach contents of 26 tiger sharks were analyzed, but 69% (18) were empty. Moreover, two stomachs were found to be everted after examination. Among non-empty guts, one shark had a Repletion Index (RI) of 25%, two sharks had a RI of 50%, three sharks had a RI of 75%, and two sharks had a RI of 100%. The items identified in the stomachs of two juvenile males (< 200 cm TL) comprised a small stingray, probably *Dasyatis centroura*, fragments of unidentified teleosts, namely eyes, jaws, otoliths, and pieces of vertebral column, and particles of coralline algae. The stomachs of three large juveniles, measuring 225−272 cm TL, contained a

balistid triggerfish weighting 0.73 kg, a whole squid, and a small cobia, *Rachycentron canadum* (Fig. SUP.6.2A,D,E). The cobia was in fact a specimen which had been recently tagged and released in this region within the scope of a different research conducted by the Fishery Oceanography Laboratory, and as the tag was still attached to the fish it could be identified. The three mature tiger sharks, measuring > 300 cm TL, showed the greatest quantity and diversity of prey items in their guts. The largest tiger shark caught had eaten one whole hawksbill turtle, *Eretmochelys imbricata* (Fig. SUP.6.2H), two marine birds, one male eagle ray, *Aetobatus narinari*, one small stingray, *Dasyatis americana* (Fig. SUP.6.2C), and one ariid catfish, all of which combined weighting 18.2 kg. A 320 cm TL male shark had one olive ridley turtle, *Lepidochelys olivacea*, one French angelfish, *Pomacanthus paru*, one puffer fish, *Diodon* sp., and one squid beak on its stomach (Fig. SUP.6.2F), whereas the stomach of a 304 cm TL male contained large pieces of a green turtle, *Chelonia mydas*, carapace and plastron, the central body of a small unidentified ray, and a whole land bird, presumably a domestic chicken, of which only the head was missing and that should have been recently ingested since most of its elements were easily identifiable (Fig. SUP.6.2B,G). Several indigestible items such as plastic bags and nylon mesh were also observed in this stomach (Fig. SUP.6.2I), whose contents weighed 0.86 kg.

The bull shark also showed a high proportion (75%) of empty guts, and one specimen had an everted stomach. Non-empty stomachs were nevertheless almost empty with RI values of 0%. Prey items identified comprised a squid beak and teleost vertebral column. In one instance, only a small teleost vertebrae was found. A 91 cm TL male blacktip shark also had a small piece of teleost vertebral column in its stomach, while a male great hammerhead shark measuring 340 cm TL had eaten two lutjanids some time before capture. Overall, few individuals of all potentially aggressive species caught had any content in their stomachs when they were examined.

6.3.4. Age and growth

Age and growth assessements were based on data obtained from recaptured potentially aggressive sharks, which was verified for tiger sharks only. Although vertebrae centra may

provide information on age and growth (Cailliet and Goldman, 2004), insufficient sample size and a large lag (>15 years) between the first and last tiger shark vertebrae collected preclude such approach at the present time, and so results on vertebrae annuli analysis are included only for one tagged shark that was recaptured by an artisanal fisherman and returned to the laboratory.

On 25 July 2009 a juvenile male tiger shark (#15) measuring 193 cm TL was caught off Recife (Fig. 6.5A). Its claspers were flaccid and puerile and measured 7 cm in length. The shark weight was estimated to be 35 kg, which was in accordance with tiger shark length-weight regressions assessed by the present study (see previous section) and by Kohler et al. (1995). The shark was fitted with a dart tag and a pop-up satellite archival tag (mk10; Wildlife Computers, Redmond WA, USA), which was attached to the first dorsal fin. More information on this procedure can be found in chapter 7. Upon release, the shark appeared to be in good health and immediately swam away from the boat. On 26 July 2011, after exactly 2 years, shark #15 was caught with gillnets by artisanal fishermen off Itamaracá, ~3.5 km from the coast and ~40 km northward from the tagging site (Fig. 6.5B). Satellite tracking showed that the shark had previously visited this region within one week after tagging (Hazin et al., 2012). Both the carcass and the numbered dart tag were recovered intact. The shark was brought into the laboratory the same day of capture and submitted to a comprehensive analysis. It had grown remarkably in size and mass. It measured 304 cm TL, which implies a growth of 55.5 $cm \cdot year^{-1}$ (Table 6.1). Total weight was calculated as the sum of different weighable parts of the shark due to scale dimension constraints, equalling 137.4 kg. This corresponds to length and weight increments of 58% and ~300%, respectively. The claspers were prominent and measured 22 cm, yet they appeared not to be functional as they were not totally calcified and did not exhibit full rotation. Nevertheless, the shark presented a convoluted epididymis and the ampulla ductus deferens contained abundant sperm already, indicating that sexual maturation should be nearly complete. The vertebral centra evidenced three distinct growth bands distally to the birth mark and a fourth band possibly forming in the outer margin of the vertebrae (Fig. 6.6). The vertebrae radius measured 16.2 mm. Also, the stomach contained several recently ingested items, including a turtle, a ray, a land bird, and pieces of plastic and nylon (see section 6.3.3). No signs of the satellite tag deployment were visible and the puncture inflicted in the dorsal fin for tag attachment had completely healed.

Table 6.1. Tag-and-recapture events for two tiger sharks caught off Pernambuco, Brazil. T-date: tagging date; TL: total length (cm); FL: fork length (cm); W: weight (kg); R-date: recapture date; TAL: time-at-liberty (year); GR: growth rate (cm L_T.year^{-1}); WR: weight increment rate (kg.year^{-1}).

Tag	Sex	T-date	TL	FL	W	R-date	TL	FL	W	TAL	GR	WR
#15	M	25−Jul−09	193	155*	35*	26−Jul−11	304	238	137.4	2.0	55.5	51.2
#116	F	12−Feb−11	110	83*	5*	22−Aug−11	172	133	21*	0.52	118.4	30.8

*estimated after Kohler et al. (1995)

On 12 February 2011 a female tiger shark (#116) was caught off Recife. It was an early juvenile measuring 110 cm TL. Its weight was estimated at 5 kg, which was again in accordance with regressions in the previous section and in Kohler et al. (1995). The small shark was hold upside down inside a water-filled tank to induce tonic immobility and an acoustic transmitter (V16; Vemco, Canada) was surgically implanted in its peritoneal cavity. Further details on this procedure can be found in chapter 7. A stainless steel dart tag was also fitted to the shark, which appeared to respond well to the procedure by swimming away from the boat immediately after being released. On 22 August 2011, after 191 days (0.52 year), shark #116 was recaptured alive roughly in the same location. The dart tag remained properly attached to the dorsal musculature, and the incision from the surgical procedure had completely healed. The shark measured 172 cm TL, which extrapolates to a growth rate of 118.4 cm·year^{-1} (Table 6.1), and its weight was estimated at ~20 kg. Similarly to shark #15, length and estimated weight increases equalled 56% and 300%, respectively. After sampling, the shark was returned to the water and released.

Both tagging and recapture events for the two sharks were plotted together with logistic growth curves assessed by previous studies for comparison purposes and both sharks showed significant deviations from the published age-at-length models, having grown considerably faster than what would be predicted by those models (Fig. 6.7). The age of shark #15 and shark #116 at recapture was conservatively estimated at 3.5 and 0.75 years, respectively. This implies that they were 1.5 and 0.25 years old at first capture, in the same order.

Figure 6.5. Aspect of a tagged-and-recaptured, male tiger shark A) at first capture (tagging), measuring 193 cm in total length (TL), and B) at recapture after 2 years at liberty, measuring 304 cm TL.

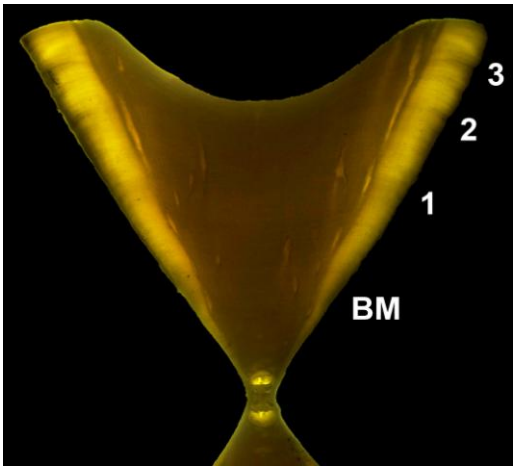


Figure 6.6. Sagittal section from the vertebrae of a 304 cm in total length, male tiger shark, evidencing the birth mark (BM) and three growth annuli (1, 2, and 3), with a fourth annulus possibly forming at the margin of the vertebrae.

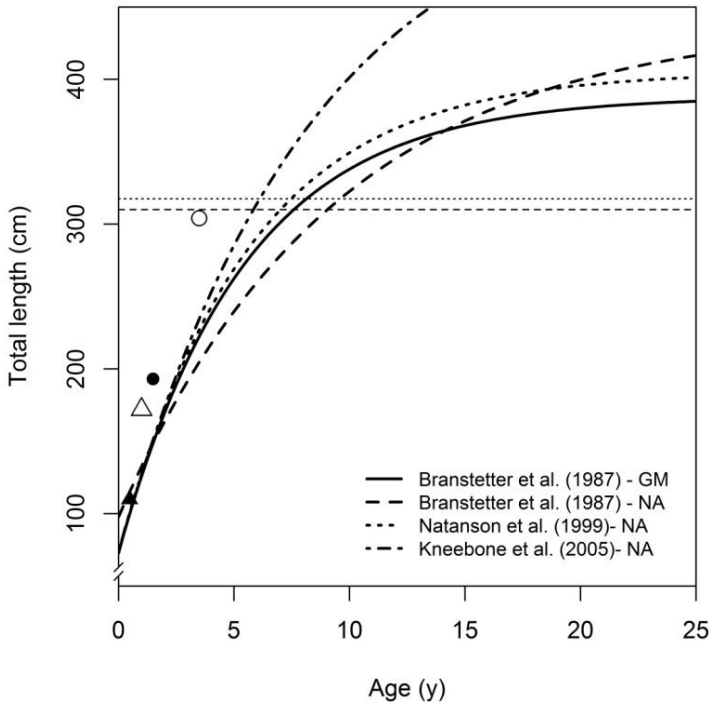


Figure 6.7. Von Bertalanffy growth models for tiger sharks from the Gulf of Mexico (thick solid line) and North Atlantic (thick dashed line, thick dotted line and thick dot-dashed line), and size at maturity for males (thin, horizontal dashed line) and females (thin, horizontal dotted line). The age and growth measured in two tagged-and-recaptured tiger sharks off Brazil are also depicted in four events, namely shark #116 tagging (▲) and recapture (Δ), and shark #15 tagging (●) and recapture (○). The age-at-tagging and age-at-recapture were conservatively estimated based on observed growth and vertebrae centra analysis.

6.4. Discussion

Elasmobranchs are typically slow growing species with late maturity and low fecundity, thus being particularly susceptible to anthropogenic disturbance (Stevens et al., 2000). Complete knowledge on elasmobranch life-history features is hence crucial for their effective conservation. However, this was not the objective of this study because the Shark Monitoring Program of Recife is mostly engaged with areas of research relying on live animals and thus only a small number of individuals were collected and dissected. In spite of small sample sizes, it is still important to understand the bioecological traits of sharks using nearshore waters, particularly in regions experiencing high incidence of attacks on humans. Therefore, the purpose of this study was to approach the most significant aspects of shark bioecology merely to the extent allowed by the collected data. Age, growth, reproduction, and diet are fundamental functions in the life-history of sharks, and knowledge on these aspects could contribute for interpreting the dynamics in shark abundance off Recife better.

Age and growth in elasmobranchs are usually determined by analysing growth annuli present in vertebral centra or other calcified structures, however validation is required for corresponding annuli with time (Cailliet and Goldman, 2004). Tag and recapture provides accurate information on growth and may allow age estimation from length if conducted intensively or when fluorescent dyes are used in conjunction (Natanson et al., 1999; Campana, 2001), but their use has been limited as they usually demand great sampling efforts. In the North Atlantic, shark tagging programs have been conducted for decades (Kohler and Turner, 2001), but virtually no tagging effort has been employed in the South Atlantic. Regarding reproduction, sexual maturation in male sharks is immediately assessed because secondary sexual characteristics such as clasper calcification and rotation and riphidion maturation are generally measurable noninvasively (Clark and von Schmidt, 1965). Females however do not possess external characteristics which could indicate sexual maturation and thus are usually dissected for the analysis of the reproductive tract unless they are visibly pregnant or otherwise carry mating evidence such as bite marks or swollen cloacas. Macroscopic and microscopic examinations of male testis, epididymis and ductus deferens, and female ovary, oviducal gland and uterus provide rigorous indicators for maturation stage and fecundity (Carrier et al., 2004).

The tiger shark, *Galeocerdo cuvier*, occurs worldwide in both tropical and temperate waters and is the largest species amongst carcharhinids, attaining 469 cm in fork length (Castro, 1983). In spite being common in coastal waters, it performs extensive migrations in the oceanic realm (Kohler et al., 2001) and is recurrently caught in pelagic longline fisheries (e.g. Afonso et al., 2011). Age and growth in the tiger shark has been investigated in several studies, but the growth rates found in this study are, to our knowledge, the greatest growth rates at the specified lengths ever measured for tiger sharks. Shark handling and tagging apparently did not hinder growth rates at all. According to published age-at-length models estimated for the North Atlantic and Gulf of Mexico (Branstetter et al., 1987; Kneebone et al., 2005; Natanson et al., 1999) and for the southwestern Indian ocean (Wintner and Dudley, 2000), shark #15 would require at least 3 to 4 years at-liberty to experience the observed growth, and shark #116 would require between 1 and 2 years. Tag and recapture data for similarly-sized tiger sharks from the North Atlantic yielded much lower growth rates than the ones herein measured, although only sharks which spent more than 0.9 years at liberty were reported (Natanson et al., 1999) and so direct

comparisons with shark #116 need caution as it spent only 0.52 years at liberty. In Australia, growth rates also assessed with tag and recapture data were greater than in other regions (Wirsing et al., 2006), but they were still less than the ones herein described. Discrepancies in growth rates between regions have been detected (Branstetter et al., 1987, Wirsing et al., 2006), which could be a response to regional differences in prey preferences and availability (Wirsing et al., 2006) and in migratory behaviour because tiger sharks would probably grow faster in productive, nearshore waters than in oceanic waters. Additionally, the vertebrae radius of shark #15 measured 16.2 mm, which is considerably less than the 18 mm radius predicted for ~300 cm TL tiger sharks (Branstetter et al., 1987). Slower growth could result in greater vertebrae radius because more time for cartilage mineralization would be available, thus a thinner vertebrae adds evidence that tiger sharks in this study grew faster than tiger sharks in the North Atlantic. In spite of fast growth in length, the increase in mass of shark #15 was even more remarkable as it quadrupled its weight by gaining over 100 kg in two years only. According to Wintner and Dudley (2002), the growth rate of tiger shark mass increases until about the 7^{th} year, when it begins to slow, while the growth rate of length decreases steadily. Thus, during the period between tag and recapture, the shark could be experiencing optimal growth rate in mass, which was nevertheless considerably higher than the one estimated by Wintner and Dudley (2002).

Published estimates of the von Bertalanffy's parameter *k* for the growth function of tiger sharks range between 0.107−0.202 (De Crosta et al., 1984; Branstetter et al., 1987; Natanson et al., 1999; Wintner and Dudley, 2002). Kneebone et al. (2008) estimated *k* to be as great as 0.283 for combined sexes, but resulting estimates of L_∞ were unrealistically small. The present results suggest that tiger sharks off Brazil could be experiencing greater growth rates than conspecifics elsewhere, adding further variability to those estimates. Juveniles from the Gulf of Mexico grow faster than juveniles from the North Atlantic (Branstetter et al., 1987), which could be related to environmental features and prey availability (Natanson et al., 1999). Growth enhancement could also be behaviourally driven if sharks spend more time in productive, coastal areas instead of performing excursions in poorer, oceanic waters, which may have been the case of the two sharks herein reported. In accordance, the stomach of shark #15 contained recently ingested items belonging to several *taxa*, suggesting that nearshore waters off Brazil provide adequate foraging grounds for tiger sharks, which could promote faster growth. However, such variability

in growth between different regions could lead to inadequate estimates of tiger shark population parameters if geographical differences are not considered. For instance, tiger sharks are born with ~70 cm TL (Branstetter et al., 1987) and it is globally accepted that shark growth rates decrease as they grow older. Thus, a conservative estimate of shark #15 age-at-recapture would be 4 years old, as the growth experienced between tagging and recapture roughly equals the implicit growth between birth and tagging. Following the same rationale, shark #116 was about 9 months old at recapture. Moreover, assuming that shark #15 vertebrae comprises four growth annuli, the age of this shark at recapture could be further reduced to about 3.5 years old because the first growth band appears 6 months after birth (Branstetter et al., 1987). So far, tiger sharks are believed to mature at 7−10 years old (Natanson et al., 1999; Kneebone et al., 2008), although Compagno (1984) reported maturation to be completed at 4−6 years old. In any case, shark #15 was nearly mature at age 3.5, which is, at the most, half the age proposed by the most recent studies. Such large difference may produce severe bias in population assessments, possibly resulting in erroneous interpretations and unsuitable management strategies. The effective modelling of tiger shark populations thus requires independent knowledge of life-history traits, particularly in regions where no such studies have yet been conducted.

The tiger shark is the only ovoviviparous carcharhinid and has a relatively high fecundity, producing 10−82 young per litter (Randall, 1992). Off Recife, the vast majority of the tiger sharks caught were juveniles and thus no attempt was made to describe the reproductive dynamics of mature sharks. During the juvenile stage, the growth in female reproductive structures does not follow growth in shark length. Indeed, the weight of ovaries and oviducal glands varies little before maturation but it seems to suddenly increase by at least one order of magnitude during adulthood. A similar but much smoother trend is observed regarding the width of these structures. Whitney and Crow (2007) also report sharp increases in oviducal gland and uterus width in females larger than 250 cm TL. As juvenile tiger sharks seem to be mostly dedicated to maximizing growth, a higher investment in somatic growth could result in the development of the reproductive tract being delayed until the shark attains a subadult size. This was however not visible in males, as clasper length and testis width and length clearly followed linear relationships with shark length. Clasper growth rate increases slightly in individuals larger than 280 cm TL (Whitney and Crow, 2007), but because few large sharks were caught such trend

could not be detected. On the other hand, Pratt (1988) reported that tiger sharks have diametric testes which grow more in length than in diameter relative to body length in order to reduce the distance the spermatozoa must traverse before being liberated to the efferent ductule network. Such tendency was not observed as testis length and width varied within the same order of magnitude relative to body length, but it is plausible that such effect is mostly visible on larger individuals. A single male shark measuring 320 cm TL was clearly mature, but one shark measuring 304 cm TL was nearly mature. Whitney and Crow (2007) reported male tiger sharks to mature at 292 cm TL, whereas other authors reported maturation to occur at 237 cm TL (Alves, 1977) or between 226−290 cm TL (Randall,1992). Whilst large differences in these estimates could imply high variability in size at maturity of male tiger sharks, this study agrees with the estimates of 305−310 cm TL proposed by Branstetter (1987) and Stevens (1984). Regarding females, size at maturity in the northwestern Atlantic Ocean and Caribbean has been reported around 297−320 cm TL (Branstetter et al., 1987; Clark and von Schmidt, 1965), but in Hawaii they appear to mature at larger sizes (Whitney and Crow, 2007). Off Recife, a single, ~350 cm TL pregnant female was caught while carrying 12 embryos, all but one in one uterus. It is possible that the shark was carrying more embryos which were aborted before the retrieval of the fishing gear, since one uterus was nearly empty. On the other hand, litter sizes usually average 30−35 embryos (Simpfendorfer, 1992; Whitney and Crow, 2007) and there is evidence of a direct relationship between litter size and maternal length (Simpfendorfer, 1992), thus this female could be too small to enjoy of optimal fecundity. The embryos measured ~70 cm TL, indicating that their gestation was nearly complete because tiger sharks are born with 70−90 cm TL (Branstetter et al., 1987; Simpfendorfer, 1992; Whitney and Crow, 2007). Late-term embryos were observed from May to August in northern Brazil (Alves, 1977) and from October to December in Australia (Simpfendorfer, 1992), whereas pupping seasons from July to September and from September to October have been reported in North Carolina (Schwartz, 1989) and Hawaii (Whitney and Crow, 2007), respectively. The length frequency distribution of tiger sharks off Recife indicates that pupping season probably occurs in the first quarter (see chapter 5), in temporal accordance with the late-term pregnancy of the referred female since it was caught in early January.

The diet of the tiger shark could not be quantitatively assessed because most stomachs were empty. This was probably related to the fishing methodology used. Sharks are able to evert their stomachs (Brunnschweiler et al., 2005) presumably as a way to expel inedible items, and hook-based fishing gear could promote such behaviour (Cortés, 1997). In accordance, the proportion of empty guts found in tiger sharks caught mostly with gillnets was considerably lower, more precisely ~30% (Simpfendorfer, 1992). Nonetheless, several *taxa* were found in the stomachs of a few, particularly larger, sharks. The prey consumed by tiger sharks off Recife comprised turtles, squids, rays, teleosts, and marine and land birds, all of which have been reported to occur in tiger shark stomachs (Simpfendorfer, 1992), including land birds (Dodrill and Gilmore, 1978), whose occurrence may result from opportunistic feeding on disoriented animals or carcasses being washed seaward by river discharge. Tiger sharks are known to feed on a diversity of animals (Bornatowski et al., 2007; DiBeneditto, 2004; Heithaus, 2001; Lowe et al., 1996; Simpfendorfer, 1992) and inclusively ingest inedible materials such as metal and plastic (Lowe et al., 1996), as it was observed in this study. There is virtually no inferences to be made with such a small sampling size, but the fact that turtles were found in the stomachs of larger sharks agrees with the ontogenetic dietary shifts described by Lowe et al. (1996) for this species.

The remaining potentially aggressive sharks were caught in low numbers and thus they were mostly examined for their maturation stage and stomachal contents. Bull sharks exhibit highest mass at specific sizes but they attain smaller lengths than tiger sharks. In spite some mature individuals were caught, no pregnant female bull sharks were identified during 8 years of survey, which disagrees with previous suggestions that female bull sharks might have been using coastal waters off Recife as a parturition ground since the construction of the Suape Port (Hazin et al., 2008). According to the results observed, bull sharks seem to mature at sizes > 190 cm TL, which is larger than the size at maturity reported by Jensen (1976). Similarly to tiger sharks, everted stomachs were also observed in bull sharks caught with longlines, and little information was obtained from their gut contents. Regarding other species, only two female blacktip sharks and one male great hammerhead were found to be mature. One 222 cm TL scalloped hammerhead was identified as a juvenile, which agrees with the size at maturity estimated by

Carrera-Fernández (2007) but disagrees with the smaller sizes at maturity estimated by previous studies (Baum et al., 2007 and references therein).

Chapter 7. Movements of the tiger shark off northeastern Brazil

An acoustic receiver deployed off Recife.

7.1. Introduction

Sharks comprise a great diversity of species using more or less extensive habitats, according to their home ranges. The *home range* concept was first introduced in reference to terrestrial mammals (Burt, 1943) and has been defined as the area over which one animal usually moves while foraging. This area may be stationary or may shift with seasons or with resource distribution, but should be persistent (Grubbs, 2010). The spatial distribution of sharks is influenced by species-specific activity and behavior patterns associated to motivational and energetic requirements, which ultimately determine essential traits such as foraging strategies and encounter rates with prey, the location of mates and timing of courtship, and habitat preferences (Sims, 2010). Spatial ecology is thus a key-component for the sustainable management of shark populations because individual movements will regulate the dynamics in the population distribution. The spatiotemporal dynamics of shark behavior is complex, involving distinct processes acting at different scales such as daily and seasonal migrations, regional variability in habitat preferences, and segregation by age or gender (Wearmouth and Sims, 2008). Knowledge on the patterns of habitat use, movement, and behavioral responses to environmental stimuli should contribute to defining spatiotemporally-integrated management measures, which could promote the sustainability of fisheries more efficiently (Mucientes et al., 2009).

Assessing movements in fish usually requires tagging them. The first efforts for tagging fish date back from the 17th century (McFarlane et al., 1990) but extensive tagging of several economically important species commenced in the 19th century and slowly expanded until about 1930 (Kohler and Turner, 2001). Generally, these tags have some sort of numeric or colored code which allows fish to be identified at recapture. While tag-and-recapture data provide precious information on some biological parameters such as age and growth (e.g. Afonso et al., 2012b), their efficacy on assessing shark movements is limited due to frequently low tag-recovering rates, which demand enormous tagging efforts. Furthermore, only the locations where the tagged animal was caught and released and caught again are known, with no information on the movements performed between those events being available. Methods to effectively assess

shark movements at higher resolutions only more recently become available since it depended on technological development.

One example of such technology pertains to acoustic telemetry, which has been used to track individual sharks since the 1960s (Carey, 1992). Currently, sound is the only effective way to transmitting a signal through seawater over appreciable distances because radio waves do not propagate efficiently in this medium (Nelson, 1990). The acoustic telemetry system comprises an acoustic transmitter, which is attached to the animal to be tracked, and a receiver unit which is able to detect and identify the emitted sound pulse. Ultrasonic frequencies (34−84 kHz) are generally used to reduce the size of transmitters, as frequency is inversely proportional to transducer diameter. Transmitters can be also equipped with sensors that measure environmental variables such as temperature and depth. An acoustic telemetry system may operate under two different approaches. Active telemetry presupposes a transmitter emitting a coded signal continuously and a human tracker equipped with a directional hydrophone and a portable transceiver. This technique provides high resolution data on shark movement rates but it greatly depends on weather conditions and is labor intensive, resulting in long tracks being generally not feasible. This brings an additional concern to this methodology because tracked individuals are usually captured and handled for transmitter deployment, and so they may experience a certain amount of post-release stress with possible influence on their behavior. Blue sharks off the U.S. northeast coast moved south and southeast following tagging and release on a seemingly seasonal migration, but it has been acknowledge that these movements could just be a behavioral reaction to capture (Carey and Scharold, 1990). Caution is therefore warranted when interpreting movement data collected during the post-release period.

Acoustic telemetry can also be used passively, in such a way that human labor is hardly required. Passive acoustic telemetry relies on stationary arrays of recording receivers equipped with omnidirectional hydrophones which can detect the presence of an animal fitted with a coded transmitter. The detection radius, i.e. the radius of the circular area around the receiver within which a transmitter will be detected, can fluctuate because it depends on seawater physical properties such as turbidity and background noise (Sims, 2010), but it commonly covers some hundreds of meters. Also, the lithium batteries used by the receivers last from 6 months to several years, thus allowing for long monitoring periods without human interference, as well as

the simultaneous monitoring of several individuals. Altogether, despite exclusively providing presence-absence data at predetermined locations, passive telemetry brings a series of advantages which allowed for a whole new focus on shark ecology. With this technique, patterns of movement and residency can be assessed at different temporal scales (i.e. diel, seasonal, and interannual) and also at broad spatial scales (Garla et al., 2006; Voegeli et al., 2001). Passive telemetry can also be used to estimate species activity spaces and home ranges provided the tracked individuals remain within the receiver array during most of the monitoring period (Heupel et al., 2004), which is not always verified (e.g. Carlson et al., 2008). Thus, this technique is mostly suited to monitor locations that coincide with the core activity space of individual sharks or locations to which sharks seasonally return (Bonfil et al., 2005; Simpfendorfer et al., 2002; Sims et al., 2006). During the last decade, a vast number of passive acoustic receivers has been deployed worldwide on both neritic and oceanic provinces as a global effort for setting up a network to monitor the migratory movements of wide-ranging species (see http://oceantrackingnetwork.org; Accessed 13 September 2012). Such initiative can greatly improve the efficacy of this methodology because a much greater area is acoustically monitored and thus researchers may obtain data relative to the movements that tagged animals perform in regions which fall beyond their individual study areas.

Acoustic telemetry provided an innovative tool for marine research but several constraints had still to be exceeded, particularly in regard to species exhibiting wide home ranges and little site attachment. It was during the 1980s that technological advances enhancing the miniaturization of data-logging computers revolutionized the study of wild fish behavior (Sims, 2010). The small size of such devices minimizes the interferences in the natural swimming behavior of tagged fish, and long-lasting batteries coupled with great, non-volatile memory capacity ensure the storage of large amounts of high-quality data. Given such aptitudes, these devices are referred to as archival tags. Environmental sensors measure temperature, pressure and ambient light-level with high accuracy at time-intervals as low as one second. With such information, it is possible to describe the movements of a shark within its depth and temperature ranges. Also, the geolocation of the shark along its track may be further estimated based on light-level, temperature, and depth data (Bradshaw et al., 2007; Hill and Braun, 2001; Hunter et al., 2004; Teo et al., 2004; West and Stevens, 2001), although these estimates produce a considerable error which vary in accuracy with latitude (Hays et al., 2001) and thus are most

effective in species that frequently move through great distances. Archival tags have been deployed extensively on the North Sea plaice, *Pleuronectes platessa* (Metcalfe and Arnold, 1997) and on Atlantic bluefin tuna, *Thunnus thynnus* (Block et al., 2001), but at that point the data retrieval depended on tags being returned by commercial fisheries, which may yield low recovery rates (Metcalfe and Arnold, 1997) and imply prohibitive investments. To overcome this issue, a hybrid device combining the functionality of data-logging archival tags with satellite transmission has been developed (Block et al., 1998). This new generation of electronic tags, known as pop-up satellite archival transmitters (PSAT), incorporated an ARGOS platform (PTT) which linked to the ARGOS constellation of satellites to stream the data into a remote ARGOS land-base. Animal tracking with ARGOS PTTs has been used for assessing the movements of birds, turtles, and cetaceans for a couple of decades (Priede and French, 1991; Watkins et al.,1999) but only more recently this technique became available for fish researchers. This is mostly due to satellite-linking being only possible at sea surface because radio waves do not propagate efficiently in seawater, and fish usually spend most time at some depth. Thus, these tags are generally programmed to pop off the animal after a certain period of time, when they float to the surface and start transmitting the summarized data to the ARGOS satellites. Other satellite tag models such as the Smart Position or Temperature Transmitting (SPOT) tag (Wildlife computers; Redmond WA, USA), may provide accurate, near real-time geolocation estimates of a tagged animal each time it surfaces during the battery life span, but consequently they are only suitable for studying species which surface frequently. All these satellite tags corresponded to an enormous methodological improvement as data retrieval was no longer dependent on commercial fisheries, and so they prompted the proliferation of studies on the long-term movements of a great diversity of wide-ranging species such as the European eel, *Anguilla anguilla* (Aarestrup et al., 2009), the striped marlin, *Kajikia audax* (Holdsworth et al., 2009), the ocean sunfish, *Mola mola* (Sims et al., 2009), the white shark, *Carcharodon carcharias* (Bruce et al., 2006), and the whale shark, *Rhincodon typus* (Gifford et al., 2007), among many others. For a review on satellite telemetry studies on sharks, see Hammerschlag et al. (2011).

Shark tagging with electronic tags has provided essential information and revealed some impressive details of the life-cycle and behavior of these apex predators, such as white sharks performing transoceanic, 10,000-km migrations in a relatively short time (Bonfil et al.,

2005) and whale sharks diving down to depths of 1.3 km (Brunnschweiler et al., 2009). Accurate information on shark movements coupled with environmental monitoring allows to assess patterns in habitat use of juveniles within coastal nursery grounds (Heupel and Hueter, 2002; Ortega et al., 2009, Wetherbee et al., 2007) and adults within larger oceanic areas (Saunders et al., 2011; Stevens et al., 2010), site fidelity (Bruce, 2006) and phylopatric behavior (Heuter et al., 2004), ontogenetic niche shifts (Chapman et al., 2007), habitat partitioning (Speed et al., 2010), sexual segregation (Sims et al., 2001), and social behavior (Guttridge et al., 2010). All this knowledge is most relevant to defining essential fish habitats (Rosenberg et al., 2000), which is indispensable to ensure the efficacy of species management strategies. Additionally, electronic tags may also provide information on post-release fishing mortality (Campana et al., 2009), thus offering a possibility to validate assumptions regarding the survival of non-target species which are alive at gear retrieval and subsequently released.

The tiger shark, *Galeocerdo cuvier*, is a large carcharhinid with circumglobal distribution at tropical and temperate latitudes which occurs in both coastal waters and the oceanic realm (Compagno, 1984). The relatively high abundance of this species off Recife (see chapter 4), together with forensic analysis (Gadig and Sazima, 2003), indicate that tiger sharks should be partly responsible for the high number of attacks on humans in this region (Hazin et al., 2008). The tiger shark is one of the three species of sharks with the highest record of attacks on humans in the world (ISAF, 2008); however, little is known about their spatial and behavioral ecology, particularly in the South Atlantic where such information is virtually inexistent. The successful management of shark attack hazard off Recife, nevertheless, strongly depends on understanding the underlying mechanisms of shark movements in this region, as well as within the much wider area that encompasses tiger shark habitats. Seasonal migrations of this species have been reported to occur in some regions (Heithaus, 2001; Wirsing et al., 2006), and evidence of transoceanic migrations have been published (Heithaus et al., 2007; Kohler et al., 1998), thus indicating that tiger sharks have wide home ranges. Tiger sharks have also been noted to exhibit a patrolling behavior throughout extensive coastal habitats, foraging over a 15−109 km section of shoreline during a period of time before leaving to a different area (Meyer et al., 2009). In addition, diel rhythmicity in tiger shark movements has been reported (Tricas et al., 1981). Such trends and behaviors have a clear relevance for the reasoning of the shark attack outbreak off Recife. Hazin et al. (2008) suggested that potentially aggressive sharks occurring off Recife were

moving downstream following northward coastal currents and that they were being attracted shoreward by commercial vessels entering the Suape port, after which they would move directly into the beaches where most attacks occurred. This hypothesis reinforces the importance of understanding tiger shark movement patterns better in order to approach shark attack mitigation measures more efficiently. Additionally, assessing the post-release behaviour of caught sharks may also contribute to evaluate and optimize the methodology used by the Shark Monitoring Program of Recife concerning fishing mortality and bather safety.

In this context, the present chapter aims at assessing horizontal and vertical movements and thermal preferences of tiger sharks caught off Recife, as well as the effect of sex, size, and some environmental factors on the spatial ecology of this species.

7.2. Material and Methods

7.2.1. Shark tagging

Tiger sharks were caught between June 2008 and September 2011 within the scope of the Shark Monitoring Program Program of Recife, whose fishing methodology is thoroughly described in chapter 4. Sharks were caught in coastal waters off Recife, 1−3 km from shore, and also about the middle continental shelf between 30−40 m isobaths, corresponding to about 15−25 km from shore. All sharks were carefully brought onboard, restrained on the deck, and eye-covered with a soaked dark tissue. Sharks caught in coastal waters were further transported offshore in order to remove them away from the area of risk. This was accomplished by accommodating sharks in a wooden tank filled with running sea water which was readily assembled after they were first sighted (Fig. SUP.7.1). The length and duration of the transport varied with oceanographic conditions and the health status of the shark, with releasing isobaths typically extending from 20 to 40 m. Before release, sharks were measured, sexed and tagged with conventional and electronic tags. Conventional tags were stainless steel, dart tags (FH-69; Floytag, Seattle, USA) with a bright colored plastic tubing holding an identification number, contact address and reward information to encourage tag returns. These tags were fitted into the dorsal musculature of the shark, just below the first dorsal fin (Fig. SUP.7.2), with a proper

applicator and should expectedly remain in the shark for several years, thus being suitable for tagging and recapture studies.

Two kinds of electronic transmitting tags were used: acoustic and radio. Acoustic tags (V16; Vemco, Halifax, Canada) were 69 KHz transmitters enclosed in a cylindrical epoxy case measuring 68 mm in length, 16 mm in width, and weighing 13 g in water (Fig. SUP.7.3). A couple of V13 transmitters (36 mm in length, 13 mm in width, and weighing 6 g in water) were also used in smaller sharks. These tags were surgically implanted in the peritoneal cavity of tiger sharks by making a midline ventral incision, about 3−4 cm long, in the postero-anterior direction with a scalp, inserting the sterilized tag, and closing the incision with a non-absorbable, monofilament, synthetic suture line (Fig. SUP.7.4). A single-layer, simple interrupted suture pattern was used. For this procedure, smaller sharks were held ventral-side up inside a water-filled, 1000 L container to induce tonic immobility. Acoustic tags were also available in a slightly longer PVC case, the so-called *shark case*, which provides attachment holes for external mounting (Fig. SUP.7.3), and this method was used when conditions did not allow the surgical procedure to be conducted or when the survival of the shark was of concern. In such situations, the tag was attached to the anterior region of the first dorsal fin by passing a coated, 2.0 mm nylon monofilament through a hole pierced with a 3.0 mm gauge needle and crimping it with a stainless steel sleeve so that the tag hanged loosely on the side of the dorsal fin. The expected life span of these acoustic tags was 715 days.

The pop-up satellite archival transmitters (PSAT) used (PAT-mk10; Wildlife computers, Redmond WA, USA) measured 175 mm in length, 40 mm in width, and weighed 75 g in air (Fig. SUP.7.5). PAT-mk10 tags withstand up to 2,000 m of pressure, thus they are equipped with an independent device which releases the tag from the animal if such depth is reached. PSAT tags were rigged with a 2.0 mm polyamide monofilament coated with high-resistance material and dark heat-shrink tubing, and were attached to sharks by passing the coated monofilament through a small hole pierced at the proximal middle portion of the first dorsal fin and crimping it with a stainless steel sleeve, similarly to the acoustic tag deployment. However, PSAT tags were placed in the sagittal plane immediately behind the first dorsal fin, and the length and slack of the monofilament were carefully adjusted and reduced to prevent the tag from crossing over the dorsal fin anteriorly while being towed by the shark (Fig. SUP.7.2).

This was believed to be the best attachment method because it is noninvasive and tags would have a minimum slack to oscillate during swimming.

7.2.2. The acoustic telemetry system

A passive acoustic system was used for monitoring tiger shark movements at specific locations, which included the already mentioned V13 and V16 transmitters and VR2W autonomous, omnidirectional receivers. Coded V16 transmitters emit acoustic ping trains that include an identification number, and VR2W receivers will record the time and presence of specific tagged sharks within the circular area limited by the detection range, which is defined by transmitter power output and seawater physical properties. The detection range was empirically measured at around 250 m in preliminary field testing. A total of 25 monitoring stations (i.e. fixed locations where acoustic receivers are installed and replaced during the study period) were strategically positioned off Recife within depths < 14 m, in an alongshore orientation in order to cover the whole distance between Paiva and Pina beaches (Fig. SUP.7.6). In the northern section of the monitored area, the presence of an alongshore channel next to the beach (see chapter 2) with considerable importance for the shark attack problem (Hazin et al., 2008) resulted in a second line of receivers being installed closer to shore (Fig. SUP.7.6). The wide extension of the study area and the small detection range did not allow a continuous coverage of the study area, and so some distance between consecutive receivers was not monitored. Additionally, receivers were also installed at other locations further away from shore, namely on three ship wrecks (*Chata de Noronha*: 7.93S, 34.72W; *Florida*: 8.02S, 34.68W; and *Walsa*: 8.13S, 34.68W) used for recreational diving, and at an offshore location (8.15S; 34.80W) where experimental cobia farming was being conducted, all of which located between 20−40 m isobaths. The receivers were attached to a moored float line, at about mid-water. Care was taken to keep the floats permanently on sub-surface regardless of tide height to prevent thefts. Data retrieval and battery replacement was conducted every 3 to 6 months.

7.2.3. Satellite tag programming and data analyzes

Satellite tags were programmed to be released between 30 and 180 days after deployment (see Table 7.2). During the tracking period, water depth (±0.5 m), temperature (±0.05ºC) and light level were recorded every second. Light level is measured as irradiance at an wavelength of 550 nm, ranging from 50^{-12} to 50^{-2} W·cm^{-2}, and was used to reconstruct the horizontal movements performed by the shark during the track. By the end of the track, the raw data were further summarized into temporal bins of 2−24 hours (see Table 7.2) for ARGOS data transmission because the narrow ARGOS receiver bandwidth does not allow the transmission of large amounts of data in due time. ARGOS-relayed data provide several types of information. First, it informs the maximum and minimum depth of the shark within each temporal bin and includes temperature measurements at eight equidistant points across the depth range (i.e., the so-called PDT profile messages). Second, it provides histograms informing the distribution of depths and temperatures at each temporal bin (i.e., the so-called time-at-depth, TAD, and time-at-temperature, TAT, histogram messages). For this, depth and temperature data were binned in 14 strata which were costumized before deployment, and the time spent at each stratum was continuously monitored. Disregarding minor variations in the first deployments, depth strata were generally arranged by classes < 1, 1−5, 5−10, 10−20, 20−40, 40−60, 60−80, 80−100, 100−125, 125−150, 150−200, 200−250, 250−300, and > 300 m, while temperature strata were arranged by classes < 12, 12−14, 14−16, 16−18, 18−20, 20−22, 22−24, 24−25, 25−26, 26−27, 27−28, 28−29, 29−30, and > 30 ºC. Heterogeneous strata sizes required temporal data to be standardized by either depth- or temperature-unit before assessing tiger shark environmental preferences. Third, a time-series of depth and/or temperature at regular, short time intervals (in this case, between 2.5 and 10 minutes) is also provided by more recent versions of this tag, and was used in a few deployments. Finally, information on light level variation during sunrise and sunset events is provided for light-based geolocation processing. If a PSAT tag is physically recovered, then the entire archived dataset will be available. Further information on PAT-mk10 tags can be found at http://www.wildlifecomputers.com/products.aspx?ID=7. A detailed description of the ARGOS system can be accessed at http://www.argos-system.org/manual.

Pop-up locations were considered to correspond to the first geolocation estimate successfully calculated by ARGOS satellites, except when a premature release was detected,

which implied a time-lag of 48−72 hours between actual pop-off and the beginning of transmissions. In such circumstances, and if the tag had been drifting prior to satellite-linking, drift direction and speed were assessed based on ARGOS geolocation estimates with location classes ≥ 1, representing an error < 1 km (Hays et al., 2001), for the first 24 h of satellite-linking. The actual pop-up location was then estimated by calculating the distance drifted by the tag during the period of time it was floating at the surface until first transmission. Otherwise, if the tag had been washed up onshore before transmitting, there were no means to estimate its actual pop-up location. Also, the movement behavior of transmitting PSAT tags was continuously monitored to assess the possibility of tag recovering (e.g. when it was transmitting from or close to land) and to verify if the shark had been caught by fishermen, which can be deduced from unnatural movements in a purportedly drifting tag.

Sharks were classified as small (< 150 cm TL), medium (≥ 150 and < 250 cm TL), and large (≥ 250 cm TL) for statistical analyzes. Large sharks were all female, so they were removed from sex comparisons. The first week of data after tagging was also discarded to minimize potential bias due to unnatural post-release behavior. Shark #1 was discarded from most analyses because its PSAT-tag was programmed with a 24-hour bin, which may not be fully comparable with other tags. Moreover, archival data from recovered PSAT tags were pooled in 3-hour bins to match the temporal resolution of ARGOS-relayed datasets from other tags. The vertical movements of tiger sharks across the study period were plotted, together with depth-temperature profiles of the water column. Although preliminary analyzes showed that data homocedasticity and normality were verified in some instances, they were generally absent, hence non-parametric statistics were used in all comparisons for consistency purposes. A Kruskal-Wallis rank sum test was used to compare tiger shark maximum depth, minimum temperature, and depth and temperature ranges between sexes and sizes (small, medium and large). For comparisons between sexes, only sharks #6, #8, #18 and #21 were considered because they corresponded to the most balanced experimental universe by comprising an equal number of males and females with matching sizes. Such strategy aimed at excluding possible influences of shark size on sex comparisons. A post-hoc procedure available in the function *kruskalmc* from the *pgirmess R* library (Giraudoux, 2011) was applied to assess which size classes were significantly different.

Also, differences in tiger shark vertical distribution across diel and lunar cycles were examined for each shark independently and for all sharks combined. To accomplish that, four surface-related ranges of water depth hierarchically selected so that the fourth depth range covered the whole surface mixed layer (SML) were defined at < 10 m, < 20 m, < 40 m, and < 60 m. Then, the proportion of time spent at each lunar phase (i.e. first quarter, full moon, last quarter, new moon) was compared for each depth range separately with a Kruskal-Wallis rank sum test. The *kruskalmc* function (Giraudoux, 2011) was further applied to assess significant differences between pairwise lunar phases. Variations in statistical significance across the four depth ranges were interpreted as to define the extent of surface-related water column exhibiting an effect across the lunar cycle. Only sharks yielding data in the four moon phases were included in this analysis. A similar approach was used to compare the proportion of time spent at each diel phase (daylight *vs* nocturnal) for each depth range, which was achieved with a Wilcoxon rank sum test. Furthermore, a modified version of the split moving window gradient analysis (SMWGA) method (Cornelius and Reynolds, 1991) with a 20,000-interaction bootstrap was used to detect significant shifts in time-at-depth (TAD) data. In this procedure, a variable-sized split window ranging from 3, 4, or 6 hours to a maximum of 8 days was used to compute dissimilarities between the two halves of the split window along the temporal units of the track. Euclidean multivariate measures of dissimilarity between all possible combinations of different half-windows were assessed, and the values of all comparisons were averaged. This average was then assigned to the centre of the window, which further moved one step forward, and the statistical significance of dissimilarities was calculated with a randomization technique and coded with 1, if significant, or 0, if non-significant. The whole process was repeated until reaching the end of the data series, and the results from each window size were finally piled in a matrix for plotting. This produces a figure which can be graphically evaluated to identify significant differences along the time-series. Whenever a significant shift in TAD data is detected, an image resembling an inverted triangle will be depicted, with its lower vertex pointing to the boundary between different behaviors. These images may not always resemble triangles (e.g. when statistical differences were weak, or when successive behavioral shifts occur in little time, which may result in superimposed triangles), thus they should be carefully scrutinized. Furthermore, this modified method has the advantage of not requiring evenly

distributed data, thus being adequate to analyze ARGOS-relayed data with temporal gaps due to incomplete data transmission (Queiroz et al., 2010).

The horizontal movements of tiger sharks were examined by assessing daily maximal rate of change in light level, which provides estimates of local time of midnight or midday and daytime duration for longitude and latitude calculations (Hill and Braun, 2001). This was accomplished with software provided by the tag manufacturer (WC-GPE global position estimator; Wildlife computers, Redmond WA, USA). Unlikely longitude estimates biased by severe light level shifts resulting from diving behavior during sunrise and sunset events were discarded. A state-space statistical model in combination with the Kalman filter (Sibert and Fournier, 2001; Sibert et al., 2003) was used to estimate the most probable track of tagged tiger sharks. This model is available as the *KFtrack* library in *R* statistical software (Nielsen and Sibert, 2004) and has been widely used because it improves light-based geolocation estimates assessed by the manufacturer software and provides movement parameters applicable to population-level models (Musyl et al, 2003; Sibert el al., 2003; Wilson et al., 2005). Different approaches which incorporate sea surface temperature (SST) data acquired from satellite imagery to match against SST data measured by the tag were also attempted. These included a KFtrack extension, available as the *KFSST R*-library (Nielsen and Sibert, 2005; Nielsen et al. 2006), and the *FindLats* algorithm developed by Teo et al. (2004). However, these SST-based approaches generally yielded poor results, probably due to the verry narrow SST range in the study area, and were not further considered.

Data analyses and plots were performed with *R* 2.12.2 (*R* development core team, 2011) and IGOR Pro 6.1© (WaveMetrics, Inc.; Lake Oswego OR, USA). The ARGOS locations of the transmitting tag and associated errors were mapped with Google Earth 6.1.0.5001© (Google Inc.; Mountain View CA, USA), and measurements of both the distance to shore and the shorter soak distance between pop-up and deployment locations were taken. The most probable tiger shark tracked movements estimated by the KFTrack algorithm were mapped with ArcMap 9.3™ (ESRI; Redlands CA, USA).

7.3. Results

7.3.1. Tagging details and diagnosis

A total of 22 tiger sharks comprising 11 males and 11 females and measuring between 90 and 295 cm in total length (TL) were tagged and released off Recife, representing a total of 15 acoustic transmitter deployments and 16 PSAT-tag deployments (Table 7.1). Most sharks were released in good health conditions except for three sharks which did not respond when released and thus had to be assisted by one person in the water, who balanced them at the sea surface and pushed them upstream until they demonstrated an autonomous swimming capacity. Also, two other sharks could not easily maintain their biological position underwater by releasing time (i.e., they tended to turn with their ventral-side up) and so they were kept in the hook next to the boat until they exhibited enough strength to be released (Table 7.1).

Satellite tags yielded a total of 865 tracked days, averaging 54 (±37.4) days per tiger shark. Nine out of the 16 PSAT-tag deployments (i.e., 56%) ended prematurely and one tag transmitted about one month after the scheduled pop-up date, resulting in tracking periods ranging from 4 to 159 days (Table 7.2). Three prematurely-released tags deployed on sharks #2 and #9 and #21 that had been drifting at the surface before initializing satellite transmissions were corrected for their pop-up positions, but corrections were not possible in the case of shark #6 because the tag did not follow a linear motion in the beginning of ARGOS transmissions, thus obscuring the direction from which the tag was drifting before transmitting. Examples of tag drifting and pop-up corrections can be found in figures SUP.7.7−9. Pop-up locations were also impossible to assess in three other prematurely-released tags and so the first ARGOS successful geolocation estimate was considered as a proxy of pop-up position in such circumstances. In one occasion, the pop-up position was informed by fishermen after capturing a tagged shark during its track. Additionally, one prematurely released tag was identified by ARGOS satellites but it uplinked an insufficient number of times and no tracking data or geolocation estimates were obtained.

Satellite-linked data streaming occurred during a total of 98 days, averaging 6 (±2.1) days per transmitting tag (Table SUP.7.1). This resulted in a total of 1,944 satellite passes with successful tag transmissions, averaging 122 (±57.4) passes per tag. Of these, 1,803 (93%)

Table 7.1. Summary of tiger sharks caught and tagged off Recife between June 2008 and September 2011, with information on total length (TL) in cm, sex, date of tagging, location of tagging, type of tag, and at-release health condition.

Shark	TL	Sex	Date	Location	Tags*	Health
#1	130	M	28−Jun−2008	8.17ºS; 34.84ºW	S	Good
#2	193	M	24−Jul−2009	8.14ºS; 34.89ºW	C,S	Good
#3	128	F	01−Jun−2010	8.20ºS; 34.77ºW	C,S	Good
#4	154	F	01−Aug−2010	8.15ºS; 34.88ºW	C,S	Good
#5	150	M	07−Aug−2010	8.17ºS; 34.88ºW	C,S	Good
#6	190	F	21−Dec−2010	8.33ºS; 34.70ºW	C,S,Ae	Good
#7	295	F	06−Jan−2011	8.21ºS; 34.70ºW	C,S,Ae	Good
#8	120	M	05−Feb−2011	8.15ºS; 34.88ºW	C,Ai	Good
#9	190	M	08−Feb−2011	8.18ºS; 34.68ºW	C,S,Ae	Poor
#10**	110	F	12−Feb−2011	8.11ºS; 34.89ºW	C,Ai	Good
#11	115	M	13−Feb−2011	8.25ºS; 34.92ºW	C,Ai	Good
#12	120	F	05−Mar−2011	8.10ºS; 34.86ºW	C,S,Ai	Good
#13	97	F	06−Mar−2011	8.15ºS; 34.88ºW	C	Good
#14	90	M	15−Mar−2011	8.15ºS; 34.79ºW	C	Good
#15	270	F	22−Mar−2011	8.20ºS; 34.68ºW	C,S,Ae	Fair
#16	156	M	03−Jul−2011	8.21ºS; 34.90ºW	C,Ai	Good
#17	125	M	11−Jul−2011	8.16ºS; 34.88ºW	C,S,Ai	Fair
#18	170	M	11−Jul−2011	8.17ºS; 34.88ºW	C,S,Ae	Poor
#19	134	F	25−Jul−2011	8.23ºS; 34.91ºW	C,S,Ai	Good
#20	156	M	14−Aug−2011	8.24ºS; 34.91ºW	C,S,Ae	Good
#21**	172	F	22−Aug−2011	8.24ºS; 34.92ºW	C,S,Ae	Good
#22	253	F	05−Sep−2011	8.15ºS; 34.88ºW	C,S,Ae	Fair

*****C = conventional; Ai-e = acoustic internal/external; S = satellite;
**Correspond to the same shark caught in different times

Table 7.2. Summary of PSAT-tag deployments off Recife between June 2008 and September 2011, with information on the programmed study span, actual track span, pop-up location, the shortest soak distance (in km) between deployment and pop-up locations, distance (in km) from pop-up location to shore, maximum depth, temperature range, number of hours per data bin, and time-series availability.

Shark	Prog span	Track span	Pop-up location	Shorter distance	Distance to shore	Max. depth (m)	ΔTemp. (ºC)	h·bin^{-1}	Time-series
#1	30 d	30 d	6.329ºS; 34.796ºW	209	23	248	13.6 – 27.0	24	No
#2	75 d	4 d	7.34ºS; 34.65ºW*	94*	16*	56	25.0 – 27.6	3	No
#3	73 d	74 d	7.979ºS; 34.667ºW	33	15	200	15.0 – 29.0	3	No
#4	50 d	42 d	***	***	***	***	***	2	No
#5‡	99 d	72 d	7.083ºS; 34.846ºW**	125**	inland**	483	8.2 – 28.0	4	No
#6	48 d	26 d	4.795ºS; 35.915ºW	442**	28**	320	9.6 – 28.2	3	Yes
#7	96 d	96 d	3.647ºS; 37.200ºW	622	104	840	4.6 – 30.0	4	No
#9	49 d	23 d	4.12ºS; 35.85ºW*	476*	103*	848	4.6 – 29.0	3	Yes
#12	70 d	70 d	6.990ºS; 34.760ºW	132	7	352	10.6 – 31.2	6	Yes
#15	120 d	159 d	2.694ºS; 42.065ºW	1193**	inland**	1112	4.0 – 30.0	12	Yes
#17‡	100 d	44 d	7.017ºS; 34.840ºW	133†	0.5†	318	10.5 – 27.4	6	Yes
#18	60 d	60 d	12.574ºS; 37.906ºW	598	9	592	6.2 – 27.8	4	Yes
#19	62 d	52 d	4.698ºS; 35.745ºW	428	43	256	12.2 – 27.2	12	Yes
#20	60 d	60 d	7.099ºS; 34.689ºW	130	13	360	9.0 – 27.0	4	Yes
#21	60 d	10 d	7.03ºS; 34.72ºW*	137*	11*	400	8.4 – 27.0	4	Yes
#22	180 d	43 d	11.745ºS; 33.733ºW	417†**	321†**	448	8.0 – 26.8	12	Yes

*estimated from tag drift; **relative to first transmission; ***tracking data not available; †captured by fishermen; ‡recovered PSAT tag

provided an ARGOS estimate of the location of the transmitting tag. The distribution of ARGOS location classes (LC) was generally consistent across deployments, with 32% (±13%) of the geolocation estimates being represented by LC = 2, 28% (±16%) by LC = 3, 21% (±19%) by LC = A and LC = B combined, 14% (±8%) by LC = 1, and 5% (±4%) by LC = 0. However, some deployments showed high proportions of poor-quality ARGOS location estimates, particularly sharks #22 and #17 (Table SUP.7.1). A total of 13,122 messages were up-linked to ARGOS satellites, averaging 820 (±504) messages per tag, but as many as five deployments yielded less than 500 messages, equaling the number of tags which transmitted more than 1,000 messages. On average, 68% (±20%) of the transmitted messages were successfully decoded by the ARGOS system (Table SUP.7.1).

7.3.2. Postrelease behavior

After being transported away from shore and released, most tiger sharks reacted well and actively moved away from the boat. Notably, many specimens stayed visibly at the surface in slow swimming for a considerable time, as long as five minutes, before diving out of sight. One specimen first headed towards land but suddenly inverted its direction, ~20 m further, and returned to the boat always at the surface, eventually diving to pass under the boat in the direction of open sea.

Most sharks moved to oceanic waters within the first 24 hours at liberty. This was clearly visible in ARGOS-relayed depth data, since sharks dove to great, > 60 m depths in the first temporal units of their respective tracks (Fig. 7.4; Fig. SUP.7.10). However, archival depth data from two recovered PSAT tags described this offshore movement with exceptional detail.

Shark #5 remained mostly at the surface for about 20 minutes after being released, and then it dove suddenly to 18 m depth, where it stayed for another 10 minutes before starting to execute oscillatory, yo-yo vertical movements spanning from the surface to 20 m depths (Fig. 7.1). This oscillatory diving behavior endured for over 12 hours, with the amplitude of vertical movements gradually increasing into deeper waters until a depth of about 60 m was reached, corresponding to the depth of the continental shelf break. By this time, the diving behavior changed dramatically, with wider vertical movements between shallow waters and depths > 100

m being continuously performed (Fig. 7.1). This wide-ranging and somewhat erratic movement pattern persisted for about seven days but it then led to a more regular pattern characterized by a higher affinity for shallower, < 60 m depth waters, periodically interrupted by short episodes of deep-diving behaviour.

Shark #17 exhibited a slightly different behavior because it performed yo-yo diving movements immediately after being released, with the amplitude of those movements increasing markedly during a ~24 h period, after which the shark dove suddenly down to ~200 m deep (Fig. 7.2). During the following week the shark exhibited a consistent diving pattern, spanning from the surface until ~60 m in depth except for a short period of time when deeper dives occurred. Also, the decreasing dive amplitudes after one week at liberty suggest that the shark may have moved shoreward to shallower waters in that period, but soon after it returned to oceanic waters and intensified the deep-diving behavior (Fig. 7.2).

Sharks #2 and #12 were the only exceptions regarding this postrelease deep-diving behavior, and apparently did not leave the continental shelf during the initial period at liberty, although they moved offshore to deeper, 40−60 m waters, as observed from diving profiles and from a cooling in water temperature in the case of shark #2 (Fig. 7.4; Fig. SUP.7.10). Interestingly, sharks #1, #3 and #5 exhibited roughly similar behavioral patterns in performing deep dives during the first 13.3 (±1.5) days at liberty and moving to shallower waters afterwards.

7.3.3. Vertical movement analysis

The distribution of tiger sharks in the water column ranged from the surface to 1,122 m in depth and was associated to a thermal gradient of 27.2ºC, ranging between 4.0 and 31.2 ºC (Table 7.2). The variation of seawater temperature with depth pooled for all PSAT tags showed a consistent profile, with the surface mixed layer (SML) extending to about 60−80 m in depth and a broad thermocline occupying depths between 80 and 500−600 m (Fig. 7.3). Temperature in the thermocline dropped nearly 20ºC throughout a depth range of about 500 m, whereas in the SML it still exhibited a considerable amplitude, exceeding 5ºC at surface waters.

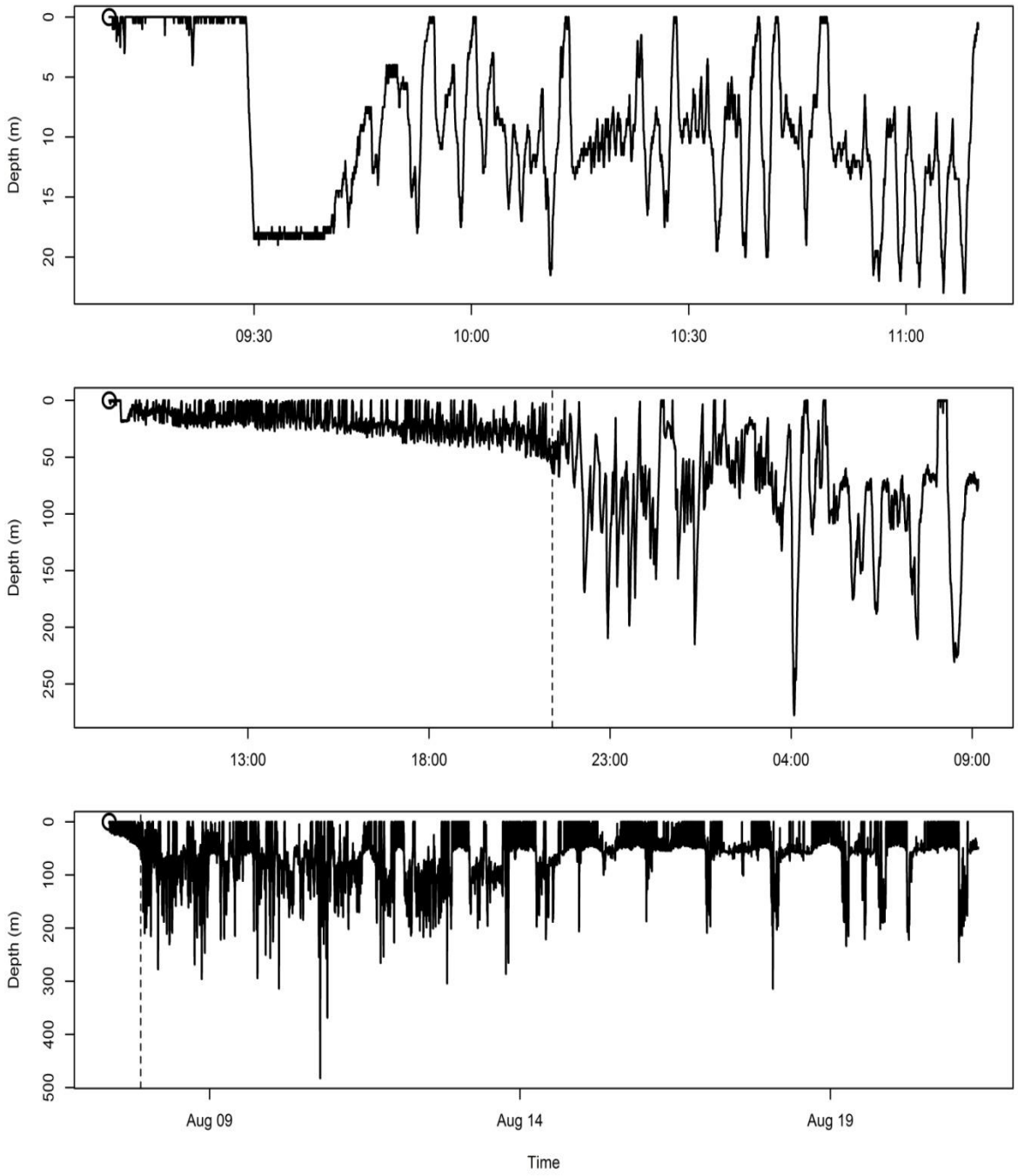


Figure 7.1. Post-release diving behavior of tiger shark #5 during the first 2 hours (top panel), the first 24 hours (middle panel) and the first two weeks after tagging. The open circle represents the beginning of the track, roughly coinciding with shark release, and the vertical dashed line represents the time at which the shark reached the shelf break.

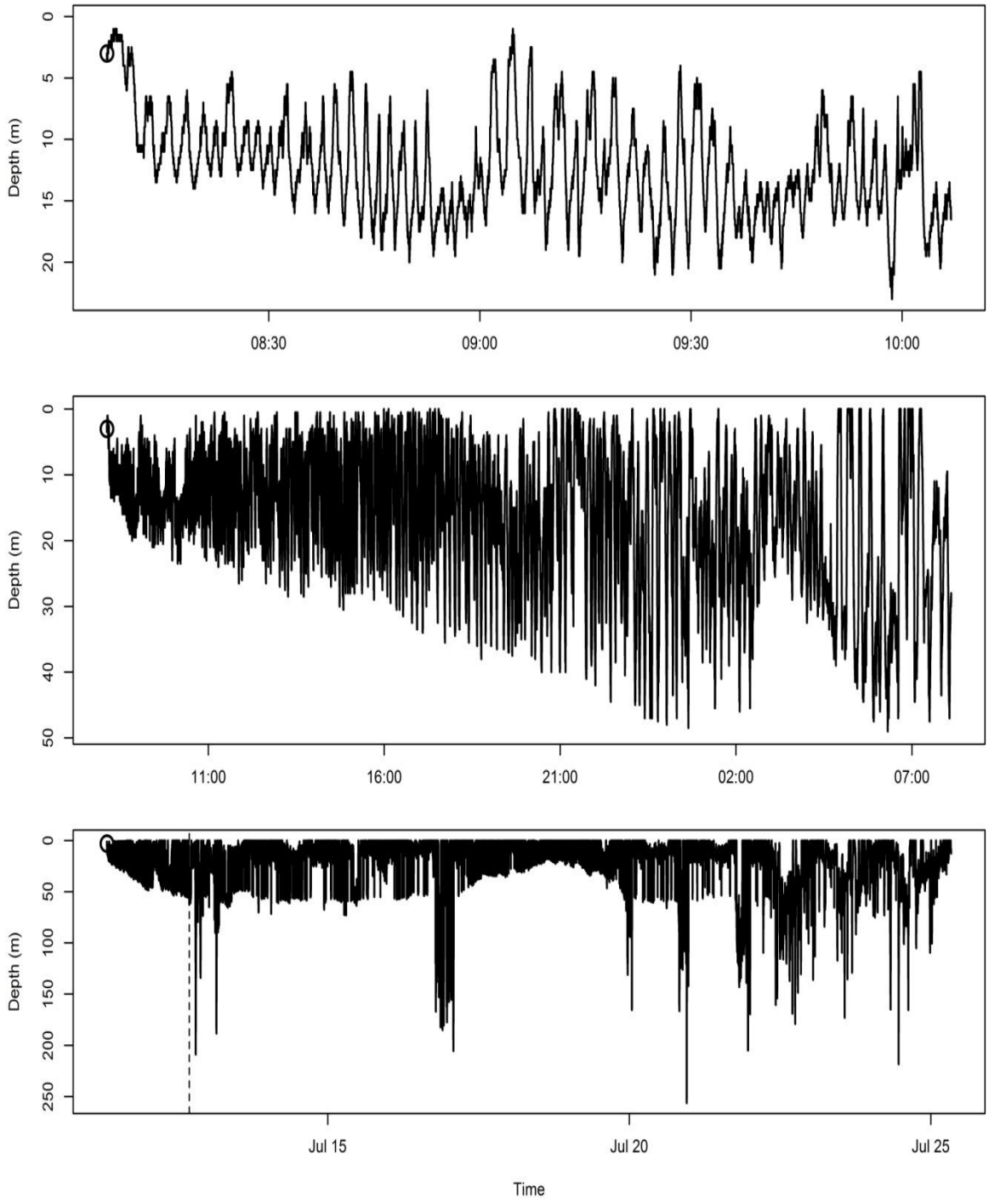


Figure 7.2. Post-release diving behavior of tiger shark #17 during the first 2 hours (top panel), the first 24 hours (middle panel) and the first two weeks after tagging. The open circle represents the beginning of the track, roughly coinciding with shark release, and the vertical dashed line represents the time at which the shark reached the continental shelf break.

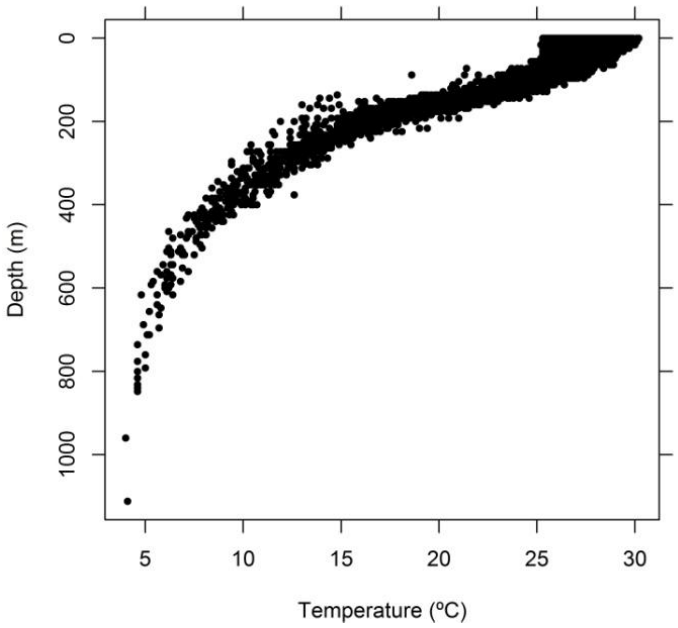


Figure 7.3. Variation of sea-water temperature across a depth range sampled by PSAT-tags attached to 16 tiger sharks off northeastern Brazil. Each dot represents a data sample.

The ARGOS-relayed depth-and-temperature (PDT) profiles of tiger shark movements exhibited gaps in data due to unsuccessful transmissions to the satellites, which precluded the examination of global trends in some deployments (Fig. 7.4; Fig. SUP.7.10). Nevertheless, nearly complete datasets were obtained for several sharks, which evidenced different patterns in diving behavior. Both sharks #1 and #3 performed > 200 m deep dives in the beginning of the track but they moved in waters less than 50 m in depth for most of the time (Fig. 7.4), similarly to sharks #5 and #12 (Fig. SUP. 7.10). The maximum dive depth of shark #2 was < 60 m, but it was tracked during four days only (Fig. 7.4). Conversely, other sharks tended to perform deep dives throughout their tracks, such as sharks #6, #9 and #21 (Fig. 7.4), and sharks #7, #15, #17, #18 and #19 (Fig. SUP.7.10). Overall, most deep dives occurred at depths between 200 and 400 m, but sharks #7, #9, #15 and #18 dove frequently into deeper, colder waters (Fig. 7.4; Fig. SUP.7.10).

Altogether, tiger sharks spent most time in the upper layer of the water column, swimming at depths shallower than 10 m for about 60% of the duration of their tracks (Table 7.3). The time spent in deeper waters decreased with depth, with depths greater than 150 m accounting for less than 1% of the monitored period. Sharks #2, #7, #9, #12, #15, #18 and #22

exhibited higher affinity for surface waters, having spent more than 50% of the time at depths < 5 m (Table 7.3). Sharks #7, #9, #15 and #22 also spent some time at depths > 100 m, together with sharks #6 and #21. Moreover, sharks #3 and #6 showed a much higher utilization of depths between 20−60 m than of adjacent water layers. All these sharks showed a bimodal distribution in time-at-depth (TAD) data, with surface waters and waters around 20−60 m in depth being most used (Table 7.3).

The thermal distribution associated to tiger shark movements evidenced a strong predominance of temperatures between 26 and 30ºC, followed by temperatures between 22 and 26ºC (Table 7.4). Sharks #6 and #12 showed a significant use of warm, > 30ºC waters, whereas sharks #7, #9, #15, #2 and #22 moved to colder, < 18ºC waters more frequently. Sharks #2 and #3 experienced the narrowest temperature range, moving in waters between 22 and 30ºC, but sharks #7 and #15 were exposed to warmest and coolest waters with comparably high frequencies (Table 7.4).

The archival data obtained from two recovered PSAT tags (sharks #5 and #17) allowed a more reliable analysis of shifts in TAD profiles throughout the tracking period by the application of the Split Moving Window Gradient Analysis (SMWGA), since their datasets have no gaps. During the first week at liberty, shark #5 used waters shallower than 200−300 m uniformly, but after one week it spent most time at specific depths, alternating between the upper 10 m of the water column and depths of 40−60 m (Fig. 7.5). During a ~3-week period, a trend for using shallower waters more often was evidenced, whereas one month after releasing onwards, the shark mostly alternated between the upper 10 m of the water column and waters between 10−20 m in depth (Fig. 7.5). The almost exclusive utilization of shallow, < 10 m waters prevailed during considerable periods of time, being most significant from 13 to 19 September and in the last three days of the track. The SMWGA procedure evidenced a clear, statistically significant shift in behaviour on 29 August, and three other moments with less clear indications of behavioural shifting, which occurred about 21 August, 9 September and 13 October (Fig. 7.5).

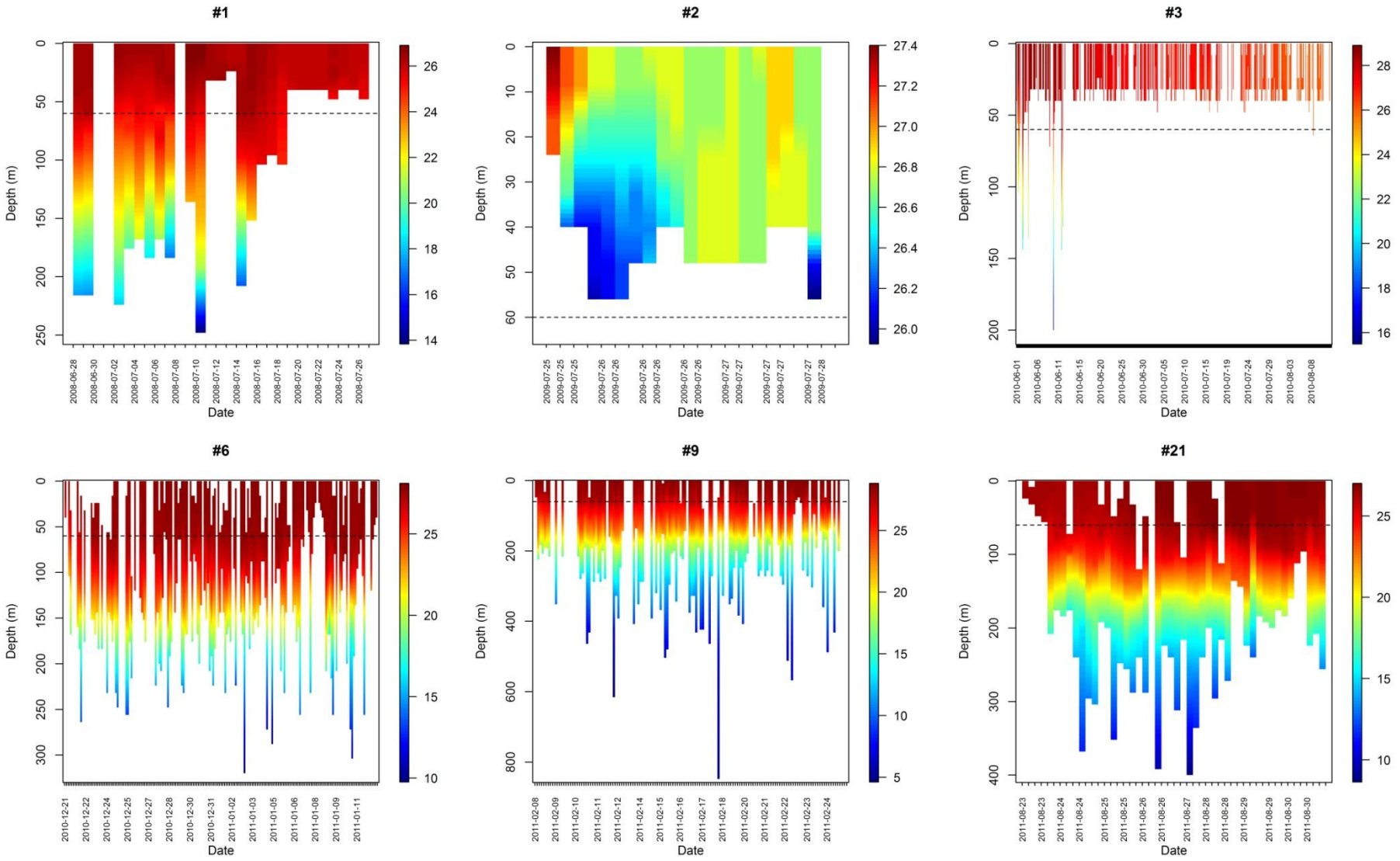


Figure 7.4. Depth-and-temperature (PDT) profiles of the movements of tiger sharks #1, #2, #3, #6, #9, and #21 assessed with PSAT tags off northeastern Brazil. Colors represent the gradient of sea water temperature. Horizontal dashed lines depict shelf break depth. Note the different scales in vertical axis and color bars.

Table 7.3. Overall proportion of time (average ± standard deviation), in percentage, spent at each depth stratum for all sharks combined and each shark separately. Data was standardized by depth unit (m) because depth strata have unequal sizes. Note that averages in each row may not always sum 100 due to accumulation of rounding errors.

Shark	0−5 m	5−10 m	10−20 m	20−40 m	40−60 m	60−100 m	100−150 m	> 150 m
All	42 (±29)	19 (±19)	11 (±15)	11 (±20)	6 (±14)	5 (±12)	5 (±13)	0.5 (±2)
#1	43 (±15)	29 (±11)	12 (±9)	9 (±7)	5 (±8)	1 (±3)	0.8 (±2)	0.1 (±0.1)
#2	71 (±14)	11 (±7)	8 (±7)	6 (±5)	4 (±5)	0	0	0
#3	38 (±24)	32 (±21)	7 (±10)	22 (±31)	0.8 (±5)	0 (±0.4)	0 (±0.1)	0
#5	31 (±25)	27 (±22)	21 (±25)	7 (±14)	9 (±21)	3 (±8)	2 (±8)	0.3 (±1)
#6	24 (±27)	7 (±8)	7 (±9)	13 (±17)	25 (±26)	15 (±22)	8 (±15)	1 (±2)
#7	59 (±31)	3 (±3)	2 (±2)	2 (±2)	4 (±6)	14 (±17)	14 (±17)	0.8 (±1)
#9	51 (±30)	10 (±12)	5 (±7)	3 (±3)	4 (±4)	10 (±12)	15 (±22)	0.7 (±1)
#12	64 (±31)	17 (±18)	10 (±16)	8 (±19)	1 (±5)	0.1 (±1)	0 (±0.5)	0 (±0.1)
#15	56 (±22)	12 (±8)	8 (±8)	4 (±11)	5 (±6)	9 (±10)	5 (±7)	0.2 (±0.2)
#17	34 (±17)	24 (±10)	27 (±18)	9 (±14)	4 (±10)	1 (±2)	0.2 (±0.6)	0 (±0.1)
#18	55 (±30)	11 (±10)	10 (±12)	11 (±17)	5 (±8)	5 (±9)	3 (±11)	0.3 (±1)
#19	38 (±20)	20 (±13)	13 (±12)	10 (±13)	12 (±20)	6 (±16)	1 (±4)	0 (±0.1)
#20	19 (±17)	26 (±20)	25 (±22)	19 (±26)	5 (±10)	3 (±7)	3 (±7)	0.3 (±1)
#21	21 (±23)	13 (±11)	12 (±13)	10 (±10)	11 (±13)	10 (±13)	18 (±24)	5 (±10)
#22	63 (±27)	13 (±9)	6 (±6)	2 (±2)	2 (±2)	4 (±4)	7 (±11)	2 (±3)

The overall diving behaviour of shark #17 was considerably different because it performed deep dives during most of its track span. In fact, the period on which this shark exclusively used waters < 50 m in depth were restricted to a few days from 17 to 19 August, and from 16 to 18 and from 20 to 23 September (Fig. 7.6). Nonetheless, shark #17 generally spent most time in the upper 10 m of the water column, followed by waters 10−20 m in depth. A greater use of depths between 20 and 30 m was also observed by the end of the track. The SMWGA procedure could not detect any significant behavioral shifts during most of the tracking period, but after one month at liberty three indications of possible shifts in the vertical distribution with a lag of about 5 days were detected (Fig. 7.6).

Table 7.4. Overall proportion of time (average ± standard deviation), in percentage, spent at each temperature stratum for all sharks combined and each shark separately. Note that the sum of each row may not always equal 100 due to accumulation of rounding errors.

Shark	< 12 ºC	12−18 ºC	18−22 ºC	22−26 ºC	26−30 ºC	> 30 ºC
All	0.2 (±1)	2 (±4)	4 (±10)	19 (±27)	73 (±34)	2 (±11)
#1	0	0.1 (±0.2)	0.4 (±1)	24 (±21)	76 (±21)	0
#2	0	0	0	5 (±22)	95 (±22)	0
#3	0	0	0	3 (±15)	97 (±15)	0
#5	0	0.2 (±1)	2 (±5)	20 (±33)	78 (±35)	0
#6	0 (±0.3)	1 (±2)	4 (±7)	18 (±22)	77 (±26)	15 (±22)
#7	1 (±3)	6 (±7)	13 (±10)	34 (±20)	46 (±25)	6 (±14)
#9	1 (±2)	4 (±5)	8 (±9)	39 (±24)	48 (±27)	0
#12	0	0.1 (±0.3)	0.1 (±1)	3 (±11)	97 (±12)	21 (±38)
#15	1 (±2)	4 (±6)	10 (±11)	32 (±19)	54 (±25)	5 (±11)
#17	0	0.4 (±3)	1 (±3)	13 (±27)	86 (±28)	0
#18	0.2 (±1)	1 (±3)	6 (±15)	39 (±38)	54 (±39)	0
#19	0	0.1 (±0.1)	2 (±5)	19 (±30)	35 (±40)	0
#20	0 (±0.2)	1 (±1)	2 (±7)	15 (±29)	83 (±31)	0
#21	0.1 (±0.3)	4 (±5)	20 (±27)	30 (±26)	46 (±36)	0
#22	0.4 (±1)	3 (±4)	13 (±14)	43 (±28)	41 (±32)	0

ARGOS-relayed time-at-temperature data were also examined for all remaining sharks but, similarly to PDT data, some deployments resulted in considerable gaps in the dataset. Shark #3 used depths between 0−10 m and 20−40 m more frequently, while depths between 10−20 m were seldom used (Fig. SUP.7.11). The SMWGA procedure detected a significant shift only after about 2 months at liberty. Shark #6 spent more time at depths between 40−60 m, but it also used waters 125−150 m in depth more frequently in some occasions (Fig. SUP.7.11). The SMWGA detected a significant shift in shark #6 behavior about 10 days after release, with some weak signs of another shift occurring one week later. Although shark #7 deployment provided little TAD data, this shark appeared to move uniformly within waters from the surface to about 200 m in depth (Fig. SUP.7.11). Still, the SMWGA detected three well defined, and a fourth less defined, shifts in behavior, which occurred around 9 and 16 January and 2 and 18 February. Sharks #12, #15, #18, and #20 also had little TAD data and generally showed similar patterns,

usually spending more time at surface waters or at depths between 30 and 50 m, but the SMWGA detected shifts after one week and two weeks at liberty for shark #12, and after about two weeks at liberty for shark #15 (Fig. SUP.7.12−13). An analogous pattern was exhibited by shark #19 (Fig. SUP.7.13). Shark #21 had a short deployment but it spent most time at depths from 100 to 150 m during the first 6 days at liberty, spending more time at surface waters afterwards, with the SMWGA detecting a significant behavioral shift ~5 days after releasing (Fig. SUP.7.13). The SMWGA was not able to detect any shift in the behavior of sharks #1, #2, #9 and #22, but shark #1 seemed to spend more time in shallower waters during the second half of its track. A similar trend was also observed for shark #2 although it was less conspicuous due to the comparably shallower dives of this specimen (Fig. SUP.7.14). Conversely, shark #9 spent more time at deeper waters (100−150 m), while shark #22 did not exhibit a preferred depth despite it also used deeper waters (Fig. SUP.7.14). Time-at-temperature (TAT) data is only shown for sharks #1, #2, #9 and #22 (Fig. SUP.7.14) to avoid including an excessive amount of information.

The sex apparently had little influence on the vertical movements of four tiger sharks, although males moved to slightly greater depths and were thus exposed to slightly lower temperatures than females (Fig. 7.7). In agreement, Kruskal-Wallis tests did not detect any significant differences in tiger shark maximum depth, minimum temperature, and both depth and temperature ranges between sexes (Table SUP.7.2). On the other hand, tiger shark size showed a clear influence on their vertical movements. Indeed, the maximum depth, minimum temperature, and depth and temperature ranges were directly proportional to shark size, with smaller specimens diving in consistently shallower, warmer waters and larger sharks progressively diving into deeper, colder waters (Fig. 7.7). Accordingly, Kruskal-Wallis tests detected significant differences between shark sizes for all variables (Table SUP.7.2), and the *kruskalmc* post-hoc procedure revealed that all pairwise comparisons yielded significant differences.

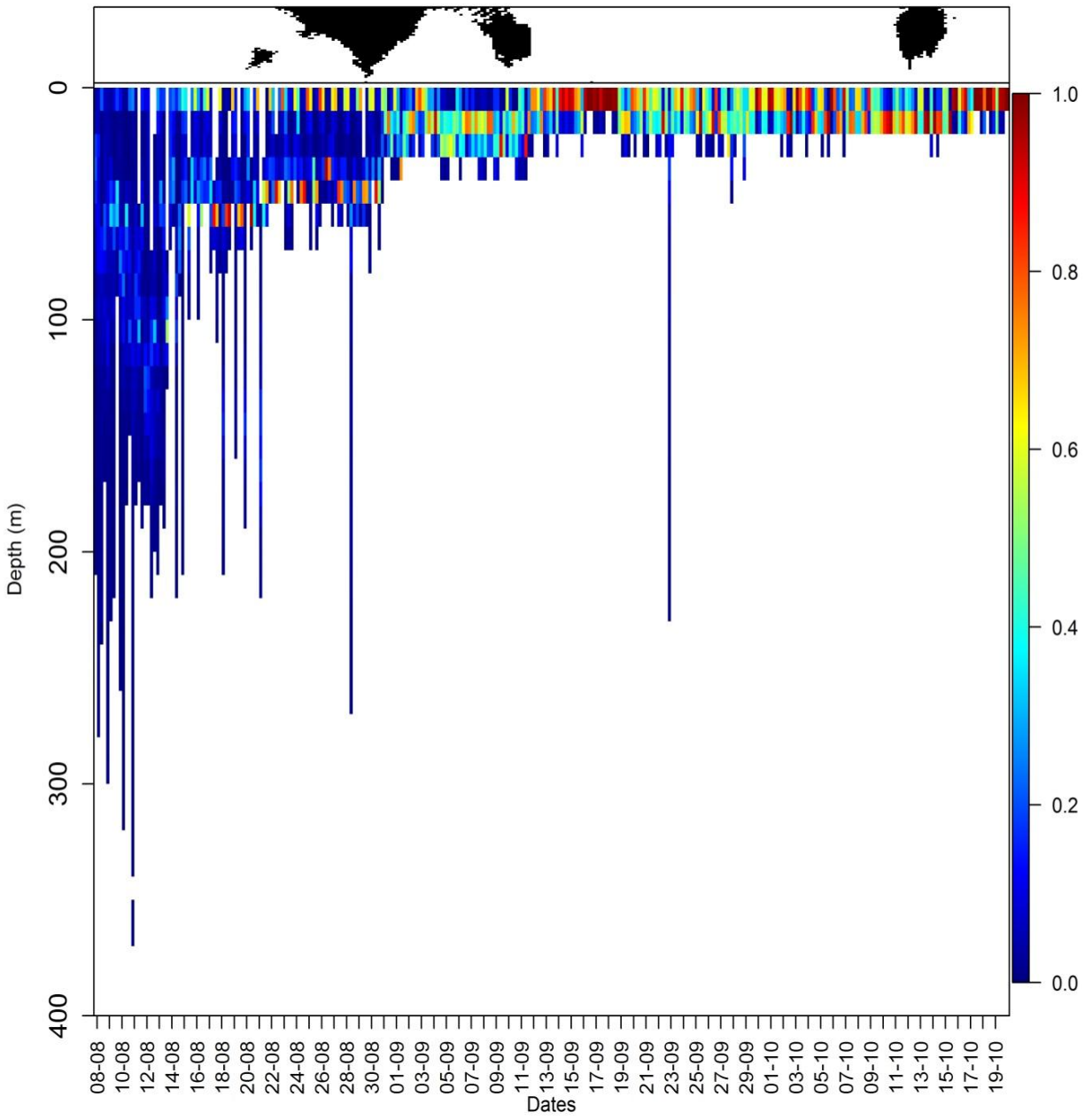


Figure 7.5. Time-at-depth (TAD) histogram of shark #5 archival data, with a 3-hour temporal resolution. Colors represent the proportion of time spent at each depth strata. The upper panel depicts results from the Split Moving Window Gradient Analysis, where inverted black triangles point to the boundary between significantly different behaviors.

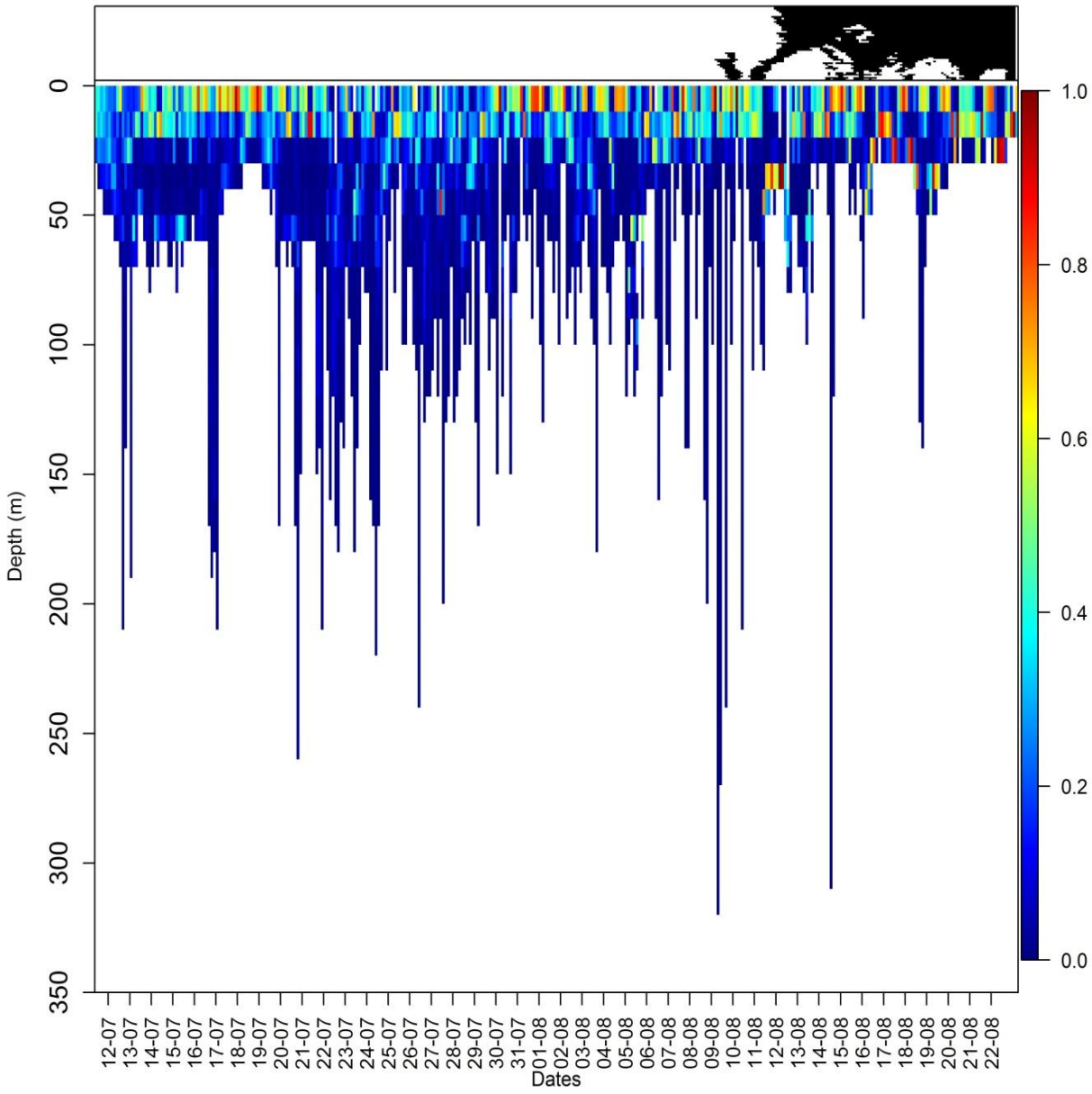


Figure 7.6. Time-at-depth (TAD) histogram of shark #17 archival data, with a 3-hour temporal resolution. Colors represent the proportion of time spent at each depth strata. The upper panel depicts results from the Split Moving Window Gradient Analysis, where inverted black triangles point to the boundary between significantly different behaviors.

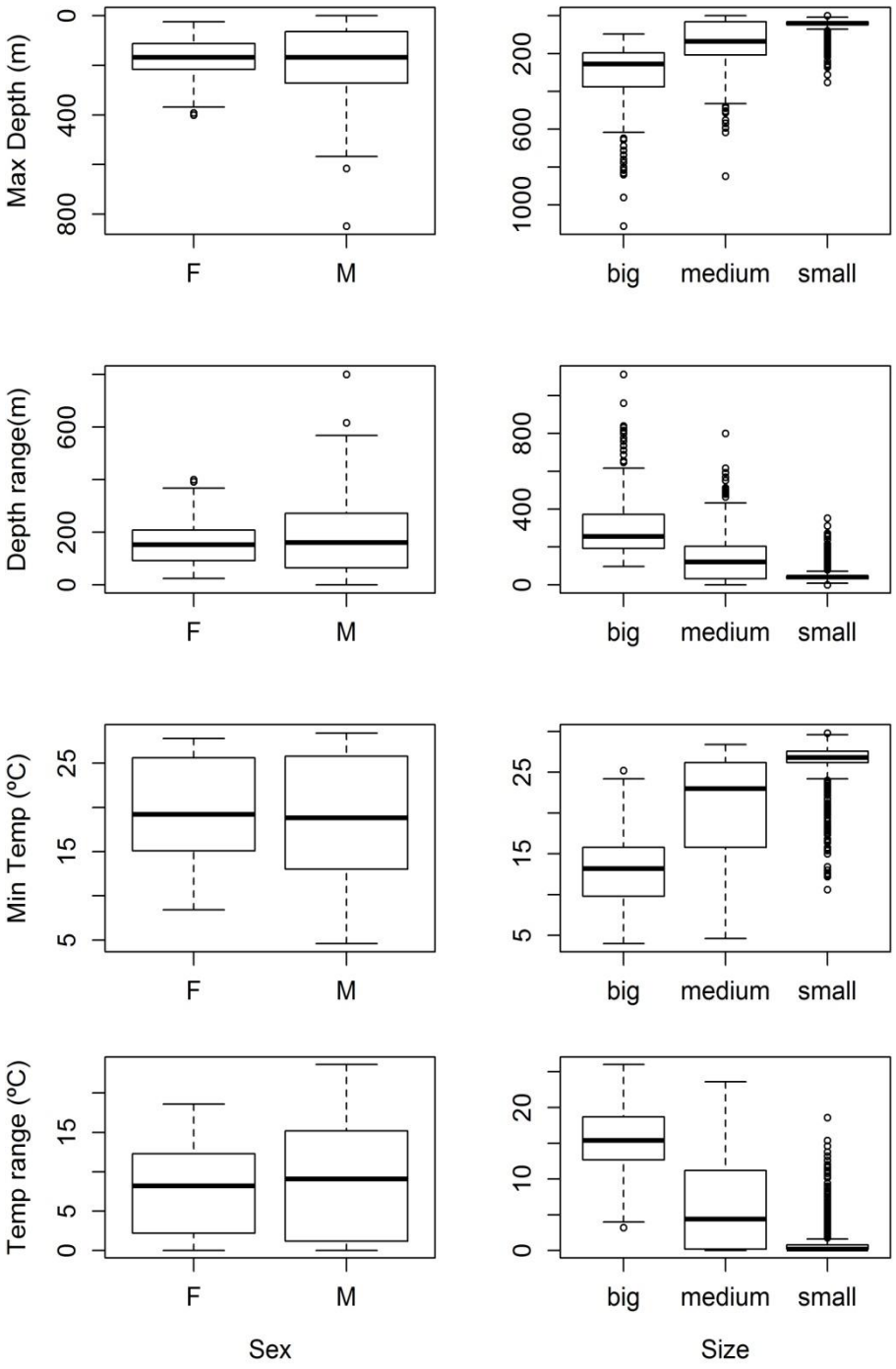


Figure 7.7. Distribution of maximum depth, depth range, minimum temperature and temperature range in tiger shark vertical movements by sex and by shark size. The thick horizontal line represents the median, the box outline represents the first and third quartiles, and the narrow horizontal lines represent data amplitude, whereas blank circles correspond to outliers.

A diel behavioral shift was apparently present in tiger sharks from this study as they tended to occupy shallower waters during the night and deeper waters during the day (Fig. 7.8). On average, tiger sharks spent most time at depths < 10 m both during the day and the night, but the amount of time spent at depths between 20 and 40 m was considerably greater during the day. Wilcoxon rank sum test detected significant differences in the proportion of time spent in shallow waters, < 20 m in depth, between diel phases for all sharks combined (Table SUP.7.3). The same test applied to each shark separately showed that sharks #12, #15, #17, and #18 followed similar patterns, but different trends were also detected which nevertheless agreed with the overall pattern in most sharks although reflecting a thinner or thicker water layer (Table SUP.7.3).

Regarding the lunar cycle, tiger sharks spent more time, on average, at shallow, < 10 m depths during the first quarter and full moon phases than during the last quarter and new moon phases, when depths > 20 m were most used (Fig. 7.9). Despite such differences being relatively small, the Kruskal-Wallis tests detected significant differences in the use of water layers shallower than 10, 20, 40 and 60 m for all tiger sharks combined, with post-hoc pairwise comparisons indicating that the first quarter and full moon phases were generally different from the last quarter and new moon phases (Table SUP.7.4). Considering sharks separately, only the first quarter and new moon were different for shark #3 and #5, whereas only the first and last quarters were different for shark #7 and only the last quarter and new moon phases were different for shark #19 (Table SUP.7.4). Shark #18 showed different use of waters < 40 m in depth between full moon and both last quarter and new moon phases. Shark #20 showed different lunar patterns at the four depth intervals considered. Some significant differences detected by Kruskal-Wallis tests, however, were not further identified by the *kruskalmc* post-hoc pairwise comparison procedure.

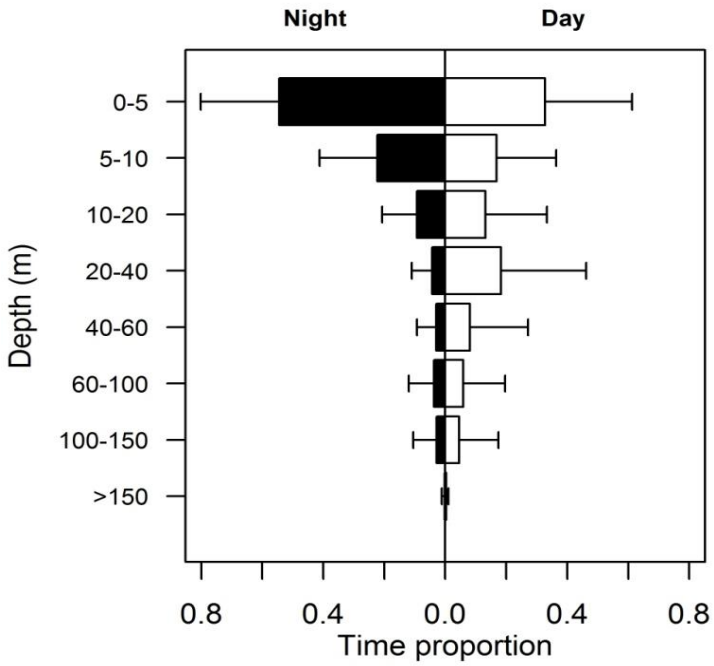


Figure 7.8. Diel variation (night *vs* day) of the average proportion of time spent by tiger sharks at specific depth intervals. Error bars represent standard deviations.

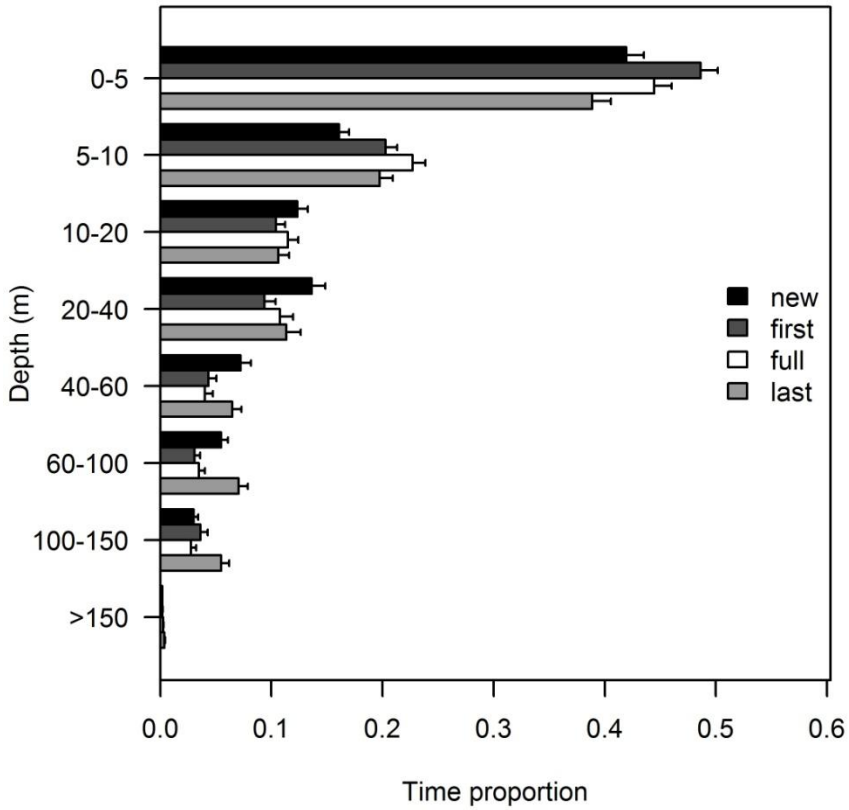


Figure 7.9. Variation of the average proportion of time spent by tiger sharks at each depth interval across the four moon phases (new moon, first quarter, full moon and last quarter). Error bars represent standard deviations.

The archival data obtained from two recovered PSAT tags allowed a thorough examination of tiger shark diving behavior at great temporal resolution (i.e., one second). For most time, shark #5 performed oscillatory, yo-yo movements continually, which usually extended from the surface to waters at varying depths (Fig. 7.10), similarly to the behavior described in section 7.3.2. Wide-ranging vertical movements were most common during the first 3 weeks at liberty and waters deeper than 60 m were only punctually visited after the initial period of tracking. Shark #17 showed the same pattern of wide-ranging vertical movements which, in this case, were performed throughout the tracking period (Fig. 7.11). However, during periods of full moon, this shark changed its behavior and moved mostly within shallow, < 50 m waters. Those shallow-water periods were characterized by progressively shallower dives followed by progressively deeper dives, which produced inverted U-shapes in depth time-series (Fig. 7.11). It is also noteworthy that both #5 and #17 sharks not always came to the surface and tended to remain at some depth for relatively brief periods of time, which was observed mostly during daylight (Figs. 7.10−11).

Some of the PSAT-tags also provided ARGOS-relayed time-series depth data, albeit insufficient numbers in successfully decoded messages frequently resulted in large gaps in the time series. Once again, a yo-yo diving behavior at varying depth ranges was present in all sharks (Fig. SUP.7.15). These movements were generally conducted in waters < 200 m in depth, with deeper dives being performed sparsely and briefly. Inverted U-shapes in depth time-series were clearly observed in sharks #6, #9, #12 and #19. Additionally, the vertical movements performed by sharks #6, #9 and #21 also exhibited regular U-shapes, with inflection points being positioned at about 50 m in depth for shark #6 and at about 100−150 m in depth for sharks #9 and #21 (Fig. SUP.7.15).

7.3.4. Horizontal movement analysis

Tiger shark horizontal movements were assessed using tag-and-recapture data and both acoustic and satellite telemetry. A total of 4 tiger sharks were recaptured after periods at-liberty as long as 2 years, corresponding to 9% of the number of sharks tagged and released. On 26 July 2011, shark #2 was caught with gillnets by artisanal fishermen off Itamaracá, ~3.5 km from the

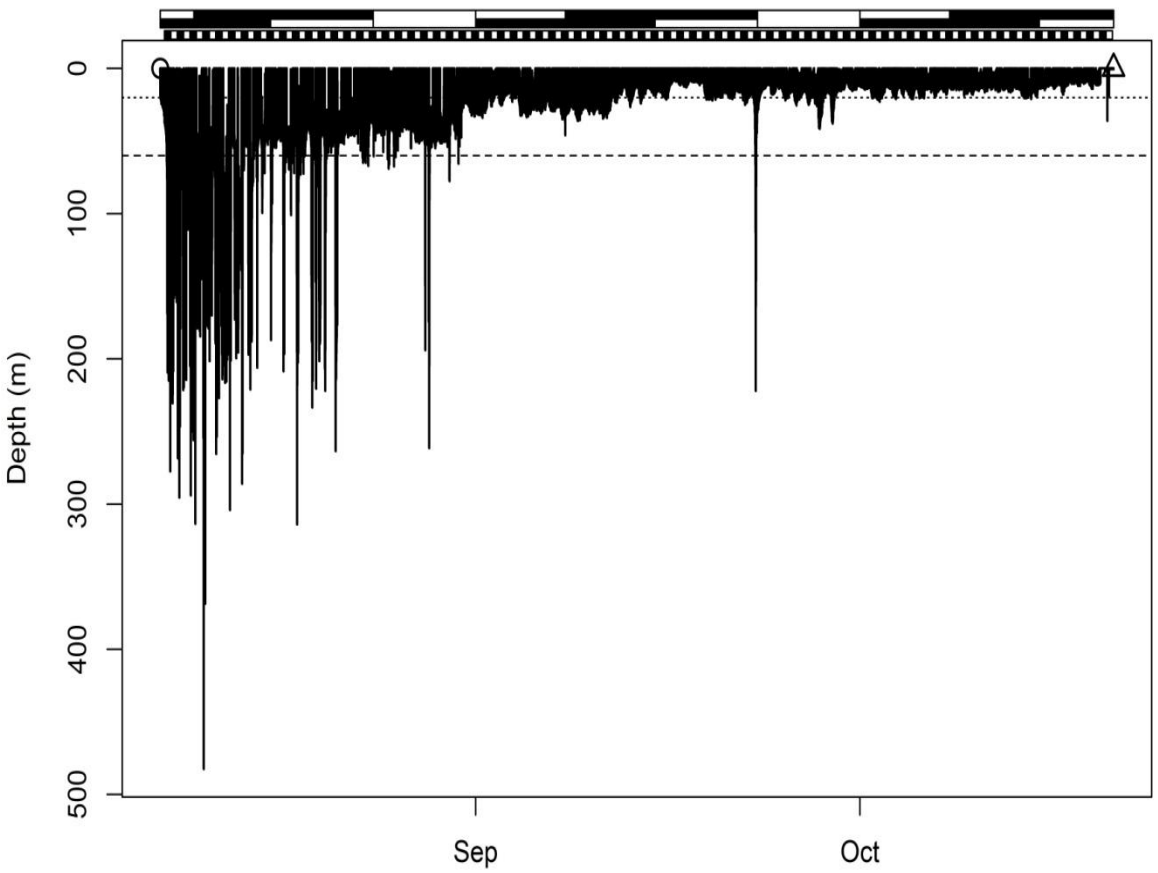


Figure 7.10. Time-series of shark #5 vertical movements, with a temporal resolution of 1 second, during its tracking period. The horizontal dashed and dotted lines represent the 60-m and 20-m isobaths, respectively, while the circle and triangle represent tagging and pop-up events, in the same order. The narrower horizontal bar with small, alternating blank and solid squares represent the diel cycle, with solid squares corresponding to nocturnal periods and blank squares corresponding to daylight periods. The wider horizontal bar with a succession of rectangular modules represent the lunar cycle, with full solid rectangles representing new moon, full blank rectangles representing full moon, and half solid rectangles representing first and last quarters in the appropriate order.

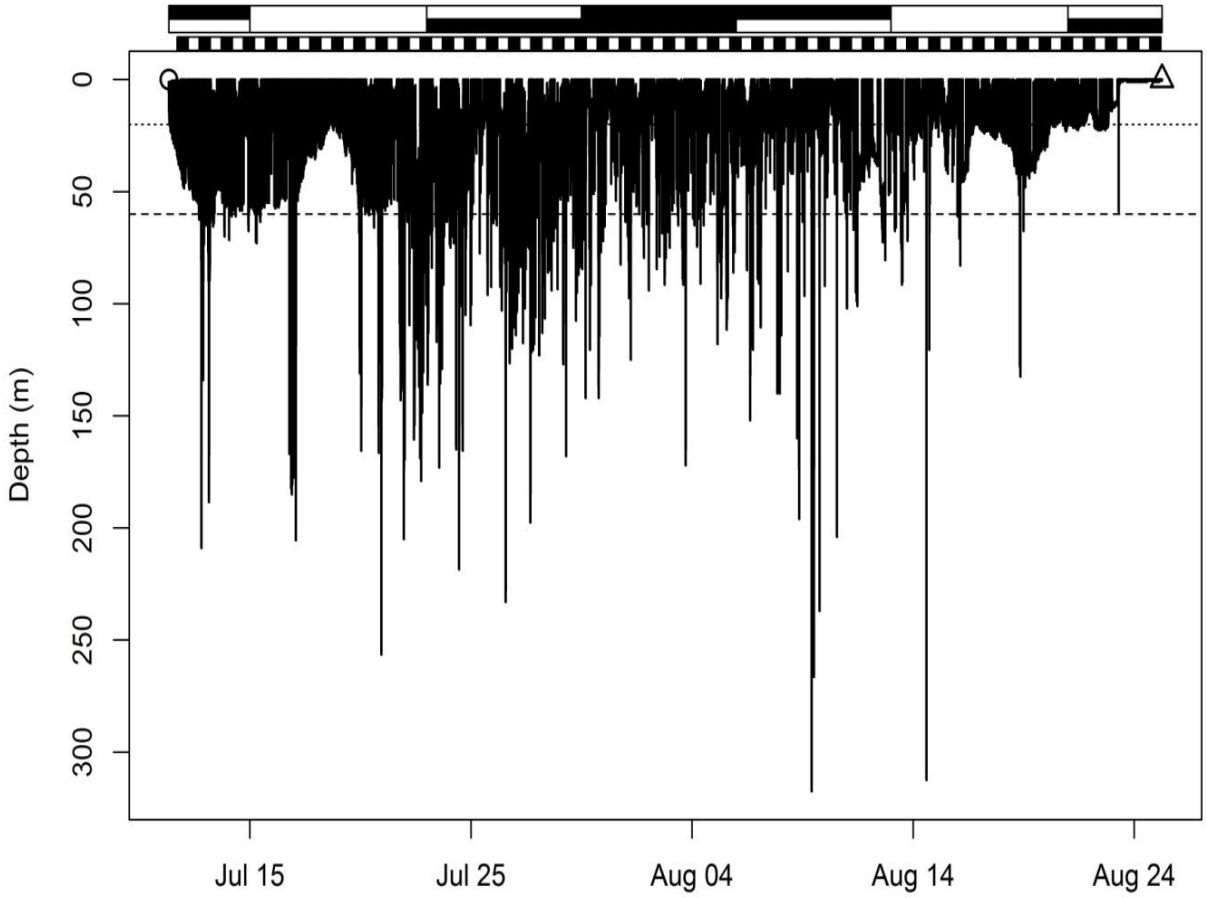


Figure 7.11. Time-series of shark #17 vertical movements, with a temporal resolution of 1 second, during its tracking period. The horizontal dashed and dotted lines represent the 60-m and 20-m isobaths, respectively, while the circle and triangle represent tagging and pop-up events, in the same order. The narrower horizontal bar with small, alternating blank and solid squares represent the diel cycle, with solid squares corresponding to nocturnal periods and blank squares corresponding to daylight periods. The wider horizontal bar with a succession of rectangular modules represent the lunar cycle, with full solid rectangles representing new moon, full blank rectangles representing full moon, and half solid rectangles representing first and last quarters in the appropriate order.

coast and ~40 km northward from the tagging site (Fig. 7.13). On 21 August 2011, shark #10 was recaptured off Recife by the Shark Monitoring Program roughly in the same location of the first capture. This shark then became shark #21. On 25 August 2011, shark #17 was caught with gillnets off João Pessoa, in the state of Paraíba, about 130 km to the north of the tagging location. The gillnets were deployed about 500 m from shore around 12−14 m isobaths. On 6 December 2011, shark #20 was also caught with gillnets off João Pessoa, roughly in the same circumstances as shark #17.

The array of acoustic receivers off Recife identified the presence of 3 acoustically-tagged tiger sharks which yielded a total of 228 detections at 6 acoustic stations. Shark #10, tagged on 12 February 2011, was detected off Recife at two acoustic monitoring stations in 25 July and from 10 to 21 August 2011. Shark #8, tagged on 5 February 2011, was detected off Recife at three acoustic stations on 16−17 February and 2−5 March 2011. Shark #12 was briefly detected on 20 October 2011, ~7 months after tagging, at one acoustic station installed away from shore at greater depths off Recife (8.01675ºS, 34.6846ºW) (Fig. SUP.7.20).

By its turn, satellite telemetry provided estimates for the horizontal movements performed by 15 tiger sharks during varied lengths of time after release, and constituted the major source of data for horizontal movement analysis. Notwithstanding, obtaining daily geolocation estimates of shark movements was frequently impossible due to gaps in the ARGOS-relayed dataset and tiger shark diving behavior during sunrise and sunset events, which may induce severe bias in luminosity-based geolocation and produce unrealistic movements. Tiger sharks were between 0.5−321 km away from shore when the tags popped-up (Table 7.2), whilst in two occasions the first ARGOS transmission occurred from land after tags were washed up ashore. The PSAT tag deployed in shark #4 did not transmit enough messages to allow geolocation, but the positions of the orbiting satellites by the time of transmissions were investigated to assess the geographic area which was then visible to the satellites, similarly to the procedure in Meyer et al. (2010). However, the pop-up position remained inconclusive because the area screened by the satellites at transmission time included the tagging location. The shortest, soak distance between deployment and successfully assessed pop-up locations ranged between 33 and 1,193 km (Table 7.2).

Virtually all sharks moved to the north after being released (Figs. 7.12−15; Figs. SUP.7.16−26), the only exceptions being shark #18, which moved south and within two months was ~600 km away from the tagging location, by the littoral of Salvador, Bahia (Fig. SUP.7.22), and shark #22 which moved southeast into oceanic waters (Fig. SUP.7.26). As already indicated by vertical movement analysis, tagged sharks tended to move offshore and leave the continental shelf after release. This behavior was most clearly evidenced by sharks #1, #3, #17, #18 and #20 (Fig. 7.12; Figs. SUP.7.16,21,22). In contrast, sharks #2 and #12 did not leave the continental platform after release (Fig. 7.13; Fig. SUP.7.20). Although shark #5 appeared not to have left the continental shelf (Fig. SUP.7.17), the time lag between consecutive geolocation estimates probably precluded the detection of post-release offshore movement because depth variation clearly demonstrated that the shark moved to oceanic waters after releasing (Fig. 7.10).

Despite most tracked tiger sharks moved to the north, distinct patterns were observed regarding trajectories and displacement rates. One common pattern was characterized by northward motion along the continental shelf, which was the case of sharks #1, #2, #3, #5, #9, #17 and #20 (Figs. 7.12−13; Figs. SUP.7.16,17,19,21). These sharks usually swam in shallow, < 60 m waters of the continental shelf, occasionally moving further offshore into deeper, oceanic waters. Also, latitudinal displacement in these sharks may have not be unidirectional, exclusively from south to north, since sharks tracked for comparatively long time periods such as shark #3 (Fig. SUP.7.16) were much closer to the tagging location than other sharks which moved far away in considerably less time, such as sharks #1 and #2 (Fig. 7.12−13). One other movement pattern was characterized by northward motion in the oceanic realm, which was the case of sharks #6, #7, #9, #15 and #19 (Figs. 7.14−15; Figs. SUP.7.18,19,23). These sharks usually performed wide-ranging movements in oceanic waters, sometimes at hundreds of kilometers away from the continental landmass, and generally covered great distances by the end of the track. A third pattern was evidenced by two sharks that did not move to the north, i.e. sharks #18 and #22 (Figs. SUP.7.22,26). Both sharks entered deep, oceanic waters soon after releasing, but while shark #18 returned to the continental landmass and moved south, shark #22 kept moving into the open ocean far away from any continental influence and exited the Brazilian Exclusive Economic Zone. Since these two tracks spanned for roughly comparable periods of time (48 *vs* 60 days), the different pop-up locations may be indicative of distinct migratory behaviors exhibited by the tracked sharks. Altogether, despite some tiger sharks performed extensive

oceanic excursions, they generally remained associated or in close proximity to the Brazilian continental landmass.

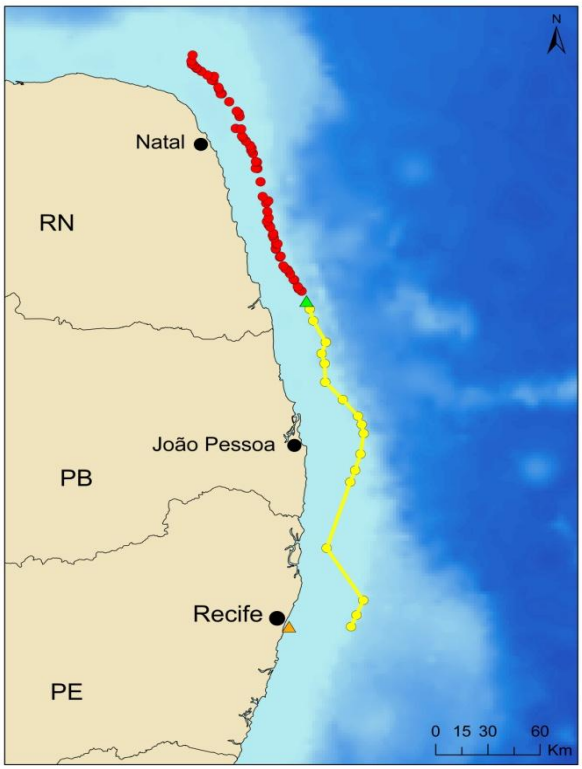


Figure 7.12. Horizontal movements of tiger shark #1 off northeastern Brazil assessed with PSAT tags. The yellow line represents shark movements estimated with light-level information, the red dots depict ARGOS geolocation estimates of the transmitting tag, the orange triangle represents the tagging location, and the green triangle represents the location of the first satellite transmission, generally coinciding with pop-up location.

Figure 7.13. Horizontal movements of tiger shark #2 off northeastern Brazil assessed with PSAT tags. The yellow line represents shark movements estimated with light-level information, the red dots depict ARGOS geolocation estimates of the transmitting tag, the orange triangle represents the tagging location, and the green triangle represents the location of the first satellite transmission, generally coinciding with pop-up location. The yellow star roughly represents the location of recapture, 2 years after tagging.

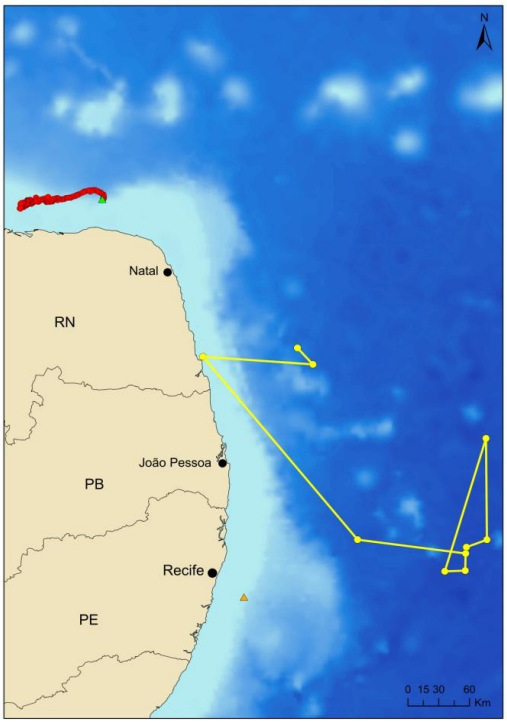


Figure 7.14. Horizontal movements of tiger shark #6 off northeastern Brazil assessed with PSAT tags. The yellow line represents shark movements estimated with light-level information, the red dots depict ARGOS geolocation estimates of the transmitting tag, the orange triangle represents the tagging location, and the green triangle represents the location of the first satellite transmission, generally coinciding with pop-up location.

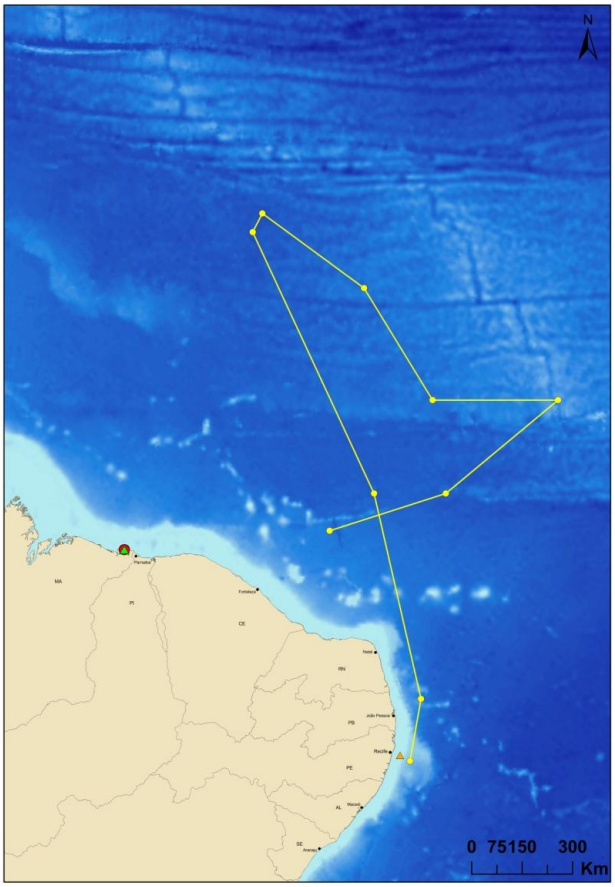


Figure 7.15. Horizontal movements of tiger shark #15 off northeastern Brazil assessed with PSAT tags. The yellow line represents shark movements estimated with light-level information, the red dots depict ARGOS geolocation estimates of the transmitting tag, the orange triangle represents the tagging location, and the green triangle represents the location of the first satellite transmission, which in this case occurred on land.

7.3.5. Natural and fishing mortality

Tiger shark tag-and-release provided valuable information regarding the mortality experienced by this species off northeastern Brazil. Out of 15 successfully satellite-tracked sharks, one episode of natural mortality was observed, corresponding to shark #19. The vertical movements of this shark were monitored for about 1.5 months, during which the shark exhibited a seemingly normal behavior, swimming between the surface and waters about 200 m in depth. However, on 8 September the shark dropped suddenly to a depth of about 1200 m, where it remained motionless for ~6 days until the PSAT tag activated the user-programmed releasing mechanism due to null depth variation. The fact that the minimum depth was never negative, which could indicate that the shark had been removed out of the water, presumably rules out the possibility that the shark was caught and discarded by fishermen.

Tiger shark fishing mortality was inspected with tag-and-recapture data and satellite telemetry data. Overall, 4 tagged sharks were recaptured by the Shark Monitoring Program of Recife and by artisanal fishermen from this region. Additionally, unnatural behavior in ARGOS geolocation estimates of shark #22 transmitting PSAT-tag (Fig. SUP.7.26) and a sudden increase in maximum temperature by the end of the tracking period (not shown in previous figures) indicated that this shark was caught, probably by a pelagic longliner. The fact that only a few messages with poor quality were successfully transmitted by this tag further suggests that it was probably stored in an enclosed space in the fishing vessel. In total, 23% of the tiger sharks tagged and released off Recife were posteriorly recaptured, in most instances within only a few months at liberty.

7.4. Discussion

This chapter aimed at assessing movement and behavior patterns of tiger sharks off northeastern Brazil using traditional tag-and-recapture techniques and electronic transmitters. Although tag-and-recapture data allowed to learn the locations of some sharks after a considerable time at liberty with high accuracy, not to mention the assessment of several important aspects of shark biology such as growth (see chapter 6), low percentages of tag returns constrained the efficacy of such sampling strategy in describing tiger shark movements and

home ranges. To be effective, tag-and-recapture studies require a great number of sharks to be tagged, a requirement which was not compatible with the numbers in the catch composition of the Shark Monitoring Program (see chapter 4). Nevertheless, the rate of recapture of tagged sharks, around 9%, was close to the rates commonly achieved in this kind of study (Kohler et al., 1998).

In turn, the electronic devices, albeit expensive, proved to be more adequate to monitor shark movements because data retrieval is not fisheries-dependent. However, electronic tags also have their own limitations that may influence their performance and thus should be taken in consideration. The detection range of acoustic receivers was empirically measured at 250 m, which is considerably lower than the detection ranges advertised by the manufacturer (500−600 m for high power, V16 tags). Since the detection range strongly depends on the physical properties of the water, local environmental features such as high turbidity and freshwater runoff from the Barra de Jangadas estuary could be attenuating the detection range and reducing the acoustically-monitored area off Recife. Acoustic transmitters with higher output power could increase the current detection range so that a continuous acoustic coverage of the study area would be achieved, given that a great number of receivers is already in use and the eventual expansion of the acoustic array could demand prohibitive human efforts and financial resources.

As expected, satellite-transmitting tags provided most tracking data. However, since PSAT tags transmit continuously after popping-up and battery exhaustion is rapidly achieved, many messages were not successfully streamed to the satellite. This produced several gaps in the dataset which could potentially compromise behavioral assessments for some sharks. A maximum of 1,250 messages is advocated by the manufacturer as the amount of messages which would be successfully transmitted to ARGOS satellites by mk10-PAT tags, but in this study an average of 820 messages by tag were transmitted and five tags yielded less than 500. Regardless of external factors being responsible for poor data transmission, e.g. when tracked tiger sharks were caught by fishermen and tags were stored in closed compartments, the fact that only five tags transmitted more than 1,000 messages strongly advises future studies to program their mk10-PAT tags to produce a more conservative amount of messages. Data transmission was not accomplished in one deployment, although the tag was identified by ARGOS satellites some days before the programmed pop-up date. This could be due to electronic failure or physical

damage to the tag (Hays et al., 2007). For example, although PSAT tags transmit at ultra-high frequency, at an wavelength of 401.65 MHz, resulting in antennas being conveniently short (Priede, 1992), any structural damage in the antenna may result in satellite transmission being no longer possible. Compromising damage may be caused by interactions with other animals or by the behavior of the tagged shark. According to Musyl et al. (2011), the reporting rates of PSAT tags are lowest in species undertaking large (~1,000 m) vertical excursions. Hammerschlag et al. (2011) reports that an average of 10% of the tags deployed in 48 shark tracking studies failed to transmit data to the satellites, being thus advisable to always anticipate such scenario when calculating the amount of tags to be deployed. Also, premature releases may always occur, either because tracked sharks are caught in fisheries or due to tag shedding. Higher tag retention rates have been associated with higher pop-off latitudes (Musyl et al., 2011), suggesting that environmental stressors such as high temperature, biofouling, and pathogenic agents may promote tag premature releases. In this study, PSAT tags were attached to tiger shark first dorsal fins, but most previous studies have chosen to rig tags with a variety of anchoring materials and inserting them into the dorsal musculature (Hammerschlag et al., 2011). This method was not attempted because it is more invasive than attaching tags to dorsal fins and could increase the susceptibility of sharks to wound infections at the site of tag insertion. Additionally, tag anchors and tethers often remain embedded in shark musculature long after the tag has detached, providing attachment sites for parasites (Hammerschlag et al., 2011). Also, a previous study on tiger shark movements showed poor tag retention performance using titanium-steel darts inserted in the dorsal musculature at the base of the dorsal fin and locked in place through the dorsal ceratotrichia (Meyer et al., 2010).

Therefore, the deployment methodology herein described seems to be preferable since it showed reasonable retention rates while being less invasive and potentially harmful to the tagged specimen. Indeed, two sharks fitted with PSAT tags through their dorsal fins which were recaptured by artisanal fishermen allowed to confirm that the puncture inflicted in their dorsal fins for tag attachment had completely healed, although the location of the puncture in the fin was discernible to the touch because the cartilage was slightly thinner, but no other signs of PSAT-tag deployments were perceived.

The depth-and-temperature profiles and time-series data clearly indicated that tiger sharks tend to move offshore and use deep, oceanic waters after being caught and released off Recife. Several sharks exhibited such behavior for periods of about 1−2 weeks before returning to shallower waters presumably in the continental shelf, a pattern which could be ascribed to specific post-release behavior in response to hooking and handling. Tiger sharks tagged and released in previous studies also moved offshore immediately after release (Holland et al., 1999; Tricas et al., 1981). Such post-release phase could implicate considerable behavioral bias in telemetry studies, thus caution is required to avoid including unnatural behaviors in the analyses. In contrast, other individuals exhibited deep-diving behavior during most of their tracking periods and no post-release behavioral effect was noticeable. In any case, it was evidenced that tiger sharks do not return to the area of risk after being released and instead move away from this region during the initial period at liberty. In only one circumstance, a small, 120 cm TL shark was detected by acoustic receivers off Recife between days 11−12 and then again between days 27−30 at liberty, but it was no further detected.

Tiger sharks off northeastern Brazil use a wide portion of the water column, descending to depths as great as 1,112 m, which seems to be the deepest published record for this species. Yet, a strong affinity for superficial waters was markedly present in most sharks, and several individuals spent long periods of time at depths < 20 m. Such distribution resulted in sharks being mainly exposed to a thermal niche of 24−28ºC in the mixed surface layer (MSL) throughout the tracking period. The lower temperatures associated to the movements of some sharks should be ascribed not only to deep-diving behavior but also to seasonal variations in the water temperature, which usually tends to be minimum in August (Hazin et al., 2000). Nonetheless, tiger sharks experienced great temperature variations during their tracks and successfully accessed cold waters below the thermocline, although episodically. Overall, tiger sharks used the upper 200 m of the water column for most of their movements and greater depths were briefly visited. Similar vertical distributions were observed in previous studies reporting data on tiger shark diving behavior (Holland et al., 1999; Holland et al., 2001; Meyer et al., 2010; Nakamura et al., 2011; Tricas et al., 1981), but small sample sizes and short track spans preclude a thorough comparison with the present study.

Although a global preference for upper layers of the water column was transversal to all sharks, differences in vertical-habitat use between individuals were observed. Whilst most sharks showed high affinity for waters < 40 m in depth, others made a considerable use of deeper layers between 60 and 150 m in depth. Most of these latter sharks spent little time at depths between 10 and 60 m but they still showed strong affinity for surface waters. Also, they were all medium or large sharks. Small sharks tended to spend less time with increasing depths and made virtually no use of waters deeper than 60 m after the first couple of weeks after releasing. In fact, the maximum dive depth was significantly correlated with shark size due to progressively greater depths being visited by larger sharks. This evidence suggests that niche expansion and segregation by size may occur in the tiger shark off northeastern Brazil, with individuals preferring deeper habitats as they grow. Ontogenetic changes in depth ranges and expansion of vertical habitats are common but physiologically demanding, and generally take two primary forms as short-term changes in vertical movement patterns (e.g. daily vertical migrations) and as long-term changes in the depths occupied (Grubbs, 2010). The southwestern equatorial Atlantic Ocean has several seamounts located at varying distances from the continental shelf, which could provide adequate foraging grounds for larger tiger sharks during oceanic excursions and compel them to use deeper waters more extensively. Unfortunately, time-at-depth (TAD) results were not reported in Meyer et al. (2010), thus it is not currently possible to determine if this pattern is also visible in tiger sharks from other regions. Nevertheless, the persistence of surface affinity coupled with permanence at deeper, colder waters is probably related to foraging strategies. Tiger sharks are known to prey upon marine birds (Carlson et al., 2002) and, as opportunistic feeders, they may consume unusual items such as disoriented land birds (Dodrill and Gilmore, 1978) or floating whale carcasses (Dudley et al., 2000), so they might benefit from visiting surface waters regularly. The yo-yo movement pattern most evidenced in depth time-series from recovered PSAT tags, therefore, could be directly related to foraging behavior. Nakamura et al. (2011) fitted tiger sharks with accelerometers and digital still cameras to investigate the reasons behind yo-yo diving behavior and came to the conclusion that it should represent a search strategy for locating prey throughout the water column rather than being a mechanism to minimize energy expenditure during swimming. It has long been suggested that negatively buoyant fish such as sharks could reduce the energetic requirements of swimming with prolonged powerless gliding during descents (Weihs, 1973), which would ultimately result

in yo-yo diving behaviour. Yet, yo-yo movements in tiger sharks seem to have a different function since they usually do not glide when descending and instead show continuous tail-beating during most of the time (Nakamura et al., 2011), although circumstancial variations in the oscillatory diving pattern could be related to energetic optimization of locomotion (Iosilevskii et al., 2012). Vertical movements in other species have been ascribed to prey-searching behavior because crossing multiple water layers would increase the odds of detecting olfactory cues to prey (e.g. Carey and Sharold, 1990), and it seems to be the most plausible explanation for tiger shark yo-yo diving behavior.

Tiger shark behavior was significantly correlated with both diel and lunar cycles. A greater use of surface waters during the night could be explained by a foraging behavior, since tiger sharks are known to be most active during nocturnal periods (Compagno,1984). Tricas et al. (1981) also detected diel shifts in tiger shark behavior, but the short track in this study should be interpreted with caution, particularly because the data were collected within 48 hours after releasing and thus the tracked shark could be performing unnatural, stress-mediated movements due to hooking and handling. In contrast, Meyer et al. (2009) found no evidence of diel rhythmicity in tiger shark activity at coastal habitats off Hawaii. Regarding the lunar cycle, surface waters were most used during the full-moon and last quarter phases, which could also be related to predatory activity since the moon phase can influence shark distribution and behavior (Ferreira et al., 2011). However, Lowry et al. (2007) found no evidence of the lunar cycle influencing the catchability of tiger sharks in a game-fishing tournament fishery, and Meyer et al. (2009) reported tiger shark activity at coastal habitats to be unrelated to the moon phase.

Tiger sharks are renowned for their ability to move in shallow, inshore waters as much as in deep oceanic basins (Compagno, 1984). Understanding the specific features that regulate tiger shark shoreward movement is of utmost importance for integrating spatiotemporal dynamics, not only in management and conservation strategies but also in shark attack mitigation measures. Besides, information on diving behavior can provide a significant contribution to understand tiger shark spatial ecology to a greater extent because shallower distributions may reflect a depth preference as much as a bathymetric constraint. The continental shelf off northeastern Brazil is relatively monotonous, slanting gently from the shoreline until a depth of about 60 m, where a steep slope abruptly starts (Fainstein and Milliman, 1979). Prolonged

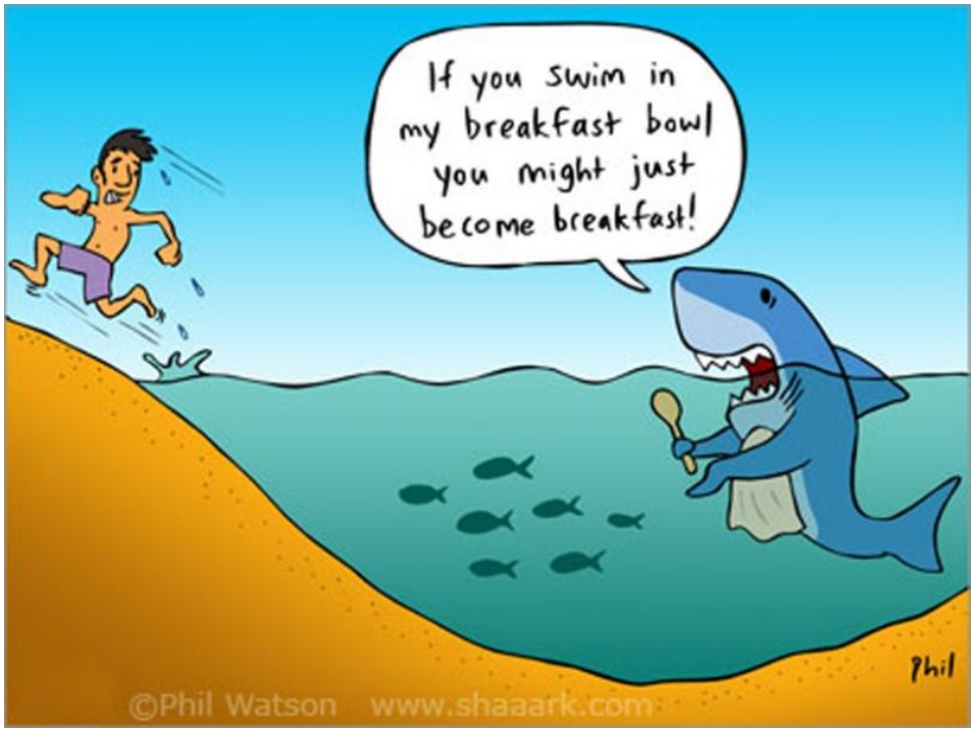
periods of time during which maximum depths are lower than 60 m may, therefore, indicate that tiger sharks are moving on the continental shelf. Such periods were frequently observed in diving profiles from several sharks. Meyer et al. (2010) also interpreted prolonged shallow diving behavior as resulting from the presence of shallow, nearshore habitat, thus imposing *depth floors* in tiger shark vertical movements. Additionally, an increase in water temperature may further indicate shoreward movement because coastal waters are typically warmer than oceanic waters. Since the continental shelf off northeastern Brazil has about 60 km in average width (Souza, 2007), a shark would have to swim around 120 km in order to access inshore waters and return to deep waters in the open ocean. Holland et al. (1999) measured the average swimming speed of six acoustically tracked tiger sharks at 0.29 body length per second, which equals 2.088 and 3.132 $km \cdot h^{-1}$ for sharks measuring 200 and 300 cm TL, respectively. Randall (1992) reported an average daily movement of 60 km per day for a tag-recaptured tiger shark, which is compatible with the estimate of Holland et al. (1999). Given these results, a minimum of between 38 and 57 hours would be required for tiger sharks measuring 200−300 cm TL to access inshore waters and return offshore, thus such movements could be easily identified using ARGOS-relayed, binned data. However, tiger sharks off northeastern Brazil could exhibit different swimming speeds than the ones reported by Holland et al. (1999) due to different current regimes in the two regions. Oceanographic currents are a main component of shark relative movements, which should always be taken into consideration when interpreting swimming speeds of free-ranging individuals. Measuring tiger shark swimming speed off northeastern Brazil would thus be advisable in order to assess the spatial ecology of this species more accurately. In any case, this approach allows to define minimum temporal windows for continuous shallow diving that may help to identify periods in ARGOS-relayed depth data during which tiger sharks may have moved to coastal waters. This task was much simplified regarding archival depth data from recovered PSAT tags because tiger shark yo-yo diving behavior clearly revealed the bathymetric constraints that progressively reduced the amplitude of the oscillatory movements during shoreward approximation. These episodes were evidenced in depth time-series as an inverted U-shape, where the first and second stems depict shoreward and seaward motion, respectively, and the summit depicts the period spent at shallowest waters. The contour of this shape adds further information on details such as the movement rate in the cross-shore component, minimum isobath visited, permanence time, and foraging behavior.

Tiger sharks off northeastern Brazil exhibited different behaviors. Several sharks clearly preferred shallower waters in the neritic province, while others made most use of oceanic waters. Despite an absolute pattern was not discernible, the utilization of oceanic waters seemed to be restricted to medium and large sharks in most occasions, which is in accordance with tiger shark population structure off Recife assessed in chapter 5. This trend was evidenced by depth-and-temperature profiles and corroborated by PSAT tag pop-up locations and by geolocation estimates from the KFtrack state-space model. The KFtrack model was used because it can generate a most probable track that is more reliable than the track generated by the manufacturer's software (Nielsen and Sibert, 2004). Other methods that attempt to correct geolocation estimates by incorporating sea surface temperature data (Domeier et al., 2005; Nielsen and Sibert, 2006; Teo et al., 2004) and unscented Kalman filtering (Lam et al., 2008) are available and were also explored, but their output generally resulted in greater, less plausible distances between successive locations. Lam et al. (2008) compared the results of different methods and found minimal differences between location estimates, thus a state-space model in combination with a regular Kalman filter could be most adequate to reconstruct tiger shark horizontal movements. Nevertheless, the performance of this model was still far from satisfactory because several estimates were clearly incorrect (e.g. they were in dry land or too far away to be reliable) and had to be discarded. Both physical (e.g. similar day lengths through the latitudinal range during the equinox, light attenuation due to water turbidity) and biological factors (e.g. diving behavior) confound light-based position estimation to a great extent, resulting in a magnitude of geolocation errors which severely limit the ability of PSAT tags in describing horizontal movements at high resolutions. Hence, light-level geolocation appears appropriate for tracking large-scale movements in the oceanic realm, but is less able to measure smaller-scale movements which constitute specific behavioral patterns (Sims, 2010). Given that tiger sharks exhibited a strong affinity for surface waters, near real-time satellite tracking may provide a better technological alternative to investigate tiger shark horizontal movements off northeastern Brazil with finer detail, as it was demonstrated by Heithaus et al. (2007) and Meyer et al. (2010).

Tiger sharks visiting coastal waters off Recife appear to be moving northward, at least on a regional scale (Hazin et al., 2012). Whether tiger sharks are coming from eastern oceanic waters, following the South Equatorial Current, or coming from south, following the Brazilian coast, is a question that remains to be answered. This species is very wide ranging and is able to

cover hundreds of kilometers in a few days (Heithaus et al., 2007; Kohler et al., 1998; Randall, 1992), as revealed by this study. In the South Atlantic, tiger sharks have been caught over oceanic seamounts (Afonso et al., 2011) and around oceanic islands such as Fernando de Noronha (Afonso et al., unpub. data). Thus, it is possible that long periods of time elapse between successive visits to the same region. One shark was recaptured not far from the tagging location after 2 years at liberty, but it was not possible to ascertain if the shark had moved to distant oceanic regions or if it remained in coastal waters during that period. Coastal patrolling behavior has been previously described in tiger sharks, with individuals swimming back and forth along 15 to 109 km of coastline (Meyer et al., 2009), thus it is plausible that some sharks which moved preferentially in the neritic province performed both northward and southward movements while foraging. Although limited to single events, shark recaptures and acoustic detections off Recife some months after tagging agree with the hypothesis of patrolling behavior, together with one shark that was less than 10 km away from the tagging location after 73 days at liberty. Nevertheless, the overall net displacement seems to result in northward motion in most cases, which could be a consequence of prevailing northward currents. Understanding large-scale movement patterns of tiger sharks in the South Atlantic and the contribution of coastal habitats to their life cycle is of utmost importance for shark attack mitigation. Therefore, further tagging efforts should be pursued in order to increase the existing database, which is still diminutive for detecting relevant aspects of tiger shark spatial ecology such as ontogenetic variations and environmental influences. Further tagging would also provide additional information on tiger shark fishing mortality. This study demonstrated tiger sharks may experience extremely high fishing mortalities in this region, which could have strong implications for management and conservation purposes. The tiger shark is classified as Near-Threatned by the International Union for the Conservation of Nature and Natural Resources (IUCN) (Simpfendorfed, 2009), thus more research is warrant to ensure the sustainability of their populations.

Chapter 8. Shark attack mitigation off Recife



Cartoon by Phil Watson; retrieved from http://www.shaaark.com, *with permission*.

8.1. Introduction

Shark monitoring and shark-meshing programs are management tools that typically emerge due to the necessity of reducing high rates of shark attacks on humans at hazardous regions. The main objective of such programs is to reduce the abundance of potentially aggressive sharks in specific shores where shark-human interaction is more likely to occur. Shark-meshing programs accomplish this by eliminating a number of sharks from local populations, consequently reducing the frequency of foraging sharks in coastal waters (Cliff and Dudley, 1992), thus they are also known as shark control programs since they aim at controlling shark populations. Vertical gillnets deployed in nearshore waters are successful in catching sharks because they do not rely on bait to be effective and will easily entangle most sharks that come across them if properly set up. However, such fishing devices are not very selective and thus catch a myriad of harmless, frequently endangered species (Dudley and Cliff, 1993a; Gribble et al., 1998; Krogh and Reid, 1996). High mortalities of sharks and non-shark *taxa* resulting from shark meshing have been widely criticized (Paterson, 1979, 1990) and efforts to address the environmental impacts of shark control programs were recently undertaken (Cliff and Dudley, 2011). Notwithstanding, the success of shark meshing in mitigating shark attack rates led to the permanent maintenance of large-scale programs in Australia and South Africa (Dudley and Cliff, 2010). In these shark control programs, shark attack rates at protected beachs were reduced by between 88 and 91% (Dudley, 1997). Despite the main goal of shark control programs being achieved, serious concerns regarding the ecological sustainability of such methods advise for the development of alternative strategies for shark attack mitigation.

This chapter aims at examining the effect of the Shark Monitoring Program of Recife (SMPR) on the local shark attack rate, and to evaluate the performance of this program in a long-term perspective. An appraisal on possible contributors to further address the shark attack issue off Recife is also included.

8.2. Shark attack mitigation off Recife

Shark attack mitigation off Recife is primarly addressed by preventing potentially aggressive sharks from entering the area of risk. The spatial configuration of the fishing gear has been carefully designed to intercept approaching sharks before they enter the alongshore channel next to the beach (see chapter 2 and 4). Bait distribution further contributes to lure sharks away from the main entrance to the channel, while preserving additional protection should a shark still swims into the risk area. The higher catch rates in the longline gear compared to drumlines indicate that such spatial configuration efficiently reduces the probability of sharks moving inshore. Previous concerns regarding baited lines attracting more sharks to inshore waters (Paterson, 1990) have not been verified as the fishing effort was strategically arranged so that sharks would be lured away from the area of peril. Differently from shark-meshing programs, the SMPR does not remove sharks from their populations, but instead it removes them away from the area of risk by transporting them to deeper waters. After releasing, sharks are expected to resume their natural movements and will no longer pose a threat to beach users, as verified by telemetry studies (see chapter 7). This methodology allows to minimize potentially deleterious

	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011
Jan		1		1							1									
Feb			1										1							
Mar		1	1							1			1							
Apr					1		1					1			1					
May						1		1			1		3		1					
Jun	1	1													1		2			1
Jul			3	1		1	1				1				1					
Aug				1									1							
Sep	2					1					1		1					1		
Oct			2		2		1				1									
Nov							1													1
Dec			3					1												
Total	3	3	10	3	3	3	4	2	0	1	5	1	7	0	4	0	2	1	0	2

Figure 8.1. Absolute frequencies of shark attacks off Recife by year and by month. The thin vertical line depicts the year when the Shark Monitoring Program was created, the wide grey vertical bars depict years with no attacks, the red and grey numbers represent shark attacks off Recife and elsewhere in the State of Pernambuco, respectively, while the blue numbers correspond to months when attacks occurred both off Recife and elsewhere in Pernambuco.

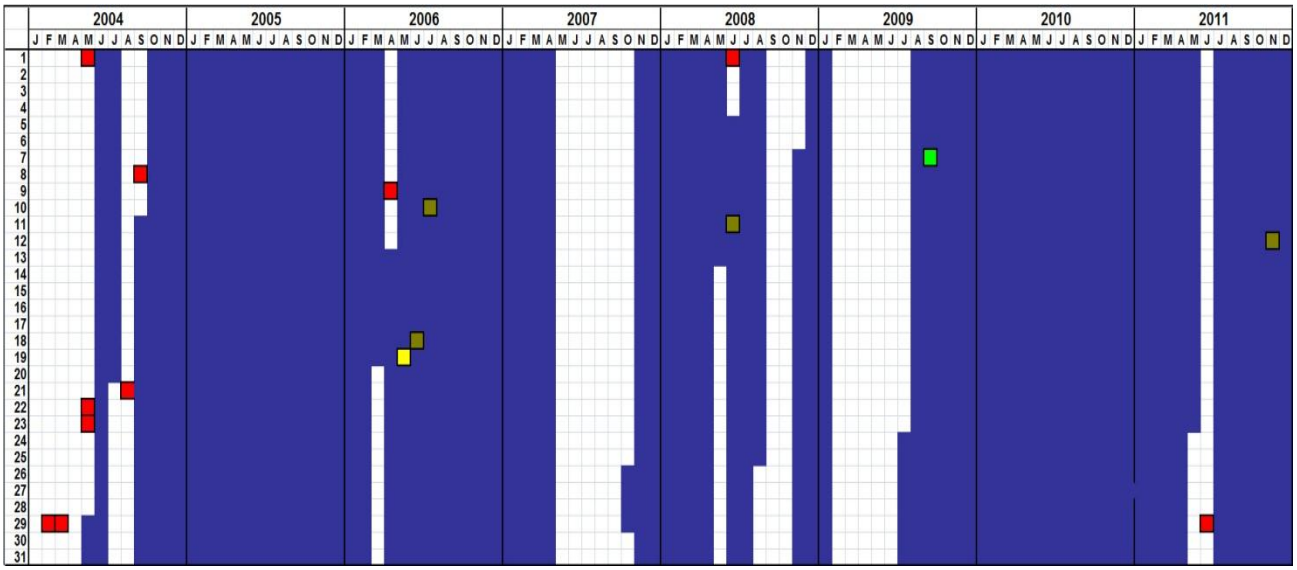


Figure 8.2. Calendar between January 2004 and December 2011, depicting periods during which the SMPR was operational, i.e. fishing (blue fields), episodes of attacks off Recife during no-fishing (red squares), episodes of attacks off Recife during fishing (yellow square), episodes of attacks elsewhere in the State of Pernambuco (gray squares), and episodes of drowning and posterior corpse scavenging by sharks off Recife (green square).

impacts of the SMPR on the local ecosystem while significantly contributing to mitigate the shark attack rate.

The fishing operations of the SMPR started in May 2004. Until then, the shark attack rate off Recife averaged 0.289 (±0.607) attacks·month^{-1} during about 12 years since 1992. Until 2004, as much as 10 attacks occurred in a single year, and attacks occurred in every year except one (Fig. 8.1). Between 2004 and 2011, the SMPR was interrupted in seven occasions of varied spans (August 2004, March−April 2006, May−September 2007, May 2008, September−October 2008, February−June 2009, and June 2011) due to discontinuity of funding. Such discontinuities provided the opportunity to compare the shark attack rate between fishing and no-fishing periods. This comparison, however, has a caveat because fishing and no-fishing periods are mutually exclusive in time, implying that temporal variability in shark attack rate cannot be accounted for in this comparison. Yet, this is the only plausible means to assess the direct effect

of the SMPR on shark attack rates given the complexity of the hypothesis being tested, which precludes a more traditional experimental design. Between January 2004 and December 2011, the program operated during 73 months and was inoperative during 23 months (~24% of whole period). While fishing was being conducted, a single attack occurred off Recife resulting in an event rate of 0.014 (±0.119) attacks·month^{-1} (Fig. 8.2). On the other hand, 10 attacks were verified during no-fishing periods, corresponding to 0.435 (±0.728) attacks·month^{-1}, which was significantly higher (about 30 times) than the former (one-tailed Mann-Whitney rank sum test; W = 1108.5, $p < 0.001$). Thus, a ~97% reduction in the monthly shark attack rate was observed when the SMPR was operational, which is higher than those achieved in other shark control programs (Dudley, 1997). If the drowning episode in 2009 (Fig. 8.2) were considered a shark attack, as it was advocated by local forensic professionals, the shark attack rate during fishing periods would equal 0.028 attacks·month^{-1}, thus corresponding to a ~94% reduction in the monthly shark attack rate, which is still considerably high. Between 1992 and 2003 (12 years), at least one attack was registered in all but one year (92%), while during 8 years of SMPR as many as four years (50%) elapsed with no incidents with sharks. Additionally, the shark attack rate during the periods since 2004 on which the SMPR was inoperative was approximated to the rate observed before its creation, suggesting that fishing operations were the prime contributor for the reduction in the number of incidents. Moreover, the monthly distribution of the catch rate of potentially aggressive sharks indicated higher abundances in March and between May−September, in reasonable accordance with the monthly frequency of shark attacks, which was higher between May−July and between September−October (Fig. 8.3). This suggests that the catch rates in the SMPR reflect the natural distribution of potentially aggressive sharks off Recife. The success of the SMPR in shark attack prevention may, however, depend on site-specific conditions as shark control programs with longlines showed no measurable effects on the rate of shark attacks in Hawaii, for instance (Wetherbee et al., 1994).

Another component of the SMPR focus on public outreach and environmental education at local beaches and community centers, thus contributing for acquainting bathers with shark attack risks and safety procedures. Other long implemented initiatives for shark attack mitigation include the local prohibition of surf, in 1995 and again in 1999 with reinforcements (Hazin et al., 2008), and posting numerous signs throughout the beaches with danger warnings and related information. However, the actual effect of these measures in shark attack reduction is

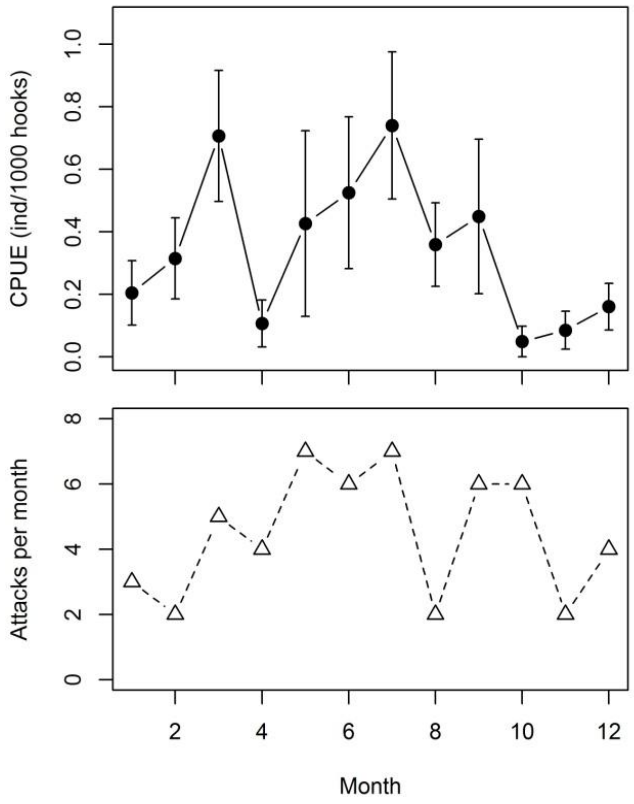


Figure 8.3. Monthly variation of the average (±SD) catch-per-unit-effor (CPUE) of potentially aggressive sharks, as the number of sharks caugth per 1000 hooks (upper panel), and absolute frequencies of attacks per month (lower panel).

difficult to be assessed, but the fact that most of the victims were local residents and were aware of the risk involved suggests that they have frequently proven to be insufficient.

Although the SMPR showed high efficiency on reducing shark attack rates compared to shark control programs in Australia and South Africa (Dudley, 1997), the magnitude of the former is much smaller, since the area of risk is restricted to a ~20 km stretch of coastline instead of spreading through several beaches and regions. Therefore, direct comparisons between these programs should allude to the structural differences between them. Anyway, the shark species most implicated in the three programs are the same, i.e. the tiger, *Galeocerdo cuvier*, and bull, *Carcharhinus leucas*, sharks, although the white shark, *Carcarodon carcharias*, is also important in South Africa and Australia (Dudley and Cliff, 2010), while it does not occur off Recife. So, the performance of the SMPR should be directly comparable to shark-meshing modules protecting a coastline with equivalent dimensions and similar human occupation, since they share the goal of preventing the same species from interacting with beach users. It seems thus reasonable to infer that the efficacy of the SMPR in shark attack mitigation is similar to or

greater than the efficacy of shark-meshing programs. Despite a clear reduction in the shark attack rate off Recife, an apparent increase in the frequency of shark attacks at northward beaches should be regarded, since 4 incidents were verified since 2004 while only one incident was reported between 1992 and 2004 (Fig. 8.2). These attacks occurred at locations several km away from the monitoring area and thus lied out of the scope of the SMPR. Nevertheless, further research is warranted to verify the likelihood of persisting shark attacks occurring elsewhere in the State of Pernambuco, which could possibly indicate a shift in the spatial distribution of shark attacks.

8.3. Perspectives on the shark attack scenario off Recife

The shark attack outbreak verified off Recife has been ascribed to several factors. One possible, immediate explanation corresponds to the demographic development of this region, which could result in more people using coastal waters and thus a higher probability of a shark-human encounter occurring. The population of Recife increased from about 1,150,000 to 1,300,000 people between 1980 and 1990, and in 2010, the year of the last demographic census, the Recife population had reached 1,537,704 people (IBGE, 2012). Although this corresponds to a populational growth of about 13% per decade, with a likely similar increase in the number of beach users, this rise is by no means sufficient to explain the sharp and sudden increase in the shark attack rate. Indeed, if shark attacks off Recife would be a simple consequence of populational growth, then a gradual increase in the shark attack rate would be expected. Instead, the annual variation of the frequency in shark attacks suggests that a sudden event and not a gradual process, such as demographic expansion, would be the cause for the shark attack outbreak.

The fact that the attacks started soon after the construction of a big portuary complex in the vicinity of Recife strongly suggests that the Suape port could be the principal agent triggering the shark attack hazard. Hazin et al. (2008) suggested that the environmental damage caused by construction activities at the estuarine system of Suape may have compelled resident sharks such as bull sharks to migrate to the nearest estuary, in this case the Barra de Jangadas estuary located in the area of risk. Also, the increase in maritime traffic to this region could contribute to attracting sharks shoreward towards Suape, since sharks are frequently found in association to

ships and port areas (Baldrigde, 1974). This could result in more sharks visiting the littoral area of Recife after departing Suape in case they follow the prevailing coastal currents to the north (Hazin et al., 2008). Tiger sharks in Hawaii exhibited a clear attraction to a portuary area (Meyer et al., 2009), and the present study demonstrated that tiger sharks caught off Recife tend to move north (see chapter 7), thus it seems reasonable to infer that, if tiger sharks are being attracted to Suape, they should be expected to further move north into the littoral of Recife. The Suape port may play a deterministic role in the shark attack problematic by artificially increasing shark abundances in coastal waters, where the natural behaviour of sharks would lead them to visit the shores off Recife. The probability of a tiger shark accessing the area of risk would then be a function of both bioecological features determining temporal variability of tiger shark abundance, and the intensity of maritime traffic to Suape, which is variable at week- and year-level. Significant statistical correlations between periods of higher maritime traffic into Suape and shark attack events off Recife have been previously evidenced (Hazin et al. 2008), which further supports this hypothesis.

However, the Suape port alone cannot be responsible for all this situation since there are larger portuary complexes placed near large urban centers elsewhere, where no shark attacks have ever occurred. Thus, local-specific features should be further involved in the case-study of Recife. The presence of the Barra de Jangadas estuary within the area of risk could contribute to attract sharks to these shores, particularly regarding species exhibiting affinity for low-salinity water such as the bull shark (Compagno, 1984). Not only the estuarine environment is attractive to some sharks, but it may also include several traits liable to attract other sharks. According to Hazin et al. (2008), a public slaughterhouse used to dump untreated effluents (blood, entrails, and associated water) directly into the Jaboatão River at an average volume of 345 m^3 per day, which endured until 2005. The Jaboatão River flows directly into the area of risk and exherts a considerable influence on the nearshore ecosystem, thus every dissolved and particulate contaminants that it carries will eventually end up at coastal waters off Recife. Besides the slaughterhouse, untreated liquid waste used to be drained from the Muribeca Waste Landfill into the Jaboatão River at an average rate between 60−72 $L \cdot min^{-1}$ during dry and rainy seasons, respectively (Hazin et al., 2008). Additionally, the urban development in this region did not contemplate treatment of waste water, resulting in sewage being directly injected in the local environment. Altogether, the amount of organic pollution in this region is a serious concern

because it resulted in severe environmental disturbance and degradation (Leite, 2007), not to mention public health issues. Also, this kind of pollution may contribute to attract sharks into the area through a process similar to chumming. Sharks are extremely sensitive to the presence of blood and other organic substances in the water, even at great dillutions, and will follow chemical trails towards their source, thus being abundant around harbours and garbage dumps (Baldridge, 1974). In Mogadishu, Somalia, a total of 30 shark attacks occurred at a single location from 1978 to 1987, and it has been suggested that the main responsible factor for this outbreak of attacks was a slaughterhouse operating in the area (Stevens, 1987). Therefore, it is most likely that the presence of the Barra de Jangadas estuary within the risk area is a factor contributing to attract sharks towards Recife. This estuary could be further involved in the shark attack outbreak due to great water siltation resulting from intense deflorestation at higher lands. Water siltation not only interfeers with primary productivity in coastal ecosystems by increasing light attenuation with depth, but it also reduces the visibility to a great extent. By its turn, lower visibility may result in a higher probability of a shark attack occurring due to prey misidentification, since sharks will not be able to rely on visual stimuli to distinguish prey from non-prey items. Water turbidity and freshwater outflow are highest during the rainy season, thus a certain seasonality in the shark attack rate could be expected. As suggested by Gilbert (1963), shark attacks are most likely to occur in regions near estuaries during periods after heavy rainfall. Although a seasonality in the number of shark attacks off Recife was not obvious, July had the highest number in shark attaks (Hazin et al., 2008) and also one of the greatest values in pluviosity (see chapter 2), further corroborating the importance of the Barra de Jangadas estuary for explaining the shark attack problem.

Although with little expression, a small artisanal fleet devoted to shrimp trawling has been exploiting nearshore demersal resources from this region for some time. Such activity could also contribute to attract sharks to these shores because it produces a considerable amount of bycatch which is discarded at short distances from the coastline, thus generating more stimuli to which sharks are likely to respond. Also, bottom trawling is known to severely impact demersal habitats (Munga et al., 2012), thus exherting additional pressure on local food webs. Despite the prohibition of shrimp trawling within 1 nautical mile from shore, poor law inforcement results in this practice being frequently conducted closer to shore.

Another feature likely contributing for the high shark attack rate off Recife pertains to the peculiar bathymetry of the area of risk. As it was evidenced in chapter 2, a deep channel extends along the shore between Piedade and Pina beaches. This channel is shaped by the presence of a shallow bank of submerged beachrocks that generates a bathymetric structure resembling a half-pipe with considerable width and about 8 m in depth. This could allow sharks to get closer to the shoreline because a greater depth is available bordering the beach. Additionally, the configuration of this channel may imply that, once inside, shark movements will be restricted to the channel because they will be less likely to swim seaward, particularly during low tides. As a consequence, sharks would be confined to inshore waters along the stretch between Piedade and Pina beaches, which would necessarily increase the probability of a shark-human encounter. Gilbert (1963) reported higher shark attack rates in regions including alongshore sandbanks that form channel-like structures close to beach, therefore it seems most likely that the presence of a channel also contributed to increase shark peril off Recife. A thorough bathymetric survey of this channel has been conducted to assess for possible entrances other than the main entrances at the southernmost and northernmost sections, which could be present along the submerged bank of beachrocks. This survey clearly evidenced that the main entrances already described, together with the bathymetric profile of deeper waters seaward to the channel, should provide the most adequate route to approaching sharks. Inclusively, the shape of the seafloor and the prevailing northward currents further suggests that sharks would most likely access to the channel through its southernmost entrance. Nevertheless, some small segments of the bank of beachrocks were found to be less shallow than the average depth of the bank (see chapter 2). These deeper segments could allow the passage of sharks, particularly during high tides, and they were located roughly in front of *hotspot* sites where most attacks occurred. Although this association is not at all conclusive, it raises the question of whether sharks are entering the channel exclusively through its main entrances or through the submerged beachrocks as well. Such question could be addressed using active acoustic tracking, since that methodology would allow to assess the movements of a shark tagged and released inside the channel with high resolution. The impossibility of attempting such strategy with potentially aggressive sharks, due to an evident risk of attack, could be overcome if using a different animal model such as the nurse or the blacknose sharks, but interspecific behavioural variability should be accounted for when interpreting results.

In conclusion, the shark attack outbreak off Recife appears to have been caused not by a single but several contributing factors whose combination resulted in a sudden increase in the probability of a shark-human interaction occurring in these waters. It seems likely that the main factor triggering this situation was the introduction of the Suape port to the south of Recife, which could have induced a higher abundance of potentially aggressive sharks in nearshore waters. Sequentially, the natural behavior of these sharks would promote their northward displacement to nearshore waters off Recife, at least regarding the tiger shark which was most abundant species among potentially aggressive sharks. Site-specific features, such as the presence of both the Barra de Jangadas estuary, with associated pollution and siltation, and the channel-like structure may have acted synergistically to further attract sharks towards inshore waters off Recife and to increase the probability of shark-human encounters and interactions. Simultaneously, other factors such as shrimp-trawling activities may have also contributed to this situation.

The bioecological component of the case-study of Recife was investigated in the present study because it expectedly comprises deterministic factors regulating the dynamics in the shark attack rate. Ultimately, the structure and dynamics of the populations of large sharks and their association with intrinsic bioecological mechanisms should be the primary contributors to shark attack hazard, as they will determine the availability of sharks at coastal waters and their propensity for interacting with a human being. According to Hazin et al. (2008), the bull shark would probably be the species responsible for most of the attacks since it was confidently implicated in six out of the seven cases in which an identification of the attacking shark was possible, whereas the tiger shark was implicated in only one incident (Gadig and Sazima, 2003). However, the much higher abundance of tiger sharks in this region suggests that they may be more important to the shark attack scenario than bull sharks, at least in more recent times after the resident bull sharks being probably removed from these waters. The initial phase of the SMPR was characterized by high catch rates of potentially aggressive sharks, including bull sharks. After the removal of the resident individuals, the SMPR has been mostly dealing with migrant sharks that approach these shores coming from other regions. In shark-meshing programs the same effect has been suggested (Dudley, 1997). Spatial variability in catch rates across a section of coast in New South Walles, Australia indicated that gillnets off northern and southern beaches consistently captured more sharks, corroborating the hypothesis that catch

primarily comprised incoming sharks (Reid et al., 2011). Since bull sharks exhibit high site-fidelity (Hammerschlag et al., 2012), their contribution to the shark attack hazard off Recife could have been most expressive before the creation of the SMPR, whereas tiger sharks continued to be important contributors since they are apparently more abundant and have wide home ranges (Meyer et al., 2009). Based on the SMPR catch composition, other large-sized species may sporadically contribute to the attacks, and their potential contribution should not be underestimated. These species include the blacktip, *Carcharhinus limbatus*, the silky, *C. falciformis*, the Caribbean reef, *C. perezi*, and both smooth, *Sphyrna lewini*, and great harmmerhead, *S. mokarran*, sharks.

Surprisingly, the overall abundance of potentially aggressive sharks off Recife is rather low. Given the high shark attack rate, high abundances of dangerous sharks would be expectable so that the probability of a shark-human encounter would be maximum, which was not the case. In Hawaii, several longline-based shark control programs aiming at reducing the populations of large sharks due to high shark attack rates had much higher catch rates than the SMPR (Wetherbee et al., 1994). The low numbers in the abundance of potentially aggressive sharks off Recife may suggest that the likelihood of an individual shark encountering a human could be maximized by mechanisms unrelated to shark abundance, such as the movement constraints imposed by the channel off Recife.

Bull sharks off Recife were generally large individuals, but previous suggestions that they could be using the Barra de Jangadas estuary for reproductive purposes (Hazin et al., 2008) were not confirmed since no pregnant females have been caught. Thus, there is currently no indication that a population of bull sharks would thrive in this region by establishing a nursery area for their youngsters. On the other hand, tiger sharks seem to make most use of the neritic province off northeastern Brazil during early juvenile stages. While no neonate tiger sharks were identified by the SMPR, young-of-the-year (YOY) sharks of growing sizes were caught during the first nine months of the year, suggesting that nearshore waters off northeastern Brazil are used as pupping areas until sharks attain a size between 150 and 200 cm TL, after when they seem to depart. Early juvenile tiger sharks in the northwestern Atlantic and Gulf of Mexico also occur in the continental shelf, although no discrete nurseries were identified (Driggers et al., 2008). Since tiger sharks have wide-ranging habitats and low site attachment even during early life-stages (see chapter 7), they should be expected to use large portions of the continental shelf

off northeastern Brazil, where they could exhibit patrolling behavior (Meyer et al., 2009) or take unidirectional courses following environmental cues, such as the prevailing northward currents. The latter seems to be the most common pattern.

The implications of tiger shark life strategy for the shark attack hazard off Recife are significant. Despite most tiger sharks visiting the area of risk were juveniles measuring less than 200 cm TL, thus being apparently less dangerous, their abundance and spatiotemporal distribution strongly suggests that they could be deeply involved in the attacks. Small sharks may still attack and cause damage to people. For example, Gilbert (1963) reports a 150 cm TL tiger shark attacking a spearfisherman in about 3 m of water off Puerto Rico, which refutes the suggestion that only tiger sharks larger than 230 cm TL would be propense to attack humans (Lowe et al., 1996). Still according to Gilbert (1963), a neonate dusky shark measuring about 90 cm TL repeatedly attacked a swimmer in Bermuda, which could be due neonate sharks frequently exhibiting frantic behaviour in the first week after hatching because they depend upon stored nourishment which would have been all absorbed at about that time, thus compeling them to be voracious. Yet, neonate sharks would hardly pose a life threat to a human being, which is not the case of larger juveniles. Tiger sharks consume a wide variety of prey and undergo through ontogenetic dietary shifts, feeding on larger, human-sized prey as they grow (Lowe et al., 1996). Tiger sharks off northeastern Brazil grow extraordinarily fast and may attain nearly 200 cm TL within the first year (Afonso et al., 2012b). Such high growth rates suggest that nearshore habitats off northeastern Brazil provide adequate foraging grounds and that the attacks are not occurring due to reduced abundances in natural prey. Since YOY seem to use nearshore waters from the first quarter to the last quarter of the year before departing to oceanic waters, they will be at their larger sizes around the third quarter, when they presumably would represent a greater threat to humans. The number of shark attacks off Recife tends to increase from January to July (Fig. 8.3), reasonably coinciding with the dynamics of YOY tiger sharks off Recife. This also suggests that the monthly distribution in shark attacks off Recife could be regulated by at least two distinct components, since the dynamics of YOY tiger sharks is notoriously different from the dynamics of larger tiger sharks or other shark species. It is important to recognize the different biological mechanisms interacting with the shark attack issue off Recife because different mechanisms may require different strategies for successful mitigation.

8.4. Optimizing shark attack mitigation off Recife

Reducing shark attack rate off Recife is achieved by reducing the likelihood of encounters between sharks and humans and/or the propensity of sharks to interact with humans. The probability of sharks encountering humans is proportional to both the number of people and sharks sharing the same area. The SMPR has been operating to regulate the amount of sharks swimming in coastal waters off Recife, thus reducing such probability. Although the SMPR has demonstrated to be widely successful in shark attack mitigation, it does not provide an absolute shark-free condition like an exclusion device would (Dudley and Cliff, 2010). Therefore, the chances of a shark bypassing the fishing gear and accessing inshore waters could be significant. Even though the probability of sharks encountering humans has been greatly reduced by the SMPR, complementary measures could further minimize such probability and enhance bathing safety off Recife.

Reducing the number of people using coastal waters off Recife would certainly contribute to minimize the probability of sharks encountering humans. However, this is frequently not feasible due to socioeconomic and cultural aspects. The great touristic revenue and the strong relationship between the local population and the beach for leisure purposes have generally hindered such approach. The surf prohibition decreeted in 1995 and 1999 (Hazin et al., 2008) resulted in widespread protest by surf practitioners and associations which continues until present time. Regardless, the shark attack outbreak modified the behaviour of beach users and life-guards. Bathers are advised e.g., not to swim into deep waters and avoid sea bath during high tides and crepuscular times, which would expectedly reduce the chances of being attacked. Yet, the persistence of shark attacks during periods on which the SMPR was inoperational leads to the conclusion that safety rules are not much respected, which could perhaps be most true after a long period with no attacks occurring. Research on the dynamics of beach utilization and the behaviour of beach users is mandatory to better integrate the human component of the shark attack issue in mitigation measures. On the other hand, the ability to predict when sharks are more likely to occur at coastal waters could contribute to reduce shark attack rates by providing a measurement of shark peril. Defining accurate time-windows when the probability of sharks visiting coastal waters off Recife is higher may offer an incentive for additional caution by bathers and life-guards.

The knowledge gathered in this study allows the tentative identification of predictors which may help to ascertain when tiger sharks should be more likely to use coastal waters off Recife (see chapter 5). In seasonal terms, the period spanning from January to September should expectedly carry higher risk of shark attack due to higher tiger shark abundances (Table 8.1), which matches the monthly distribution of shark attacks reasonably (March−October) (Fig. 8.3). At smaller temporal scales, the juxtaposition of abundance modelling and tracking data indicates that the period between new moon and full moon should represent a higher risk of shark attack (Table 8.1), which is in accordance with higher shark attack rates verified between new moon and full moon phases (Hazin et al., 2008). Also, nocturnal periods should be more dangerous because tiger sharks tend to spend more time at shallow waters during the night (see chapter 7), although few people will use coastal waters off Recife at that time. Other environmental variables such as tidal amplitude, pluviosity and wind direction may have a positive influence on tiger shark abundance within particular ranges (Table 8.1). The continuous monitoring of such variables could allow to antecipate periods of higher risk of shark attack and to activate additional preventive measures. However, the proposed predictors and conditions are based on a yet small tiger shark catch, thus additional sampling would be required to improve the accuracy of the predictors and the applicability of this strategy.

Table 8.1. Proposed predictors and value ranges for higher shark peril off Recife, based on Generalized Additive Modelling (GAM) of tiger shark abundance and on tiger shark affinity for shallow, < 10 m water measured with PSAT tags.

Predictor	Value range	Source
Month	January − September	GAM
Lunar phase	New moon − first quarter	GAM
Lunar phase	First quarter − full moon	PSAT-tag
Diel phase	Night	PSAT-tag
Tidal amplitude	0 − 1.4 m and 2 − 2.4 m	GAM
Pluviosity	0 − 50 mm	GAM
Wind direction	130 − 220º	GAM

The use of typical shark exclusion devices for providing small, shark-free areas off the beaches of Recife raises several concerns which fall beyond the scope of this thesis. Therefore, such mitigation strategy will not be herein addressed. However, the bathymetric profile of the area of risk may grant a distinct, innovative approach to shark exclusion devices. If sharks access inshore waters off Recife exclusively through the main entrances of the channel (i.e., the northern and southern entrances), a condition which remains to be determined, then it would be possible to generate a vast, shark-free area along the channel by imposing shark exclusion devices at the main entrances of the channel. If feasible, this solution could be effective in providing extensive areas with low or null risk and therefore avoiding issues regarding the management of small-scale shark exclusion devices. However, the entrances of the channel, particularly the southern one, are wide and exposed to strong hydrodyamics. In this perspective, the most adequate solution for a long-term installment would probably rely on concrete structures resembling tetrapods used worlwide for wave energy dissipation at coastal areas. These artificial structures would necessarily have to be configured so that they would form a submerged reef connected to the beachrock structure that shapes the channel off Recife (see chapter 2), but in such way that they would allow the passage of smalller, harmless species when stacked. Yet, the development of this solution requires a coastal engineering approach assuring that no significant impacts associated to sediment transport or to the distribution and behaviour of local communities would occur.

One important assumption in the case-study of Recife pertains to the role of the Suape port, which presumably promotes an artificially high abundance of sharks in nearshore waters from this region. It would be important to ascertain the validity of this assumption, since this scenario could allow to improve the performance of the SMPR. If sharks are indeed coming from Suape, then it may be profitable to extend the longline monitoring to strategical locations southward from Recife in order to increase the probability of capturing potentially aggressive sharks before they approach the littoral of Recife. Moreover, the presence of the *Parque dos Naufrágios Artificiais de Pernambuco* (PNAPE; Park of Artificial Shipwrecks of Pernambuco) on the continental shelf could also contribute to attract sharks seaward. The PNAPE comprises several shipwrecks which were sank at strategic locations, roughly between the 20-m and 40-m isobaths, with the purpose of providing hard substrate for biotic colonization. These hotspots in the middle of a continental shelf dominated by soft substrate are expected to attract sharks to

deeper waters. Further extensions of PNAPE could thus improve its efficacy as shark attractors, but research is required to understand how sharks use those shipwrecks in order to design PNAPE extensions more effectively.

Finally, the shark attack rate off Recife could be further mitigated through local environmental recovery and restoration. Severe organic pollution coupled with abundant discarding from shrimp trawling could be eliciting sharks to engage a predatory state. Additionally, chronic siltation greatly reducing the visibility in the area of risk could further promote shark-human interactions due to prey-misidentification. Although presupposing an enormous task, the recovery of this coastal ecosystem may correspond to the only means to actuate upon reducing the likelihood of sharks interacting with humans. Because the abundance of potentially aggressive sharks off Recife is rather small, the high shark attack rate could imply a great probability of sharks interacting with humans when an encounter is verified. In such circumstances, shark-human interactions could probably be reduced by increasing water visibility and reducing the amount of both dissolved and particulate organic matter in the water column.

The magnitude and complexity of the shark attack problemat in Recife require the commitment of governments, stakeholders, and third parties to achieve the best, most desirable solution to approach this issue in a long-term perspective. While the SMPR can provide an immediate response to shark attack mitigation, the conjunction of the previously referred measures could result in a considerable reduction in shark peril. Since the mechanism promoting high shark attack rates in this region apparently follows several consecutive stages (i.e., sharks being attracted towards Suape, then moving north, then being attracted towards Recife and finally entering the area of risk), chain-reductions in the probability of sharks accessing to the next stage which will drive them closer to inshore waters off Recife may have a synergistic effect on shark attack mitigation. The fact that multiple factors are acting to promote high shark attack rates suggests that effective mitigation may depend on several measures being taken simultaneously. A permanent solution to this problem may however be unreachable, at least while the effects of some keystone factors persevere.

Conclusions and final remarks

Shark attacks on humans generally promote severe damage to local socioeconomics and human welfare, particularly in persistently hazardous regions. Gillnet-based shark control programs have provided satisfactory effects on shark attack mitigation in Australia and South Africa, but low gear selectivity and high fishing mortality resulted in a large number of harmless, frequently endangered *taxa* being removed from coastal ecosystems. Hook-based fishing gear such as longlines or drumlines performed better because they are more selective and less traumatogenic than gillnets. Also, optimization of longline and drumline gear increased both selectivity towards potentially aggressive sharks and survival, which was achieved by using circle hooks and suspending the hooks in the water column. Such configuration significantly reduced bycatch and allowed a large number of individuals to be released.

Altogether, the Shark Monitoring Program of Recife (SMPR) provides an effective solution to increase bathing safety at local beaches with minimal ecological consequences.
This fishing methodology combined with bioecological research (e.g. tag-recapture, telemetry, environmental control) allows crucial information for the reasoning of the shark attack outbreak to be collected. Thorough examinations of the sharks which do not survive to the fishing gear add further information on several important traits of shark bioecology such as reproduction, diet, and growth. Understanding the structure and dynamics of the shark assemblage off Recife may allow to approach preventive measures more efficiently and contribute to further decreasing shark peril.

Tiger sharks seem to currently be reponsible for most of the attacks, but bull sharks were implicated in several attacks and may have been most important before the creation of the SMPR. Other potentially dangerous species were also present but in low numbers. In this region, tiger sharks have wide home-ranges and move preferentially to the north, which could be related to the prevailing northward current regime. This species seems to use the continental shelf off northeastern Brazil mostly during early juvenile stages, where they quickly grow between January and September before departing to oceanic waters. Older tiger sharks seem to make most

use of deeper oceanic waters but they also visit nearshore and coastal areas frequently to forage. The depth distribution of tiger sharks was correlated with both diel and lunar cycles, which could be usefull in determining periods when tiger sharks are more likely to occur at coastal waters. Additionally, tiger shark abundance off Recife was correlated with month, lunar phase, tidal amplitude, pluviosity and wind direction. All this information may contribute to predict periods of higher risk of shark attack and consequently to reinforce preventive measures.

This study corroborates the hypothesis that the presence of the Suape port to the south of Recife could be contributing to increase the abundance of sharks in nearshore waters. The natural movements of tiger sharks would consequently lead them to visit the littoral of Recife. Local-specific features such as the Barra de Jangadas estuary and high levels of pollution could further attract sharks to inshore waters, where high water siltation and the presence of a channel next to the beaches could promote the probability of sharks interacting with humans. The SMPR actuates by intercepting sharks before they access to the area of risk and by transporting them to deeper waters for releasing. Since tiger sharks swam away to oceanic waters and followed northward routes after releasing in most occasions, this methodology seems to be effective to significantly enhance bathing safety. The success of the SMPR in shark attack prevention may, however, depend on site-specific features, since previous longline-based shark control programs in other regions (e.g. Hawaii) showed no measurable effects on the rate of shark attacks.

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Supplementary tables

Table SUP.5.1. Approximated logarithmic marginal likelihoods, *logE*, of single models with one predictor variable for all species and predictors, assessed with non-inflated Generalized Additive Models (GAM), zero-inflated Generalized Additive Models (ZIGAM), and constrained zero-inflated Generalized Additive Models (COZIGAM). The lowest *logE* for each species and predictor is typed in bold face. NA's correspond to unsuccessfully fitted models which did not provide an output.

Species	Predictor	GAM	ZIGAM	COZIGAM
Carcharhinus acronotus	Year	−203.526	**−186.97**	−371.308
	Month	−233.725	**−192.835**	−305.444
	Lunar day	−231.402	**−206.348**	−213.932
	Temperature	−231.379	**−192.142**	−297.501
	Salinity	−206.893	**−193.537**	−214.203
	Visibility	−231.569	**−203.118**	−214.324
	Pluviosity	−231.491	**−207.035**	−217.949
	Tidal amplitude	−231.438	−206.501	**−204.998**
	Wind direction	−223.608	**−197.384**	−200.750
	Solar radiation	−230.833	**−206.058**	−218.846
	Wind speed	−211.495	**−193.497**	NA
Ginglymostoma cirratum	Year	−297.338	**−282.258**	−815.652
	Month	−310.557	**−300.78**	−540.733
	Lunar day	−312.917	**−302.46**	−435.343
	Temperature	−309.956	**−302.012**	−545.362
	Salinity	−306.540	**−290.829**	−296.893
	Visibility	−299.013	**−288.377**	NA
	Pluviosity	−312.857	**−303.905**	NA
	Tidal amplitude	−312.821	**−303.751**	NA
	Wind direction	−309.104	**−296.706**	−829.089
	Solar radiation	−313.923	**−294.462**	−797.744
	Wind speed	−309.396	**−290.800**	−302.599
Galeocerdo cuvier	Year	−127.749	**−124.151**	−260.078
	Month	−132.918	**−126.782**	−171.675
	Lunar day	−133.486	**−130.147**	−346.171
	Temperature	−136.727	**−132.579**	NA
	Salinity	−133.734	**−131.848**	−368.931
	Visibility	−131.901	**−126.988**	−471.958
	Pluviosity	−135.513	**−125.94**	NA
	Tidal amplitude	−135.688	**−119.908**	NA
	Wind direction	−129.589	**−117.531**	−462.808
	Solar radiation	−135.297	**−132.786**	−279.408
	Wind speed	−124.665	**−120.939**	−274.774
Dasyatis spp.	Year	−124.910	−116.515	**−116.135**
	Month	−127.809	**−120.358**	−166.916
	Lunar day	−129.925	**−121.663**	−437.909
	Temperature	−129.499	**−120.246**	−139.977
	Salinity	−127.451	**−116.155**	NA
	Visibility	−129.455	**−121.078**	−207.457
	Pluviosity	−129.078	**−119.789**	−153.048
	Tidal amplitude	−127.621	**−119.614**	−139.67
	Wind direction	−129.515	**−119.841**	−130.387
	Solar radiation	−128.521	**−120.757**	−138.286
	Wind speed	−126.052	**−116.322**	−116.569

Table SUP.5.2. Summary of correlation analysis between continuous variables to assess for problematic interdependencies. Results are shown for t-statistics, degrees of freedom (d.f.), *p*-value, 95% confidence intervals (± C.I.), Pearson's product-moment correlation coefficient (*r*), and Spearman's rank correlation coefficient (ρ). Covariates exhibiting high, possible problematic correlations are typed in boldface.

Covariate 1	Covariate 2	t-stat.	d.f.	*p*-value	− C.I.	+ C.I.	*R*	ρ
Temperature	Salinity	2.7682	241	0.0061	0.05082	0.2948	0.176	0.358
Temperature	**Visibility**	**13.3331**	**332**	**< 0.001**	**0.51592**	**0.6562**	**0.591**	**0.600**
Temperature	Tidal amplitude	0.2304	452	0.8179	−0.0812	0.1027	0.011	0.016
Temperature	Pluviosity	−4.1042	408	< 0.001	−0.2903	−0.104	−0.199	−0.203
Temperature	Wind speed	−0.4315	418	0.6664	−0.1165	0.0747	−0.022	−0.034
Temperature	Wind direction	−4.2665	418	< 0.001	−0.2942	−0.110	−0.204	−0.191
Temperature	Solar radiation	4.0375	349	< 0.001	0.10898	0.3090	0.211	0.242
Salinity	Visibility	0.1619	223	0.8715	−0.1201	0.1414	0.011	0.198
Salinity	Tidal amplitude	0.8364	241	0.4038	−0.0725	0.1784	0.054	0.036
Salinity	Pluviosity	−2.9906	226	0.0031	−0.3169	−0.066	−0.195	−0.211
Salinity	Wind speed	2.5685	228	0.0109	0.03919	0.2907	0.168	0.206
Salinity	Wind direction	−0.4042	228	0.6865	−0.1555	0.1029	−0.027	−0.078
Salinity	Solar radiation	2.8123	202	0.0054	0.05829	0.3228	0.194	0.151
Visibility	Tidal amplitude	−0.1309	376	0.8959	−0.1075	0.0941	−0.007	0.009
Visibility	Pluviosity	−3.4035	336	< 0.001	−0.2837	−0.077	−0.183	−0.172
Visibility	**Wind speed**	**−11.536**	**342**	**< 0.001**	**−0.6013**	**−0.448**	**−0.529**	**−0.520**
Visibility	**Wind direction**	**−6.0066**	**342**	**< 0.001**	**−0.4015**	**−0.210**	**−0.309**	**−0.319**
Visibility	Solar radiation	1.9835	279	0.0483	0.00092	0.2317	0.118	0.113
Pluviosity	Wind speed	−0.4643	462	0.6427	−0.1124	0.0695	−0.022	−0.154
Pluviosity	**Wind direction**	**7.8201**	**462**	**< 0.001**	**0.25893**	**0.4198**	**0.342**	**0.353**
Wind speed	Wind direction	8.6982	472	< 0.001	0.29137	0.4467	0.372	0.187
Wind direction	Solar radiation	−5.3213	397	< 0.001	−0.3473	−0.164	−0.258	−0.288
Tidal	Lunar day	−5.7111	516	< 0.001	−0.3231	−0.161	−0.244	−0.229

Table SUP.7.1. Summary of ARGOS-linked transmissions performed by PSAT tags deployed on tiger sharks off Recife between June 2008 and September 2011, with information on the number of transmitting days, number of satellite passes, number of ARGOS locations assessed and the respective distribution of ARGOS location classes (LC), and the number of messages received with the successfully decoded percentage.

Shark	Days of transm	Satellite passes	ARGOS locations	Location class (LC)					Messages (% decoded)
				3	2	1	0	A+B	
#1	3	69	64	7	28	18	7	4	524 (88%)
#2	8	202	186	34	89	40	10	13	1794 (79%)
#3	6	163	150	19	72	31	14	14	1176 (70%)
#4	3	4	0	0	0	0	0	0	4 (0%)
#5	6	98	85	41	22	7	5	10	537 (81%)
#6	7	173	151	32	73	30	6	10	1448 (76%)
#7	10	148	142	47	46	16	3	30	997 (65%)
#9	8	202	179	26	87	37	10	19	1377 (67%)
#12	5	140	137	34	42	17	6	38	897 (67%)
#15	4	66	60	35	11	2	0	12	363 (83%)
#17	7	112	105	38	12	3	5	47	456 (84%)
#18	4	114	109	34	35	16	1	23	731 (64%)
#19	5	138	136	28	49	25	9	25	934 (65%)
#20	9	61	59	29	14	7	2	7	427 (69%)
#21	8	185	183	63	62	21	3	34	1289 (70%)
#22	5	69	57	1	3	1	7	45	168 (63%)

Table SUP.7.2. Summary of Kruskal-Wallis rank sum tests (χ^2 statistics and associated *p*-value) to compare the maximum depth, depth range, minimum temperature and temperature range in tiger shark vertical movements between sexes and 3 size classes.

Variable	Sex		Size	
	χ^2	*p*-value	χ^2	*p*-value
Maximum depth	0.0001	0.9909	519.45	< 0.001
Depth range	1.0657	0.3019	518.5208	< 0.001
Minimum temperature	1.8572	0.1729	693.8818	< 0.001
Temperature range	1.383	0.2396	580.4897	< 0.001

Table SUP.7.3. Summary of Wilcoxon rank sum tests (W statistics and associated *p*-value) to compare the proportion of time spent by tiger sharks at depths shallower than 10, 20, 40 and 60 m between diel phases (day *vs* night).

Shark	10 m		20 m		40 m		60 m	
	W	*p*-value	W	*p*-value	W	*p*-value	W	*p*-value
All	109653.5	< **0.001**	134651	< **0.001**	203364.5	0.1763	212776.5	0.9734
#3	2520	< **0.001**	3414	< **0.001**	14131.5	**0.0050**	11979	0.9555
#5*	1504	< **0.001**	2610.5	0.6198	2623.5	0.6038	2839.5	0.6139
#6	523	< **0.001**	525	< **0.001**	807.5	< **0.001**	1545.5	0.1795
#7	2712	< **0.001**	2679	< **0.001**	2624	< **0.001**	2539	< **0.001**
#9	474	0.7675	472	0.7466	416	0.2743	341	**0.0337**
#12	835	< **0.001**	1263	**0.0024**	1894.5	0.8446	2106	0.1961
#15	380	**0.0103**	421	**0.0397**	438	0.0645	435	0.0594
#17*	599	**0.0014**	687	**0.0131**	884	0.3853	1099	0.3639
#18	539	< **0.001**	632	**0.0067**	887.5	0.5707	960	0.9732
#19	104	< **0.001**	158.5	**0.0012**	212.5	**0.0239**	344	0.8903
#20	497	**0.0033**	681	0.2556	984	0.0742	1129.5	**0.0013**
#21	6	1	7	0.8571	8	0.6286	12	0.0571

*Archival data

Table SUP.7.4. Summary of Kruskal-Wallis rank sum tests (χ^2 statistics and associated *p*-value) to compare the proportion of time spent by tiger sharks at depths shallower than 10, 20, 40 and 60 m between moon phases (1 = first quarter, F = full moon, 3 = last quarter, N = new moon). The six columns on the right present results from a post-hoc procedure, *kruskalm*c (Giraudoux, 2011), which informs the significance (T = true, F = false) of each pairwise comparisons when *p*-value < 0.05.

Shark	Depth	KW χ^2	*p*-value	1−F	1−3	1−N	F−3	F−N	3−N
All	10 m	35.9941	< **0.001**	F	T	T	T	T	F
	20 m	32.3874	< **0.001**	F	T	T	T	T	F
	40 m	29.569	< **0.001**	F	T	T	T	T	F
	60 m	29.4785	< **0.001**	F	T	T	T	F	F
#3	10 m	6.6462	0.0840						
	20 m	9.2561	**0.0261**	F	F	T	F	F	F
	40 m	11.1692	**0.0109**	F	F	F	F	F	F
	60 m	10.5536	**0.0144**	F	F	F	F	F	F
#5*	10 m	9.2421	**0.0262**	F	F	T	F	F	F
	20 m	1.0601	0.7867						
	40 m	2.5913	0.459						
	60 m	2.817	0.4207						
#7	10 m	12.0829	**0.0071**	F	T	F	F	F	F
	20 m	11.0377	**0.0115**	F	T	F	F	F	F
	40 m	10.3913	**0.0155**	F	T	F	F	F	F
	60 m	9.818	**0.02018**	F	T	F	F	F	F
#12	10 m	1.0698	0.7844						
	20 m	8.8565	**0.0313**	F	F	F	F	F	F
	40 m	7.4125	0.0599						
	60 m	9.4814	**0.0235**	F	F	F	F	F	F
#15	10 m	0.5796	0.9011						
	20 m	3.4416	0.3284						
	40 m	6.3531	0.0956						
	60 m	6.064	0.1085						
#17*	10 m	7.3895	0.0605						
	20 m	0.7968	0.8502						
	40 m	0.3946	0.9413						

	60 m	0.9353	0.8169						
#18	10 m	5.0123	0.1709						
	20 m	3.3579	0.3397						
	40 m	15.8023	**0.0012**	F	F	F	T	T	F
	60 m	25.7216	< **0.001**	F	F	F	F	F	F
#19	10 m	1.8286	0.6087						
	20 m	7.4064	0.0600						
	40 m	9.0909	**0.0281**	F	F	F	F	F	T
	60 m	3.4781	0.3236						
#20	10 m	15.3471	**0.0015**	F	F	T	F	T	T
	20 m	23.4899	< **0.001**	F	F	T	T	T	F
	40 m	28.1845	< **0.001**	F	T	F	T	T	F
	60 m	13.7523	**0.0033**	F	F	T	F	T	T

*Archival data

Supplementary figures

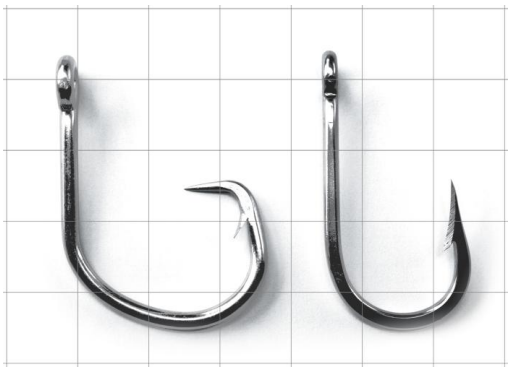

Figure SUP.3.1. Circle and J-style hooks used in the longline experiment. Squares of the superimposed grid are 2.0 x 2.0 cm.

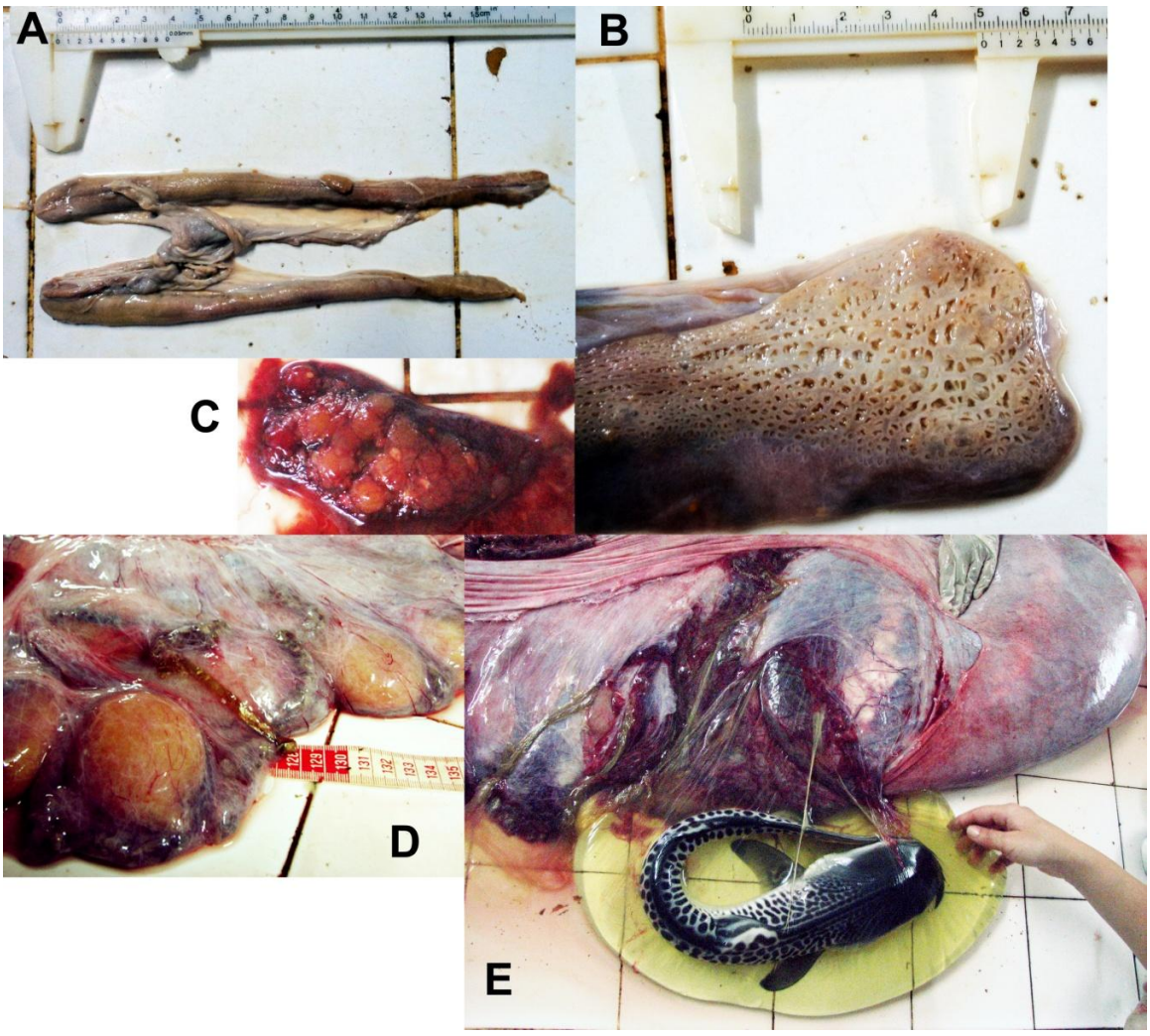

Figure SUP.6.1. Details on the reproductive tract of tiger sharks caught off Recife, namely A) testes; B) an incipient ovary developing on the epigonal organ; C) a mature ovary with vitellogenic oocytes; D) uterus containing large, yolked eggs; and E) a late-term embryo being removed from the compartmentalized uterus.

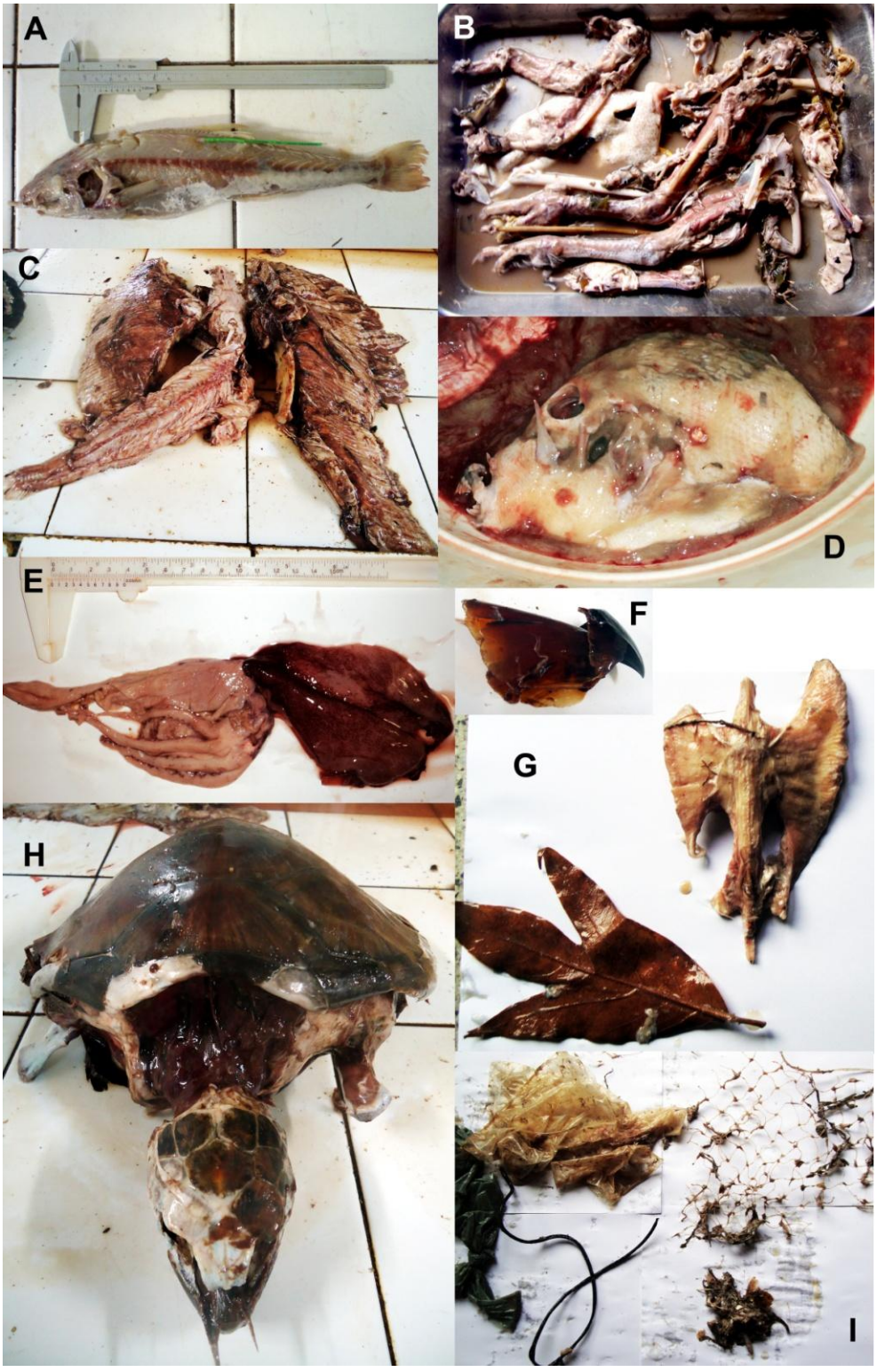

Figure SUP.6.2. Stomachal contents of tiger sharks caught off Recife, namely A) a cobia, *Rachycentron canadum*, which had been tagged and release in the same region; B) a land bird, presumably a domestic chicken; C) a stingray, *Dasyatis americana*; D) a balistid triggerfish; E) a squid; F) a squid beak; G) a small ray and a tree leaf; H) an hawksbill turtle, *Eretmochelys imbricata*; and I) pieces of a gillnet mesh and garbage.

Figure SUP.7.1. Details on the water-filled wooden taken assembled on the deck of the R/V Sinuelo for transporting potentially aggressive sharks caught in coastal waters off Recife to deeper waters.

Figure SUP.7.2. Aspects of tiger shark tagging, depicting an yellow, conventional, stainless steel dart tag inserted in the dorsal musculature of the shark, and a satellite tag fitted to its first dorsal fin.

Figure SUP.7.3. Aspect of the coded, acoustic transmitters used for monitoring tiger shark movements, namely V13 (top) and V16 (middle) transmitters for surgical implantations and V16 transmitter with shark-case (bottom) for external attachment. Scale is in centimeters.

Figure SUP.7.4. Aspect of the surgical implantation of an acoustic transmitter in the peritoneal cavity of a tiger shark.

Figure SUP.7.5. Aspect of the pop-up satellite archival transmitter (PSAT) tag used for monitoring tiger shark movements. Scale is in centimeters.

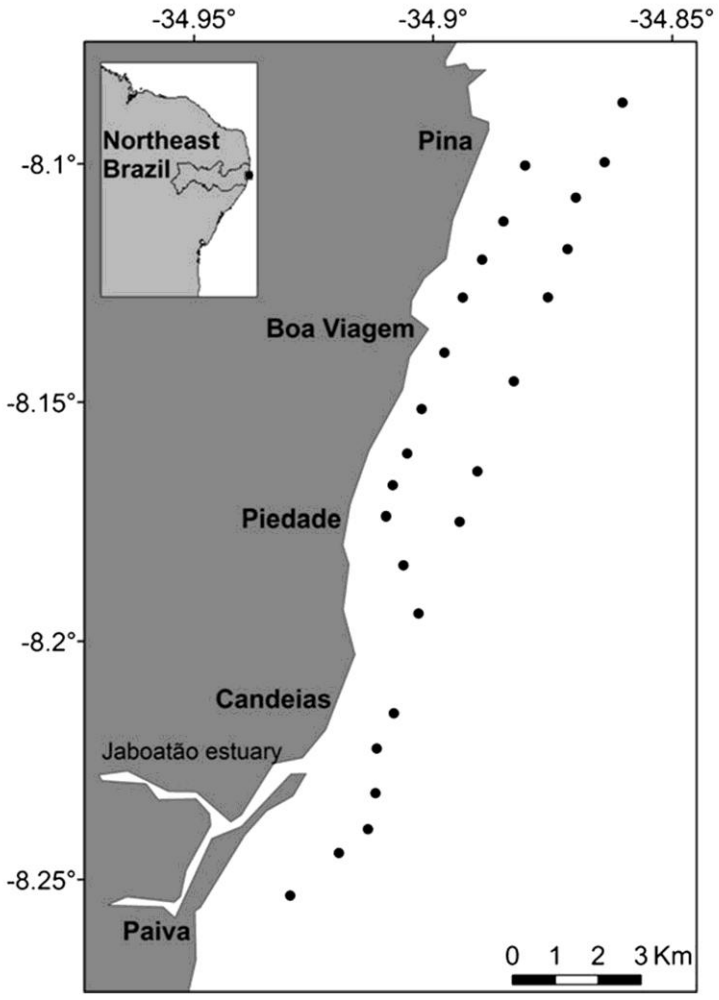

Figure SUP.7.6. Map of the coastal region of the Metropolitan Region of Recife depicting the location of acoustic monitoring stations (black dots). Four other acoustic stations located further offshore at 20-40 m isobaths are not included due to scale constraints. Adapted from Ferreira et al. (2012).

Figure SUP.7.7. ARGOS geolocation estimates for shark #9 prematurely-released PSAT-tag westward drifting following pop-up off northeastern Brazil. An estimate of the actual pop-up location is also shown.

Figure SUP.7.8. ARGOS geolocation estimates for shark #21 prematurely-released PSAT-tag northward drifting following pop-up off northeastern Brazil. An estimate of the actual pop-up location is also shown.

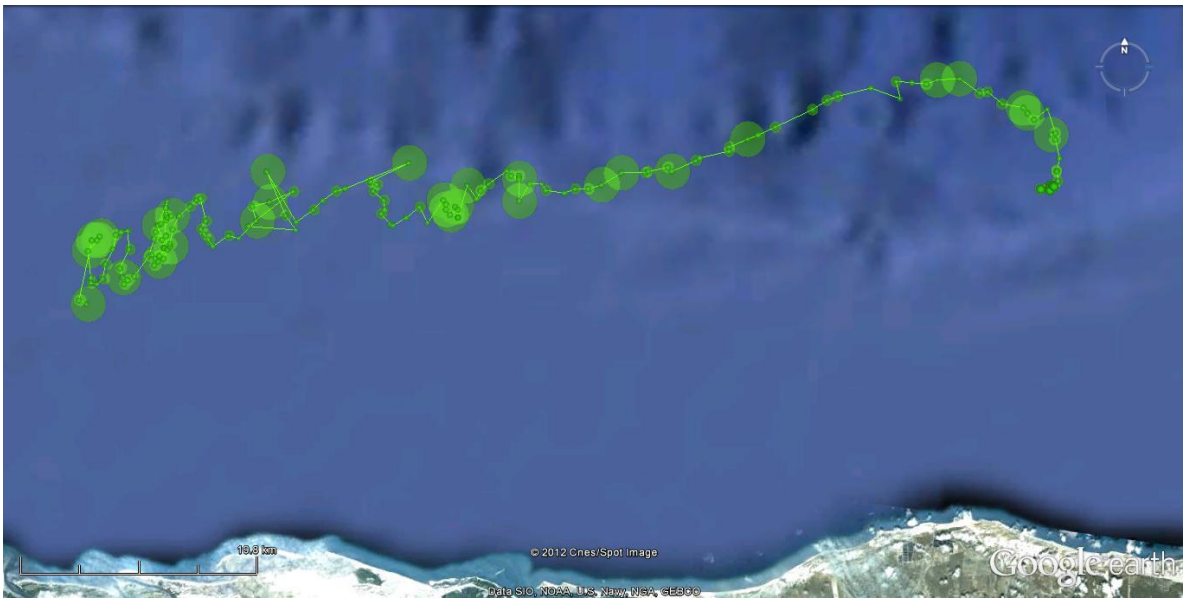

Figure SUP.7.9. ARGOS geolocation estimates for shark #6 prematurely-released PSAT-tag westward drifting following pop-up off the northern coast of Rio Grande do Norte, Brazil. The actual pop-up location was impossible to assess due to nonlinear motion in the beggining of the drift. Green circles correspond to confidence intervals for ARGOS estimates.

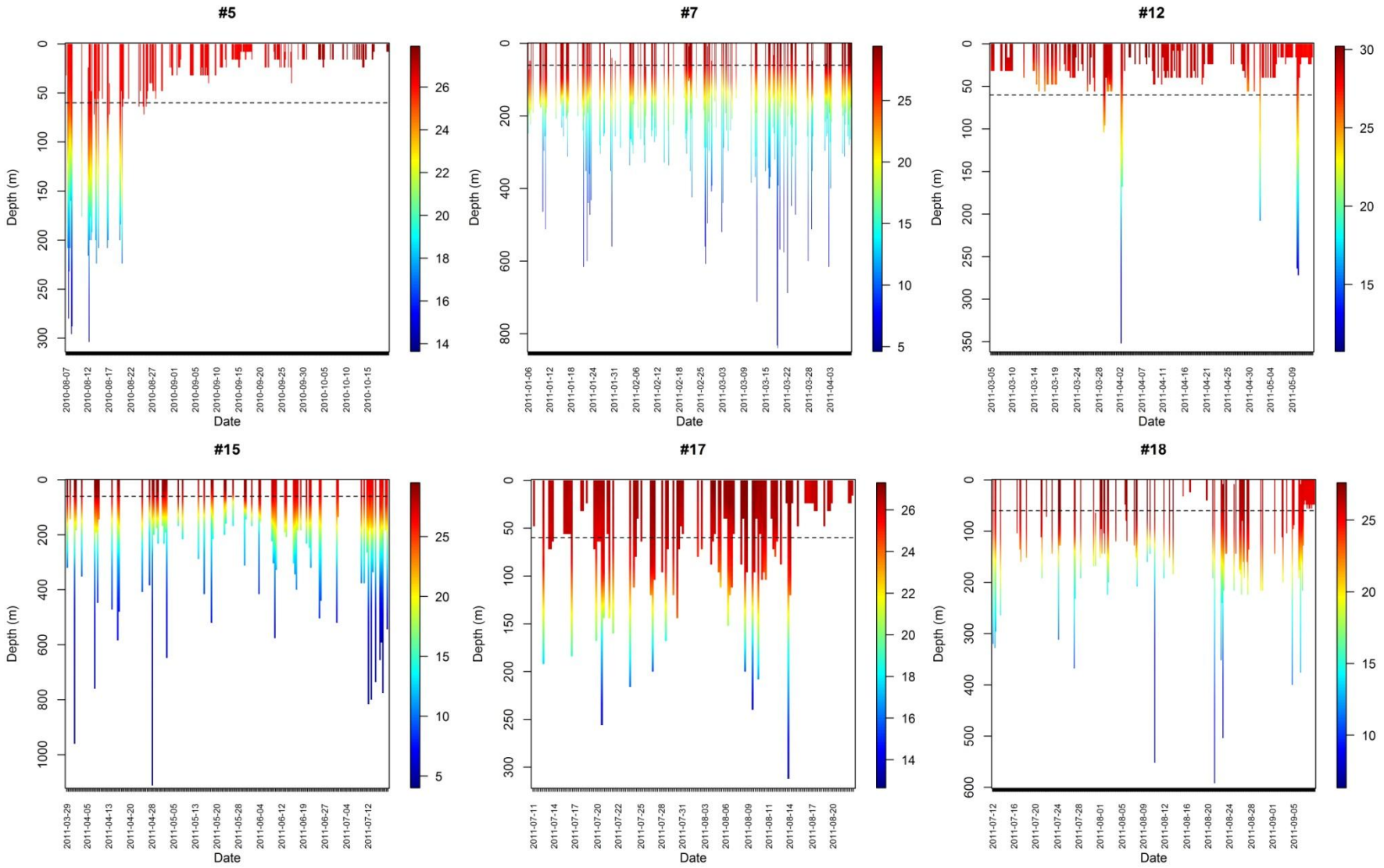

Figure SUP.7.10. Depth-and-temperature (PDT) profiles of the movements of tiger sharks #5, #7, #12, #15, #17, #18, #19, #20, and #22 assessed with PSAT tags off northeastern Brazil. Colours represent the gradient of sea water temperature. Horizontal dashed lines depict shelf break depth. (continues on next page)

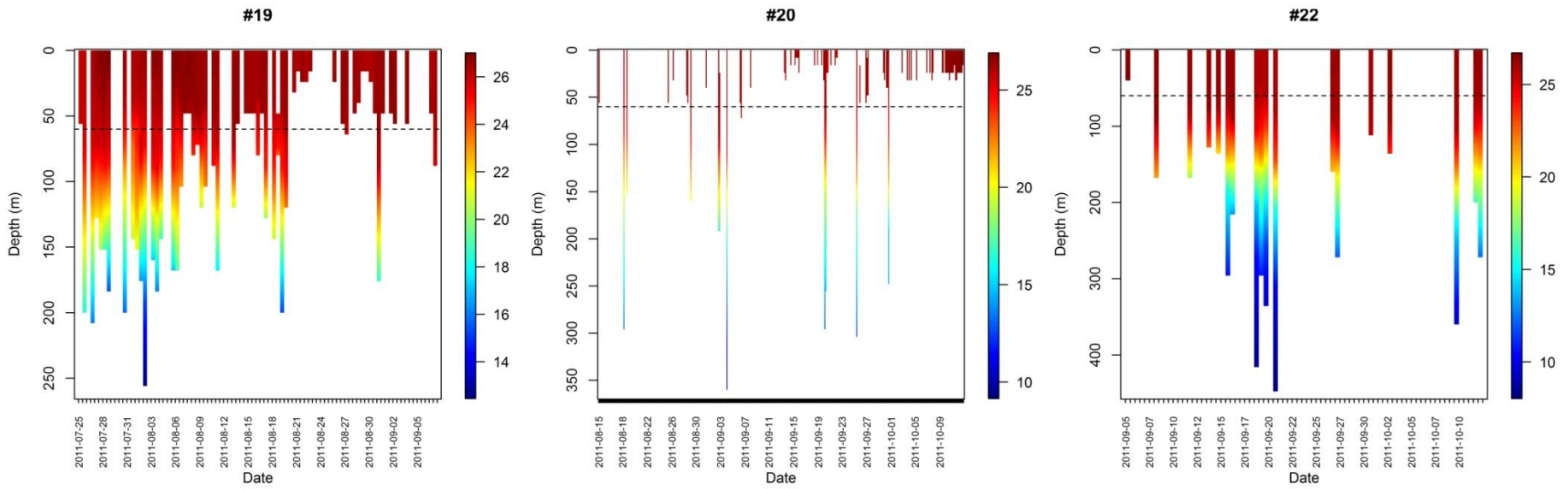

Figure SUP.7.10. Continuation Depth-and-temperature (PDT) profiles of the movements of tiger sharks #5, #7, #12, #15, #17, #18, #19, #20, and #22 assessed with PSAT tags off northeastern Brazil. Colours represent the gradient of sea water temperature. Horizontal dashed lines depict shelf break depth.

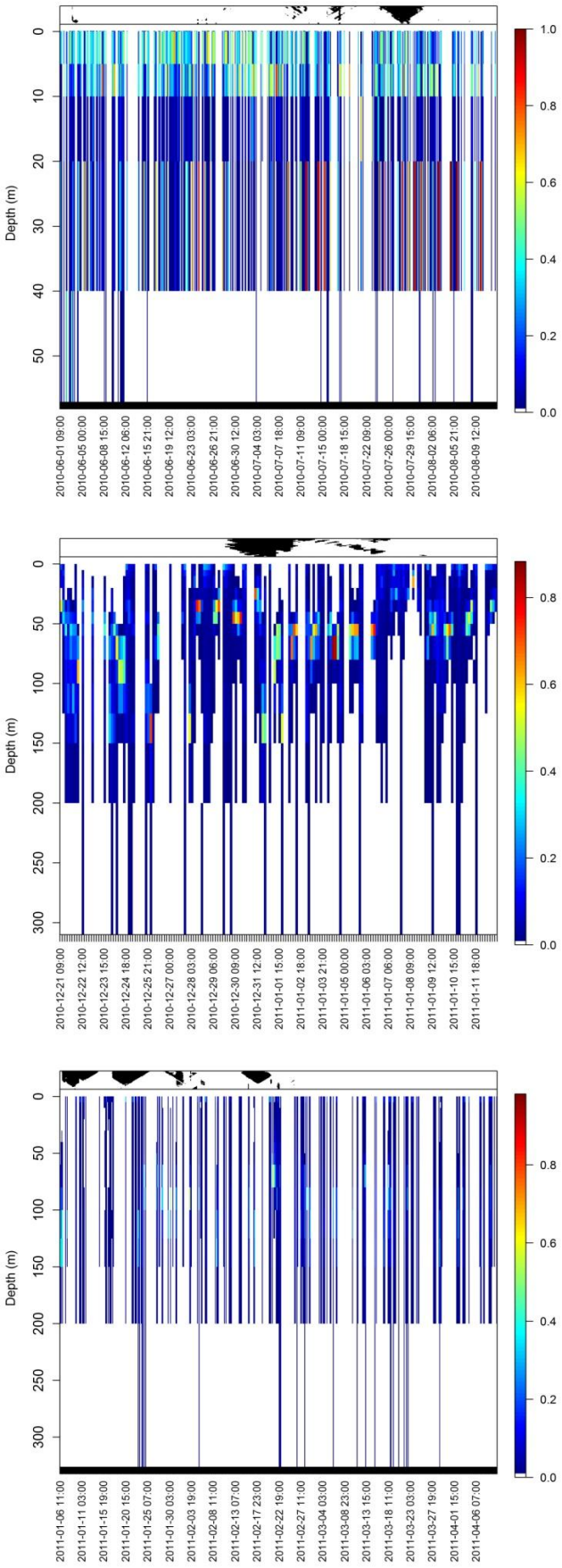

Figure SUP.7.11. Time-at-depth (TAD) histograms for sharks #3 (top panel), #6 (middle panel), and #7 (bottom panel) ARGOS-relayed data. Colours represent the proportion of time spent at each depth strata. The rectangle above each histogram depicts results from the Split Moving Window Gradient Analysis, where inverted black triangles point to the boundary between significantly different behaviours.

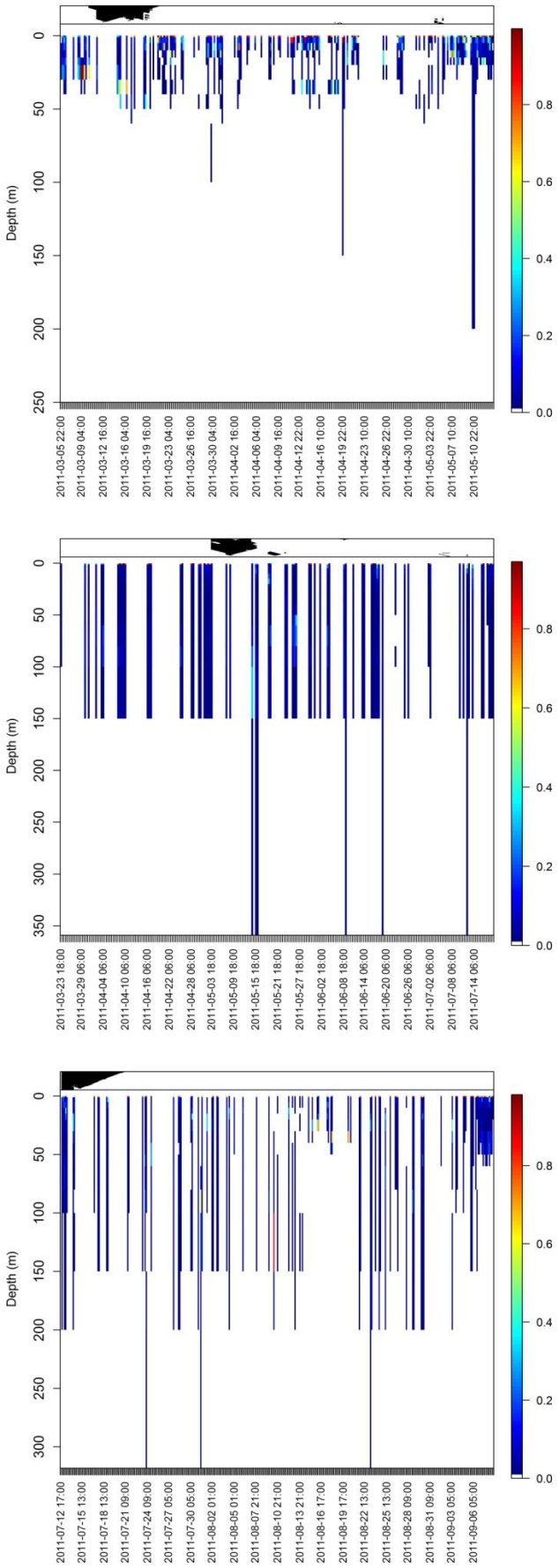

Figure SUP.7.12. Time-at-depth (TAD) histograms for sharks #12 (top panel), #15 (middle panel), and #18 (bottom panel) ARGOS-relayed data. Colours represent the proportion of time spent at each depth strata. The rectangle above each histogram depicts results from the Split Moving Window Gradient Analysis, where inverted black triangles point to the boundary between significantly different behaviours.

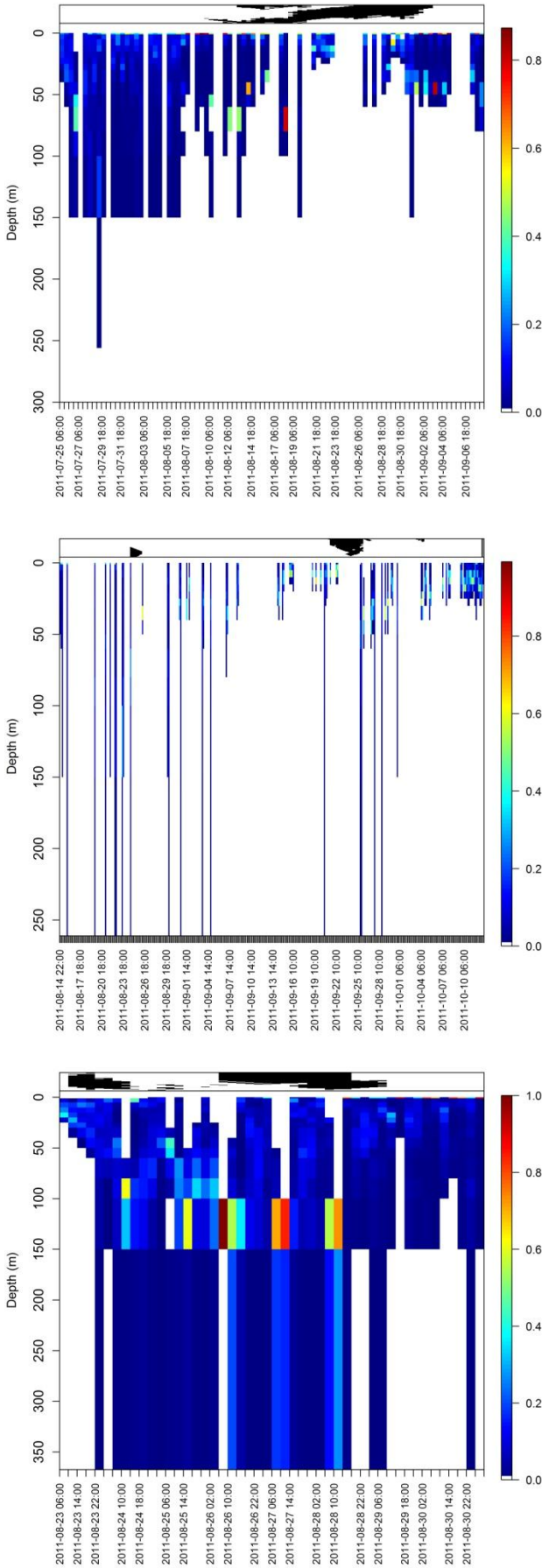

Figure SUP.7.13. Time-at-depth (TAD) histograms for sharks #19 (top panel), #20 (middle panel), and #21 (bottom panel) ARGOS-relayed data. Colours represent the proportion of time spent at each depth strata. The rectangle above each histogram depicts results from the Split Moving Window Gradient Analysis, where inverted black triangles point to the boundary between significantly different behaviours.

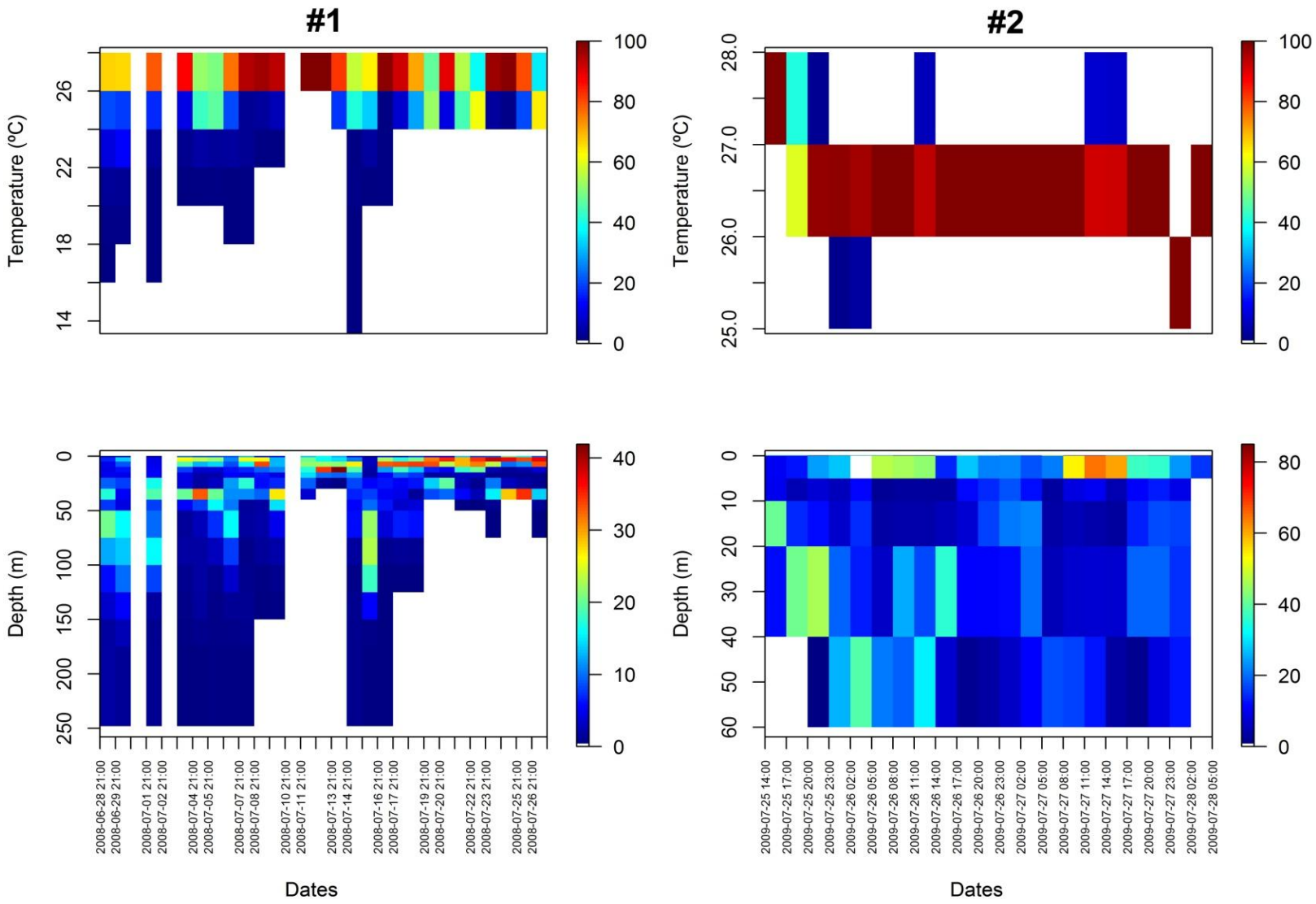

Figure SUP.7.14. Time-at-temperature (TAT; upper panel) and time-at-depth (TAD; lower panel) histograms for sharks #1, #2, #9 and #22 ARGOS-relayed data. Colours represent the proportion of time spent at each depth strata.

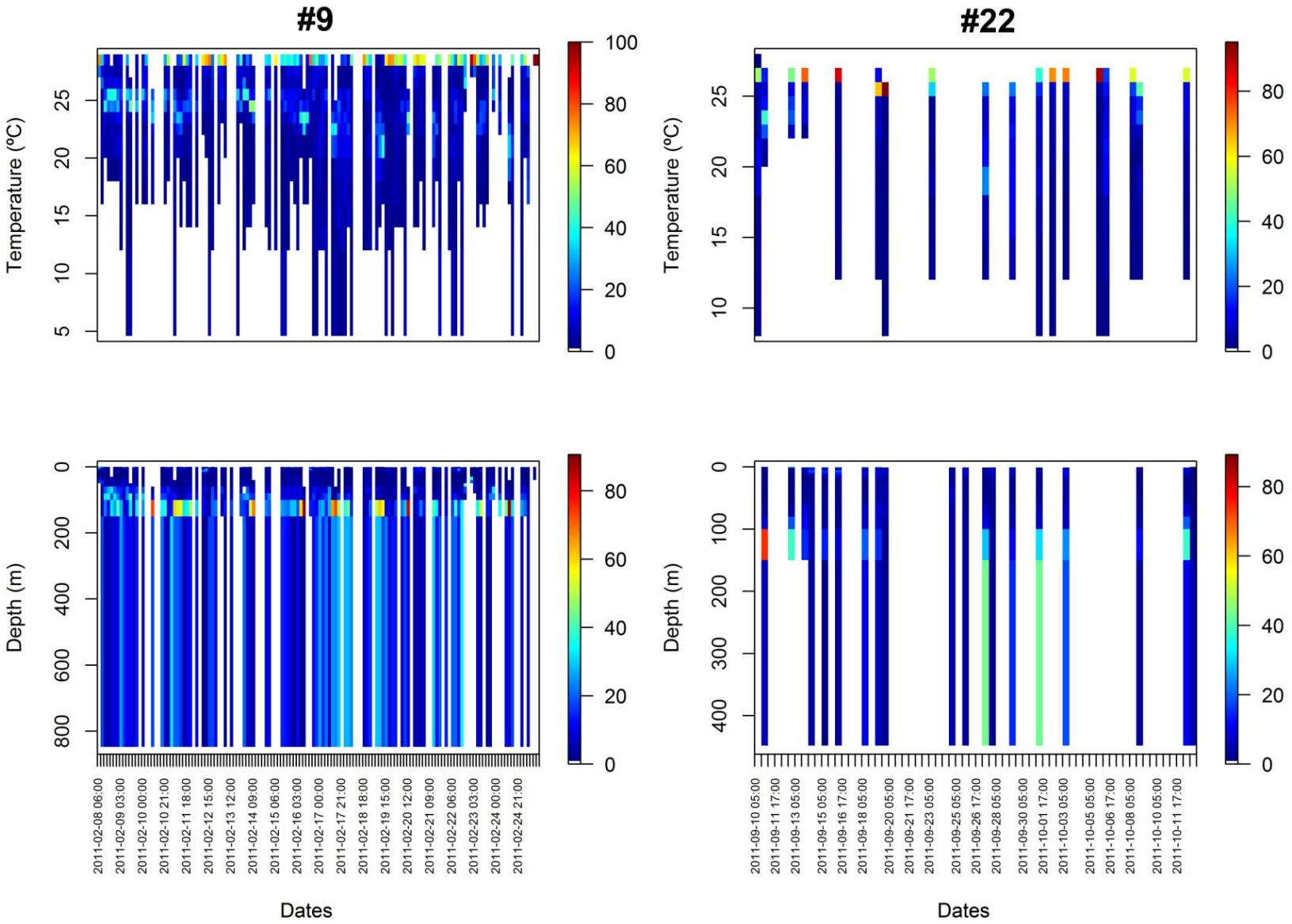

Figure SUP.7.14. Continuation. Time-at-temperature (TAT; upper panel) and time-at-depth (TAD; lower panel) histograms for sharks #1, #2, #9 and #22 ARGOS-relayed data. Colours represent the proportion of time spent at each depth strata.

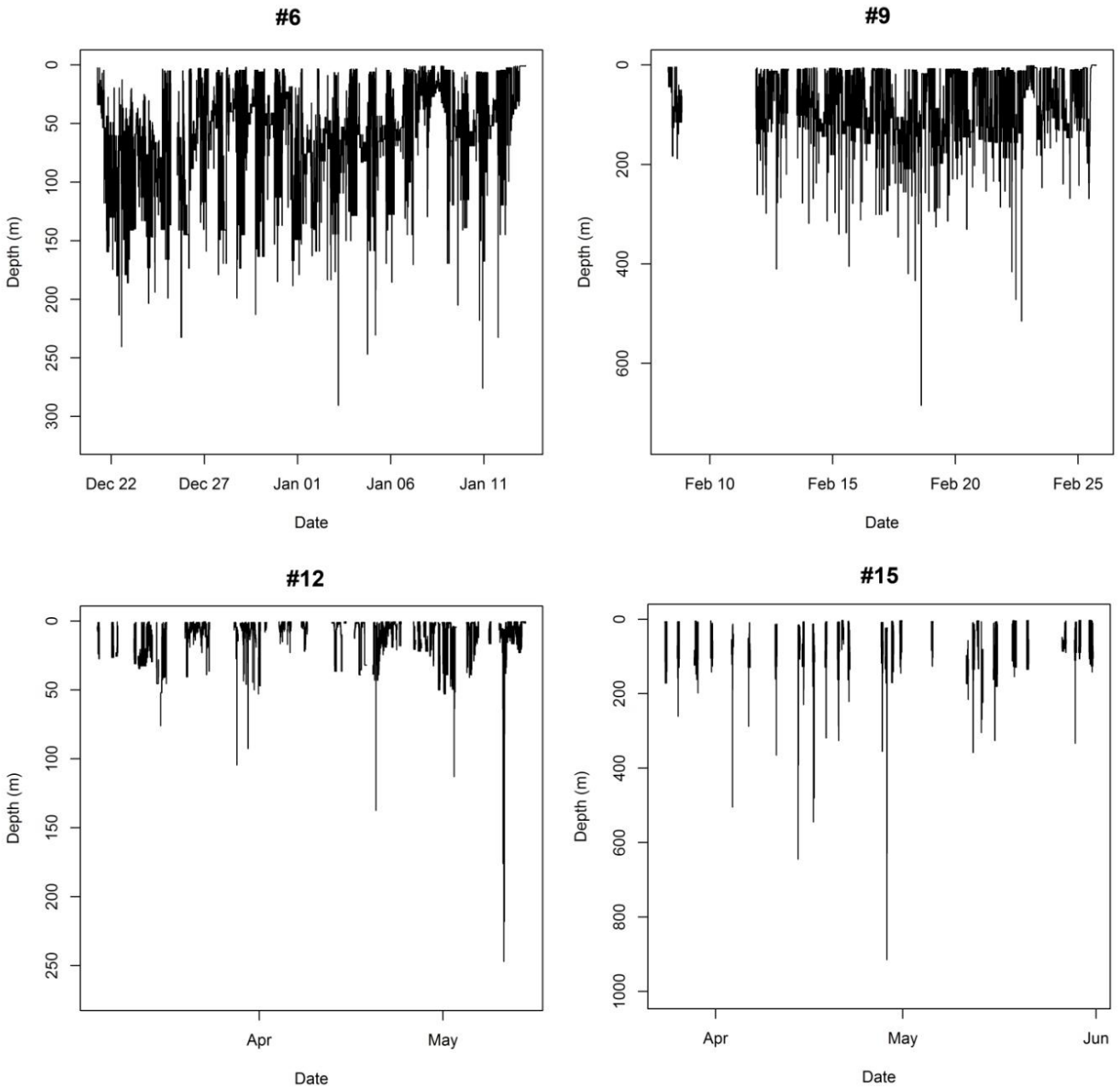

Figure SUP.7.15. Time-series of sharks #6, #9, #12, #15, #18, #19, #20 and #21 vertical movements, with a temporal resolution between 2.5-5 minutes, during the respective tracking period. (continues on next page)

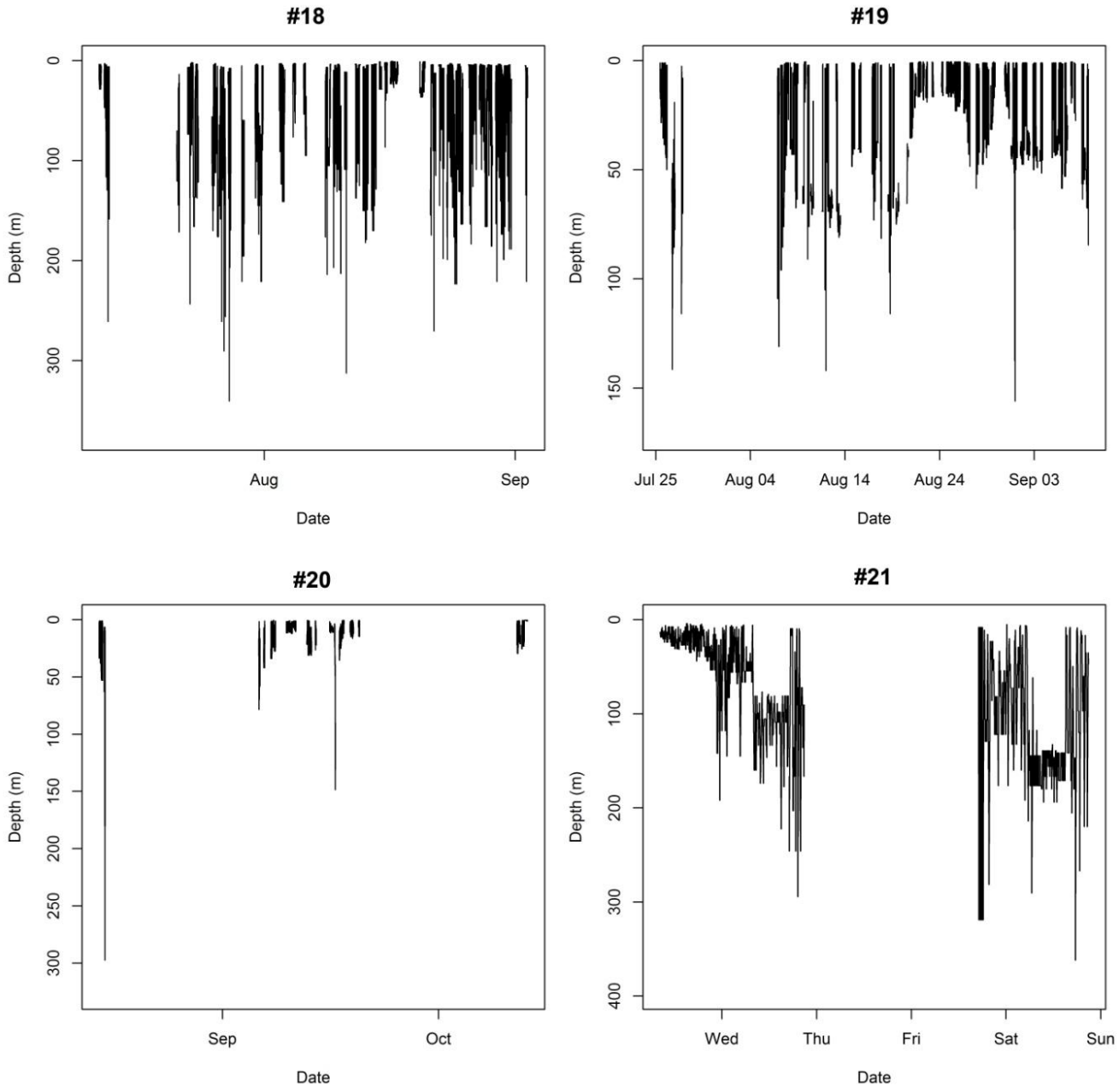

Figure SUP.7.15. Continuation. Time-series of sharks #6, #9, #12, #15, #18, #19, #20 and #21 vertical movements, with a temporal resolution between 2.5-5 minutes, during the respective tracking period.

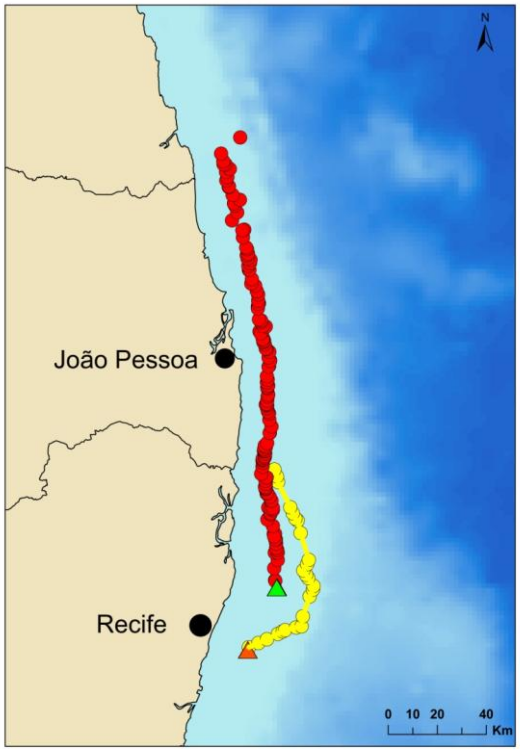

Figure SUP.7.16. Horizontal movements of tiger shark #3 off northeastern Brazil assessed with PSAT tags. The yellow line represents shark movements estimated with light-level information, the red dots depict ARGOS geolocation estimates of the transmitting tag, the orange triangle represents the tagging location, and the green triangle represents the location of the first satellite transmission, generally coinciding with pop-up location.

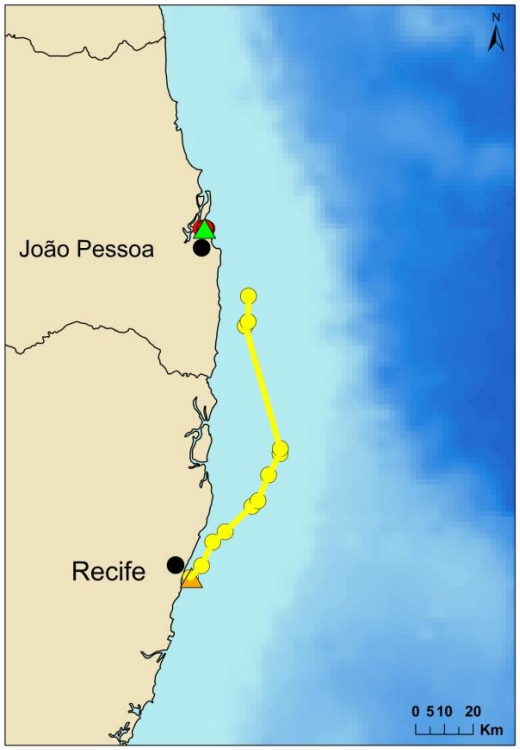

Figure SUP.7.17. Horizontal movements of tiger shark #5 off northeastern Brazil assessed with PSAT tags. The yellow line represents shark movements estimated with light-level information, the red dots depict ARGOS geolocation estimates of the transmitting tag, the orange triangle represents the tagging location, and the green triangle represents the location of the first satellite transmission, which in this case ocurred on land.

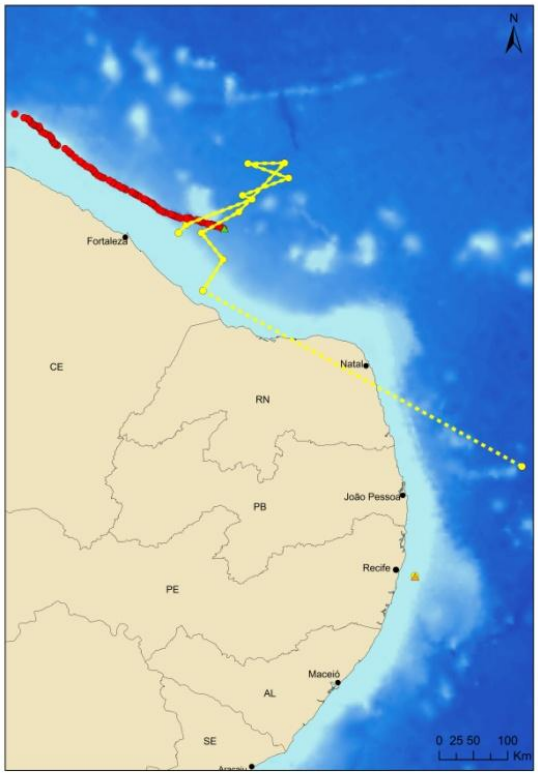

Figure SUP.7.18. Horizontal movements of tiger shark #7 off northeastern Brazil assessed with PSAT tags. The yellow line represents shark movements estimated with light-level information, the red dots depict ARGOS geolocation estimates of the transmitting tag, the orange triangle represents the tagging location, and the green triangle represents the location of the first satellite transmission, generally coinciding with pop-up location.

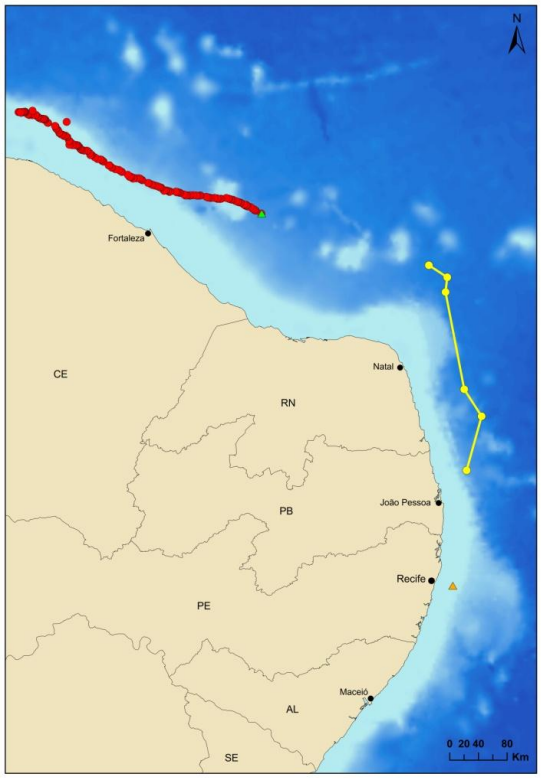

Figure SUP.7.19. Horizontal movements of tiger shark #9 off northeastern Brazil assessed with PSAT tags. The yellow line represents shark movements estimated with light-level information, the red dots depict ARGOS geolocation estimates of the transmitting tag, the orange triangle represents the tagging location, and the green triangle represents the location of the first satellite transmission, generally coinciding with pop-up location.

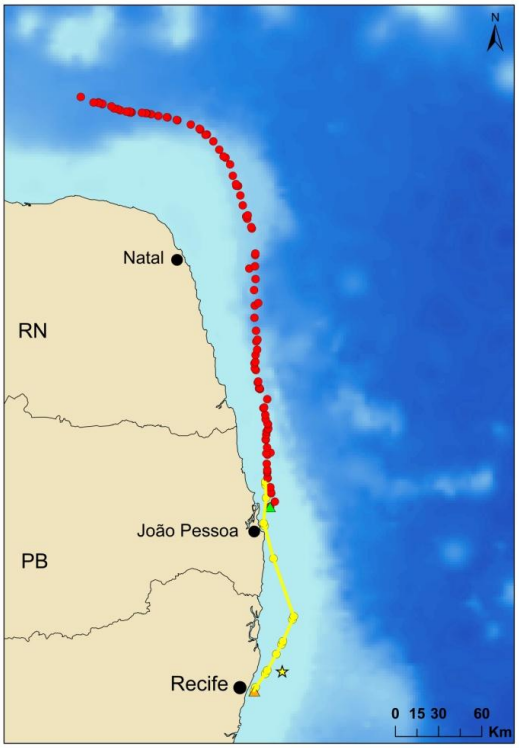

Figure SUP.7.20. Horizontal movements of tiger shark #12 off northeastern Brazil assessed with PSAT tags. The yellow line represents shark movements estimated with light-level information, the red dots depict ARGOS geolocation estimates of the transmitting tag, the orange triangle represents the tagging location, and the green triangle represents the location of the first satellite transmission, generally coinciding with pop-up location. The yellow star represents the location of an acoustic receiver which detected the presence of shark #12.

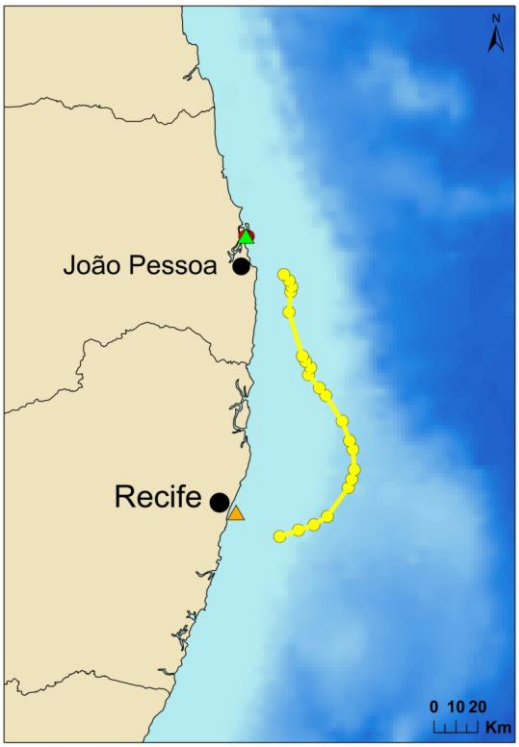

Figure SUP.7.21. Horizontal movements of tiger shark #17 off northeastern Brazil assessed with PSAT tags. The yellow line represents shark movements estimated with light-level information, the red dots depict ARGOS geolocation estimates of the transmitting tag, the orange triangle represents the tagging location, and the green triangle represents the location of the first satellite transmission, generally coinciding with pop-up location.

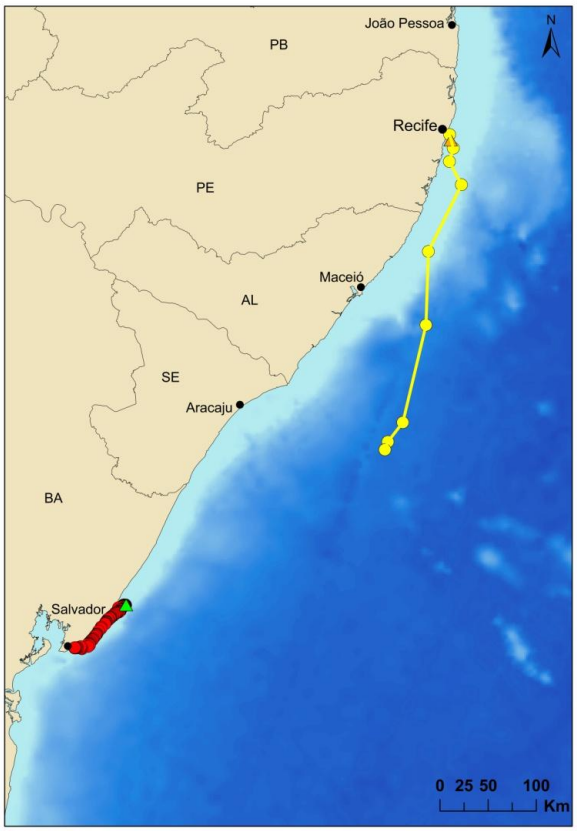

Figure SUP.7.22. Horizontal movements of tiger shark #18 off northeastern Brazil assessed with PSAT tags. The yellow line represents shark movements estimated with light-level information, the red dots depict ARGOS geolocation estimates of the transmitting tag, the orange triangle represents the tagging location, and the green triangle represents the location of the first satellite transmission, generally coinciding with pop-up location.

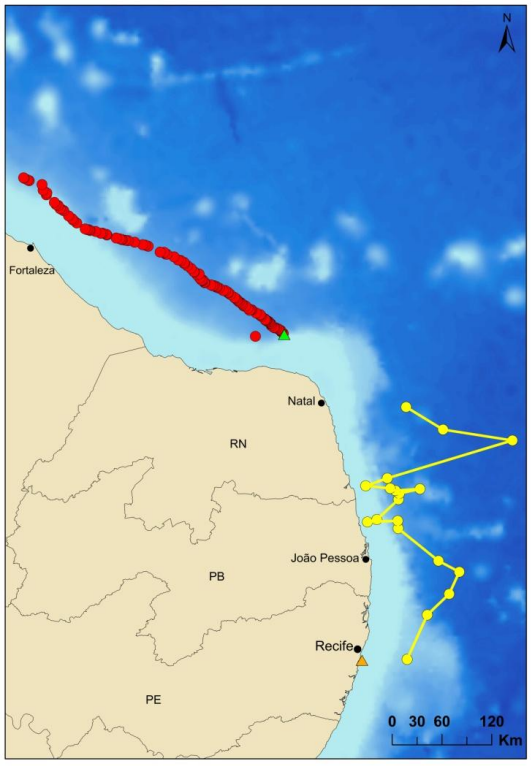

Figure SUP.7.23. Horizontal movements of tiger shark #19 off northeastern Brazil assessed with PSAT tags. The yellow line represents shark movements estimated with light-level information, the red dots depict ARGOS geolocation estimates of the transmitting tag, the orange triangle represents the tagging location, and the green triangle represents the location of the first satellite transmission, generally coinciding with pop-up location.

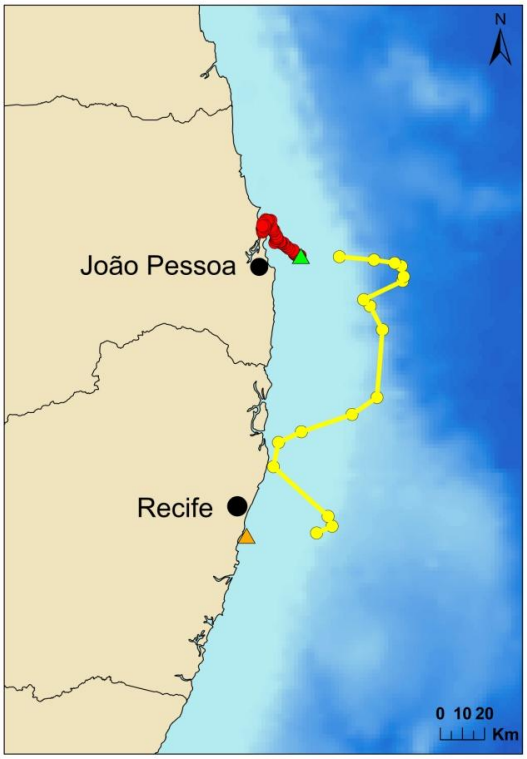

Figure SUP.7.24. Horizontal movements of tiger shark #20 off northeastern Brazil assessed with PSAT tags. The yellow line represents shark movements estimated with light-level information, the red dots depict ARGOS geolocation estimates of the transmitting tag, the orange triangle represents the tagging location, and the green triangle represents the location of the first satellite transmission, generally coinciding with pop-up location.

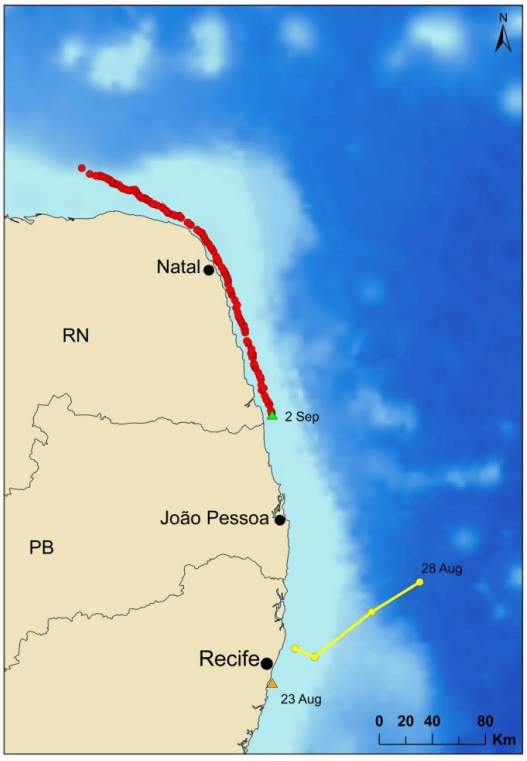

Figure SUP.7.25. Horizontal movements of tiger shark #21 off northeastern Brazil assessed with PSAT tags. The yellow line represents shark movements estimated with light-level information, the red dots depict ARGOS geolocation estimates of the transmitting tag, the orange triangle represents the tagging location, and the green triangle represents the location of the first satellite transmission, generally coinciding with pop-up location.

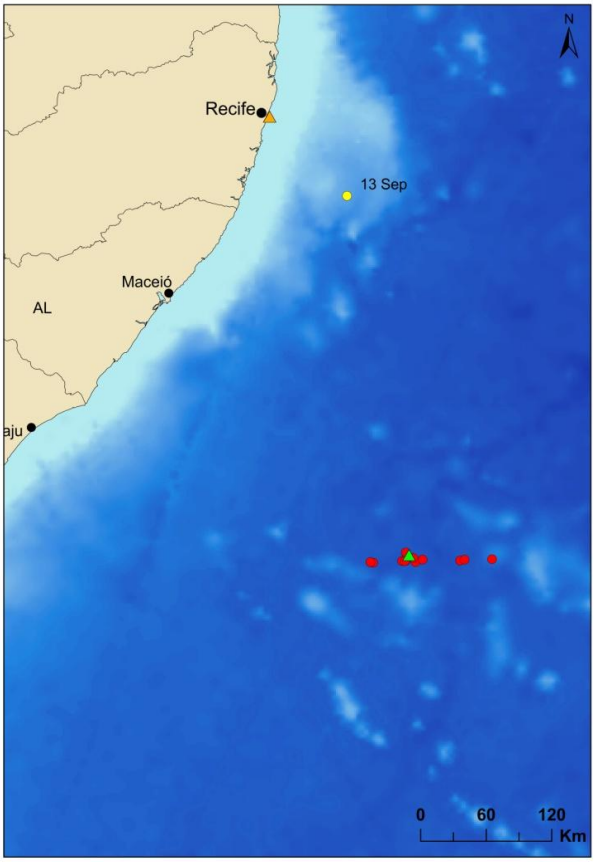

Figure SUP.7.26. Horizontal movements of tiger shark #22 off northeastern Brazil assessed with PSAT tags. The yellow line represents shark movements estimated with light-level information, the red dots depict ARGOS geolocation estimates of the transmitting tag, the orange triangle represents the tagging location, and the green triangle represents the location of the first satellite transmission, generally coinciding with pop-up location.

Annex I : Publications and presentations resulting from the thesis

Publications in peer-review journals*

Afonso AS, Hazin FHV, Carvalho F, Pacheco J C, Hazin H, Kerstetter D, Murie D and Burgess GH. 2011. Fishing gear modifications to reduce elasmobranch mortality in pelagic and bottom longline fisheries off Northeast Brazil. Fisheries Research, 108: 336-343.

Afonso AS, Santiago R, Hazin H, Hazin FHV. 2012. Shark bycatch and mortality and hook bite-offs in pelagic longlines: Interactions between hook types and leader materials. Fisheries Research, 131-133: 9-14.

Afonso AS, Hazin FHV, Santana FM, Barreto R, Lessa RP. 2012. Extraordinary growth in tiger sharks from the South Atlantic Ocean. Journal of Fish Biology, 81: 2080-2085.

Hazin FHV, Afonso AS, Ferreira LC, Castilho PC, Macena B. 2012. Regional movements of the tiger shark, *Galeocerdo cuvier*, off northeastern Brazil: Inferences regarding shark attack hazard. Anais da Academia Brasileira de Ciências, *in press*.

Ferreira LC, Afonso AS, Castilho PC and Hazin FHV. 2012 Habitat use of the nurse shark, *Ginglymostoma cirratum*, off Recife, Northeast Brazil: a combined survey with longline and acoustic telemetry. Environmental Biology of Fishes, pp. 11. doi:10.1007/s10641-012-0067-5

Papers in preparation for being submitted to peer-review journals

Afonso AS, Agrelli H, Hazin FHV. Structure and dynamics of the elasmobranch assemblage off Recife, Brazil.

Afonso AS, Hazin FHV. Movement patterns and behavior of the tiger shark, *Galeocerdo cuvier*, off northeastern Brazil.

Afonso AS, Santana FM, Barreto R, Hazin FHV, Lessa RP. Bioecological traits of tiger sharks, *Galeocerdo cuvier*, caught in the South Atlantic Ocean.

Afonso AS, Hazin FHV. A green methodology for shark attack mitigation off Recife, Brazil.

*also comprises publications not directly included in the thesis

Presentations at scientific meetings

Carvalho F, Hazin FHV, Pacheco JC, Afonso AS, Kerstetter D, Murie D, Burgess G. 2008. Fishing Gear Modifications to Reduce Elasmobranch Mortality in Pelagic and Bottom Longline Fisheries, off Northeast Brazil. Joint Meeting of Herpetologist and Ichthyologist –American Elasmobranch Society, Montréal,Canada, August 2008. (oral)

Afonso AS, Carvalho F, Pacheco JC, Castilho PC, Coxey M, Ferreira LC, Hazin FHV. 2008. Movimentações em larga escala de um tubarão tigre, *Galeocerdo cuvier*, capturado no litoral de Recife, Pernambuco. VI Reunião da Sociedade Brasileira para o Estudo de Elasmobrânqueos, Fortaleza, Brazil, Novembro 2008. (oral)

Carvalho F, Hazin FHV, Pacheco JC, Fisher A, Afonso AS, Burgess G. 2008. Shark Monitoring Program off the Coast of Pernambuco, Brazil. VI Reunião da Sociedade Brasileira para o Estudo de Elasmobrânqueos, Fortaleza, Brazil, Novembro 2008. (oral)

Afonso AS, Ferreira LC, Castilho PC, Hazin FHV. 2009. Short note on large-scale movements of the tiger shark, G*aleocerdo cuvier*, in the South Atlantic Ocean. III Workshop de Investigação em Elasmobrânquios, Associação para o Estudo e Conservação de Elasmobrânquios (APECE), Cascais, Portugal, Setembro 2009. (oral)

Ferreira LC, Castilho PC, Afonso AS, Hazin FHV. 2010. Estudos preliminares sobre o monitoramento acústico do tubarão lixa, *Ginglymostoma cirratum*, no litoral do Recife, Pernambuco. Congresso Brasileiro de Oceanografia, Rio Grande, Brazil, Maio 2010. (poster)

Afonso AS, Hazin FHV. 2010. Shark Monitoring Program off Recife, Brazil. I Sharks International, Cairns, Australia, June 2010. (oral)

Afonso AS, Ferreira LC, Castilho PC, Hazin FHV. 2010. Large-scale movements of the tiger shark, *Galeocerdo cuvier*, in the Southwest Atlantic: implications for shark attack hazard management. I Sharks International, Cairns, Australia, June 2010. (poster)

Afonso AS, Hazin FHV, Carvalho F, Pacheco JC, Kerstetter D, Murie D, Burgess G. 2011. Fishing gear modifications to reduce elasmobranch mortality in pelagic and bottom longline fisheries off Northeast Brazil. Circle Hook Symposium – NOAA, Miami, USA, May 2011. (oral)

Ferreira, L, Afonso, A, Castilho, P, Hazin, F. 2012. Habitat use of the nurse shark, *Ginglymostoma cirratum*, off Recife, Northeast Brazil: a combined survey with longline and acoustic telemetry. Joint Meeting of Herpetologist and Ichthyologist –American Elasmobranch Society, Vancouver, Canada, August 2012. (oral)

Hazin FHV, Afonso AS. 2012. Shark Monitoring Program of Recife, Brazil. Joint Meeting of Herpetologist and Ichthyologist –American Elasmobranch Society, Vancouver, Canada, August 2012. (oral)

Afonso AS, Hazin FHV, Santana FM, Barreto R, Lessa RP. 2012. Extraordinary growth in tiger sharks from the South Atlantic Ocean. Congresso Brasileiro de Oceanografia, Rio de Janeiro, Brasil, November 2012. (poster)

Afonso AS, Ferreira LC, Silva ARF; Carvalho ACC; Arújo CBB, Vedova CD, Carapeba DCB, Rodrigues DSAV, Santiago RJO, Hazin FHV. 2012. A bathymetric survey for assessing hot-spots in a seashore with high incident of shark attacks on humans. Congresso Brasileiro de Oceanografia, Rio de Janeiro, Brasil, November 2012. (poster)