UNIVERSIDADE FEDERAL DE PERNAMBUCO
CENTRO DE BIOCIÊNCIAS
DEPARTAMENTO DE ZOOLOGIA
PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA ANIMAL

KAREN MARINA SILVA LUCCHINI

ELUCIDANDO A COMUNICAÇÃO TÁTIL EM PEIXE-BOI MARINHO (*Trichechus manatus manatus*): UMA ABORDAGEM ETOLÓGICA COMO FERRAMENTA PARA CONSERVAÇÃO *EX SITU* E *IN SITU* DA ESPÉCIE NO NORDESTE DO BRASIL

Recife
2021

KAREN MARINA SILVA LUCCHINI

ELUCIDANDO A COMUNICAÇÃO TÁTIL EM PEIXE-BOI MARINHO (*Trichechus manatus manatus*): UMA ABORDAGEM ETOLÓGICA COMO FERRAMENTA PARA CONSERVAÇÃO *EX SITU* E *IN SITU* DA ESPÉCIE NO NORDESTE DO BRASIL

Dissertação apresentada ao Programa de Pós-graduação em Biologia Animal da Universidade Federal de Pernambuco como requisito parcial para a obtenção do título de Mestre em Biologia Animal.
Orientadora: Profª. Drª. Bruna Martins Bezerra

Recife
2021

Catalogação na Fonte:
Bibliotecário Bruno Márcio Gouveia, CRB-4/1788

Lucchini, Karen Marina Silva
Elucidando a comunicação tátil em peixe-boi marinho (*Trichechus manatus manatus*) : uma abordagem etológica como ferramenta para conservação *ex situ* e *in situ* da espécie no Nordeste do Brasil / Karen Marina Silva Lucchini. - 2021.

107 f. : il.

Orientadora: Profa. Dra. Bruna Martins Bezerra.
Dissertação (mestrado) – Universidade Federal de Pernambuco. Centro de Biociências. Programa de Pós-graduação em Biologia Animal, Recife, 2021.
Inclui referências.

1. Fauna marinha. 2. Mamífero marinho. 3. Comunicação animal. 4. Animais – comportamento. I. Bezerra, Bruna Martins (orientadora) II. Título.

597.64 CDD (22.ed.) UFPE/CB-2021-048

KAREN MARINA SILVA LUCCHINI

ELUCIDANDO A COMUNICAÇÃO TÁTIL EM PEIXE-BOI MARINHO (*Trichechus manatus manatus*): UMA ABORDAGEM ETOLÓGICA COMO FERRAMENTA PARA CONSERVAÇÃO *EX SITU* E *IN SITU* DA ESPÉCIE NO NORDESTE DO BRASIL

Dissertação apresentada ao Programa de Pós-graduação em Biologia Animal da Universidade Federal de Pernambuco como requisito parcial para a obtenção do título de Mestre em Biologia Animal.
Orientadora: Profª. Drª. Bruna Martins Bezerra

Data de aprovação: ____/____/____

BANCA EXAMINADORA

Titulares:

____

Drª. Maria Adélia Oliveira Monteiro da Cruz (Externo) - UFRPE

____

Dr. Valdir Luna da Silva (Externo) – Fisiologia UFPE

____

Dr. Diego Astúa de Moraes (Interno) – PPGBA UFPE

Suplentes:

____

De. João Pedro Souza Alves (Interno) – PPGBA UFPE

____

Drª. Monique Bastos de Araújo (Externo) – CPB ICMBio

AGRADECIMENTOS

Agradeço aos meus pais, Adilson e Maria, e às minhas irmãs, Carla e Flavia, por sempre me darem apoio e todo amor do mundo, muito além do que eu poderia merecer. Agradeço ao meu parceiro de vida, Carlos, e toda sua família por terem sempre me abraçado como família e me dado amor, suporte e apoio desde que cheguei por aqui.

Agradeço também à minha orientadora, Professora Dr. Bruna Martins Bezerra, e ao Professor Dr. Paulo Parreira dos Santos por todo aprendizado, ajuda, orientação, ensinamentos e paciência durante essa jornada. A Rebecca por ser minha amiga, companheira e parceira de campo nessa caminhada e por me ensinar tanto sobre esses animais incríveis. À Iara, Fernanda, Fábia, toda a equipe do Projeto Peixe-boi em Itamaracá e da APA Costa dos Corais em Porto de Pedras pelo suporte e por possibilitar e a execução desse projeto. À toda equipe do Laboratório de Ecologia, Comportamento e Conservação por terem me acolhido na equipe e por compartilharem tantos conhecimentos.

Agradeço à Universidade Federal de Pernambuco, ao Programa e Pós-Graduação em Biologia Animal, ao Instituto Chico Mendes de Conservação da Biodiversidade, ao Centro Nacional de Pesquisa e Conservação da Biodiversidade Marinha do Nordeste, ao Conselho Nacional de Desenvolvimento Científico e Tecnológico e à Coordenação de Aperfeiçoamento de Pessoal de Nível Superior por possibilitar a execução desse trabalho e prover estrutura, suporte técnico e financeiro para isso.

E não menos importante, agradeço aos peixes-boi por sempre propiciarem experiências fabulosas enquanto os tentava compreender.

RESUMO

Sinais táteis têm sido negligenciados em estudos sobre animais aquáticos, embora sejam uma importante modalidade de comunicação. Objetivamos com essa dissertação, elucidar o conhecimento sobre comunicação tátil em peixe-boi marinho. Para essa espécie, em particular, investigamos o repertório de comportamentos táteis e o orçamento desses comportamentos. Além disso, testamos dois diferentes estímulos como enriquecimento ambiental para estimular a prática de comportamentos táteis. Esta dissertação está organizada em quatro capítulos. No capítulo inicial, apresento uma revisão de literatura, elucidando o estado da arte sobre comunicação tátil em mamíferos aquáticos e também apresentando a espécie alvo deste estudo. No segundo capítulo, apresento o repertório com 17 comportamentos táteis, que representam 14.03% do orçamento de atividade da espécie em indivíduos de cativeiro e semi-cativeiro no Nordeste do Brasil. Apresento também nesse segundo capítulo, a investigação de fatores que influenciaram na detecção e performance desses comportamentos, como método de observação, idade, sexo e tipo de habitação. No capítulo 3, é apresentado o experimento de exposição dos animais a dois diferentes estímulos (boia e modelo de infante), e a avaliação da eficiência dos estímulos em incentivar a execução de comportamentos táteis. Neste capítulo, comparo os efeitos dos estímulos na prática dos comportamentos, suas diferentes fases experimentais e comportamentos parentais direcionados ao estímulo do modelo de infante por machos e fêmeas. No último capítulo, apresento uma síntese dos principais resultados encontrados nos demais capítulos, e proponho recomendações para estudos voltados para a comunicação tátil e manejo de peixes-boi marinhos em cativeiro e semi-cativeiro. Recomendamos também a escolha cuidadosa do método de observação ao investigar as diferentes categorias de comportamentos táteis da espécie. Atividades táteis não devem ser desprezadas em processos de reabilitação e reintrodução de peixes-boi. O uso de práticas de enriquecimento ambiental é recomendado para estimular a realização de comportamentos táteis naturais relacionados à exploração e investigação, comportamentos fundamentais para a sobrevivência da espécie, além de evitar estereotipia de cativeiro.

Palavras-chave: Comportamento animal. Mamíferos marinhos. Sirenia. Ecologia comportamental. Enriquecimento ambiental.

ABSTRACT

Tactile signals have been neglected in aquatic animal studies, although they are an important mode of communication. In this dissertation, we aimed to elucidate knowledge about tactile communication on the Antillean manatee. For this species, in particular, we investigate the repertoire of tactile behaviors and the budget of those. In addition, we tested two different stimuli as environmental enrichment to stimulate tactile behaviors. This dissertation is organized in four chapters. In the opening chapter, I present a literature review, elucidating the state of the art on tactile communication in aquatic mammals and also presenting the target species of this study. In the second chapter, I present the behavioral repertoire with 17 tactile behaviors, which represent 14.03% of the species' activity budget in captive and semi-captive individuals in Northeast Brazil. I also present in this second chapter, the investigation of factors that influenced the detection and performance of these behaviors, such as observation sampling method, age, sex and housing condition. In chapter 3, the experiment of exposure of animals to two different stimuli (floating device and infant manatee model) is presented, and the evaluation of the stimuli efficiency in encouraging the practice of tactile behaviors. In this chapter, I compare the effects of the different stimuli in behaviors performances, their experimental phases, and the usage of parenting behaviors directed to the infant model stimulus between males and females. In the last chapter, I present a summary of the main results and propose recommendations for studies related to tactile communication and captive and semi-captive Antillean manatee management. We also recommend a careful choice of the observation method when investigating the different categories of tactile behaviors of the species. Tactile behaviors should not be taken for grant in manatee rehabilitation and reintroduction processes. The use of environmental enrichment practices is recommended to stimulate the performance of natural tactile behaviors related to exploration and investigation, fundamental behaviors for the species’ survival, and also to avoid stereotypy.

Key-words: Animal behaviour. Marine mammals. Sirenia. Behavioral ecology. Environmental enrichment.

LISTA DE FIGURAS

PART 1 – ARTIGO 1: TACTILE COMMUNICATION IN AQUATIC MAMMALS: A REVIEW

PART 2

ARTIGO 2: THE ROLE OF TOUCH IN CAPTIVE AND SEMI-CAPTIVE ANTILLEAN MANATEE (*Trichechus manatus manatus*)

LISTA DE TABELAS

PART 1 – ARTIGO 1: TACTILE COMMUNICATION IN AQUATIC MAMMALS: A REVIEW

ARTIGO 2: THE ROLE OF TOUCH IN CAPTIVE AND SEMI-CAPTIVE ANTILLEAN MANATEE (*Trichechus manatus manatus*)

SUMÁRIO

1 THEORETICAL REVIEW

1.1 PART 1 – ARTIGO 1: TACTILE COMMUNICATION IN AQUATIC MAMMALS: A REVIEW

Nota: Esta parte da dissertação, em formato de artigo, será submetido para periódico científico. Entretanto, regras usuais de formatação foram flexibilizadas para facilitar a leitura pela banca. Por exemplo, figuras e tabelas foram inseridas no corpo do texto. O resumo foi suprimido para evitar repetições com o resumo da dissertação. A numeração de linhas também foi suprimida. Este trabalho é fruto da colaboração de pesquisadores da Universidade Federal de Pernambuco.

1.1.1 Introduction

Marine mammals are often gregarious, conventionally classified as social or semi-social (e.g., Moore, 1956; Ling, 1977; Winn & Schneider, 1978; and Dudzinski, 1998). Socialization is essential for their survival, with communication systems not only based on vocal signaling (Scott 1958). Aquatic animals can communicate through acoustic, chemical, tactile, and visual signals, and the use of those signals varies according to the species and the environmental conditions (Liley, 1982; Zelick et al., 1999). Aquatic mammals often have well-developed acoustic and tactile communication signals because the environment does not favor chemical and visual communication senses (Dehnhardt, 2002; Reynolds & Rommel, 1999).

Most marine mammal olfactory anatomy is not suitable for chemical communication underwater, with some species even lacking olfactory structures to support this communication mode (Anderson, 1969; Reynolds & Rommel, 1999). For instance, sirenians, pinnipeds, and cetaceans close their nasal openings while in water, and many of them have a rudimentary olfactory system, leading to the possible use of taste for chemoreception, which is suggested to be a result of ancestry (Reynolds & Rommel, 1999; Berta et al., 2006; Dudzinski et al., 2008). Coprophagy might also be a manner to obtain information about reproductive and dominance status in some species (cetaceans and sirenians) (Reynolds & Rommel, 1996; Bauer & Reep, 2018). Yamasaki et al. (1980) have described the presence of distinct papillae in manatee tongues, called "Spiegeln" papillae, and these structures may function as tactile and chemical organs.

The visual system of marine mammals that perform behaviors above the water surface, such as the pinnipeds, can be slightly improved (Reidenberg, 2007). However, vision is often limited due to water refraction caused by suspended material in the water (Walls, 1963; Bauer et al., 2003; Mass & Ya Supin, 2007). Some marine mammals, such as the cetaceans, have developed anatomical adaptations (i.e., shape and structure of the pupil, cornea, and lens) for vision under the water and became able to communicate visually even in low light conditions. These adaptations, combined with other senses including hearing (echolocation in cetaceans) and tactile senses (hydrodynamic stimuli in pinnipeds and sirenians) (Anderson, 1969; Herman et al., 1975; Mass & Ya Supin, 2007; Reidenberg, 2007; Gaspard et al., 2013), improve communication underwater. Reidenberg (2007) also highlighted structural adaptations (e.g., fat pads distribution and tympanic structure – membrane and ossicles) developed for hearing and producing sound waves underwater.

Acoustic communication includes non-vocal and vocal signals (Dudzinski et al., 2008). Thus, some animals may produce a wide variety of vocalizations, as well as use body parts to hit the own body or water surface and tooth gnashing, or scratching the environment (Riedman & Estes, 1990; Richardson et al., 1995). Vocal repertoires in aquatic mammals are often complex and can reveal individual motivational status, age, and behavior (e.g., feeding, socializing, learning, and echolocating) (Au, 1993; Blomqvist et al., 2005; Umeed et al., 2018).

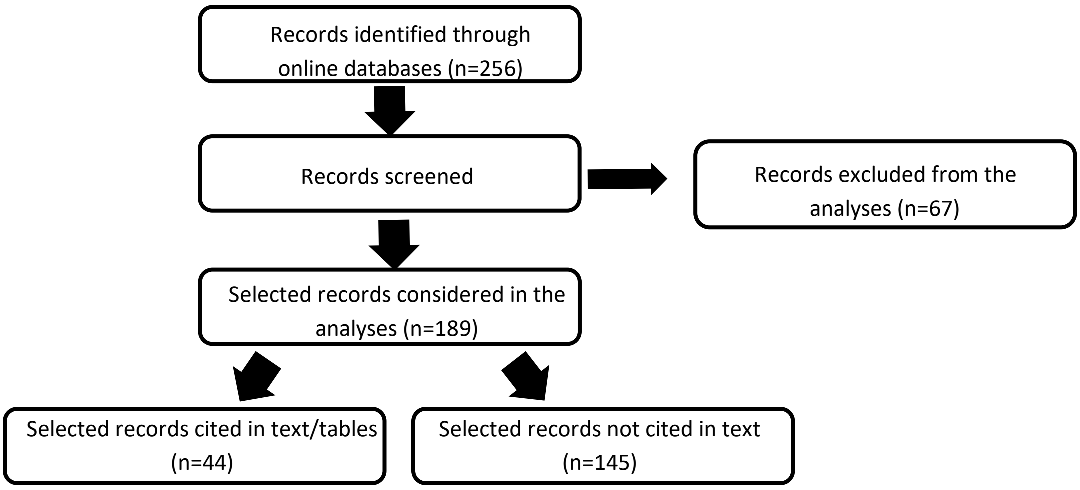
The use tactile communication in aquatic mammals might be a consequence of poor visual acuity and water turbidity in marine and freshwater environments (Reep et al., 2002; Dudzinski et al., 2008). Due to the poor visual acuity, environmental conditions, and social structure of these animals, a well-developed repertoire of tactile signals may be needed. However, the usage of tactile signals can also be associated to related species evolutionary characteristics, once elephants and hyrax also relies part of their communication and socialization in tactile modality (Kleinschmidt et al., 1986; Langbauer, 2000; Schulte, 2000; Poole & Granli, 2011). Tactile signals relate to a diversity of contexts, including mother-calf bond, courtship, reproduction, self-pleasure (masturbation and play), self-maintenance, foraging, prey detection, dominance, competition, navigation, orientation, and environmental exploration (Hartman, 1979; Dehnhardt et al., 1998; Dudzinski et al., 2008; Bauer at al., 2018).

Considering the habitat complexity and the potential for information transmission through tactile signals, we aimed to review the tactile communication systems in marine mammals - a modality of communication that has been relatively ignored despite its evident importance. We compiled data from 43 marine mammals to elucidate our knowledge of their tactile signals' adaptations, contexts, and functions, this is the total number of species found during the systematic search.

1.1.2 Material and Methods

We carried out a systematic search in the Google Scholar and PubMed platforms, using 40 keyword combinations. Keywords were tactile behavior related topics (e.g., Tactile behavior; tactile communication; touch behavior; anatomic tactile structure) associated with the marine mammal group (Cetacea, Pinnipedia, and Sirenia) and general groups (aquatic mammals and marine mammals), in English and Portuguese. The search started on April 24th, 2020 and finished on November 16th, 2020, using "by relevance" and "best match" tools, respectively. Only articles in the first three pages of results were analyzed for information on marine and aquatic mammals' tactile communication and behaviors, as the results beyond the third page were not relevant as subject of this review paper. We screened a total of 256 articles. We excluded articles covering topics not relevant to this study (Figure 1). Articles classified as not relevant were the ones not related to the subject of this review. From the selected articles, we compiled information on the target marine mammal group and species (when available), the relative percentage of studied species per groups, housing condition/analyzed material condition, institution location where the authors were affiliated, general area of research, type of study and decade of publication. We compiled all screened articles obtained in our search in an Excel spreadsheet, and we characterized them and discussed our findings below.

Figure 1. Diagram illustrating the process of record inclusion in the current review paper. Records were identified through the use of database searches (Google and PubMed).



Source: The author (2021).

1.1.3 Results

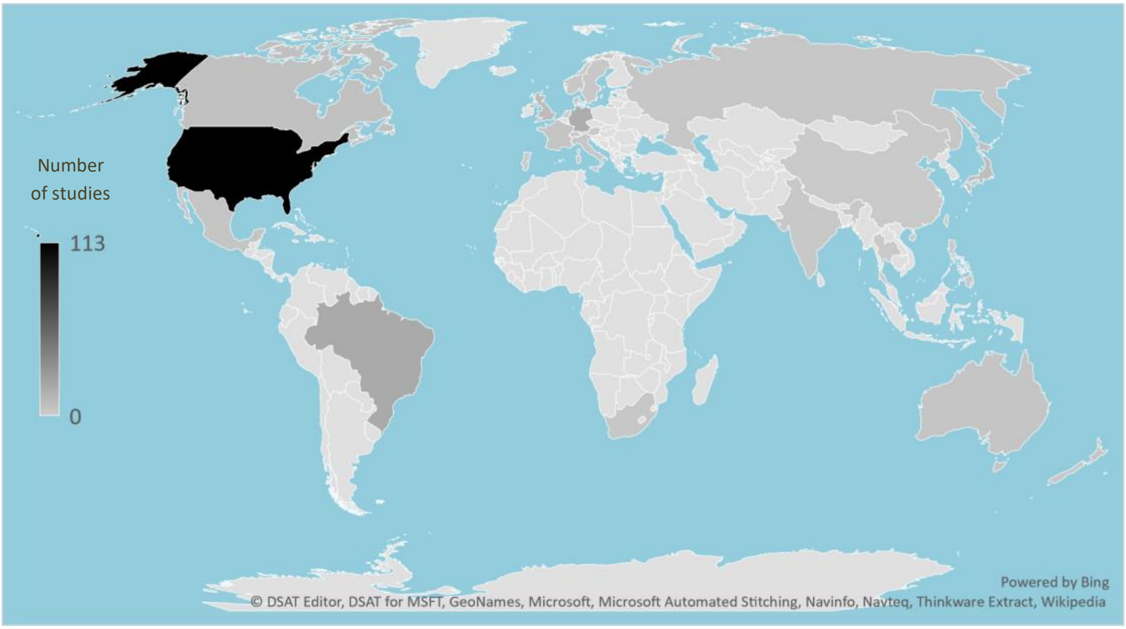
1.1.3.1 Characterization of the studies

Out of the screened articles, some were focused on more than one marine mammal group. The most common group with studies about tactile behavior was Cetacea with a total of 67 out of the 189 articles inspected, followed by Sirenia (48), Pinnipedia (29), Mustelidae (2), and Ursidae (1). Sirenia articles covered 75% of the group species (3), while Pinnipedia covered 30.3% (10) and Cetacea 19.8% (17). Mustelidae and Ursidae were not considered in this comparison due to non-aquatic species' occurrence in the groups. These analyses revealed that a greater number of studies were performed on species of aquatic mammals that are considered more easily accessible and cosmopolitan, such as *Tursiops truncatus* (10) and *Phoca vitulina* (7). However, *Trichechus manatus manatus* (6) and *Trichechus manatus latirostris* (18) were also subjects of a significant number of studies, even though they are species with a more restricted distribution, which could lead to a stronger relationship with the tactile communication and behavior topics of our search.

The studies included research on reintroduced and wild (46) and captive (43) individuals/populations. However, in some of them, carcasses and fixed material were also analyzed (28). Individuals in captivity could make it easier to test hypotheses and perform closer observations on a specific topic, structure, or behavior. Some tactile behaviors are easier to observe and test in captive animals. If the study objective is to understand these behaviors' functions and usage, it is essential that the environment is controlled and the visibility does not interfere with the observations. However, some behaviors might only be possible to observe *in situ*, such as the ones affected by captivity routines, or that rely on a natural source of interactions, feeding habits, and reproductive behaviors. Besides, studies of tactile behaviors in captivity might assist with individuals' welfare during rehabilitation and reintroduction processes, facilitate the understanding of responses to environmental interferences and public awareness (Jiang et al., 2007; Anzolin et al., 2014; Flint & Bonde, 2017).

We also collected information about the countries where the studies were conducted, considering observations, experiments, and laboratory analysis processes. A total of 29 countries were listed as authors' affiliation locality. Institutions within the USA were the most common (113), followed by Brazil's (19) and Germany's (17) institutions (Figure 2). The higher number of scientific articles produced by research groups in the United States (113) may be related to the easier access to research funding and public and private investments in research institutions and infrastructure, and a higher number of academic institutions (IOC-UNESCO, 2017). The same pattern was observed in studies included in a review on marine mammals' acoustic communication (Umeed et al., *under review*).

Figure 2. Countries in which screened studies' authors were affiliated.

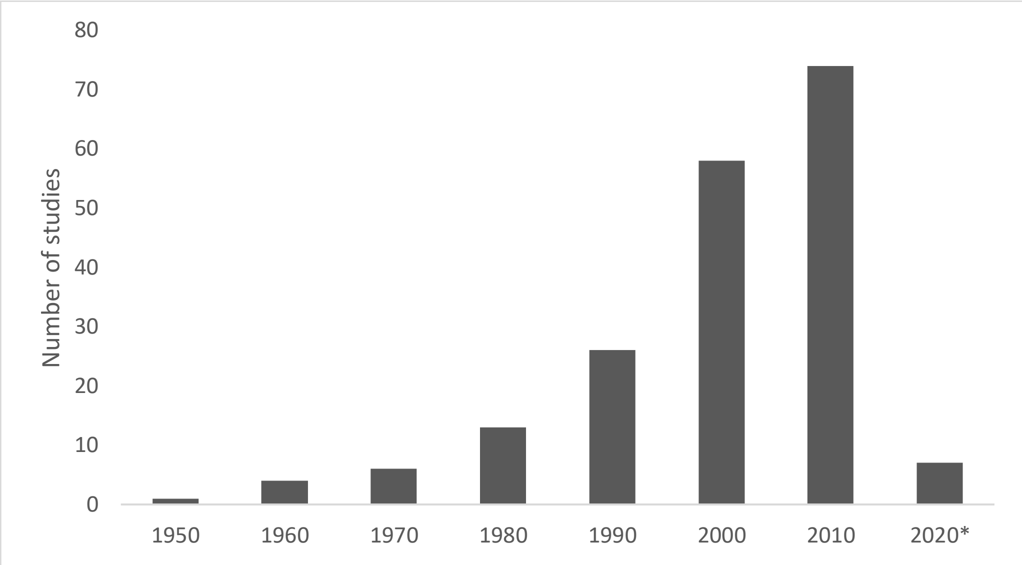


Source: The author (2021).

The decades the studies were published were also evaluated with records dating from the 1950s to the 2020s. Studies on the 2010s were the most numerous (74) (Figure 3), when availability of funds, research internationalization, dissemination channel access, and public interest and awareness about research importance were increasing (IOC-UNESCO, 2017). The 2020s (7) were considered in this analysis; however, it is an ongoing decade, and this is the cause of one of the lowest publication rates on our search.

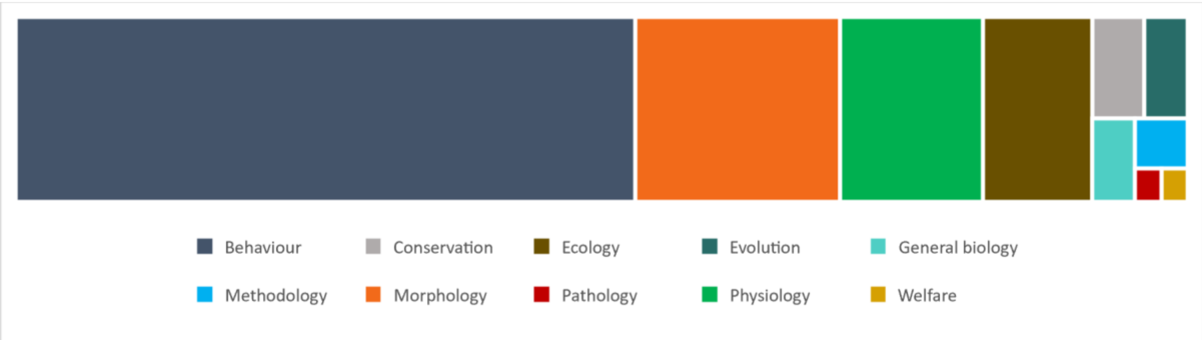
We examined the type of study (Descriptive/Report, Experimental, Review/Survey, Book/Chapter, and Comment/Note), the majority was Descriptive/Report (92), Review/Survey and Book/Chapter in second (44), Experimental (34), and the minority of the studies was Comment/Note (3). We also analyzed the general research area, where ten research areas were registered. Studies on Behaviour topics were the most screened (130), followed by Morphology (43) and Physiology (30) (Figure 4). These results possibly are due to our search structure, which was mostly associated with behavioral analysis, tactile structures, and their functionality, which is revealed by the three most common areas of research the screened studies covered.

Figure 3. The number of screened studies published per decade. *Ongoing decade.



Source: The author (2021).

Figure 4. The general research area of screened studies.



Source: The author (2021).

1.1.3.2 Context of tactile behaviors

Tactile behaviors are categorized in agonistic and affiliative interactions (Langbauer, 2000). Agonistic interactions refer to any interaction that uses or involves aggression, domination, disciplining, or threatening of other individuals (Young, 2019). Affiliative interactions use pacific and pleasant approaches between individuals to establish or maintain a social relationship (Jasso del Toro & Nekaris, 2019). The performance of agonistic and affiliative tactile interactions will depend on the social context, which can be mating, nursing, grooming, playing, self-pleasure, and competition for resources (Weber, 1973; Langbauer, 2000; Dudzinski at al., 2008). These behaviors are also classified into two types according to the touch reception, passive (when something touches the individual) and active (when the individual chooses to touch, it is purposive or goal-directed) (Prescott et al., 2015). Both touch reception types might occur on integument receptors (skin sensitivity) or through vibrissae complex movement (Bauer et al., 2018).

Marine mammal species are known to perform a wide range of tactile behaviors according to the context they are inserted in, such as maternal, sexual, amicable behaviors, pushing, and severe attacks (Poole, 1985). Each group we considered in this review developed unique sense organs and usage schemes according to their social system and activities performed (Dehnhardt and Mauck, 2008) (Table 1). For example, Pinnipedia is a well-studied group when we consider tactile sensorial structures and sensibility. They possess many long mystacial vibrissae, also entitled whiskers (Ling, 1966; Dehnhardt & Kaminski, 1995; Bauer et al., 2018). This suborder is known to use this modality of communication for objects' texture and shape exploration, identification, play, and might use the vibrissae complex as an acoustic sensor (Winn & Schneider, 1978). Dehnhardt et al. (2001) tested this group and reinforced its ability to follow hydrodynamic trails to forage and navigate. Thermoregulation was also studied for the vibrissae complex and revealed a heat concentration in the vibrissae complex concentration region (Dehnhardt et al., 1998). Ladygina et al. (1985) also registered a highly sensitive body surface for different types of mechanical stimulation.

Most of Mustelidae are classified as semi-social, they perform a variety of touch behaviors that include licking, forepaw contact with general body surface due to the oily fur cleaning process, copulation, maternal grooming, vibrissae usage for foraging, and environmental investigation (Winn & Schneider, 1978; Riedman & Estes, 1990; Strobel et al., 2018).

Although cetaceans hold a greatly reduced or even absent vibrissae complex, they possess a highly sensitive integument, as well as follicle crypts that also provide support for tactile communication (Breathnach, 1960; Ling, 1977; Ridgway & Carder, 1990). Contexts including competition, sexual stimulation (reproduction and masturbation), mother-calf relationship, and mechanoreception are known to be part of the repertoire of this group (Silva Jr., 2005; Caffery, 2013; Drake et al., 2015; Hill et al., 2016; DelFour, 2017). The Ursidae aquatic member is the *Ursus maritimus*, the polar bear. Polar bears are commonly solitary, but strong adult friendships and mother-calf bonds were registered (Matthews, 1993; Bauer et al., 2018). These contexts are briefly studied for the species, however little is known about the non-vocal communication system (Dudzinski et al., 2008).

Hartman (1979) and Lucchini et al. (2021) gathered many contexts for tactile behaviors registered for Florida manatee (*Trichechus manatus latirostris*) and Antillean manatees (*T. manatus manatus*), respectively, classifying most of them as social and exploratory behaviors. Activities such as mouthing for grooming and greeting, embracing, mounting, and playing were listed as important contexts for manatees' maintenance and providing pleasurable sensations (Moore, 1956; Hartman, 1979). Tactile behaviors in manatees are believed to strengthen bonds and support individual activities and contexts (Herman et al., 1975; Reynolds & Odell, 1991). Reports of strong bonds between adult wild Florida manatees (*Trichechus manatus latirostris*) show that manatees are more social than previously believed (Koelsch, 1997). Also, behaviors based on the mother-calf relationship support a strong bond for years and include learning processes about recognition, location, foraging, and body maintenance and play (Hartman, 1979; Bengtson, 1981; Wells et al., 1999). Along with the idea of learning about environmental conditions and skills from conspecifics, calves are considered to build a social map of learning and tactile signalization (Bengtson, 1981; Harper & Schulte, 2005).

Table 1. Aquatic mammal species, their respective social systems, and tactile behaviors contexts.

Group	Species	Social system	Contexts of tactile behaviors	References
Cetacea	*Balaena mysticetus*	Semi-social	Mother-calf, spatial orientation, navigation, and prey detection	Drake et al., 2015;
	Delphinapterus leucas	Social	Mother-calf, reproduction, and exploration	Krasnova et al., 2009; Hill & Ramirez, 2014; Hill et al., 2016
	Stenella frontalis	Social	Mother-calf, play, reproduction, and competition	Dudzinski, 1998
	Stenella longirostris	Social	Mother-calf, play, reproduction, masturbation, competition, spatial orientation, and navigation	Silva Jr., 2005
	Steno bredanensis	Social	Mother-calf, play, reproduction, masturbation, and competition	Caffery, 2013
	Tursiops truncatus	Social	Mother-calf, play, reproduction, masturbation, competition, and exploration	DelFour, 2017
Mustelidae	*Enhydra lutris*	Solitary	Mother-calf, play, reproduction, foraging, exploration, spatial orientation, and navigation	Winn & Schneider, 1978; Riedman & Estes, 1990; Strobel et al., 2018
	Lontra felina	Solitary	Mother-calf, play, reproduction, foraging, exploration, spatial orientation, and navigation	Bauer et al., 2018
Pinnipedia	*Erignathus barbatus*	Social	Mother-calf, reproduction, prey detection, foraging, and exploration	Ling, 1977; Fay, 1982; Marshall, 2016
	Odobenus rosmarus	Social	Mother-calf, reproduction, foraging, socialization, and exploration	Fay, 1982; Sjare & Stirling, 1996
	Eumetopias jubata	Social	Mother-calf, play, reproduction, foraging, socialization, and exploration	Farentinos, 1971
	Phoca vitulina	Social	Mother-calf, reproduction, foraging, socialization, exploration, hydrodynamic trails following, and thermoregulation	Dehnhardt & Kaminski, 1995; Dehnhardt et al., 1998
Sirenia	*Dugong dugon*	Semi-social	Mother-calf, play, reproduction, foraging, spatial orientation, and navigation	Reynolds, 1979; Moore, 1956; Reynolds, 1981; Bauer & Reep, 2018
	Trichechus inunguis	Semi-social	Mother-calf, play, reproduction, foraging, spatial orientation, and navigation	Reynolds, 1979; Moore, 1956; Reynolds, 1981; Bauer & Reep, 2018
	Trichechus manatus	Semi-social	Mother-calf, play, reproduction, foraging, spatial orientation, navigation, and exploration	Moore, 1956; Hartman, 1979; Reynolds, 1979; Reynolds, 1981; Marshall et al., 1998; Bauer & Reep, 2018
	Trichechus senegalensis	Semi-social	Mother-calf, play, reproduction, foraging, spatial orientation, and navigation	Moore, 1956; Reynolds, 1979; Reynolds, 1981; Bauer & Reep, 2018
Ursidae	*Ursus maritimus*	Solitary	Mother-calf, play, prey detection, foraging, hierarchy competition, spatial orientation, and navigation	Matthews, 1993; Bauer et al., 2018

1.1.3.3 Tactile communication structures

Tactile communication is accompanied by specific sensorial systems that can be found in some species (vibrissae complex, hairs, tubercles, integument receptors, follicle crypts, and "Spiegeln" papillae) (Table 2). Some species, e.g., seals, manatees, otters, toothed, and baleen whales, have developed adaptations for this communication mode at some phase of development, called vibrissae (Ling, 1977; Winn & Schneider, 1978; Reep et al., 1998; Reeb et al., 2007). These structures consist of several innerved sensorial hairs along with the individuals' bodies. They are responsible for receiving and processing environmental conditions, structure, hydrodynamic stimuli, sources of information for orientation and navigation, interindividual signals, and low-frequency acoustic energy (Hyvarien, 1995; Gerstein et al., 1999; Bauer & Reep, 2018). Some studies suggested that vibrissae complex functions analogously to the lateral line system in fish (Hartman, 1979; Reynolds, 1979; Hyvarien, 1995; Reep et al., 2002).

In marine mammals, vibrissae typically cover the oral and perioral muscular region, thus, supporting feeding and manipulative/oripulative behaviors, using prehensile movement in some species (Peterson & Bartholomew, 1967; Dehnhardt & Kaminski, 1995; Marshall et al., 1998). These sensorial structures might be used combined with intensity modulation, body part usage, and other signalling modes, responding and processing mechanical and hydrodynamical stimuli (Reep et al., 1998; Reep et al., 2011; Bauer & Reep, 2018).

Table 2. Tactile structures in marine mammal species.

Tactile structure	Species	References
Vibrissae complex (Bristle/Whisker)	*Eubalaena australis*	Reeb et al., 2007
	Stenella attenuata	Thewissen & Heyning, 2007
	Enhydra lutris	Winn & Schneider, 1978; Marshall et al., 2014; Strobel et al. 2018
	Odobenus rosmarus	Ling, 1977; Milne et al., 2020; Kastelein et al., 1990
	Erignathus barbatus	Ling, 1977
	Ommatophoca rossii	Ling, 1972
	Zalophus californianus	Gläser et al., 2011; Milne et al., 2020; Dehnhardt, 1994
	Eumetopias jubata	Milne, 2019

	Eschrichtius robustus	Berta et al., 2015
	Mirounga leonina	Ling, 1966
	Phoca vitulina	Dehnhardt & Kaminski, 1995; Milne et al., 2020
	Dugong dugon	Reep et al., 1998
	Trichechus sp.	Reep et al., 1998
Hair	*Inia geoffrensis*	Simpson & Gardner, 1972; Layne and Caldwell, 1964
	Balaena mysticetus	Slijper, 1962
	Balaenoptera borealis	Nakai & Shida, 1948
	Trichechus sp.	Reep et al., 1998
Tubercle	*Megaptera novaeangliae*	Mercado, 2014
Integument receptor	*Delphinus delphis*	Kolchin & Bel'kovich, 1973
	Tursiops truncatus	Lende & Welker, 1972; Kolchin & Bel’kovich, 1973
	Stenella longirostis	Silva Jr., 2005
	Eubalaena australis	Reeb et al., 2007
	Stenella attenuata	Thewissen & Heyning, 2007
	Enhydra lutris	Strobel et al., 2018
Follicle crypt	*Sotalia fluviatilis*	Mauck et al., 2000
	Tursiops truncatus	Palmer & Weddell, 1964
	Delphinus delphis	Palmer & Weddell, 1964
	Sotalia guianensis	Czech-Damal et al., 2012
Large-sized fungi-form papillae (Spiegeln)	Sirenia	Yamasaki et al., 1980

1.1.4 Discussion and Conclusion

Marine mammals use a diversity of anatomical structures as tactile mechanisms and behavior according to different contexts. Related species appear to use body structures and behaviors similarly. All species covered in the studies screened by this review showed specific tactile behaviors for the mother-calf relationship. The majority of the species were also recorded performing tactile behaviors in social (play, reproduction, and competition), foraging/feeding, and navigation/orientation activities. The vibrissae system is the most common structure among the species listed here, and it is generally associated with exploratory and investigative activities using oral and perioral body parts. We show that experimental studies often target tactile communication in captivity animals – where it is possible to have a more controlled setting. Animals in captivity benefit from these studies to help their reproduction, rehabilitation and reintroduction programs, and welfare in captivity, in case of animals not suited to return to the wild and animals returning to their natural environment. Our review emphasizes a gap in the knowledge about the usage and function of tactile behaviors and communication systems in some species (i.e. *Trichechus manatus manatus*, *Trichechus manatus inunguis*, and *Trichechus senegalensis*). This gap also includes a lack of knowledge about tactile responses to different stimuli and context exposure in captive and wild animals. Therefore, we highly encourage experimental studies on species' tactile responses to different stimuli (e.g., physical, spatial, and social stimuli) to address this lack of knowledge on tactile behavior and provide support for management, rehabilitation and reintroduction programs, and conservation strategies. Such studies may contribute to the implementation of effective environmental enrichment practices in captive facilities.

1.1.5 References

Anderson, H. T. L. (1969). The biology of marine mammals. Pergamon Press, New York.

Anzolin, D. G., Carvalho, P. S. M. de, Viana-Jr., P. C., Normande, I. C. & Souto, A. S. (2014). Stereotypical behaviour in captive West Indian manatee (*Trichechus manatus*). – J. Mar. Biol.l Assoc. U.K. 94: 1133-1137.

Au, W. W. L. (1993). The sonar of dolphins. Springer-Verlag, New York.

Bauer, G. B. & Reep, R. (2018). Sirenia sensory systems. In Encyclopedia of animal cognition and behavior. Springer, Cham.

Bauer, G. B., Colbert, D. E., Gaspard, II, J. C., Littlefield, B. & Fellner, W. (2003). Underwater visual acuity of Florida manatees (*Trichechus manatus latirostris*). – Int. J. Comp. Psychol. 16: 130–142.

Bauer, G. B., Reep, R. L. & Marshall, C. D. (2018). The tactile senses of marine mammals. - Int. J. Comp. Psychol. 31: 1–28.

Bengtson, J. L. (1981). Ecology of manatees (*Trichechus manatus*) in the St. Johns River, Florida. (Ph.D. thesis). University of Minnesota, MN, USA.

Berta A., Sumich J. L., & Kovacs K. M. (2006). *Marine mammals: evolutionary biology*, San Diego, CA: Associated Press.

Berta, A., Ekdale, E. G., Zellmer, N. T., Deméré, T. A., Kienle, S. S., & Smallcomb, M. (2015). Eye, nose, hair, and throat: external anatomy of the head of a neonate gray whale (Cetacea, Mysticeti, Eschrichtiidae). – Anat. Rec. 298: 648-659.

Blomqvist, C., Mello, I. & Amundin, M. (2005). An acoustic play-fight signal in bottlenose dolphins *(Tursiops truncatus)* in human care. – Aquat. Mamm. 31:187-194.

Breathnach, A. S. (1960). The cetacean central nervous system. – Biol. Rev. 35:187-230.

Caffery, K. A. (2013). Tactile Behavior in a Group of Captive Rough-Toothed Dolphins as a Function of Opportunities to Play with Objects. (PhD dissertation). University of Southern Mississippi, MS, USA. <https://aquila.usm.edu/dissertations/507>

Czech-Damal, N. U., Liebschner, A., Miersch, L., Klauer, G., Hanke, F. D., Marshall, C., Dehnhardt, G. & Hanke, W. (2012). Electroreception in the Guiana dolphin (*Sotalia guianensis*). – Proc. Royal Soc. B. 279: 663-668.

Dehnhardt, G. (1994). Tactile size discrimination by a California sea lion (*Zalophus californianus*) using its mystacial vibrissae. – J. Comp. Physiol. 175: 791-800.

Dehnhardt, G. (2002) Sensory systems. In A. R. Hoelzel ed. Marine mammal biology: an evolutionary approach. Oxford: Blackwell, pp. 116-141.

Dehnhardt, G. & Kaminski, A. (1995). Sensitivity of the mystacial vibrissae of Harbour Seals (*Phoca vitulina*) for size differences of actively touched objects. – J. Exp. Biol. 198: 2317-2323.

Dehnhardt, G. & Mauck, B. (2008). Mechanoreception in secondarily aquatic vertebrates. In Sensory evolution on the threshold: adaptations in secondarily aquatic vertebrates, pp. 295-314.

Dehnhardt, G., Mauck, B. & Hyvarinen, H. (1998) Ambient temperature does not affect the tactile sensitivity of mystacial vibrissae in harbour seals. – J. Exp. Biol. 201: 3023-3029.

Dehnhardt, G., Mauck, B., Hanke, W. & Bleckmann, H. (2001). Hydrodynamic trail-following in harbor seals (*Phoca vitulina*). – Science, 293:102-104.

DelFour, F. (2017). Object manipulation and play behavior in bottlenose dolphins (*Tursiops truncatus*) under human care. – Int. J. Comp. Psychol. 30.

Drake, S. E., Crish, S. D., George, J. C., Stimmelmayr, R. & Thewissen, J. G. M. (2015). Sensory hairs in the bowhead whale, *Balaena mysticetus* (Cetacea, Mammalia). – Anat. Rec. 298(7): 1327-1335.

Dudzinski, K. M. (1998). Contact behavior and signal exchange in Atlantic spotted dolphins (*Stenella frontalis*). – Aquat. Mamm. 24: 129-142.

Dudzinski, K. M., Thomas, J. A., & Gregg, J. D. (2008) Communication in marine mammals. In Encyclopedia of marine mammals. San Diego, CA: Academic Press, pp. 260-269.

Fay, F. H. (1982). Ecology and biology of the Pacific walrus, *Odobenus rosmarus divergens.* Illiger. – N. Am. Fauna 74 :1-279.

Flint, M. & Bonde, R. K. (2017). Assessing welfare of individual sirenians in the wild and in captivity. In A. Butterworth ed. Marine Mammal Welfare. Animal Welfare, vol 17. Springer, Cham.

Gaspard, J. C., Bauer, G. B., Reep, R. L., Dziuk, K., Read, L. & Mann, D. A. (2013). Detection of hydrodynamic stimuli by the Florida manatee (*Trichechus manatus latirostris*). – J. Comp. Psychol. 199(6): 441-450.

Gerstein, E. R., Gerstein, L., Forsythe, S. E. & Blue, J. E. (1999). The underwater audiogram of the West Indian manatee (*Trichechus manatus*). – J. Acoust. Soc. Am. 105: 3575-3583.

Gläser, N., Wieskotten, S., Otter, C., Dehnhardt, G. & Hanke, W. (2011). Hydrodynamic trail following in a California sea lion (*Zalophus californianus*). – J. Comp. Physiol. 197: 141–151.

Harper, J. Y. & Schulte, B. A. (2005). Social interactions in captive female Florida manatees. – Zoo Biol. 24: 135–144.

Hartman, D. S. (1979). Ecology and behavior of the manatee (*Trichechus manatus*) in Florida. American Society of Mammologists, Special Publications.

Herman, L. M., Peacock, M. F., Yunker, M. P. & Madsen, C. J. (1975). Bottlenosed dolphin: double-slit pupil yields equivalent aerial and underwater diurnal acuity. – Science 189: 650–652.

Hill, H. & Ramirez, D. (2014). Adults play but not like their young: The frequency and types of play by belugas (*Delphinapterus leucas*) in human care. – Anim. Cogn. 1: 166-185.

Hill, H. M., Alvarez, C. J., Dietrich, S. & Lacy, K. (2016). Preliminary findings in beluga (*Delphinapterus leucas*) tactile interactions. – Aquat. Mamm. 42(3). <https://aquila.usm.edu/dissertations/507>.

Hyvarinen, H. (1995). Structure and function of the vibrissae of the ringed seal (*Phoca hispida* L.). In Sensory systems of aquatic mammals (ed. by R.A. Kastelein, J.A. Thomas and P.E. Nachtigall), De Spil Publishers, Woerden, The Netherlands.

IOC-UNESCO (2017). Global Ocean Science Report - The current status of ocean science around the world. L. Valdés et al. (eds), Paris, UNESCO Publishing.

Jasso del Toro, C. & Nekaris, K.AI. (2019) Affiliative behaviors. In J. Vonk, T. Shackelford, eds. Encyclopedia of animal cognition and behavior. Springer, Cham.

Jiang, Y., Lück, M. & Parsons, E. C. M. (2007). Public awareness, education, and marine mammals in captivity. – Tour. Rev. 11: 237-249.

Kastelein, R. A., Stevens, S. & Mosterd, P. (1990). The tactile sensitivity of the mystacial vibrissae of a Pacific walrus (*Odobenus rosmarus divergens).* Part 2: Masking. – Aquat. Mamm. 16: 78-87.

Kleinschmidt, T., Czelusniak, J., Goodman, M. & Braunitzer, G. (1986). Paenungulata: a comparison of the hemoglobin sequences from elephant, hyrax, and manatee. – Mol. Biol. Evol. 3: 427-435.

Koelsch, J. K. (1997). The seasonal occurrence and ecology of Florida manatees (Trichechus manatus latirostris) in coastal waters near Sarasota, Florida. (Masters dissertation). University of South Florida, Sarasota, FL, USA.

Kolchin, S. P. & Bel'kovich, M. (1973). Tactile sensitivity in *Delphins delphis.* – Zool. Zhurnal 52: 620–622.

Krasnova, V. V., Bel'Kovich, V. M., & Chernetskii, A. D. (2009). Formation of behavior in the White Sea beluga calf, *Delphinapterus leucas*, during early postnatal ontogenesis. – Russ. J. Mar. Biol. 35: 53-59.

Ladygina, T. F., Popov, V. V. & Supin, A. (1985). Topical organization of somatic projections to the cerebral cortex of the seal *Callorhinus ursius*. – Neurophysiology 17: 344-351.

Langbauer, W. R. Jr. (2000). Elephant communication. – Zoo Biol. 19: 425-445.

Layne, J. N. & Caldwell, D. K. (1964). Behavior of the Amazon dolphin, *Inia geoffrensis* (Blainville) in captivity. – Zool. Sci. Contrib. N. Y. Zool. Soc. 49: 81-108.

Lende, R. A. & Welker, W. I. (1972). An unusual sensory area in the cerebral neocortex of the bottlenose dolphin, *Tursiops truncatus*. – Brain Res. 45: 555–560.

Liley, N. R. (1982). Chemical communication in fish. – Can. J. Fish. Aquat. Sci. 39: 22-35.

Ling, J. K. (1966). The skin and hair of the southern elephant seal, *Mirounga leonina* (Linn.) I. The facial vibrissae. – Aust. J. Zool. 14: 855-866.

Ling, J. K. (1972). Vibrissa follicles of the Ross seal. – British Antarctica Survey B 27: 19–24.

Ling, J. K. (1977). Vibrissae of marine mammals. In R. Harrison, ed. Functional anatomy of marine mammals. Vol. 3. Academic Press, New York, NY.

Marshall, C. D., Huth, G. D., Edmonds, V. M., Halin, D. L. & Reep, R. L. (1998). Prehensile use of perioral bristles during feeding and associated behaviors of the Florida manatee (*Trichechus manatus latirostris*). – Mar. Mamm. Sci. 14: 274–289.

Marshall, C. D., Rozas, K., Kot, B. & Gill, V.A. (2014). Innervation patterns of sea otter (*Enhydra lutris*) mystacial follicle-sinus complexes. – Front. Neuroanat. 8: 121.

Marshall, C. D. (2016). Morphology of the bearded seal (*Erignathus barbatus*) muscular–vibrissal complex: A functional model for phocid subambient pressure generation. – Anat. Rec. 299: 1043-1053.

Mass, A. M. & Ya Supin, A. (2007) Adaptive features of aquatic mammals' eye. – Anat. Rec. 290: 701–715.

Matthews, D. (1993). Polar Bear. San Francisco, CA: Chronicle Books.

Mauck, B., Eysel, U. & Dehnhardt, G. (2000). Selective heating of vibrissal follicles in seals (*Phoca vitulina*) and dolphins (*Sotalia fluviatilis guianensis*). – J.Exp. Biol. 203(14): 2125-2131.

Mercado III, E. (2014). Tubercles: What sense is there? – Aquat. Mamm. 40: 95-103.

Milne, A. O. (2019). Active touch sensing in pinnipeds. (Ph.D. dissertation) Manchester Metropolitan University, Manchester, UK.

Milne, A. O., Smith, C., Orton, L. D., Sullivan, M. S. & Grant, R. A. (2020). Pinnipeds orient and control their whiskers: a study on Pacific walrus, California sea lion and Harbor seal. J. Comp. Physiol. 206: 441-451.

Moore, J. C. (1956). Observations on manatees in aggregations. – Amer Mus. Novit. 1811: 1-24.

Nakai, J. & Shida, T. (1948). Sinus hairs of the sei-whale (*Balaenoptera borealis*). Scientific Reports of the Whales Research Institute, Tokyo, 1: 41-47.

Palmer, E. & Weddell, G. (1964). The relationship between structure, innervation and function of the skin of the bottlenose dolphin (*Tursiops truncatus*). – J. Zool. 143: 553–568.

Peterson, S. & Bartholomew, G.A. (1967). The natural history and behavior of the California sea lion. Special Publication No. 1, The American Society of Mammalogists. Lawrence, KS.

Poole, T. B. (1985). Senses and Social Communication. In Social Behaviour in Mammals. Springer, Boston, MA.

Poole, J. H. & Granli, P. (2011). Signals, gestures, and behavior of African elephants. In The Amboseli elephants: A long-term perspective on a long-lived (Moss, C. J.; Croze, H. J. & Lee, P. C., eds.). - University of Chicago Press, Chicago, p. 109-124.

Prescott, T. J., Mitchinson, B. & Grant, R. A. (2015). Vibrissal behavior and function. In Scholarpedia of touch. Scholarpedia, Atlantis Press, Paris, pp. 103-116.

Reeb, D., Best, P. B. & Kidson, S. H. (2007). Structure of the integument of southern right whales, *Eubalaena australis*. – Anat. Rec. 290: 596-613.

Reep, R. L., Marshall, C. D. & Stoll, M. L. (2002). Tactile hairs on the postcranial body in Florida manatees: A mammalian lateral line? – Brain Behav. Evol. 59: 141-154.

Reep, R. L., Marshall, C. D., Stoll, M. L. & Whitaker, D. M. (1998). Distribution and innervation of facial bristles and hairs in the Florida manatee (*Trichechus manatus latirostris*). – Mar. Mamm. Sci. 14: 257-273.

Reep, R. L., Gaspard, J. C. III, Sarko, D., Rice, F. L., Mann, D. A. & Bauer, G. B. (2011). Manatee vibrissae: evidence for a "lateral line" function. Annals of the New York Academy of Sciences, 1225. New York, USA.

Reidenberg, J. S. (2007). Anatomical adaptations of aquatic mammals. – Anat. Rec. 290(6): 507-513.

Reynolds III, J. E. (1979). The semisocial manatee. – Nat. Hist. 88: 44-53.

Reynolds III, J. E. (1981). Aspects of the social behaviour and herd structure of a semi-isolated colony of West Indian manatees, *Trichechus manatus*. – Mammalia 45(4): 431-452.

Reynolds III, J. E. & Odell, D.E. (1991). Manatees and dugongs, facts on file**.** New York, USA.

Reynolds III, J. E. & Rommel, S. A. (1996). Structure and function of the gastrointestinal tract of the Florida manatee, *Trichechus manatus*. – Anat. Rec. 245: 539-558.

Reynolds III, J. E. & Rommel, R. (1999). Biology of Marine Mammals. Smithsonian Institution Press, Washington, DC.

Richardson, W. J., Greene, C. R., Malme, C. I. & Thomson, D. H. (eds.) (1995). Marine Mammals and Noise. Academic Press, New York.

Ridgway, S. H. & Carder, D. A. (1990). Tactile sensitivity, somatosensory responses, skin vibrations, and the skin surface ridges of the bottle-nose dolphin, *Tursiops truncatus*. In Sensory abilities of cetaceans. Springer, Boston, MA.

Riedman, M. L. & Estes, J. A. (1990). The sea otter (*Enhydra lutris*): Behavior, ecology, and natural history. US Fish Wildlife Serv., Biol. Rep. 90, 126p.

Schulte, B. A. (2000). Social structure and helping behavior in captive elephants. – Zoo Biol. 19: 447–60.

Scott, J. P. (1958). Animal Behavior. University of Chicago Press, Chicago, USA.

Silva Jr., J. M. D. (2005). Ecologia comportamental do golfinho-rotador (*Stenella longirostris*) em Fernando de Noronha. (Master's thesis) Universidade Federal de Pernambuco.

Simpson, J. G. & Gardner, M. B. (1972). Comparative microscopic anatomy of selected marine mammals. In S. H. Ridgway, ed. Mammals of the sea. Biology and Medicine. Springfield, IL: C.C. Thomas.

Sjare, B. & Stirling, I. (1996). The breeding behavior of Atlantic walruses, *Odobenus rosmarus rosmarus*, in the Canadian High Arctic. Can. J. Zool. 74(5): 897-911.

Slijper, E. J. 1962. Whales. New York: Basic Books.

Strobel, S. M., Sills, J. M., Tinker, M. T. & Reichmuth, C. J. (2018). Active touch in sea otters: in-air and underwater texture discrimination thresholds and behavioral strategies for paws and vibrissae. – J. Exp. Biol. 221(18).

Thewissen, J. G. M., & Heyning, J. (2007). Embryogenesis and development in *Stenella attenuata* and other cetaceans. In D.L. Miller, ed. Reproductive biology and phylogeny in cetacea, whales, dolphins and porpoises. CRC Press, Florida.

Umeed, R., Attademo, F. L. N. & Bezerra, B. (2018) The influence of age and sex on the vocal repertoire of the antillean manatee (*Trichechus manatus manatus*) and their responses to call playback. – Mar. Mamm. Sci. 34(3): 577-594.

Walls, G. L. (1963). The vertebrate eye and its adaptive radiation. Hafner Publ. Co., New York.

Weber, I. (1973) Tactile communication among free-ranging langurs. – Am. J. Phys. Anthropol. 38(2): 481-486.

Wells, R. S., Boness, D. J. & Rathbun, G. B. (1999). Behavior. In J. E. Reynolds III & S. A. Rommel, eds. Biology of marine mammals. Smithsonian Institution Press, Washington, DC.

Yamasaki, F., Komatsu, S. & Kamiya, T. (1980). A comparative morphological study on the tongues of Manatee and Dugong (Sirenia). – Sci. Rep. Whales Res. Inst. 32: 127-144.

Young C. (2019). Agonistic Behavior. In J. Vonk & T. Shackelford, eds. Encyclopedia of Animal Cognition and Behavior. Springer, Cham.

Zelick R., Mann D. A. & Popper A. N. (1999). Acoustic Communication in Fishes and Frogs. In R. R. Fay, A. N. Popper, eds. Comparative Hearing: Fish and Amphibians. Springer Handbook of Auditory Research, vol 11. Springer, New York, NY.

1.2 PART 2

1.2.1 Study species: *Trichechus manatus manatus*

1.2.1.1 Taxonomy and distribution

Sirenia order uniquely comprises herbivorous aquatic mammals and probably ascended during the middle Eocene Epoch (45-50my) (Hartman, 1979; Reynolds et al., 2008). The closest orders which are related to Sirenia are Proboscidea (elephants) and Hyracoidea (hyraxes). Together they belong to the Paengulata (Kleinschmidt et al., 1986). Sirenia is a monophyletic taxon with two families, Dugongidae and Trichechidae (Rosas & Pimentel, 2001). *Dugong dugon* is a single living species comprised of the Dugongidae family, while Trichechidae includes three species (*Trichechus manatus*, *Trichechus senegalensis*, and *Trichechus inunguis*) (Nishiwaki & Marsh, 1985).

Sirenia systematics:

Kingdom Animalia

Filo Chordata

Class Mammalia

Order Sirenia Illiger, 1811

Family Dugongidae

Subfamily Dugongidae

Genus Dugong

Species *Dugong dugon* (Muller, 1776)

Genus Hydrodamalis

Species *Hydrodamalis gigas* (Zimmermann, 1780)

Family Trichechidae

Subfamily Trichechine

Genus Trichechus

Species *Trichechus manatus* Linnaeus, 1758

Subspecies *Trichechus manatus manatus* Linnaeus, 1758

Trichechus manatus latirostris (Harlan, 1824)

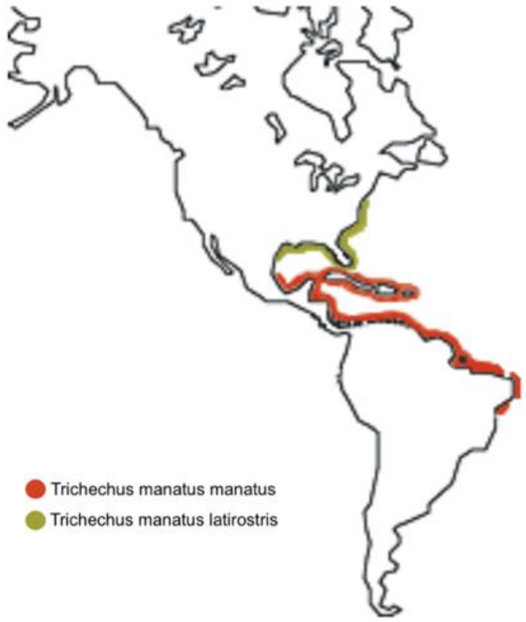
*Trichechus sen*egalensis Link, 1795

Trichechus inunguis (Natterer, 1883)

Hatt (1934) proposed two subspecies for *Trichechus manatus*. Domning & Hayek (1986) and Garcia-Rodriguez et al. (1998) conducted morphological and mitochondrial DNA studies that provided support for the subspecies establishment (*T. manatus manatus* and *T. manatus latirostris*). However, Barros et al. (2016) highlight morphometric and karyological differences between *T. manatus manatus* members from different locations, disagreeing with the current subspecies division proposed by Hatt (1934). These subspecies distribution covers tropical and subtropical shallow warm waters, in rivers, estuaries, and marine environments between Central America and the north-eastern coast of Brazil, and south-eastern coast of the USA (mainly Florida waters), respectively (Ronald et al., 1978) (Figure 5).

T. manatus manatus, also called Antillean manatee, occurs along the north-eastern Brazilian coast. The species inhabit murky estuaries and clear oceanic shallow waters (Husar, 1977; Pause, 2007). Antillean manatee stranding frequently occurs along the beaches. Thus, studies on rehabilitation and reintroduction represent a continuous need for manatee conservation in the country (Balensiefer et al., 2017).

Figure 5. *Trichechus manatus manatus* and *Trichechus manatus latirostris* distribution



Adapted from Costa, 2006.

1.2.1.2 Morphology

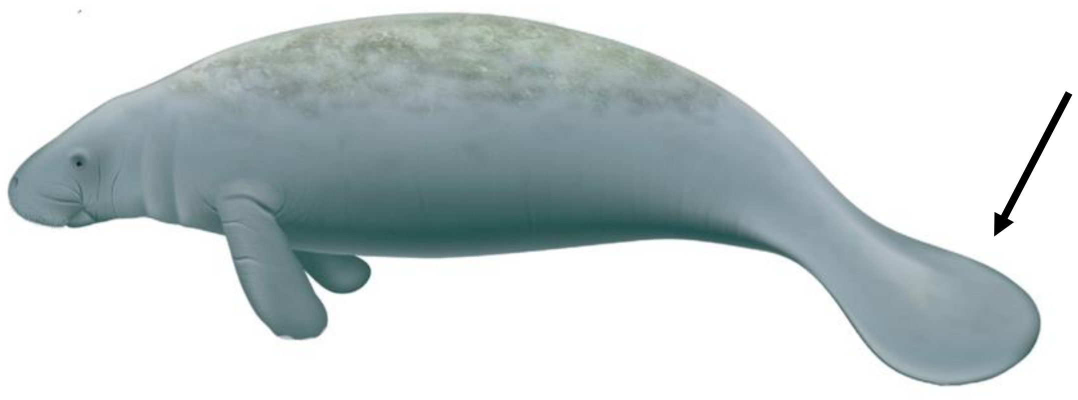
Manatee's body is anatomically adapted to aquatic environments (Reynolds et al., 2008). They have a large fusiform hydrodynamic rounded-shaped body, covered by a thick grey skin, which might facilitate heat conservation (Husar, 1977). The tail is paddle-shaped and is responsible for propulsion in locomoting (Reynolds & Odell, 1991) (Figure 6). Anatomical adaptations to support manatee's herbivory include molariform teeth with a continuous distomesial replacement, enlarged lips composed of prehensile muscular-vibrissal complex, and gastrointestinal tract expansion for hindgut fermentation (Domning, 1982; Reynolds et al., 2008; Beatty et al., 2012).

Sensory structures in manatees include vibrissae throughout their bodies and snout, covering the perioral area, prehensible and flexible lips, and a tongue with tactile sensors (Ling, 1977; Hartman, 1979; Reynolds & Odell, 1991;

Marshall et al., 1998; Sarko et al., 2007a) (Figure 7). Also, manatee's eyes are relatively small, and its eyesight is poor (Walls, 1963; Bauer et al., 2003). Well-developed tactile sensors may counterpart manatee's visual limitations (Dehnhardt & Mauck, 2008; Reynolds et al., 2008) (Figure 7). Manatee's tactile sensory system may function analogously to the lateral line system in fish due to the capability of detecting detailed environmental and external information (Reep et al., 2002). The tactile sensory system can detect information about other animals' proximity and movement, stationary features (obstacles, feeding, and resting areas), water currents, tidal flows, low-frequency sound waves, and conspecifics recognition by direct contact or water movement/particle displacement (Hartman, 1979; Bachteler & Dehnhardt, 1999; Reep et al., 2002; Kikuchi et al., 2011; Bauer & Reep, 2018).

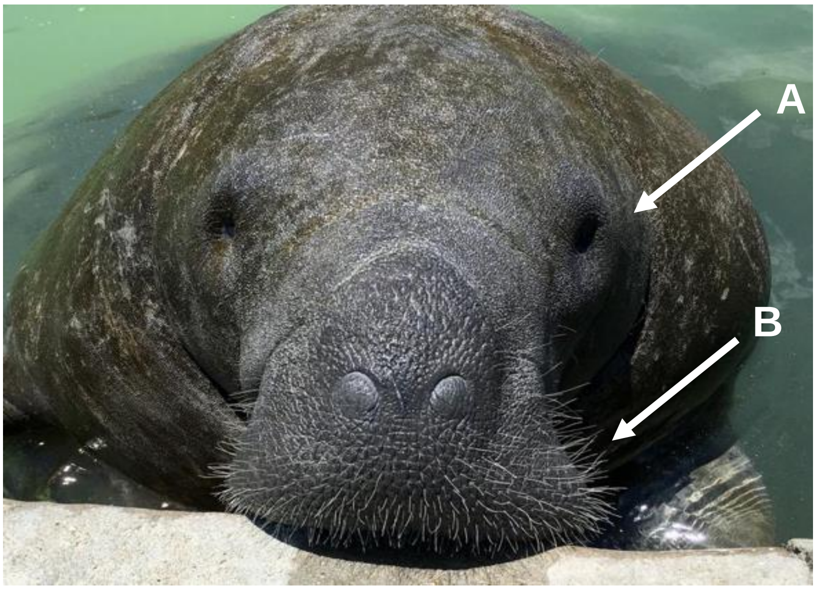
Neuroanatomical studies on manatee's brain revealed with a large somatosensorial area, which supports the importance of tactile sense (Sarko et al., 2007a). The cerebral cortical region is also responsible for long-term memory and information processing (Purves et al., 2001; Reep & Bonde, 2006). Migratory patterns, source, refuge information, and location are some of the information that might be kept for manatees' survival (Pause, 2007).

Figure 6. *Trichechus manatus* external morphology of the body. The arrow shows the paddle shaped tail of the manatee.



Source: Adapted from Reynolds et al. (2017).

Figure 7. *Trichechus manatus manatus* facial morphology. The arrows show the small eyes (A) and the vibrissal complex distribution (B).



Source: The author (2021).

1.2.1.3 Ecology

Manatees are exclusively herbivorous, and due to this characteristic, some adaptations on physiology and ecology favor their survival, low metabolic rates, and intestinal tract size, for example (O'Shea & Reep, 1990). Low-energy diets require high quantities of vegetation to maintain metabolism working (Pause, 2007). Between manatees' diet are seagrasses, algae, freshwater plants, and some terrestrial branches (Best & Teixeira, 1982; Reynolds & Odell, 1991; Paludo, 1998; Lima, 1999). Consequently, manatee's distribution is also limited by food distribution and water availability (Hartman, 1979; Reynolds & Odell, 1991). Water temperature, depth, currents, and tidal flow are also limiting factors (Hartman, 1979; Lefebvre et al., 2001; Olivera-Gómez & Mellink, 2005).

Tactile behaviors in manatees (*Trichechus manatus manatus* and *Trichechus manatus latirostris*) include hugging and touching for sexual activities, mouthing and rubbing during socialization, mouthing and scratching for social grooming and body touch during journeys, playing, feeding, and to help the calf breathe until it assumes its breathing rhythm (Hartman, 1979; Marshall et al., 1998; Wells et al., 1999; Reeves et al., 2002; Silva et al., 1992). Social interactions seem essential for social recognition in manatees (Hénaut et al., 2010). Furthermore, there are also solitary tactile behaviors such as self-grooming, investigating objects, and environment recognition and assessment (Reynolds & Odell, 1991; Marshall et al., 1998).

An essential context that involves tactile signals in manatees is the mother-calf interaction, which can last up to three years counting from birth (Hartman, 1979; Bengtson, 1981; Wells et al., 1999). Antillean manatees depend on a mother-calf relationship for cognition development and adult bonding for reproduction and tradition transmitting based on long-term memory (Wells et al., 1999). Moore (1951) registered a mother lifting the newborn on her tail to establish a breathing rhythm. Nuzzling and mouthing behaviors and synchronous breathing are also considered a mother-calf relationship reinforcement (Reynolds, 1981). Synchronized behaviors are described as a mechanoreceptor interpretation of the vibrissae complex (Hartman, 1971). Play behaviors require no apparent stimuli, thus being an individual initiative (Marler & Hamilton, 1966).

Studies focused on tactile investigation described a tactile scanning process using the oral disk's sensorial hairs, sometimes accompanied by muscular movements (Marshall et al., 1998; Bauer & Reep, 2018). Marshall et al. (2003) suggest that the muscular-vibrissal complex's grasping motion may function in feeding and surface/object exploration, sometimes assisted by flipper usage to hold themselves, conspecifics, vegetation, or objects. Moreover, some authors suggested that rubbing behavior could leave a chemical track (Hartman, 1979; Wells et al., 1999). Thus, scanning environmental features could be related to chemoreception and individual recognition, playing a significant role in socialization and reproduction together with coprophagy behavior (Reynolds & Rommel, 1996; Wells et al., 1999; Bauer & Reep, 2018).

Texture and shape sensibility experiments have increased our understanding of tactile communication in manatees (Bachteler & Dehnhardt, 1999; Bauer et al., 2012; Bauer et al., 2018). Social interactions and habitat enrichment in captivity stimulate tactile communication performance (Harper & Schulte, 2005). High frequencies of social behaviors in captivity could be a consequence of the high density of animals in the pools, as previously observed in Florida manatees (Harper & Schulte, 2005). Additionally, environmental enrichment is also a useful tool for promoting tactile behavior in captivity (Anzolin et al., 2014).

Although manatees are considered as "tactile specialists", they also use other senses to supplement poor visual acuity, such as hearing and vocalizing, chemoreception (as mentioned above) (Sarko et al., 2007b, Umeed et al., 2017). According to Umeed et al. (2017), Antillean manatees present sexual and age differences in the repertoire of vocalizations, which supports a complex and complete acoustic communication system varying appropriately to the context animals face, feeding, mother-calf calls, alarm, etc. Identity calls and individual recognition were also registered for manatees, which points to a possible relation to cerebral cortex development for long-term memory (Reynolds, 1981; Reep & Bonde, 2006; Sousa-Lima et al., 2008).

Chemical communication sense has not been largely investigated in manatees. However, some studies suggest that tactile behavior could be related to chemical information (Hartman, 1979; Wells, 1999). Although chemoreception is challenging to track due to the nostrils closing underwater, "Spiegeln" papillae and other tongue structures might convey chemical information for social and reproductive behaviors (Yamasaki et al., 1980; Reynolds & Rommel, 1996; Bauer & Reep, 2018).

Currently, Antillean manatees are considered endangered to extinction (Self-Sullivan & Mignucci-Giannoni, 2008). Thus, this species is targeted in many national policies for fauna conservation. Although there are controlling plans, human activities (habitat loss, fishing gear, and boat injuries) are still threats to species stability and protection (Reeves et al., 2002). Associated with these threats, low reproduction rate, and species docility contribute to its vulnerability (Self-Sullivan & Mignucci-Giannoni, 2008). Consequently, the species is considered endangered and declining.

1.2.1.4 Ethograms

Behavioral studies are founded on ethograms, a catalog containing the complete and detailed description of the behaviors performed by an animal (Scott, 1958; Banks, 1982). Ethograms are crucial for designing and testing hypotheses for quantitative and qualitative behavioral studies. They support essential assessment studies with animals in captivity and seminatural environments and any behavioral deviation analyses associated with a higher density of animals, intensive management, and group size in these circumstances (Altmann, 1974; Ruby & Niblick, 1994). Ethograms also provide accurate measurements and scientific documentation of performed behaviors, thereby supporting research on functional and sexual and age group variations of behavioral patterns (Altmann, 1974; Banks, 1982; Lehner, 1992).

Furthermore, ethograms define the behavioral profile of the individual or the entire population observed. Thus, they make comparisons possible between individuals, populations, and species once they record the particularities of the analyzed group (Barlow, 1977). Sutherland (1998) drew a list of 20 subjects to which behavioral studies can support and significantly contribute with a better understanding and management practices. Behavioral studies provide valuable information to support studies on neurobiology, animal welfare, biomedicine, conservation biology, management plans, and public policies (Sutherland, 1998; Silva, 2014; Davis et al., 2015; Attademo et al., 2020). Conservation widely benefits from behavioral studies, which help the understanding of population extinctions (Allee, 1931; McLain et al., 1995), fragmentations and dispersions (Harrison et al., 1993), animals' responses to environmental changes (Goss-Custard & Sutherland, 1997), captive welfare and breeding (Synder et al., 1996; Durrant, 1995) and environmental education (Bell, 1994).

1.2.2 References

Allee, W. C. (1931). Animal Aggregations: A Study in General Sociology. Chicago: Chicago University Press.

Altmann, J. (1974). Observational study of behaviour: sampling methods. – Behaviour 49: 227-267.

Anzolin, D. G., Carvalho, P. S. M. de, Viana-Jr., P. C., Normande, I. C. & Souto, A. S. (2014). Stereotypical behaviour in captive West Indian manatee (Trichechus manatus). – J. Mar. Biolog. Assoc. U. K. 94: 1133-1137.

Attademo, F. L. N., Gomes, G. L., Silva, F. J. L., Modeira, A. B., Freire, A. C. B., Leitão, H. C. M. S. & Luna, F. O. (2020). Comportamento de peixes-bois|Guia ilustrado. Instituto Chico Mendes de Conservação da Biodiversidade, Brazil.

Bachteler, D. & Dehnhardt, D. (1999). Active touch performance in the Antillean manatee: evidence for a functional differentiation of facial tactile hairs. – Zoology (Jena) 102: 61–69.

Balensiefer, D. C., Attademo, F. L. N., Sousa, G. P., Freire, A. C. D. B., da Cunha, F. A. G. C., Alencar, A. E. B., Silva, F. J. L. & Luna, F. D. O. (2017). Three decades of Antillean manatee (*Trichechus manatus manatus*) stranding along the Brazilian coast. – Trop. Conserv. Sci. 10: 1940082917728375.

Banks, E. M. (1982). Behavioral research to answer questions about animal welfare. – J. Anim. Sci. 54: 434–455.

Barlow, G. W. (1977). Modal action patterns. In T. A. Sebeok, ed. How Animals Communicate. Bloomington, Indiana: Indiana University Press.

Barros, H. M. D. R., Meirelles, A. C., Luna, F. O., Marmontel, M., Cordeiro-Estrela, P., Santos, N., & Astúa, D. (2017). Cranial and chromosomal geographic variation in manatees (Mammalia: Sirenia: Trichechidae) with the description of the Antillean manatee karyotype in Brazil. – J. Zoolog. Syst. Evol. 55: 73-87.

Bauer, G. B. & Reep, R. (2018). Sirenia sensory systems. In Encyclopedia of Animal Cognition and Behavior. Springer, Cham.

Bauer, G. B., Colbert, D. E., Gaspard, II, J. C., Littlefield, B. & Fellner, W. (2003). Underwater visual acuity of Florida manatees (*Trichechus manatus latirostris*). – Int. J. Comp. Psychol. 16: 130–142.

Bauer, G. B., Gaspard III, J. C., Colbert, D. E., Leach, J. B., Stamper, S. A., Mann, D. & Reep, R. (2012). Tactile discrimination of textures by Florida manatees (*Trichechus manatus latirostris*). – Mar. Mamm. Sci. 28: E456-E471.

Bauer, G. B., Reep, R. L. & Marshall, C. D. (2018). The tactile senses of marine mammals. – Int. J. Comp. Psychol. 31: 1-28.

Beatty, B. L., Vitkovski, T., Lambert, O., & Macrini, T. E. (2012). Osteological associations with unique tooth development in manatees (Trichechidae, Sirenia): a detailed look at modern *Trichechus* and a review of the fossil record. – Anat. Rec. 295: 1504-1512.

Bell, B. (1994). Translocation of fluttering shearwaters: developing a method to re-establish seabird populations. In M. Serena, ed. Reintroduction Biology of Australian and New Zealand Fauna. Chipping Norton: Surrey Beatty & Sons, pp. 143-148.

Bengtson, J. L. (1981). Ecology of manatees (*Trichechus manatus*) in the St. Johns River, Florida. (Ph.D. thesis). University of Minnesota, MN, USA.

Best, R. C. & Teixeira, D. M. (1982). Notas sobre a distribuição e status aparente dos peixes-bois (Mammalia, Sirenia) nas costas amapaenses brasileiras. Bol. FBCN, Rio de Janeiro, 17: 41-47.

Costa, A. F. (2006). Distribuição espacial e status do peixe-boi marinho, *Trichechus manatus manatus,* (Sirenia: Trichechidae) no litoral leste do Estado do Ceará. (MSc. dissertation) Instituto de Ciências do Mar, Universidade Federal do Ceará, Fortaleza.

Dehnhardt, G. & Mauck, B. (2008). Mechanoreception in secondarily aquatic vertebrates. Sensory evolution on the threshold: adaptations in secondarily aquatic vertebrates, pp. 295-314.

Domning, D. P. (1982). Evolution of manatees: a speculative history. – J. Paleontol. 56: 599-619.

Domning, D. P. & Hayek, L. A. C. (1986). Interspecific and intraspecific morphological variation in manatees (Sirenia: *Trichechus*). – Mar. Mamm. Sci. 2: 87-144.

Durrant, B. S. (1995). Reproduction in mammals: captive perspectives. In E. F. Gibbons Jr., B. S. Durrant & J. Demarest, eds. Conservation of Endangered Species in Captivity. Albany, New York: State University of New York Press.

Garcia-Rodriguez, A. I., Bowen, B. W., Domning, D., Mignucci, A. A., Marmontel, M., Montoya, R. A., Morales-Vela, B., Rudin, M., Bonde, R. K., Mc-Guire, P. M. (1998). Phylogeography of the West Indian manatee (*Trichechus manatus*): How many populations and how many taxa? – Mol. Ecol. 7: 1137-1149.

Goss-Custard, J. D. & Sutherland, W. J. (1997). Individual behaviour, populations and conservation. In J. R. Krebs & N. B. Davies, eds. Behavioural Ecology. Oxford: Blackwells, pp. 373-395.

Hatt, R. (1934). A manatee collected by the American Museum Congo Expedition, with observations on the recent manatees. – Bull. Am. Mus. Nat. Hist. 66: 533-566.

Harper, J. Y. & Schulte, B. A. (2005). Social interactions in captive female Florida manatees. – Zoo Biol. 24: 135–144.

Harrison, S., Stahl, A. & Doark, D. (1993). Spatial models and spotted owls: exploring some biological issues behind recent events. – Conserv. Biol. 7: 950-953.

Hartman, D. S. (1971). Behavior and ecology of the Florida manatee, *Trichechus manatus latirostris* (Harlan), at Crystal River, Citrus County. (Ph.D. dissertation) Cornell University, Ithaca, NY.

Hartman, D. S. (1979). Ecology and behavior of the manatee (*Trichechus manatus*) in Florida. American Society of Mammologists, Special Publications.

Hénaut, Y., Lopez, S. P. B., Machkour-M'Rabet, S., Morales-Vela, B., Winterton, P. & Delfour, F. (2010). Activities and social interactions in captive Antillean manatees in Mexico. – Mammalia 74: 141-146.

Husar, S. L. (1977). The West Indian manatee (*Trichechus manatus*). United States Fish and Wildlife Service, Wildl. Res. Rept. 7: 1-22.

Kikuchi, M., Suzuki, M., Ueda, K., Miyahara, H. & Uchida, S. (2011). The differences in behavioral responses to a net obstacle between day and night in captive manatees; does entanglement happen at night? – Fish. Sci. 77:795.

Kleinschmidt, T., Czelusniak, J., Goodman, M. & Braunitzer, G. (1986). Paenungulata: a comparison of the hemoglobin sequences from elephant, hyrax, and manatee. – Mol. Biol. Evol. 3: 427-435.

Lefebvre, L.W., Marmontel, M., Reid, J.P., Rathbun, G.B. & Domning, D.P. (2001). Status and biogeography of the West Indian manatee, In C. A. Woods & F. E. Sergile, eds., 2nd ed. Biogeography of the West Indies: patterns and perspectives, CRC Press.

Lehner, P.N. (1992). Sampling methods in behavior research. – Poult. Sci. 71: 643-649.

Lima, R. P. (1999). Peixe-boi marinho (*Trichechus manatus*): Distribuição, status de conservação e aspectos tradicionais ao longo do litoral nordeste do Brasil. Meio Ambiente em Debate Series, 30, Brasília: Ed. IBAMA.

Ling, J. K. (1977). Vibrissae of marine mammals. In R. Harrison, ed. Functional anatomy of marine mammals. Vol. 3. Academic Press, New York, NY.

Marler, P & Hamilton, W.J. III (1966). Mechanisms of animal behavior. Wiley, New York, NY.

Marshall, C. D., Huth, G. D., Edmonds, V. M., Halin, D. L. & Reep, R. L. (1998). Prehensile use of perioral bristles during feeding and associated behaviors of the Florida manatee (*Trichechus manatus latirostris*). – Mar. Mamm. Sci. 14: 274–289.

Marshall, C. D., Maeda, H., Iwata, M., Furuta, M., Asano, S., Rosas, F. & Reep, R. L. (2003). Orofacial morphology and feeding behaviour of the dugong, Amazonian, West African and Antillean manatees (Mammalia: Sirenia): functional morphology of the muscular-vibrissal complex. – J. Zool. 259: 245-260.

McLain, D. K., Moulton, M P. & Redfearn, T. P. (1995). Sexual selection and the risk of extinction of introduced birds on oceanic islands. – Oikos 74: 27-34.

Moore, J. C. (1951). The status of the manatee in the Everglades National Park, with notes on its natural history. – J. Mammal. 32: 22-36.

Nishiwaki, M. & Marsh, H. (1985). *Dugong dugon* (Müller 1776). In S. H. Ridgway & S. R. Harrison, eds. Handbook of Marine Mammals. London: Academic Press.

O'Shea, T. J. & Reep, R. L. (1990). Encephalization quotients and life-history traits in the Sirenia. – J. Mammal. 71: 534-543.

Olivera-Gómez, L. D. & Mellink, E. (2005). Distribution of the Antillean manatee (*Trichechus manatus manatus*) as a function of habitat characteristics, in Bahía de Chetumal, Mexico. – Biol. Conserv. 121: 127-133.

Paludo, D. (1998). Estudos sobre ecologia e conservação do peixe-boi marinho (*Trichechus manatus manatus)* no Nordeste do Brasil. Brasília: Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis. 70pp.

Pause, K. C. (2007). Conservation genetics of the Florida manatee, *Trichechus manatus latirostris.* (Ph.D. dissertation) University of Florida, USA.

Purves, D., Augustine, G. J., Fitzpatrick, D., Katz, L. C., LaMantia, A-S., McNamara, J. O. & Williams, S.M. (2001). Neuroscience, Second ed. Sinauer Associates, Inc., Sunderland, MA, USA.

Reep, R. L. & Bonde, R. K. (2006). The Florida manatee: biology and conservation. Gainesville: University Press of Florida.

Reep, R. L., Marshall, C. D. & Stoll, M. L. (2002). Tactile hairs on the postcranial body in Florida manatees: A mammalian lateral line? – Brain Behav. Evol. 59(3): 141-154.

Reeves, R. R., Stewart, B. S., Clapham, P. J. & Powell, J. A. (2002). National Audubon Society guide to Marine Mammals of the World. New York: National Audubon Society, USA.

Reynolds III, J. E. (1981). Aspects of the social behaviour and herd structure of a semi-isolated colony of West Indian manatees, *Trichechus manatus*. – Mammalia 45(4): 431-452.

Reynolds III, J. E. & Odell, D.E. (1991). Manatees and dugongs, facts on file**.** New York, USA.

Reynolds III, J. E. & Rommel, S. A. (1996). Structure and function of the gastrointestinal tract of the Florida manatee, *Trichechus manatus*. – Ant. Rec. 245: 539-558.

Reynolds III, J. E., Powell, J. A. & Taylor, C. R. (2008). Manatees: *Trichechus manatus, T. senegalensis*, and *T. inunguis*. In Encyclopedia of marine mammals. Academic Press, San Diego, CA, USA.

Reynolds III, J. E., Powell, J. A., Keith Diagne, L. W., Barton, S. L., & Scolardi, K. M. (2017). Manatees. In Encyclopedia of Marine Mammals. Academic Press, San Diego, CA, USA.

Ronald, K., Selley, L. J. & Amoroso, E. C. (1978). Biological Synopsis of the Manatee. Faculdade de Ciências Biológicas, Universidade de Guelf, Ontário.

Rosas, F. C. W. & Pimentel, T. L. (2001). Order Sirenia (Manatees, Dugongs, Sea cows). In M. E. Fowler & Z. S. Cubas, eds. Biology, medicine, and surgery of South American wild animals. Blackwell Publishing, Iowa.

Ruby, D. E. & Niblick, H. A. (1994). A behavioral inventory of the desert tortoise: development of an ethogram. – Herpetol. Monogr. 8: 88-102.

Sarko, D. K., Johnson, J. I., Switzer III, R. C., Welker, W. I. & Reep, R. L. (2007a). Somatosensory nuclei of the manatee brainstem and thalamus. – Anat. Rec. 290: 1138-1165.

Sarko, D. K., Reep, R. L., Mazurkiewicz, J. E., & Rice, F. L. (2007b). Adaptations in the structure and innervation of follicle-sinus complexes to an aquatic environment as seen in the Florida manatee (*Trichechus manatus latirostris*). – J. Comp. Neurol. 504: 217-237.

Self-Sullivan, C. & Mignucci-Giannoni, A. (2008). *Trichechus manatus* ssp. *manatus*. The IUCN Red List of Threatened Species 2008: e.T22105A9359161. Available at: <http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T22105A9359161.en>.

Scott, J.P. (1958). Animal Behavior. University of Chicago Press, Chicago, USA.

Silva, K. G., Paludo, D., Oliveira, E. M. A., Lima, R. P. & Soavinski, R. J. (1992). Distribuição e ocorrência do peixe-boi marinho (*Trichechus manatus*) no estuário do rio Mamanguape, Paraíba – Brasil. – Periódico Peixe-boi/ IBAMA – FMM, 1: 6-18.

Silva, F. J. L. (2014). Manual de métodos de estudo de comportamento de cetáceos. Natal: Offset Editora.

Sousa-Lima, R. S., Paglia, A. P. & Fonseca G. A. B. da (2008). Gender, age, and identity in the isolation calls of Antillean manatees (Trichechus manatus manatus). – Aquat. Mamm. 34: 109-122.

Sutherland, W. J. (1998). The importance of behavioural studies in conservation biology. – Anim. Behav. 56(4): 801-809.

Synder, N. F. R., Derrickson, S. R., Beissinger, S. R., Wiley, J. W., Smith, T. M., Toone, W. D. & Miller, B. (1996). Limitations of captive breeding in endangered species recovery. – Conserv. Biol. 10: 338-348.

Umeed, R., Attademo, F. L. N. & Bezerra, B. (2017). The influence of age and sex on the vocal repertoire of the Antillean manatee (*Trichechus manatus manatus*) and their responses to call playback. – Mar. Mamm. Sci. 34(3): 577-594.

Walls, G. L. (1963). The vertebrate eye and its adaptive radiation. Hafner Publ. Co., New York.

Wells, R.S., Boness, D.J. & Rathbun, G.B. (1999). Behavior. In J. E. Reynolds III & S. A. Rommel, eds. Biology of marine mammals. Smithsonian Institution Press, Washington, DC.

Yamasaki, F., Komatsu, S. & Kamiya, T. (1980). A comparative morphological study on the tongues of Manatee and Dugong (Sirenia). – Sci. Rep. Whales Res. Inst. 32: 127-144.

2 OBJETIVOS

2.1 OBJETIVO GERAL

Usando uma abordagem etológica, objetivamos investigar, avaliar e descrever o repertório de sinais de comunicação tátil usado por peixes-boi marinhos e entender como esses sinais variam em função da idade, sexo e contexto comportamental dos animais.

2.2 OBJETIVOS ESPECÍFICOS

1. Descrever o repertório de sinais táteis de comunicação do peixe-boi marinho, identificando as funções dos diferentes sinais táteis por associação com os diferentes contextos comportamental e social dos animais; e identificando a representatividade dos sinais táteis no orçamento comportamental da espécie.

2. Investigar se existe diferenças individuais, sexuais e etárias no padrão de uso dos sinais táteis (i.e., diferenças nos tipos de sinais e na frequência de uso dos mesmos);

3. Confirmar, experimentalmente, a função de alguns sinais táteis através da exposição controlada de diferentes estímulos (e.g., exposição de novos objetos e modelo de infante).

4. Frente aos resultados obtidos, sugerir medidas de manejo *ex situ* para promover exposição dos animais a estímulos que incentivem a produção de sinais de comunicação tátil na espécie.

3 ARTIGO 2: THE ROLE OF TOUCH IN CAPTIVE AND SEMI-CAPTIVE ANTILLEAN MANATEE (*Trichechus manatus manatus*)

Nota: Esse capítulo é fruto da colaboração de pesquisadores da Universidade Federal de Pernambuco e do Centro Nacional de Pesquisa e Conservação de Mamíferos Aquáticos no Nordeste (CEPENE). O capítulo foi publicado no formato de artigo no periódico Behaviour – DOI 10.1163/1568539X-bja10069, e tem como autores Karen Lucchini, Rebecca Umeed, Luana Guimarães, Paulo Santos, Iara Sommer e Bruna Bezerra.

3.1 INTRODUCTION

Socially organized animals must maintain contact with their conspecifics (Scott, 1958). Studies during the 1950s started showing the importance of all animal communication modalities, including tactile, visual, vocal, and chemical communication. Tactile communication is related to the information individuals communicate via their sense of touch (Frank, 1958). As with any other communication type, during tactile contact, a sender directs specific information towards a receiver, altering the receiver’s behaviour (Frank, 1958; Jones, 2011). Langbauer (2000) showed that tactile behaviour plays a role in maintaining elephant social groups, establishing alliances and well- being. This communication system can also be associated with greetings and recognition between individuals and self-grooming and interaction with the environment (Dudzinski, 1998; Sakai et al., 2006).

Animals perform tactile signals in various contexts, from sexual activities, socialization, and parental care to environmental exploration and aggression. Thus, tactile signalling plays an important role in cognitive development (Hartman, 1979; Silva et al., 2011). The presence of sensorial structures throughout the bodies of sirenians, proboscideans, pinnipeds, and cetaceans, highlights the importance of tactile communication for these animals (Reynolds & Odell, 1991; Dehnhardt & Kaminski, 1995; Dudzinski, 1998; Marshall et al., 1998; Poole & Granli, 2011). Combined with intensity modulation and different body part usage, tactile signalling is usually associated with other types of signals, often operating as sensors of mechanical and hydrodynamic stimuli (Reep et al., 1998, 2011). Bauer et al. (2018) reviewed and highlighted the use of touch and sensory hairs in Sirenians. Among the functions highlighted were mother-calf bonding, indicated as a primary social interaction, oripulation for object control, feeding behaviours, hydrodynamic stimuli, and navigation (Bauer et al., 2018). The sensory hairs of manatees are equivalent to a lateral line (Reep et al., 2011; Bauer et al., 2018) — they are relatively simple structures but have a powerful effect on manatee behaviour, socialization, and survival.

Anatomical studies on manatees revealed the presence of vibrissae throughout their body and snout, covering the perioral area, as well as the presence of prehensible and flexible lips and a tongue filled with tactile sensors (Hartman, 1979; Reynolds & Odell, 1991; Marshall et al., 1998; Sarko et al., 2007). Tactile social behaviours in Antillean and Florida manatees (*Trichechus manatus manatus* and *Trichechus manatus latirostris*, respectively) include hugging and touching for sexual activities, mouthing and rubbing during socialization, mouthing and scratching for social grooming, body touches during journeys, playing, and feeding (Hartman, 1979; Marshal et al., 1998; Wells et al., 1999; Reeves et al., 2002; Silva et al., 2011). Female manatees also help calves breathe until they assume a breathing rhythm (Hartman, 1979; Wells et al., 1999; Reeves et al., 2002; Harper & Schulte, 2005). There are also solitary tactile behaviours such as self- grooming, investigating objects, and environment assessment (Reynolds & Odell, 1991; Marshal et al., 1998). Furthermore, tactile behaviours can play a role in learning processes (key location and referential), social interactions necessary for survival and reproductive activities, and self-maintenance associated with parasite removal (Bengtson, 1981; Dudzinski et al., 2008).

We know relatively little about Antillean manatee tactile behaviours, with information on sexual variation and patterns associated with their functionality, contextualization, and environment still lacking. Therefore, to fill some of these gaps in knowledge, the aim of this study was to (i) investigate the representativeness of tactile behaviours in the general activity budget of Antillean manatees; (ii) test whether the observation method influences the detection of tactile behaviours; (iii) investigate if age, housing conditions and sex influence the use of specific tactile behaviours; and (iv) investigate if tactile patterns can differentiate animals in the different sex-enclosure con- ditions (i.e., captive females, captive males, and semi-captive males).

We predicted that sex differences would result in distinct performances of tactile behaviours, in which females would perform more tactile signals com-pared to males due to the mother-calf relationship previously recorded by several studies on other manatee species (Hartman, 1979; Wells et al., 1999; Reeves et al., 2002; Silva et al., 2011). Female manatees are more tolerant of body contact and tactile communication than males, possibly due to the existence of this mother-calf relationship (Wells et al., 1999; Harper & Schulte, 2005). Such relationships may transmit environmental information and some skills from adults to calves, resulting in learned behaviour (Bengtson, 1981). Nevertheless, some sexual and agonistic behaviours are likely to be most frequently performed by males due to sexual competition and sexual maturity (Hartman, 1979). Furthermore, some studies have shown sexual variations in the performance of other types of communication signals in West Indian manatees (e.g., vocal communication signals — Bengtson, 1981; Bengtson & Fitzgerald, 1985; Henaut et al., 2010; Sousa-Lima et al., 2008; Umeed et al., 2017). This reinforces the notion that there may also be variations in the performance of tactile behaviours. Thus, animals in captivity in an oceanarium may perform tactile behaviours more frequently due to the higher density of animals in the pools compared to animals in semi-natural conditions, where pools are larger, have fewer animals, and are under natural tide regimes. Amazonian manatee (*Trichechus inunguis*) group composition may be influenced by river regimes and stochastic hydrological conditions (Da Silva, 1996; Kendall et al., 2014), suggesting that manatees may be more social when occurring in higher densities or favourable conditions, such as feeding and resting areas.

3.2 MATERIAL AND METHODS

3.2.1 Animals and study site

We carried out the study at two sites: (1) the oceanarium of the Centro Nacional de Pesquisa e Conservação de Mamíferos Aquáticos do Instituto Chico

Mendes de Conservação da Biodiversidade (ICMBio/CMA) on Itamaracá Island, Pernambuco, Brazil; (2) the semi-natural pools of the Área de Proteção Ambiental Costa dos Corais in Porto de Pedras, Alagoas, Brazil. We conducted the observations between October 2018 and April 2019. We saw no apparent variation in water visibility between the different enclosures. The water in the oceanarium pools was not completely clear (supplementary material 1; supplementary material 4), resulting in similar water conditions in the captive and semi- depth of the semi-natural pools did not pose a noticeable variation in water clarity due to tide and estuarine regimes.

We investigated 11 adult manatees in the oceanarium, four males and seven females, kept in separate pools according to their sex (Table 3). The male pool was composed of two rectangular pools connected by a gate and had total dimensions of 8 × 5 m and 4 m deep (density of 0.0250 individuals/m3). The female pool was "L" shaped, composed of two rectangular 10 × 5 m and depth ranging from 2 to 4 m pools interconnected by two gates and a 5 m long and 2 m deep square pool in the adjoining corner (see supplementary material 1). During the observations, the females remained in one of the rectangular pools and the small square pool (density of 0.0350 individuals/m3). The animals were not exposed to general public visits during the study.

We also investigated four adult male manatees equally distributed in two semi-natural pools (see supplementary material 2). One pool had dimensions of 25 × 15 m (density approximately 0.004 individuals/m3) and the other one 30 × 25 m (density approximately 0.002 individuals/m3), and the depth varied from 1 to 1.5 m in the Tatuamunha River estuary bed, according to the tide regime. We individually identified the animals through natural anatomic variations, such as size, head and back shapes, and scars (Table 3).

Table 3. Captive and semi-captive Antillean manatees included in the present study at the oceanarium of the *Centro Nacional de Pesquisa e Conservação da Mamíferos Aquáticos/Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio/CMA*) on Itamaracá Island, Pernambuco, Brazil and at the semi-natural pools of the Área de Proteção Ambiental Costa dos Corais in Porto de Pedras, Alagoas, Brazil. *Estimated age of the animals at the beginning of the observations in October 2018. **Time in captivity refers to time spent in confinement. All individuals were either born in captivity or arrived at captive Centers when they were a calf/less than 1 year old (a few days/weeks as estimated by the rehab center).

Individual	Sex	Estimated age (yr.)*	Housing condition	Time in captivity (yr.)**
Bela	Female	8	Oceanarium	Born in captivity
Canoa	Female	14	Oceanarium	14
Carla	Female	22	Oceanarium	Born in captivity
Paty	Female	4	Oceanarium	4
Sheila	Female	22	Oceanarium	Born in captivity
Vitória	Female	4	Oceanarium	4
Xuxa	Female	32	Oceanarium	32
Daniel	Male	9	Oceanarium	9
Parajuru	Male	6	Oceanarium	6
Poque	Male	27	Oceanarium	27
Zoé	Male	14	Oceanarium	14
Assu	Male	19	Semi-natural	19
Arati	Male	9	Semi-natural	9
Netuno	Male	28	Semi-natural	28
Raimundo	Male	8	Semi-natural	8

Source: The author (2021).

3.2.2 Observations of animals

To construct the list of tactile behaviours, we spent 100 hours observing the manatees at the oceanarium using the ad libitum sampling method (Altmann, 1974). We conducted these observations from November 2018 to April 2019, between 8 am and 2 pm, an average of 2.5 h of sampling per sampling day. We did not carry out observations when keepers or veterinarians were inter- acting with the manatees. We recorded manatee tactile behaviours, made precise descriptions for each behaviour, and video recorded the animals whenever possible. We conducted the observations from a position that provided a complete view of the enclosures, avoiding any physical interaction between the subjects and the observer. Furthermore, we conducted a literature review on ethograms and behavioural definitions for manatees, where we listed Hartman (1979), Gomes et al. (2008), Henaut et al. (2010), Umeed et al. (2017), and Attademo et al. (2019) to help standardize the categorization and definition of the behaviours.

We also observed the animals for 100 hours using a scan sampling method (Altmann, 1974). Behavioural records were taken every five minutes to obtain the representativeness of tactile behaviours in the Antillean mana- tee activity budget. We conducted these observations from October 2018 to April 2019, between 8 am and 3 pm.

We also conducted observations using the focal animal sampling method (Altmann, 1974) to assess potential differences in the frequencies of tactile behaviour according to age/time in captivity, sex, and housing conditions. We conducted 20 focal sessions of 10-minute duration per individual over 20 days (in captivity, five days in April and eight days in May 2019; in semi- natural pools, seven days in February 2019).

The observer KL conducted ad libitum sampling observations, and the observer RU performed scan sampling observations. Focal animal sampling was performed by KL and RU, who were both experienced at observing the manatees and contributed equally to the final sample size. KL and RU used the same ethogram developed from ad libitum observations (supplementary material 3). We performed an Intraclass Correlation Coefficient (ICC) to estimate inter-observer reliability. The two observers (i.e., KL and RU) independently scored 3 hours of video footage of the captive manatees’ behaviours, and we used such data for the ICC (Average ICC = 0.997).

3.2.3 Statistical Analyses

We present descriptive statistics using percentages, means, and standard errors. We calculated the percentage of each of the behavioural categories and performed a Chi-square test, using Microsoft Excel Version 16.29.1, to test whether the observation method influenced the scoring of tactile behaviours. Here we considered the behavioural category frequencies for each observation sampling method (ad libitum, scan, and focal animal).

Using data from focal animal sampling, we used a Spearman correlation to investigate the influence of animal ages on the performance of tactile behaviours. We conducted Mann–Whitney U-tests to investigate the influence of housing condition type and sex on the frequency of specific tactile behaviours performed by Antillean manatees. We only considered data from males in the comparison between housing conditions to avoid sex bias as females were absent in the semi-natural enclosures. Moreover, we only considered the behaviours performed by both males and females for the sexual comparison (see supplementary materials 3 and 4).

We conducted a Permutational Analysis of Variance (PERMANOVA) based on Bray-Curtis dissimilarities, through Primer® 6 with add-on PERMANOVA+, to evaluate whether the tactile behavioral pattern obtained from focal animal observations of Antillean manatees could significantly separate distinct groups detected in a distance-based Redundancy Analysis (dbRDA). In the dbRDA analysis, we considered time in captivity, housing conditions, and sex as explanatory variables, along with the behaviors used to generate the Bray-Curtis dissimilarity matrix. We used all 15 tactile behaviors observed in the repertoire of our study of Antillean manatees in the multivariate analysis as they define the pattern of each group. Finally, we used permutational *t*-tests for *post hoc* pairwise comparisons. For all *post hoc* analyses, we used 999 random permutations with statistical significance given by the Monte Carlo test. Significance was attained when $p \leq 0.05$ in all tests.

3.3 RESULTS

3.3.1 List of tactile related behaviors

We registered a total of 5936 events of tactile behaviours in our ad libitum observations, representing 17 types of different behaviours, distributed in three main categories: ‘Social’ (N = 2397), ‘Environment exploration’ (N = 3373), and ‘Self-maintenance’ (N = 166) (supplementary material 3 and 4). The category ‘Social’ included affiliative and agonistic interactions between the manatees. The category ‘Environment exploration’ included any type of interaction with the environment and environmental investigation. The category ‘Self-maintenance’ included behaviours related to self-pleasure and behaviours that did not involve interaction between individuals or the environment.

3.3.2 Representativeness of tactile behaviors in the activity budget of Antillean manatees and influence of observation method

We registered a total of 9290 behavioural records during scan observations (mean of 1.13 ± 0.004 behaviours per scan). Out of these, 1304 were tactile behaviours, representing 14.03% of the Antillean manatees’ activity budget. A total of 3688 behaviours were registered during focal animal observations (mean of 12.29 ± 0.46 behaviours per focal animal session), 734 represented tactile behaviours (19.90%). Ad libitum observations were focused on tactile behaviours.

Using the ad libitum sampling method, we registered 5936 tactile behavioural records distributed across the ‘Environmental exploration’ (56.82%), ‘Self-maintenance’ (2.8%), and ‘Social’ (40.38%) categories. Using the scan sampling method, we registered 1304 tactile behavioural records (69.78% ‘Environment exploration’; 1.77% ‘Self-maintenance’; and 28.45% ‘Social’). Using the focal animal sampling method, we registered a total of 734 tactile behavioural records (46.18% ‘Environment exploration’; 22.08% ‘Self-maintenance’; and 31.74% ‘Social’). The Chi-square test revealed a significant difference between the sampling method frequencies for the ‘Self-maintenance’ category ($\chi^2 = 29.49$;

df = 2; p < 0.05), but not for the 'Environment exploration' ($\chi^2 = 4.85$; df = 2; $p > 0.05$) and the 'Social' ($\chi^2 = 2.26$; df = 2; $p > 0.05$) categories.

3.3.3 Influence of age on the performance of tactile behaviors

There was no correlation between Antillean manatee age and the frequency of most tactile behaviours, except for the behaviour 'Hanging', which negatively correlated with age (Table 4). 'Masturbation' and 'Attempted copulation' were not registered during focal animal sessions and were, therefore, not included in this or any of the following analyses.

Table 4. Correlation of the frequency of tactile behaviors and age in Antillean manatees. The row in gray shows the behavior that was significantly different between ages (p<0.05). N=15.

Category	Behavior	r	p-value
Social	Snout touch	-0.153	0.586
	Flipper touch	-0.148	0.599
	Pushing	-0.035	0.900
	Mouthing	0.027	0.923
	Body touch	0.061	0.829
	Tail touch	0.165	0.556
	Embrace	0.203	0.469
Environment exploration	Hanging	-0.529	0.043
	Body on the wall	-0.245	0.378
	Slapping water	-0.197	0.481
	Interaction with wall/gate	-0.037	0.896
	Checking object	0.083	0.769
Self-maintenance	Chewing flipper	-0.120	0.669
	Spinning	-0.117	0.678
	Moving mouth	-0.029	0.918

Source: The author (2021).

3.3.4 Influence of housing conditions on the performance of tactile behaviors

Housing conditions did not influence the frequency of tactile behaviours in male Antillean manatees, with no significant differences observed for the ten behaviours that occurred in both captive and semi-captive conditions (supplementary material 5). Nevertheless, other behaviours not included in supplementary material 5 were exclusive to one of the sex-housing conditions. 'Body on the wall', 'Moving mouth', 'Tail touch', and 'Chewing flippers' were performed only by the captive animals. In contrast, 'Checking object' was only performed by the semi-captive animals due to natural objects occurring in the environment.

3.3.5 Influence of sex on the performance of tactile behaviors

The frequency of only two of the 15 tactile behaviours differed between males and females in the oceanarium (Table 5): 'Body on the wall' was more frequently performed by males, while 'Tail touch' was performed more frequently by females. For the analysis of the influence of sex on the performance of tactile behaviours, we considered the captive and semi-captive individuals due to the lack of differences in the specific behaviours reported above for housing conditions.

Table 5. Comparison of the frequency of tactile behaviors performed by male and female manatees. The rows in gray show the behaviors that were significantly different between sexes (p<0.05). $N_{females}$=7 and N_{males}=8.

Category	Tactile behaviors	Mean frequency of tactile behaviors ± SE		Mann-Whitney *U* test	p-value
		Females	Males		
Social	Body touch	0.51 ± 0.09	0.06 ± 0.02	13.0	0.078
	Mouthing	0.30 ± 0.03	0.13 ± 0.05	14.5	0.115
	Snout touch	0.18 ± 0.04	0.14 ± 0.04	19.0	0.290
	Tail touch	0.09 ± 0.02	0.01 ± 0.01	4.0	0.002
	Embrace	0.08 ± 0.04	0.04 ± 0.02	27.5	0.950

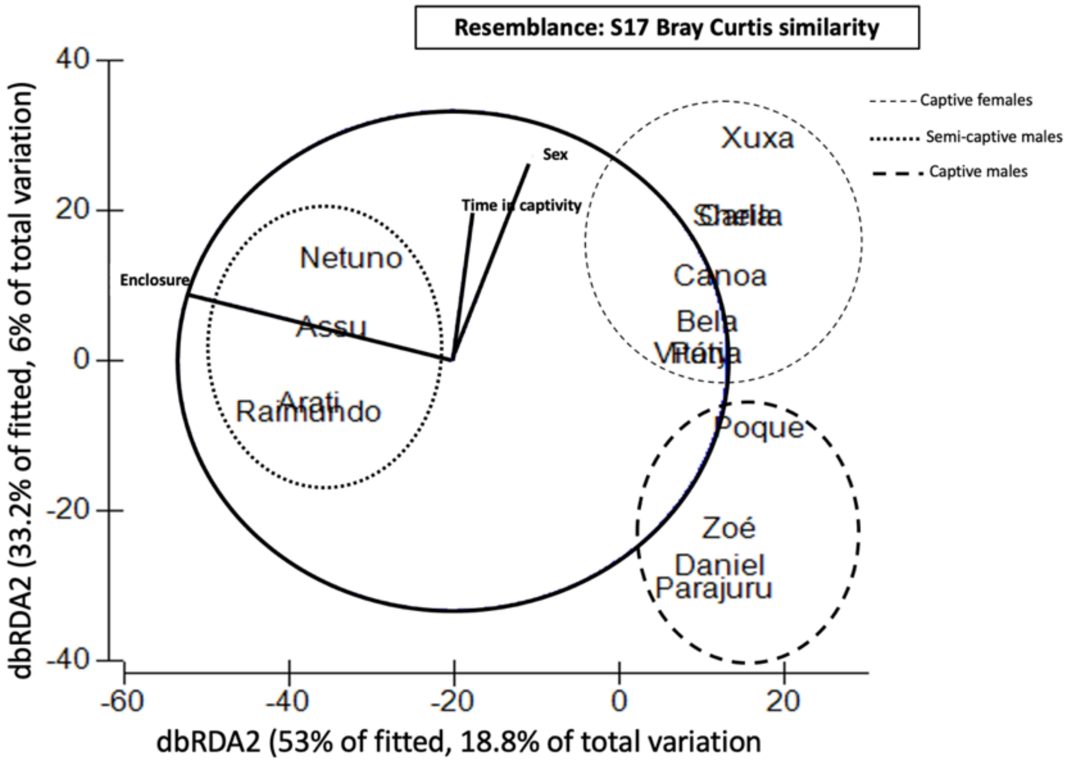
	Pushing	0.03 ± 0.01	0.03 ± 0.02	24.5	0.648
	Flipper touch	0.02 ± 0.01	0.01 ± 0.01	23.0	0.480
Environment exploration	Interacting with wall/gate	1.34 ± 0.96	0.86 ± 0.35	20.0	0.354
	Hanging	0.05 ± 0.04	0.11 ± 0.06	20.5	0.325
	Checking object	0.03 ± 0.02	0.18 ± 0.14	26.0	0.766
	Slapping water	0.01 ± 0.01	0.02 ± 0.01	25.5	0.724
Self-maintenance	Spinning	0.26 ± 0.13	0.34 ± 0.21	25.5	0.765
	Body on the wall	0.14 ± 0.04	0.24 ± 0.18	10.5	0.037
	Chewing flippers	0.06 ± 0.03	0.01 ± 0.01	14.5	0.061
	Moving mouth	0.04 ± 0.03	0.02 ± 0.01	22.0	0.406

Source: The author (2021).

3.3.6 Influence of time in captivity, sex, and housing condition on the tactile behavioral pattern

The tactile behavioural pattern of the three groups detected by dbRDA (i.e., captive males, semi-captive males, and captive females; Figure 8) differed according to the PERMANOVA (Pseudo-F = 2.3592; df = 2; 12; p = 0.0046; 9999 random permutations). Permutational t-tests showed that the tactile pattern of captive females differed from the pattern of semi-captive males (*t* = 1.7498, *P* (MC)= 0.0221), the pattern of captive females did not differ from the pattern of captive males (*t* = 1.2944, *P* (MC)= 0.1679), and the pattern of captive males did not differ from the pattern of semi-captive males (*t* = 1.5243, *P* (MC)= 0.087).

Figure 8. Distance-based Redundancy Analysis showing the captive males, semi-captive males and captive females as separate groups. Enclosure type, sex and time in captivity were the explanatory variables.



Source: The author (2021).

3.4 DISCUSSION

We listed 17 tactile behaviours out of 33 behaviours in the activity budget of the Antillean manatees studied. The tactile behaviours were distributed across three functional categories: social, self-maintenance, and environmental exploration. They represented 14.03% of the Antillean manatees' activity budget, reflecting the anatomical structures specialized to feel touch in the species (Bauer et al., 2018). Wild Florida manatees (Hartman, 1979; Harper & Schulte, 2005) and Antillean manatees in semi-natural enclosures in Mexico (Henaut et al., 2010) showed behaviours similar to the ones we classified as 'Environment exploration' and 'Social' categories. Despite genetic differences, the external morphology and anatomy of Antillean and Florida manatees present similarities (Garcia-Rodriguez et al., 1998), which may favour the existence of similar tactile behaviours.

Self-maintenance tactile behaviours represented less than 2% of the tactile activity budget of Antillean manatees. The detection rate of these behaviours was higher using focal animal and ad libitum sampling methods than when using the scan sampling method. This agrees with Bernstein (1991), who pointed out that under near optimum conditions for observations, ad libitum and focal animal sampling methods agree. The ad libitum method of observation allows for the registration of a large amount of data, such as ordinal frequencies, over a short period (Bernstein, 1991). The focal animal method may generate data for different analyses (i.e., duration and frequency) (Bern- stein, 1991).

Environmental exploration behaviours represented nearly 70% of the tac- tile behavioural budget in captive Antillean manatees. Such behaviours are essential for locating feeding areas and for self-location (Ramirez-Jiménez et al., 2017). Manatee vibrissae are sensitive to water currents and may receive environmental information using low-frequency vibrations and pressure waves (Hartman, 1979; Bauer et al., 2018). Although the majority of the 'Environment exploration' behaviours may be related to actual environmental conditions and learning, behaviours such as 'Interacting with wall/gate' could be a captive stereotypy as suggested by Anzolin et al. (2014). Courbis & Worthy (2003), on the other hand, suggest that such exploratory behaviour on enclosure walls plays an essential role in feeding habits (Courbis & Worthy, 2003). Our study included the behaviour 'Interacting with wall/gate' as an exploratory activity (potentially related to feeding) since chewing movements could also accompany the behaviour, as observed in Florida manatees. Furthermore, our study animals were not repeatedly hitting their head on the wall, as Anzolin et al. (2014) described for their study animals.

Social behaviours represented 28.5% of the tactile activity budget of the Antillean manatees. Behaviours included in this category can be related to social recognition, commonly observed in cetaceans (Mercado & Delong, 2001), or can even be associated with sexual activities (Henaut et al., 2010). Some associations within captive manatees seem to be similar to associations found for captive African elephants (*Loxodonta africana*) (Schulte, 2000). However, time spent in the oceanarium was not suggested to influence manatee activity patterns (Young, 2001). Manatees in oceanariums are more sociable than wild ones and show greater tolerance and acceptance of other individuals who are not partaking in a mother-calf relationship (Harper & Schulte, 2005). On the other hand, Koelsch (1997) supports a stronger association than previously believed for wild manatees, with reports of adult bonding during activities such as traveling together without reproductive intention. This might explain the variety of social behaviours that we were able to register in our study. Nevertheless, we cannot rule out that the high number of social behaviours could be related to manatee density inside each pool. Previous studies have associated greater contact rates between mana- tees with a high density of animals in pools (Harper & Schulte, 2005).

We found that younger individuals performed ‘Hanging’ more frequently than older individuals, which could be related to the captive oceanarium routine. Young manatees at the oceanarium are fed using nursing bottles at the pools’ side, which encourages the performance of ‘Hanging’ behaviour. A juvenile male manatee rescued in Mexico also performed behaviours that were affected by feeding hours and the daily rhythm activities of the captive centre where it was held (Mercadillo-Elguero et al., 2014). Some tactile behaviours depend on the presence of enrichment stimuli in the captive pools or natural stimuli inside the semi-captive pools. For instance, the behaviour ‘checking object’ was not registered for captive males in Itamaracá due to the absence of environmental enrichment and natural objects (coconuts, trees, branches, and leaves). Even simple stimuli like coconuts floating on the water favour the performance of tactile behaviours related to environmental exploration. Such behaviours are important for the stimulation of different sensorial structures throughout manatee bodies, which have been suggested to help individuals navigate their habitats (Bauer et al., 2018). Manatees seem to be aware of the spatial configuration of their habitats and may use objects in the environment as a cue for navigation (Slone et al., 2012).

When we compared the tactile behaviours in both captive and semi-captive enclosures, we found that housing conditions did not influence the performance of behaviours by males. Sex influenced the specific frequency of only two behaviours (i.e., ‘Tail touch’ was the most frequent in females; ‘Body on the wall’ was the most frequent in males). Nevertheless, based on the complete tactile activity pattern, we could identify three distinct groups of manatees (i.e., captive females, captive males, and semi-captive males) in our multivariate analysis. ‘Sex and housing conditions’ played a more prominent role than ‘time in captivity’ (and consequently age, for the study animals) in the observed tactile activity pattern. Despite nearing the significance level, the housing condition variable was not enough to discriminate between the tactile behavioural patterns of captive and semi-captive males. It did however, discriminate between the tactile pattern of captive females and semi-captive males. Overall, females tended to perform more tactile behaviours than males, indicating a possible higher tolerance to body con- tact in females, which agrees with the literature available for tactile and other types of communication signals in Antillean manatees (Hartman, 1979; Bengtson, 1981; Wells et al., 1999; Reeves et al., 2002; Henaut et al., 2010; Sousa-Lima et al., 2008; Silva et al., 2011; Umeed et al., 2017).

We conclude that tactile behaviours represent nearly 15% of the activity budget of the study Antillean manatees. Furthermore, the type of observation method influences the detection of self-maintenance tactile behaviours, the least frequent category of tactile activities. Individuals in the oceanarium, particularly the females, performed a wider range of tactile behaviours com- pared to males. We believe the high density of females in the pool may have played a role in their tactile activity budget, as also pointed out by Da Silva (1996) and Kendall et al. (2014) in their studies with *Trichechus inunguis*. The tactile activity pattern of manatees could differentiate between individuals in captivity and semi-captivity. Several researchers highlight the importance of behavioural studies, focusing on captive and semi-captive animals, in order to monitor natural and altered behaviours. Such studies focus on the animals’ needs, as they often try reducing ethological restrictions by providing stimuli-rich surroundings through environmental enrichment (Breland & Breland, 1961; Mellen & Ellis, 1996; Carlstead, 1998; Mellen & MacPhee, 2001). We hope our findings will contribute to manatees’ well-being as they can be used in rehabilitation programs, providing a better understanding of manatee tactile behaviours and activity budgets.

We suggest that ad libitum and focal animal methods may be the best options when specifically investigating self-maintenance tactile behaviours in manatees, as they favour the detection of such behaviours. Nevertheless, different sampling techniques complement each other, and only a detailed evaluation of the aims of the study in question will determine which observation sampling method is the most adequate. We recommend using objects as routine environmental enrichment in manatee oceanariums to stimulate sensory structures and the performance of exploratory tactile behaviours. Such behavioural and morpho-physiological stimulation could be key for manatee survival after their reintroduction to the wild. Future studies investigating semi-captive female Antillean manatees would help us further clarify the influence of sex and housing conditions on manatee tactile repertoires. Furthermore, considering the convincing effect of the presence of objects in both captive and semi-captive pools observed in our study, further studies should focus on how Antillean manatees respond to different objects used as environmental enrichment. Touch must never be taken for granted in rehabilitation and reintroduction programs of Antillean manatees and should be encouraged. Understanding how different communication types (i.e., vocal and tactile) are connected may also clarify and support rehabilitation and reintroduction processes, backing up management and conservation pro- grams using behavioural approaches as tools.

3.5 SUPPLEMENTARY MATERIALS

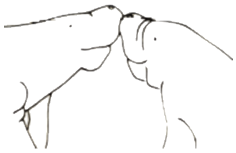
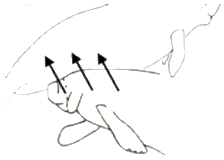
Supplementary material 1. Oceanarium pools at the *Centro Nacional de Pesquisa e Conservação da Mamíferos Aquáticos/Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio/CMA*) at Itamaracá Island, Pernambuco, Brazil. (I) Males' pool; (II) Females' pool.

Source: The author (2021).

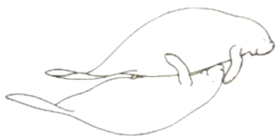
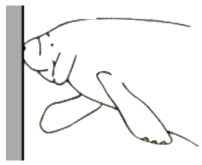
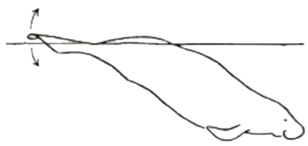
Supplementary material 2. Semi-natural pools at the Área de Proteção Ambiental Costa dos Corais at Porto de Pedras, Alagoas, Brazil.


Source: The author (2021).

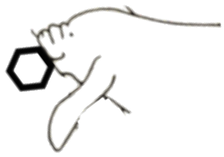
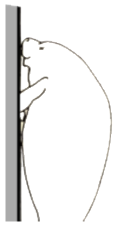
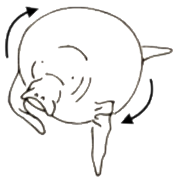
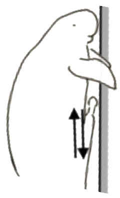
Supplementary material 3. List of tactile behaviors performed by Antillean manatees and their descriptions. To aid in comparisons, we based our definitions and/or illustrations in Hartman (1979), Gomes et al. (2008), Henaut et al. (2010), Umeed et al. (2017) and Attademo et al. (2019) whenever possible. N= number of times the behavior was registered in the *ad libitum* observations.

Tactile behavior **N**	**Category**	**Description**	**Illustration of the behavior**
Body touch **N=885**	Social	The individual's body touches another one's body without pushing it. It normally happens during resting hours ("Nuzzling" in Hartman, 1979).	
Mouthing **N=565**	Social	The individual snout touches any of the body parts of another individual with exception of its snout, with or without chewing movement ("Touch snout" in Gomes et al., 2008).	
Snout touch **N=347**	Social	The snout of one individual specifically touches the snout of another, without chewing movement ("Kissing" in Hartman, 1979).	
Pushing **N=312**	Social	An individual uses strength to move another manatee, using head, back, flippers or tail ("Push away" in Gomes et al., 2008 and "Empurrar" in Attademo et al., 2019).	

Supplementary material 3. Cont.

Tactile behavior N	Category	Description	Illustration of the behavior
Tail touch **N=145**	Social	The individual's tail gently touches the body of another individual without pushing it.	
Flipper touch **N=111**	Social	The individual touches another's body with one flipper only, sometimes scratching it.	
Embrace **N=31**	Social	The animal uses both flippers to hold another individual ("Abraçar" in Attademo et al., 2019).	
Attempted copulation **N=1**	Social	A male embraces another individual in ventral embrace in position to copulate, but despite male genital exposure, no penetration occurs ("Montar em outro animal" in Attademo et al., 2019). *Only observed between males in our study sites.	
Interacting with wall/gate **N=2428**	Environment exploration	The individual touches the wall/gate with snout, with or without chewing movement.	
Hanging **N=379**	Environment exploration	The individual holds on to the edge of wall/gate/pool/fence using one flipper, lying still against side of pool/ground.	
Slapping water **N=43**	Environment exploration	The individual hits the water surface using its tail or body.	

Supplementary material 3. Cont.

Tactile behavior **N**	**Category**	**Description**	**Illustration of the behavior**
Checking object **N=22**	Environment exploration	The individual approaches an object handling it with snout and lips, with or without chewing movements. Captive females were observed performing this behavior due to an exclusive habitat enrichment in the female pools. Semi-captive males were observed performing the behavior due to natural objects floating on the water.	
Body on the wall **N=459**	Self-maintenance	The individual touches the wall with the entire body. It can be performed with the animal in a still position or in gentle up and down or side to side movement.	
Chewing flippers **N=88**	Self-maintenance	The individual gently bites its own flippers (“Auto-groom” in Gomes et al., 2008).	
Moving mouth **N=66**	Self-maintenance	The individual’s gently moves the mouth in a chewing movement, attempting to remove food remains or anything that is trapped around the lips.	
Spinning **N=42**	Self-maintenance	The individual rolls around its own axis completely or partially creating a spiral current around it (“Rotation” in Henaut et al., 2010, “Corkscrew” in Gomes et al., 2008 and “Movimento em parafuso” in Attademo et al., 2019).	
Masturbation **N=12**	Self-maintenance	The individual rubs its genital area in a rhythmic thrusting motion against the wall/gate. *Only observed for males and they can expose their genitals.	

Source: The author (2021).

Supplementary material 4. Video of 13 of the 17 tactile behaviors we registered during the observations. Video link <http://dx.doi.org/10.6084/m9.figshare.13603016>

Supplementary material 5. Comparison of the mean frequency of tactile behaviors between male manatees living in the oceanarium pool and semi-natural pools (considering data from focal animal sampling). N=4 for semi-captive individuals and captive individuals.

Category	**Tactile behaviors**	**Mean frequency of tactile behaviors ± SE**		***Mann-Whitney U test***	**p-value**
		Semi-natural pools	**Oceanarium pools**		
Social	Mouthing	0.11 ± 0.07	0.15 ± 0.08	5.5	0.457
	Snout touch	0.06 ± 0.05	0.21 ± 0.05	4.0	0.243
	Body touch	0.06 ± 0.04	0.06 ± 0.03	5.5	0.454
	Embrace	0.01 ± 0.01	0.06 ± 0.03	3.5	0.155
	Pushing	0.01 ± 0.01	0.05 ± 0.04	5.5	0.405
	Flipper touch	0.01 ± 0.01	0.01 ± 0.01	8.0	1.000
Environment exploration	Interacting with wall/gate	0.29 ± 0.09	1.43 ± 0.58	8.0	1.000
	Hanging	0.01 ± 0.01	0.20 ± 0.11	4.0	0.215
	Slapping water	0.01 ± 0.01	0.03 ± 0.01	6.0	0.495
Self-maintenance	Spinning	0.04 ± 0.02	0.64 ± 0.39	3.0	0.139

Source: The author (2021).

3.6 REFERENCES

Altmann, J. (1974). Observational study of behavior: sampling methods. – Behaviour 49: 227-267.

Anzolin, D. G., Carvalho, P. S. M. de, Viana-Jr., P. C., Normande, I. C. & Souto, A .S. (2014). Stereotypical behaviour in captive West Indian manatee (*Trichechus manatus*). – J. Mar. Biol. Assoc. UK 94: 1133-1137.

Attademo, F. L. N., Gomes, G. L., Silva, F. J. L., Modeira, A. B., Freire, A. C. B., Leitão, H. C. M. S. & Luna, F. O. (2019). Comportamento de peixes-bois | Guia ilustrado. Instituto Chico Mendes de Conservação da Biodiversidade, Brazil.

Bauer, G .B., Reep, R .L. & Marshall, C. D. (2018). The tactile senses of marine mammals. – Int. J. Comp. Psychol. 31. Retrieved from https://escholarship.org/uc/item/1vk1c9z1

Bengtson, J. L. (1981). Ecology of manatees (*Trichechus manatus*) in the St. Johns River, Florida. (Ph.D. thesis). – University of Minnesota, MN, USA.

Bengtson, J. L. & Fitzgerald, S. M. (1985). Potential role of vocalizations in West Indian manatees. – J. Mammal. 66: 816-819.

Bernstein, I. S. (1991). An empirical comparison of focal and ad libitum scoring with commentary on instantaneous scans, all occurrence and one-zero techniques. – Anim. Behav. 42: 721-728.

Breland, K. & Breland, M. (1961). The misbehavior of organisms. – Am. Psychol. 16: 681-4.

Carlstead, K. (1998). Determining the causes of stereotypic behaviors in zoo carnivores: Toward appropriate enrichment strategies. In: Shepherdson, D. J., Mellen, J. D. & Hutchins, M. editors. Second nature: Environmental enrichment for captive animals. Washington, DC: Smithsonian Institution Press. p. 172-83.

Courbis, S. S. & Worthy, G. A. J. (2003). Opportunistic carnivory by Florida manatees (*Trichechus manatus latirostris*). – Aquat. Mamm. 29: 104-107.

Da Silva, V. M. F. (1996). Os mamíferos aquáticos da Amazônia, sua organização social e comportamento. In: Anais de Etologia, v. 14. Uberlândia, Brasil, p. 263-273.

Dehnhardt, G. & Kaminski, A. (1995). Sensitivity of the mystacial vibrissae of Harbour seals (*Phoca vitulina*) for size differences of actively touched objects. – J. Exp. Biol. 198: 2317-2323.

Dudzinski, K. M. (1998). Contact behavior and signal exchange among Atlantic spotted dolphins (*Stenella frontalis*). – Aquat. Mamm, 24: 129-142.

Dudzinski, K. M., Thomas, J. A. & Gregg, J. D. (2008). Communication in marine mammals. – In: Encyclopedia of marine mammals. Academic Press, p. 260-269.

Frank, L. K. (1958). Tactile communication. – ET Cetera 16: 31-79.

Garcia-Rodriguez, A. I., Bowen, B. W., Domning, D., Mignucci-Giannoni, A., Marmontel, M., Montoya-Ospina, A., Morales-Vela, B., Rudin, M., Bonde, R. K. & McGuire, P. M. (1998). Phylogeography of the West Indian manatee (*Trichechus manatus*): How many populations and how many taxa? – Mol. Ecol. 7: 1137–1149.

Gomes, F. F. A., Vergara-Parente, J. E. & Ferrari, S. F. (2008). Behavior patterns in captive manatees (*Trichechus manatus manatus*) at Itamaracá Island, Brazil. – Aquat. Mamm. 34: 269–276.

Harper, J. Y. & Schulte, B. A. (2005). Social interactions in captive female Florida manatees. – Zoo Biol. 24: 135–144.

Hartman, D. S. (1979). Ecology and behavior of the manatee (*Trichechus manatus*) in Florida. American Society of Mammologists, Special Publications.

Henaut, Y., Lopez, S. P. B., Machkour-M'Rabet, S., Morales-Vela, B., Winterton, P. & Delfour, F. (2010). Activities and social interactions in captive Antillean manatees in Mexico. – Mammalia 74: 141-146.

Jones, L. A. (2011). Tactile communication systems: optimizing the display of information. – Prog. Brain Res. 192: 113-128.

Kendall, S., Ahue, C., Orozco, D. L. & Pena, L. H. (2014). Conservación y monitoreo de los manatíes en los humedales de Tarapoto. In: Los humedales de Tarapoto. Serie Humedales de la Amazonia y la Orinoquia (Trujillo, F. & Duque, S., eds.). F. Omacha/Corpoamazonía/Universidad Nacional de Colombia.

Koelsch, J. K. (1997). The seasonal occurrence and ecology of Florida manatees (*Trichechus manatus latirostris*) in coastal waters near Sarasota, Florida. (Master's dissertation). - University of South Florida, Sarasota, FL, USA.

Langbauer, W. R. Jr. (2000). Elephant communication. – Zoo Biol. 19: 425-445.

Marshall, C. D., Huth, G. D., Edmunds, V. M., Halin, D. L. & Reep, R. L. (1998). Prehensile use of the perioral bristles during feeding and associated behaviors of the Florida manatee (*Trichechus manatus latirostris*). – Mar. Mammal Sci. 14: 274-289.

Mellen, J. & Ellis, S. (1996). Animal learning and husbandry training. In: Kleiman, D., Allen, M., Thompson, K. & Lumpkin, S. (eds). Wild mammals in captivity: principles and techniques. Chicago: The University of Chicago Press. p. 88–99.

Mellen, J. & MacPhee, M. S. (2001). Philosophy of environmental enrichment: past, present, and future. – Zoo Biol. 20(3): 211-226.

Mercadillo-Elguero, M. I., Castelblanco-Martínez, D. N. & Padilla-Saldívar, J. A. (2014). Behavioral patterns of a manatee in semi-captivity: Implication for its adaptation to the wild. – JMATE 7: 31–41.

Mercado, E. III & Delong, C. M. (2001). Experiments are the key to understanding socially acquired knowledge in cetaceans. – Behav. Brain Sci. 24: 345.

Poole, J. H. & Granli, P. (2011). Signals, gestures, and behavior of African elephants. In: The Amboseli elephants: A long-term perspective on a long-lived (Moss, C. J.; Croze, H. J. & Lee, P. C., eds.). - University of Chicago Press, Chicago, p. 109-124.

Ramirez-Jiménez, H. H., Olivera-Gómez, L. D. & Cueva, H. D. L. (2017). Habitat use by the Antillean manatee (*Trichechus manatus*) during an extreme dry season in an urban lake in Tabasco, Mexico. – Therya 8(1): 19-26.

Reep, R. L., Gaspard, J. C. III, Sarko, D., Rice, F. L., Mann, D. A. & Bauer, G. B. (2011). Manatee vibrissae: evidence for a "lateral line" function. – Ann. N. Y. Acad. Sci. 1225: 101-109.

Reep, R. L., Marshall, C. D., Stoll, M. L. & Whitaker, D. M. (1998). Distribution and innervation of facial bristles and innervation of facial bristles and hairs in the Florida manatee (*Trichechus manatus latirostris*). – Mar. Mamm. Sci. 14: 257-273.

Reeves, R. R., Stewart, B. S., Clapham, P. J. & Powell, J. A. (2002). National Audubon society guide to marine mammals of the world. A.A. Knopf, Random House, New York, USA.

Reynolds, J. E. III & Odell, D. E. (1991). Manatees and dugongs, facts on file**.** New York, USA.

Sakai, M., Hishii, T., Takeda, S. & Kohshima, S. (2006). Flipper rubbing behaviors in wild bottlenose dolphins (*Tursiops aduncus*). – Mar. Mammal Sci. 22: 966- 978.

Sarko; D. K., Reep, R. L., Mazurkiewicz, J. E. & Rice, F. L. (2007). Adaptations in the structure and innervation of follicle-sinus complexes to an aquatic environment as seen in the Florida manatee (*Trichechus manatus latirostris*). – J. Comp. Neurol. 504: 217–237.

Schulte, B. A. (2000). Social structure and helping behavior in captive elephants. – Zoo Biol. 19: 447–60.

Scott, J. P. (1958). Animal Behavior. - University of Chicago Press, Chicago, USA.

Silva, K. G., Paludo, D., Oliveira, E. M. A., Lima, R. P. & Soavinski, R. J. (2011). Distribuição e ocorrência do peixe-boi marinho (*Trichechus manatus*) no estuário do rio Mamanguape, Paraíba, Brasil. – Nat Resources 1: 5-14.

Slone, D. H., Reid, J. P., Kenworthy, W. J., di Carlo, G. & Butler, S. M. (2012). Manatees mapping seagrass. – Seagrass-Watch. 46: 8–11.

Sousa-Lima, R. S., Paglia, A. P. & Fonseca, G. A. B. (2008). Gender, age, and Identity in the isolation calls of Antillean Manatees (*Trichechus manatus manatus*). – Aquat. Mamm. 34: 109-122.

Umeed, R., Attademo, F. L. N. & Bezerra, B. (2017). The influence of age and sex on the vocal repertoire of Antillean manatee (*Trichechus manatus manatus*) and their responses to call playback. – Mar. Mamm. Sci. 34: 577-594.

Wells, R. S., Boness, D. J. & Rathbun, G. B. (1999). Behavior. In: Biology of marine mammals (Reynolds, J. E. III & Rommel, S. A., eds.). Smithsonian Institution Press, Washington, DC, p. 324–422.

Young, J.S. (2001). An investigation of captive Florida manatee (*Trichechus manatus latirostris*) behavior and social interactions. (Master's dissertation). Georgia Southern University, Statesboro, USA.

4 ARTIGO 3: TACTILE RESPONSES TO ENVIRONMENTAL ENRICHMENT IN CAPTIVE ANTILLEAN MANATEE (*Trichechus manatus manatus*)

Nota: Esta parte da dissertação, em formato de artigo, será submetido para periódico científico. Entretanto, regras usuais de formatação foram flexibilizadas para facilitar a leitura pela banca. Por exemplo, figuras e tabelas foram inseridas no corpo do texto. O resumo foi suprimido para evitar repetições com o resumo da dissertação. A numeração de linhas também foi suprimida. Este trabalho é fruto da colaboração de pesquisadores da Universidade Federal de Pernambuco e do Instituto Chico Mendes de Conservação da Biodiversidade/Centro Nacional de Pesquisa e Conservação de Mamíferos Aquáticos (ICMBio/CMA).

4.1 INTRODUCTION

Touch in aquatic mammals is classified as a communication modality, modulated by or associated with other modalities, such as visual and acoustics (Reep et al., 2002). The development of the tactile system in aquatic animals relates to environmental pressures, e.g., some species occupy waters with high turbidity resulting in poor visual acuity (Reep et al., 2002; Dudzinski et al., 2008). Social pressures also play a role in tactile communication in the marine environment. For example, marine mammals' sociability is often very high, with groups varying from a few to hundreds of individuals and classified as semi-social or social (Moore, 1956; Dudzinski, 1998). Close touch contact between group members may facilitate group coordination.

Tactile communication usually includes a complex and well-developed repertoire and is conventionally divided into agonist and affiliative interactions, and according to its reception, passive or active (Langbauer, 2000; Prescott et al., 2015). These signals are important in a diversity of contexts, from the mother-calf relationship, reproduction, self-maintenance, foraging, and navigation (Hartman, 1979; Dehnhardt et al., 1998; Bauer et al., 2018). There are also various sensorial structures, including the vibrissae complex and hairs (Reep et al., 1998). Vibrissae are innerved sensory hairs distributed along the animal's body, usually concentrated on the oral and perioral area (Peterson & Bartholomew, 1967; Marshall et al., 1998; Reep et al., 1998). Vibrissae are responsible for receiving and processing information from environmental conditions to orientation and navigation and assist in detecting low-frequency acoustic energy

(Hyvarinen, 1995; Gerstein et al., 1999; Bauer & Reep, 2018). Marine mammals possess a broad collection of tactile performances related to the species general behavior, habitat, and organization (Poole, 1985). Among the marine mammal groups that rely significantly on tactile behavior is Sirenia, the manatees and dugong group (Hartman, 1979; Bengtson, 1981; Reynolds & Odell, 1991).

West Indian manatees (*Trichechus manatus*) possess relatively poor vision and well-developed tactile systems, possibly to overcome visual limitations (Walls, 1963; Bauer et al., 2003). However, they use tactile behavior mostly for social activities (e.g., grooming and greeting, embracing, and playing). Previous reports show that they can use this system to detect other animals, movements, stationary features, currents, sound waves, and for individual identification (Hartman, 1979; Bachteler & Denhardt, 1999; Reep et al., 2002; Kikuchi et al., 2011; Bauer & Reep, 2018). Also, some studies point to the vibrissae system being analogous to the fish lateral line system (e.g., Reep et al., 2002). Additionally, much of the mother-calf bond is based on tactile interactions. For instance, the mother often lifts the calf to breathe until it assumes a proper breathing rhythm (Hartman, 1979; Wells et al., 1999; Reeves et al., 2002; Harper & Schulte, 2005).

Environmental enrichment is recognized to stimulate species-appropriate behaviors, recover natural behaviors, and avoid stereotypies caused by captivity routines (Breland & Breland, 1961; Mellen & MacPhee, 2001). We know relatively little about the use of tactile behaviors by Antillean manatees (*Trichechus manatus manatus*) in response to environmental enrichment in captivity. Thus, here we assessed captive Antillean manatees' responses to two stimuli (i.e., an infant manatee model and a floating device) to evaluate their potential to stimulate the production of tactile behaviors. Furthermore, we investigated Antillean manatees' gender's influence on specific behaviors performed in response to the infant manatee model. We focused on the "infant lifting" related behaviors because female manatees perform infant lifting towards newborn calves. We expected that captive females would try lifting the infant model more often than males. We hope our study will contribute to the understanding of tactile behavior use and evolution in Antillean manatees.

4.2 MATERIAL & METHODS

4.2.1 Animals and study site

We carried out the study at the oceanarium of the *Centro Nacional de Pesquisa e Conservação da Biodiversidade Marinha do Nordeste/Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio/CEPENE)* on Itamaracá Island, Pernambuco, Brazil. We investigated eight adult manatees in the oceanarium (four males and four females above ten years old – the age range was 10-33 yrs). The animals were kept separately in two pools according to sex. The female pool dimensions were 10 x 5 m and 4 m deep, and the male pool was composed of two pools connected with total dimensions of 8 x 5 and 4 m deep. The density of animals in the females' enclosure was 0.030 manatees/m^3. There were two other females under ten years of age housed together with the females analyzed in our study. We did not consider these two young females' responses to the stimuli to avoid age biases in the analysis. The density of animals in the males' pool was 0.025 manatees/m^3. We identified all animals individually based on their natural marks.

4.2.2 Experimental design

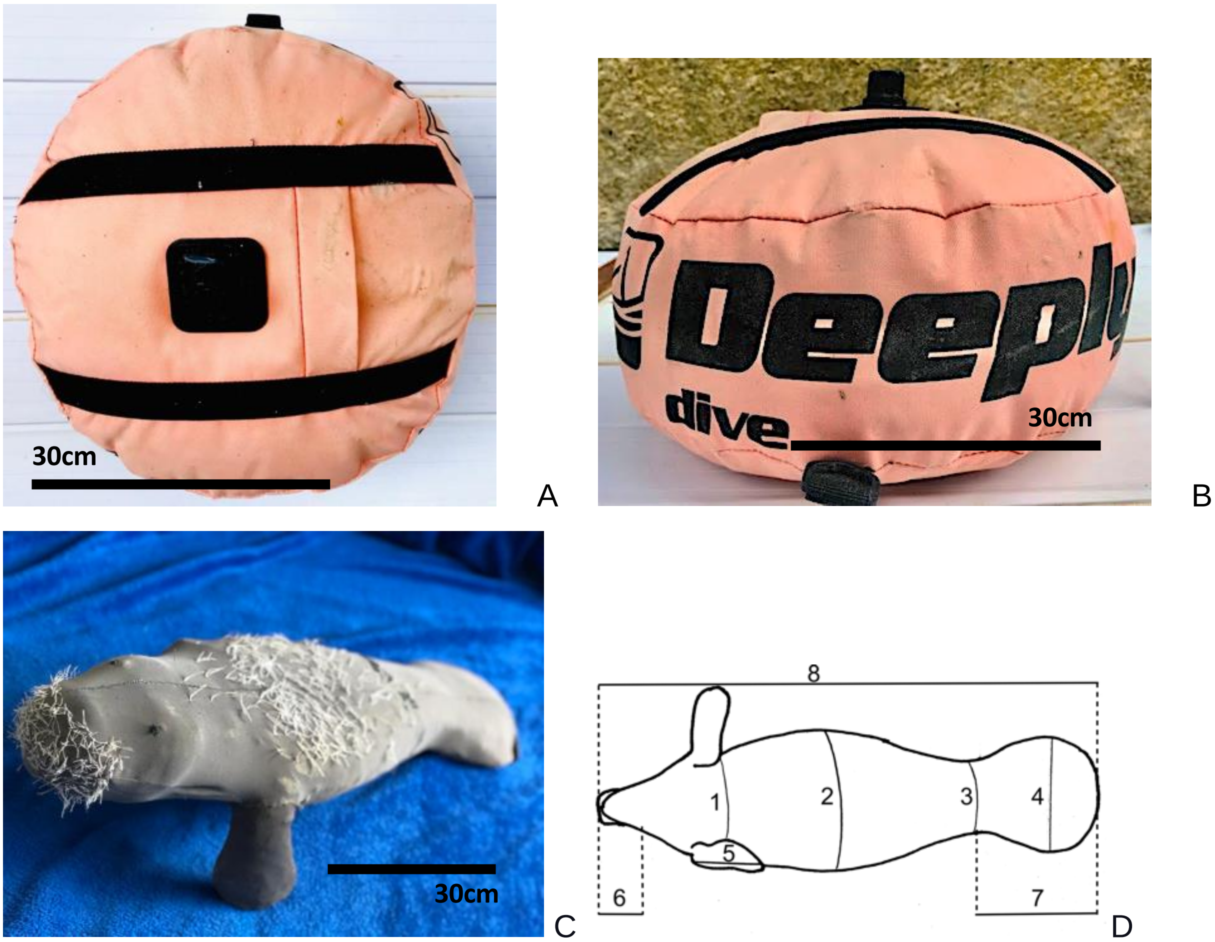
We conducted our experiments from January to February 2020, and the water visibility was similar over the experimental period. We presented two different stimuli to the animals: an ordinary floating device (i.e., an orange scuba dive buoy, Figures 9A and B) and an infant manatee model (i.e., a life-size infant made of styrofoam covered with grey lycra fabric, Figures 9C and D).

We conducted six repetitions of the presentation of the stimuli. We performed repetitions (hereafter called "experimental sessions") with at least a 48-hour interval to minimize manatees' habituation to stimuli exposure. Each experimental session lasted 15 minutes: We video-recorded the animal for five minutes before stimulus exposure, five minutes during stimulus exposure, and five minutes after stimulus exposure. We treated the preexposure time as the control period and the post-stimulus time as the follow-up period.

We recorded exploratory and social tactile behaviors performed by the Antillean manatees in the pool during the experimental sessions. We considered the exploratory and social tactile behaviors as described in Lucchini et al. (2021). Briefly, as exploratory behavior, we considered the behavior "interacting with wall-gate". We choose this behavior because it relates to the enclosure's exploration, simulating an active exploration of the environment. We also considered the exploratory behaviors directed to the stimuli during their presentation (i.e., push the stimulus with the head or snout, embrace the stimulus, interact with the cord tied to the stimulus). We considered any behavior performed by one manatee towards another as considered social.

Observations were conducted by two experienced observers (i.e., KL and RU), which contributed equally to the records. We performed an Intraclass Correlation Coefficient (ICC) to estimate inter-observer reliability, as two observers recorded behaviors. KL and RU independently scored behaviors during 3 hours of video footage of the manatees at the Center, and ICC was based on this data (Average ICC = 0.997).

Figure 9. Experimental stimuli presented to captive Antillean manatees. A/B: Floating device represented by an orange scuba dive buoy; C: Infant manatee model made of styrofoam covered with grey lycra fabric and sewing thread around the perioral area and body to simulate the vibrissae; Scale bars = 30cm; D: Infant manatee model measurements – 1 (Axillary circumference) = 28cm; 2 (Ventral circumference) = 31cm; 3 (Peduncular circumference) = 20cm; 4 (Tail width) = 26cm; 5 (Flipper length) = 23cm; 6 (Head length) = 20cm; 7 (Tail length) = 29cm; 8 (Total length) = 100cm; Approximate weight = 4kg.



Source: The author (2021).

4.2.3 Statistical analyses

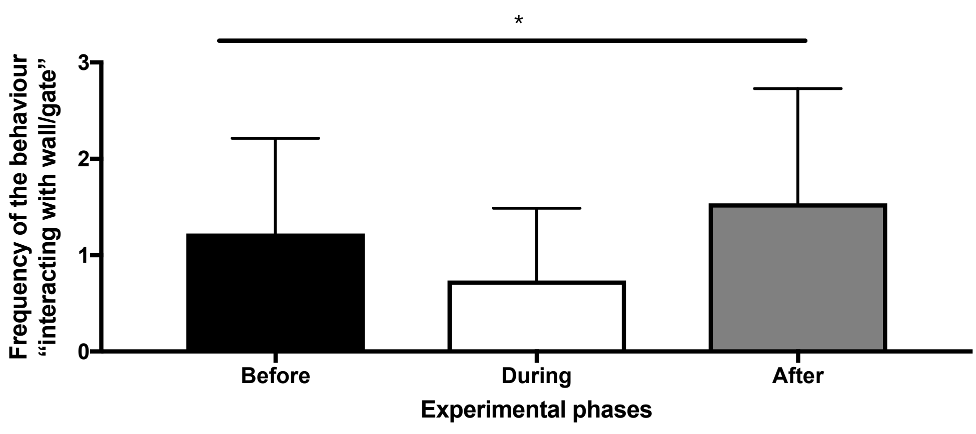
We considered exploratory and social behaviors separately in our analysis. First, we compared the frequency of the behavior "interacting with wall-gate" before, during, and after presenting the stimulus using Friedman tests. To test which stimulus type most triggered exploratory behaviors, we compared the frequency of new exploratory behaviors directed to the stimuli during their presentation using a Wilcoxon test. We then compared the frequency of social behaviors before, during, and after presenting each stimulus using Friedman's test. We also compared social behaviors between stimuli, considering the different phases of the experiment. Finally, we conducted a Chi-square test to analyze if females performed more "infant model lifting" than males. Significance was attained when $p \leq 0.05$ in all tests.

4.3 RESULTS

4.3.1 Exploratory behaviors

The frequency of the behavior "interacting with wall-gate" varied when comparing the time "before, during, and after" the infant manatee model's exposure. The lowest frequency of the behavior occurred "during" the stimulus presentation (Friedman test=6.645; p=0.0323; n=8 individuals, Figure 10). Dunn’s multiple comparisons show: Before vs. During (Rank sum difference 6.5; p=0.3125); Before vs After (Rank sum difference -3.5; p=>0.9999); During vs After (Rank sum difference -10; p=0.0373).

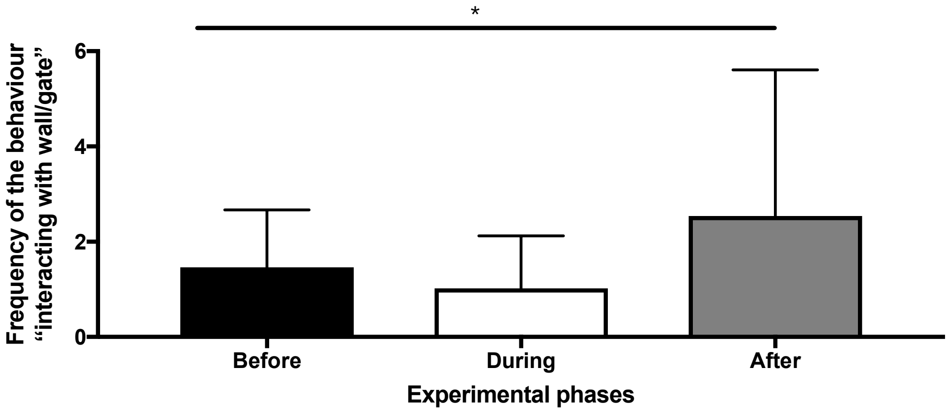
Figure 10. Frequency of occurrence of the exploratory behavior "interacting with wall-gate" when using the infant manatee model in the experimental session.



Source: The author (2021).

The frequency of the behavior "interacting with wall-gate" varied "before, during, and after" the floating device's presentation. The lowest frequency of the behavior occurred "during" the stimulus presentation (Friedman test=6.414; p=0.0368, n=8 individuals, Figure 11). Dunn’s multiple comparisons show: Before vs. During (Rank sum difference 7.5; p=0.1834); Before vs After (Rank sum difference -1.5; p=>0.9999); During vs After (Rank sum difference -9; p=0.0733).

Figure 11. Frequency of occurrence of the exploratory behavior "interacting with wall-gate" when using the floating device in the experimental session.



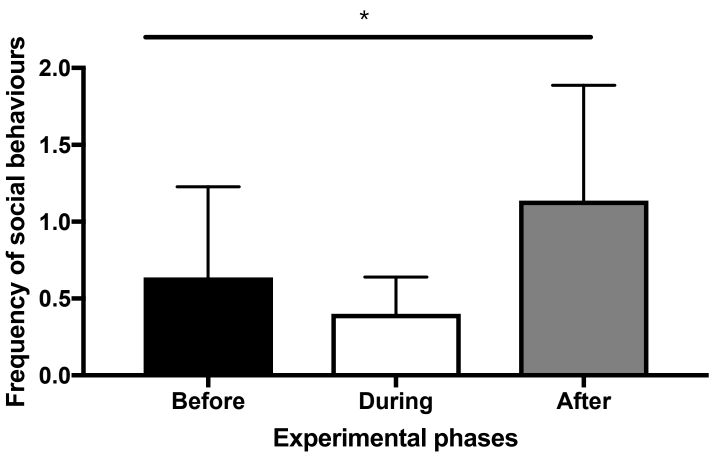
Source: The author (2021).

The infant manatee model and the floating device triggered the same amount of new exploratory behaviors towards them (Wilcoxon test: Z=-0.485; p>0.999).

4.3.2 Social behaviors

The frequency of social behaviors varied "before, during, and after" the presentation of the manatee model, with the lowest frequency of social behavior occurring during the stimulus presentation (Friedman test=7.462; p=0.0177; n=8 individuals, Figure 12). Dunn's multiple comparisons show: Before vs. During (Rank sum difference 2.5; p>0.999); Before vs. After (Rank sum difference -7, p=0.2404); During vs. After (Rank sum difference -9.5; p=0.526).

Figure 12. Frequency of occurrence of social behaviors when using the infant manatee model in the experimental session.



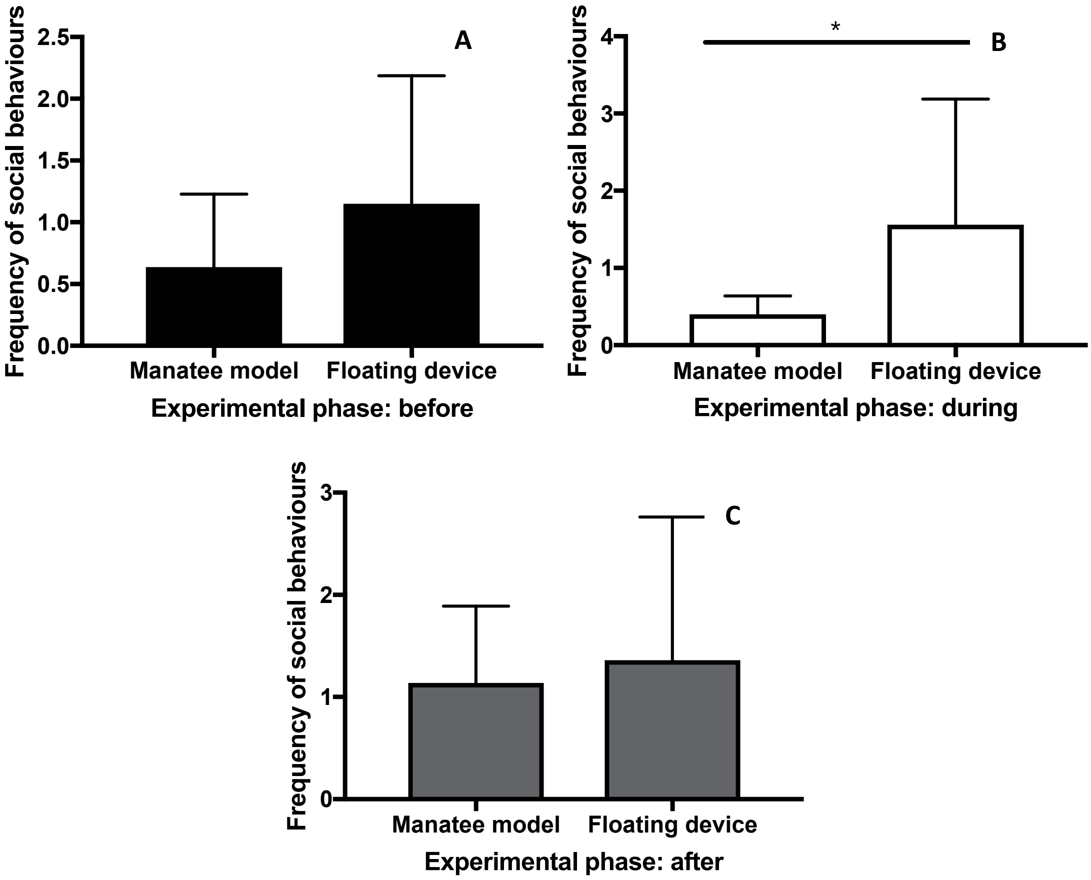
Source: The author (2021).

The frequency of the social behaviors did not vary "before, during, and after" the floating device's presentation (Friedman test=0.06667; p=0.9906; n= 8 individuals).

When comparing the manatee model and the floating device, the frequency of social behaviors did not vary before (Wilcoxon test: Z=0.15; p=1250, Figure 13a) or after (Wilcoxon test: Z=-0.1; p=0.7578, Figure 13c) stimuli presentation. Nevertheless, the frequency of social behaviors varied during stimuli presentation, with the lowest frequencies of social behaviors occurring during the manatee model presentation (Wilcoxon test: Z=-0.45; p=0.0156, Figure 13b).

The Chi-square analysis revealed that female manatees performed a parenting-related behavior of lifting the infant model significantly more frequently than males during the infant manatee model presentation experimental phase (χ^2=10.79; df=1; p<0.005).

Figure 13. Comparison of the frequencies of social behaviors "before, during, and after" stimulus presentation. Experimental session phases: A – Before; B – During; C – After.



Source: The author (2021).

4.4 DISCUSSION

Both stimuli tested as environmental enrichment stimulated tactile behaviors in the study of captive Antillean manatees. During stimuli exposure, the Antillean manatees reduced the frequency of exploratory behaviors directed at the enclosure and started performing exploratory behaviors towards the stimuli. Exploratory behaviors are known to be part of various contexts, from navigation and orientation to recognition and foraging (Hartman, 1979; Bengtson, 1981; Wells et al., 1999). Also, manatees hold low visual acuity due to their habitat water turbidity (Bauer et al., 2003). Thus, tactile exploratory behaviors play an important role in habitat and conspecific recognition (Hartman, 1979; Bengtson, 1981). The use of exploratory behaviors by animals in rehabilitation programs is important to develop natural recognition processes and natural behaviors recovery or development in the case of animals born in captivity

(Breland & Breland, 1961; Bengtson, 1981; Wells et al., 1999). The reduction of exploratory behaviors towards the enclosure and their increasing towards the stimuli show that our study individuals were interested in the stimuli, highlighting our object presentation's efficiency in stimulating natural behaviors of exploring new features/structures. Thus, we emphasize the importance of developing *ex-situ* and *in* situ behavioral studies to support rehabilitation programs and animal welfare. Considering the species' natural history and natural behaviors helps develop specific and efficient environmental enrichment practices that properly stimulate animals during their time in captivity.

The captive manatees studied reduced social behaviors towards each other during the presentation of the infant manatee model, but they increased the behaviors directed at the model. It shows that the manatees were more interested in the infant model than in the other animals in the same enclosure. The floating device did not influence social behavior frequencies. This interest in the infant manatee model could be a result of the differentiation of the stimulus silhouette. Even though the manatees hold poor visual acuity (Bauer et al., 2003), they possibly recognized the infant silhouette from the model and directed more attention and more exploratory behaviors towards it. The use of the model for parenting-related behaviors stimulation is particularly important for females, once they are responsible for their calves after giving birth (Hartman, 1979; Reynolds, 1979, 1981; Odell, 2008). Accordingly, females in rehabilitation programs should be strongly stimulated to perform parenting-related behaviors.

The parenting-related behavior of lifting the infant manatee model during its presentation could be seen as a reproduction of the natural female behavior of lifting the calf to breathe until it assumes a breathing rhythm. The study female Antillean manatees probably performed this behavior due to the mother-calf relationship, once only females are believed to support calves during early ages (Hartman, 1979; Wells et al., 1999; Reeves et al., 2002; Harper & Schulte, 2005; Odell, 2008; Bonde, 2017). Parental care in female marine mammals is more common than in males (Berta et al., 2006). In fact, marine mammal males are rarely involved in parenting (Berta et al., 2006). Marine mammal males' energetic allocation during reproduction is usually directed at the mating competition, while females allocate their energy during gestation and lactation (Mann, 2008). In the case of female sirenians, energy is also spent on infant protection and mother-infant information transfer (Berta et al., 2006; Mann, 2008; Odell, 2008). According to this information, stimulating parenting-related activities in females is advantageous to rehabilitation and release processes.

The knowledge of Antillean manatees' tactile behavioral responses to different stimuli provides a valuable tool for rehabilitating and reintroducing these animals. The captive setting ethologically deprives captive manatees, but the stimuli used in our study as environmental enrichment trigged the performance of different exploratory tactile behaviors. Such exploratory behaviors may be crucial for survival post-release in the wild because they may increase habitat perception. Using stimuli related to natural situations, such as the contact between females and infants simulated by the infant model, may help to revert stereotyped behaviors or stimulate the display of appropriate behaviors. We recommend studies about Antillean manatees' behavioral responses to stimuli combination such as an infant model and infant calls together to arouse different communication channels. Furthermore, we recommend studies on the usage of age and sex specific stimuli (based on the particular ethological patterns of animals of varying sex and age) to help manage Antillean manatees in captivity. Considering the importance of tactile communication for Antillean manatees, we recommend the stimulation of tactile behaviors as a common practice in captive centers and during rehabilitation and reintroduction programs.

4.5 REFERENCES

Bachteler, D. & Dehnhardt, D. (1999). Active touch performance in the Antillean manatee: evidence for a functional differentiation of facial tactile hairs. – Zoology (Jena) 102: 61–69.

Bauer, G. B. & Reep, R. (2018). Sirenia Sensory Systems. In Encyclopedia of Animal Cognition and Behavior. Springer, Cham.

Bauer, G. B., Colbert, D. E., Gaspard, II, J. C., Littlefield, B. & Fellner, W. (2003). Underwater visual acuity of Florida manatees (*Trichechus manatus latirostris*). – Int. J. Comp. Psychol. 16: 130–142.

Bauer, G. B., Reep, R. L. & Marshall, C. D. (2018). The tactile senses of marine mammals. – Int. J. Comp. Psychol. 31: 1-28.

Bengtson, J. L. (1981). Ecology of manatees (*Trichechus manatus*) in the St. Johns River, Florida. (Ph.D. thesis). University of Minnesota, MN, USA.

Berta A., Sumich J. L., & Kovacs K. M. (2006). *Marine mammals: evolutionary biology*, Associated Press, San Diego, CA, USA.

Bonde, R. K. (2017). Sirenian life history. In: Encyclopedia of marine mammals (pp. 859-861). Academic Press, San Diego, CA, USA.

Breland, K. & Breland, M. (1961). The misbehavior of organisms. – Am. Psychol. 16: 681-4.

Dehnhardt, G., Mauck, B. & Hyvarinen, H. (1998) Ambient temperature does not affect the tactile sensitivity of mystacial vibrissae in harbour seals. – J. Exp. Biol. 201: 3023-3029.

Dudzinski, K. M. (1998). Contact behavior and signal exchange in Atlantic spotted dolphins (*Stenella frontalis*). – Aquat Mamm. 24: 129-142.

Dudzinski, K. M., Thomas, J. A., & Gregg, J. D. (2008) Communication in marine mammals. In Encyclopedia of marine mammals. Academic Press, San Diego, CA, USA.

Gerstein, E. R., Gerstein, L., Forsythe, S. E. & Blue, J. E. (1999). The underwater audiogram of the West Indian manatee (*Trichechus manatus*). – J. Acoust. Soc. Am. 105: 3575-3583.

Harper, J. Y. & Schulte, B. A. (2005). Social interactions in captive female Florida manatees. – Zoo Biol. 24: 135–144.

Hartman, D. S. (1979). Ecology and behavior of the manatee (*Trichechus manatus*) in Florida. American Society of Mammologists, Special Publications.

Hediger, H. (1950). Wild animals in captivity. London: Butterworths. 207 p.

Hediger, H. (1969). Man and animal in the zoo. London: Routledge and Kegan Paul. 303 p.

Hyvarinen, H. (1995). Structure and function of the vibrissae of the ringed seal (*Phoca hispida* L.). In Sensory systems of aquatic mammals (ed. by R.A. Kastelein, J.A. Thomas and P.E. Nachtigall), De Spil Publishers, Woerden, The Netherlands.

Kikuchi, M., Suzuki, M., Ueda, K., Miyahara, H. & Uchida, S. (2011). The differences in behavioral responses to a net obstacle between day and night in captive manatees; does entanglement happen at night? – Fish. Sci. 77: 795.

Langbauer, W. R. Jr. (2000). Elephant communication. – Zoo Biol. 19: 425-445.

Lucchini, K., Umeed, R., Guimaraes, L., Santos, P., Sommer, I. & Bezerra, B. (2021). The role of touch in captive and semi-captive Antillean manatees *(*Trichechus manatus manatus*). – Behaviour, 1*(aop): 1-23. <https://doi.org/10.1163/1568539X-bja10069>

Mann, J. (2008). Parental behavior. In Encyclopedia of marine mammals (pp. 830-836). Academic Press, San Diego, CA, USA.

Marshall, C. D., Huth, G. D., Edmonds, V. M., Halin, D. L. & Reep, R. L. (1998). Prehensile use of perioral bristles during feeding and associated behaviors of the Florida manatee (*Trichechus manatus latirostris*). – Mar. Mamm. Sci. 14: 274–289.

Mellen, J. & Ellis, S. (1996). Animal learning and husbandry training. In: Kleiman, D., Allen, M., Thompson, K. & Lumpkin, S. (eds). Wild mammals in captivity: principles and techniques. Chicago: The University of Chicago Press. p 88–99.

Mellen, J. & MacPhee, M.S. (2001). Philosophy of environmental enrichment: past, present, and future. – Zoo Biol. 20(3): 211-226.

Moore, J. C. (1956). Observations on manatees in aggregations. – Amer Mus. Novit. 1811:1-24.

Odell, D. K. (2008). Sirenian life history. In Encyclopedia of marine mammals. Academic Press, San Diego, CA, USA, pp. 1019-1021

Peterson, S. & Bartholomew, G.A. (1967). The natural history and behavior of the California sea lion. Special Publication No. 1, The American Society of Mammalogists. Lawrence, KS.

Poole, T. B. (1985). Senses and social communication. In Social behaviour in mammals. Springer, Boston, MA.

Prescott, T. J., Mitchinson, B. & Grant, R. A. (2015). Vibrissal behavior and function. In Scholarpedia of touch. Scholarpedia, Atlantis Press, Paris, pp. 103-116.

Reep, R. L., Marshall, C. D. & Stoll, M. L. (2002). Tactile hairs on the postcranial body in Florida manatees: A mammalian lateral line? – Brain Behav, Evol. 59: 141-154.

Reep, R. L., Marshall, C. D., Stoll, M. L. & Whitaker, D. M. (1998). Distribution and innervation of facial bristles and hairs in the Florida manatee (*Trichechus manatus latirostris*). – Mar. Mamm. Sci. 14: 257-273.

Reeves, R. R., Stewart, B. S., Clapham, P. J. & Powell, J. A. (2002). National Audubon Society guide to Marine Mammals of the World. New York: National Audubon Society, USA.

Reynolds III, J. E. (1979). The semisocial manatee. – Nat. Hist. 88: 44-53.

Reynolds III, J. E. (1981). Aspects of the social behaviour and herd structure of a semi-isolated colony of West Indian manatees, *Trichechus manatus*. – Mammalia 45: 431-452.

Reynolds III, J. E. & Odell, D.E. (1991). Manatees and dugongs, facts on file**.** New York, USA.

Walls, G. L. (1963). The Vertebrate Eye and Its Adaptive Radiation. Hafner Publ. Co., New York, USA.

Wells, R.S., Boness, D.J. & Rathbun, G.B. (1999). Behavior. In J. E. Reynolds III & S. A. Rommel, eds. Biology of marine mammals. Smithsonian Institution Press, Washington, DC, USA.

5 CONCLUSÕES GERAIS E RECOMENDAÇÕES PARA O MANEJO *EX-SITU* DE PEIXES-BOI

5.1 OBJETIVOS DESTA SESSÃO

1. Sintetizar os principais resultados apresentados nesta dissertação de mestrado, evidenciando o impacto dos mesmo para os avanços no estudo da comunicação tátil de peixes-boi.
2. Sugerir medidas para o manejo *ex-situ* para promover a exposição de peixes-boi marinhos a estímulos que incentivem a produção de sinais de comunicação tátil na espécie.

5.2 SÍNTESE DOS PRINCIPAIS RESULTADOS

No capítulo 1, evidenciamos a carência de estudos voltados para comunicação tátil em mamíferos marinhos, em especial em ambiente natural. Além disso, foi possível notar a carência de informações sobre sistemas de comunicação tátil e não tátil para os membros da família Trichechidae, com exceção de *Trichechus manatus latirostris*, o peixe-boi da Flórida. Essa carência pode ser resultado da dificuldade de observação desses animais em ambiente natural. O ambiente de cativeiro, nesse sentido, vem trazendo informações sobre o uso e potenciais funções dos sinais táteis dos mamíferos aquáticos, e vem possibilitando a execução de estudos experimentais controlados.

No capítulo 2, mostramos que peixes-boi marinhos apresentam um repertório de comportamentos táteis com 17 comportamentos, distribuídos em 3 categorias funcionais: social, exploração e autocuidado. Os comportamentos táteis representam cerca de 15% do orçamento comportamental da espécie. Mostramos ainda que o método de observação influencia na detecção de comportamentos táteis em peixe-boi, sendo recomendado o método animal focal quando o objetivo é relacionado aos comportamentos de autocuidado. Além disso, destacamos a importância de um planejamento adequado para definição do método de observação a ser utilizado pelo estudo. Mostramos que comportamentos táteis não sofrem influência do tipo de recinto, porém o padrão de atividades pode variar entre semi-cativeiro e cativeiro; sexo e idade, por sua vez, influenciaram na execução de comportamentos táteis. Neste capítulo também destacamos a importância de estudos comportamentais visando o bem-estar e programas de manejo mais efetivos em ambientes de cativeiro e semi-cativeiro.

Já no capítulo 3, evidenciamos o uso de práticas de enriquecimento ambiental para o estímulo de comportamentos táteis em animais de cativeiro. Dessa forma, os objetos oferecidos se mostraram eficientes para estimular comportamentos exploratórios voltados ao objeto. Mostramos também que a silhueta/forma do estímulo pode ter influência na tomada de decisão para exploração. O modelo de infante se mostrou mais eficiente em estimular comportamentos exploratórios, comportamentos sociais entre indivíduos do recinto cedeu espaço para comportamentos exploratórios do modelo de infante. As fêmeas se aproximaram do modelo com mais afinco e realizaram mais frequentemente comportamentos relacionados a cuidado parental. Aqui também destacamos a relevância de estudos sobre respostas comportamentais e evidenciamos a necessidade do uso de práticas de enriquecimento ambiental para animais cativos ou em processos de reabilitação e reintrodução.

5.3 RECOMENDAÇÕES PARA OS ESTUDOS E O MANEJO DE PEIXES-BOI MARINHOS

A partir dessas informações acima destacadas, trazemos recomendações específicas para o aumento de estudos voltados para comunicação tátil e para um manejo efetivo de animais em cativeiro e semi-cativeiro:

1. Estudos devem ser direcionados para o esclarecimento sobre as respostas táteis dos peixes-boi marinhos a diferentes estímulos de enriquecimento ambiental (estímulos espaciais, físicos e sociais). Também recomendamos a execução de estudos para a identificação de como diferentes modalidades de comunicação se relacionam. Esses estudos podem possibilitar o desenvolvimento de métodos mais eficientes para programas de manejo, reabilitação, reintrodução e, consequentemente, as estratégias de conservação da espécie.

2. Para os peixes-boi marinhos em cativeiro e em processo de reabilitação, se torna essencial o estímulo de comportamentos táteis, tendo em vista a relevância dos mesmos no orçamento comportamental da espécie. A implementação de práticas de

enriquecimento ambiental na rotina dos centros de animais cativos e em reabilitação é importante para estimular as estruturas sensoriais e comportamentos exploratórios. O uso de fontes de estímulo diversas se faz necessário para o promover a execução de comportamentos táteis sob diferentes contextos, como cuidado parental, exploração, socialização e forrageio. Além disso, essa prática pode também vir a favorecer a reversão de comportamentos estereotipados e/ou influenciados pela rotina dos centros, visando o bem-estar e qualidade de vida dos animais cativos e em processos de reabilitação;

3. Recomendamos a observação contínua do padrão de comportamentos táteis exploratórios, visto que esses podem ser determinantes para adaptação dos animais pós-soltura e sua consequente sobrevivência em ambiente natural. Essa prática também favorece animais que permanecerão em cativeiro, uma vez que possibilita um acompanhamento das atividades executadas pelos indivíduos, podendo servir como diagnóstico de alterações comportamentais a diferentes medicações, práticas e estímulos sociais por inclusão de novos animais nos recintos. Recomendamos que o monitoramento de comportamentos táteis deve ser considerado em planos de manejo, reabilitação e reintrodução dos peixes-boi marinhos.

REFERÊNCIAS

ALLEE, W. C. **Animal Aggregations:** A Study in General Sociology. Chicago: Chicago University Press, 1931.

ALTMANN, J. Observational study of behavior: sampling methods. **Behaviour,** v. 49, p. 227-267, 1974.

ANDERSON, H. T. L. **The biology of marine mammals**. New York: Pergamon Press, 1969.

ANZOLIN, D. G.; CARVALHO, P. S. M. DE; VIANA-JR., P. C.; NORMANDE, I. C.; SOUTO, A. S. Stereotypical behaviour in captive West Indian manatee (*Trichechus manatus*). J**. Mar. Biol.l Assoc. U.K**., v. 94, p. 1133-1137, 2014.

ATTADEMO, F. L. N.; GOMES, G. L.; SILVA, F. J. L.; MODEIRA, A. B.; FREIRE, A. C. B.; LEITÃO, H. C. M. S.; LUNA, F. O. **Comportamento de peixes-bois|Guia ilustrado. Instituto Chico Mendes de Conservação da Biodiversidade**, Brasil, 2020.

AU, W. W. L. **The sonar of dolphins**. New York: Springer-Verlag, 1993.

BACHTELER, D.; DEHNHARDT, D. Active touch performance in the Antillean manatee: evidence for a functional differentiation of facial tactile hairs. **Zoology (Jena)**, v. 102, p. 61–69, 1999.

BALENSIEFER, D. C.; ATTADEMO, F. L. N.; SOUSA, G. P.; FREIRE, A. C. D. B.; DA CUNHA, F. A. G. C.; ALENCAR, A. E. B.; SILVA, F. J. L.; LUNA, F. D. O. Three decades of Antillean manatee (*Trichechus manatus manatus*) stranding along the Brazilian coast. **Trop. Conserv. Sci.**, v. 10, ID. 1940082917728375, 2017

BANKS, E. M. Behavioral research to answer questions about animal welfare. **J. Anim. Sci.,** v. 54, p. 434–455, 1982.

BARLOW, G. W. Modal action patterns. *In:* T. A. SEBEOK (ed.) **How Animals Communicate**. Bloomington: Indiana University Press, 1977.

BARROS, H. M. D. R.; MEIRELLES, A. C.; LUNA, F. O.; MARMONTEL, M.; CORDEIRO-ESTRELA, P.; SANTOS, N.; ASTÚA, D. Cranial and chromosomal geographic variation in manatees (Mammalia: Sirenia: Trichechidae) with the description of the Antillean manatee karyotype in Brazil. **J. Zoolog. Syst. Evol.**, v. 55, p. 73-87, 2017.

BAUER, G .B.; REEP, R .L.; MARSHALL, C. D. The tactile senses of marine mammals. **Int. J. Comp. Psychol.** v. 31, 2018.

BAUER, G. B.; REEP, R. Sirenia sensory systems. *In:* VONK., J; SHACKELFORD, T (eds.). **Encyclopedia of animal cognition and behavior**. Springer, Cham, 2018.

BAUER, G. B.; COLBERT, D. E.; GASPARD III, J. C.; LITTLEFIELD, B.; FELLNER, W. Underwater visual acuity of Florida manatees (*Trichechus manatus latirostris*). **Int. J. Comp. Psychol.**, v. 16, p. 130–142, 2003.

BAUER, G. B.; GASPARD III, J. C.; COLBERT, D. E.; LEACH, J. B.; STAMPER, S. A.; MANN, D.; REEP, R. Tactile discrimination of textures by Florida manatees (*Trichechus manatus latirostris*). **Mar. Mamm. Sci.**, v. 28, e456-e471, 2012.

BAUER, G. B.; REEP, R. L.; MARSHALL, C. D. The tactile senses of marine mammals. **Int. J. Comp. Psychol.** v. 31, p. 1–28, 2018.

BEATTY, B. L.; VITKOVSKI, T.; LAMBERT, O.; MACRINI, T. E. Osteological associations with unique tooth development in manatees (Trichechidae, Sirenia): a detailed look at modern *Trichechus* and a review of the fossil record. **Anat. Rec.**, v. 295, p. 1504-1512, 2012.

BELL, B. Translocation of fluttering shearwaters: developing a method to re-establish seabird populations. *In*: SERENA, M. (ed.) **Reintroduction Biology of Australian and New Zealand Fauna.** Chipping Norton: Surrey Beatty & Sons, p. 143-148, 1994.

BENGTSON, J. L. **Ecology of manatees (*Trichechus manatus*) in the St. Johns River, Florida.** Ph.D. thesis - University of Minnesota, MN, USA, 1981.

BENGTSON, J. L.; FITZGERALD, S. M. Potential role of vocalizations in West Indian manatees. **J. Mammal.**, v. 66, p. 816-819, 1985.

BERNSTEIN, I. S. An empirical comparison of focal and ad libitum scoring with commentary on instantaneous scans, all occurrence and one-zero techniques. **Anim. Behav**., v. 42, p. 721-728, 1991.

BERTA, A.; SUMICH, J. L.; KOVACS, K. M. **Marine mammals: evolutionary biology**, San Diego, CA: Associated Press, 2006.

BERTA, A.; EKDALE, E. G.; ZELLMER, N. T.; DEMÉRÉ, T. A.; KIENLE, S. S.; SMALLCOMB, M. Eye, nose, hair, and throat: external anatomy of the head of a neonate gray whale (Cetacea, Mysticeti, Eschrichtiidae). **Anat. Rec.**, v. 298, p. 648-659, 2015.

BEST, R. C.; TEIXEIRA, D. M. Notas sobre a distribuição e status aparente dos peixes-bois (Mammalia, Sirenia) nas costas amapaenses brasileiras. **Bol. FBCN, Rio de Janeiro,** v. 17, p. 41-47, 1982.

BLOMQVIST, C.; MELLO, I.; AMUNDIN, M. An acoustic play-fight signal in bottlenose dolphins *(Tursiops truncatus)* in human care. **Aquat. Mamm.** v. 31, p. 187-194, 2005.

BONDE, R. K. Sirenian life history. *In*: WÜRSIG, B; THEWISSEN, J. G. M.; KOVACS, K. (eds.) **Encyclopedia of marine mammals.** Academic Press, San Diego, CA, USA, 2017. p. 859-861.

BREATHNACH, A. S. The cetacean central nervous system. **Biol. Rev.,** v. 35, p. 187-230, 1960.

BRELAND, K.; BRELAND, M. The misbehavior of organisms. **Am. Psychol.**, v. 16, p. 681-684, 1961.

CAFFERY, K. A. **Tactile behavior in a group of captive rough-toothed dolphins as a function of opportunities to play with objects**. PhD dissertation - University of Southern Mississippi, MS, USA, 2013.

CARLSTEAD, K. Determining the causes of stereotypic behaviors in zoo carnivores: Toward appropriate enrichment strategies. *In*: SHEPHERDSON, D. J.; MELLEN, J. D.; HUTCHINS, M. (eds.) **Second nature: Environmental enrichment for captive animals.** Washington, DC: Smithsonian Institution Press, 1998. p. 172-183.

COSTA, A. F. **Distribuição espacial e status do peixe-boi marinho, *Trichechus manatus manatus,* (Sirenia: Trichechidae) no litoral leste do Estado do Ceará.** M.Sc. dissertation - Universidade Federal do Ceará, Fortaleza, 2006.

COURBIS, S. S.; WORTHY, G. A. J. Opportunistic carnivory by Florida manatees (*Trichechus manatus latirostris*). **Aquat. Mamm.**, v. 29, p. 104-107, 2003.

CZECH-DAMAL, N. U.; LIEBSCHNER, A.; MIERSCH, L.; KLAUER, G.; HANKE, F. D.; MARSHALL, C.; DEHNHARDT, G.; HANKE, W. Electroreception in the Guiana dolphin (*Sotalia guianensis*). **Proc. Royal Soc. B**., v. 279, p. 663-668, 2012.

DA SILVA, V. M. F. Os mamíferos aquáticos da Amazônia, sua organização social e comportamento. In: **Anais de Etologia [...]**, v. 14. Uberlândia, Brasil, p. 263-273, 1996.

DEHNHARDT, G. Tactile size discrimination by a California sea lion (*Zalophus californianus*) using its mystacial vibrissae. **J. Comp. Physiol.**, v. 175, p. 791-800, 1994.

DEHNHARDT, G. Sensory systems. *In:* HOELZEL, A. R. (ed.) **Marine mammal biology: an evolutionary approach.** Oxford: Blackwell, 2002. p. 116-141.

DEHNHARDT, G.; KAMINSKI, A. Sensitivity of the mystacial vibrissae of Harbour Seals (*Phoca vitulina*) for size differences of actively touched objects. **J. Exp. Biol.**, v. 198, p. 2317-2323, 1995.

DEHNHARDT, G.; MAUCK, B. Mechanoreception in secondarily aquatic vertebrates. *In*: THEWISSEN, J.G.M; NUMMELA, S. (eds.) **Sensory evolution on the threshold: adaptations in secondarily aquatic vertebrates**. , 2008. p. 295-314.

DEHNHARDT, G.; MAUCK, B.; HYVARINEN, H. Ambient temperature does not affect the tactile sensitivity of mystacial vibrissae in harbour seals. **J. Exp. Biol.**, v. 201, p. 3023-3029, 1998.

DEHNHARDT, G.; MAUCK, B.; HANKE, W.; BLECKMANN, H. Hydrodynamic trail-following in harbor seals (*Phoca vitulina*). **Science**, v. 293, p. 102-104, 2001.

DELFOUR, F. Object manipulation and play behavior in bottlenose dolphins (*Tursiops truncatus*) under human care. **Int. J. Comp. Psychol.**, v. 30, 2017.

DOMNING, D. P. Evolution of manatees: a speculative history. **J. Paleontol.**, v.56, p. 599-619, 1982.

DOMNING, D. P.; HAYEK, L. A. C. Interspecific and intraspecific morphological variation in manatees (Sirenia: *Trichechus*). **Mar. Mamm. Sci.**, v. 2, p. 87-144, 1986.

DRAKE, S. E.; CRISH, S. D.; GEORGE, J. C.; STIMMELMAYR, R.; THEWISSEN, J. G. M. Sensory hairs in the bowhead whale, *Balaena mysticetus* (Cetacea, Mammalia). **Anat. Rec**., v. 298, p. 1327-1335, 2015

DUDZINSKI, K. M. Contact behavior and signal exchange among Atlantic spotted dolphins (*Stenella frontalis*). **Aquat. Mamm,,** v. 24, p. 129-142, 1998.

DUDZINSKI, K. M.; THOMAS, J. A.; GREGG, J. D. Communication in marine mammals. *In:* PERRIN, W. F.; WÜRSIG, B.; THEWISSEN, J. G. M. (eds.) **Encyclopedia of marine mammals**. San Diego, CA: Academic Press, 2008. p. 260-269.

DURRANT, B. S. Reproduction in mammals: captive perspectives. *In:* GIBBONS Jr., E. F.; DURRANT, B. S.; DEMAREST, J. (eds.) **Conservation of Endangered Species in Captivity.** Albany, New York: State University of New York Press, 1995.

FAY, F. H. Ecology and biology of the Pacific walrus, *Odobenus rosmarus divergens.* Illiger. **N. Am. Fauna**, 74, p. 1-279, 1982.

FLINT, M.; BONDE, R. K. Assessing welfare of individual sirenians in the wild and in captivity. *In*: BUTTERWORTH, A. (ed.) **Marine Mammal Welfare. Animal Welfare**, vol 17. Springer, Cham, 2017.

FRANK, L. K. Tactile communication. **ET Cetera,** v. 16, p. 31-79, 1958.

GARCIA-RODRIGUEZ, A. I.; BOWEN, B. W.; DOMNING, D;, MIGNUCCI, A. A.; MARMONTEL, M.; MONTOYA, R. A.; MORALES-VELA, B.; RUDIN, M.; BONDE, R. K.; MC-GUIRE, P. M. Phylogeography of the West Indian manatee (*Trichechus manatus*): How many populations and how many taxa? **Mol. Ecol.,** v. 7, p. 1137-1149, 1998.

GASPARD, J. C.; BAUER, G. B.; REEP, R. L.; DZIUK, K.; READ, L.; MANN, D. A. Detection of hydrodynamic stimuli by the Florida manatee (*Trichechus manatus latirostris*). **J. Comp. Psychol.**, v. 199, p. 441-450, 2013.

GERSTEIN, E. R.; GERSTEIN, L.; FORSYTHE, S. E.; BLUE, J. E. The underwater audiogram of the West Indian manatee (*Trichechus manatus*). **J. Acoust. Soc. Am.**, v. 105, p. 3575-3583, 1999.

GLÄSER, N.; WIESKOTTEN, S.; OTTER, C.; DEHNHARDT, G.; HANKE, W. Hydrodynamic trail following in a California sea lion (*Zalophus californianus*). **J. Comp. Physiol.,** v. 197, p. 141–151, 2011

GOMES, F. F. A.; VERGARA-PARENTE, J. E.; FERRARI, S. F. Behavior patterns in captive manatees (*Trichechus manatus manatus*) at Itamaracá Island, Brazil. **Aquat. Mamm.,** v. 34, p. 269–276, 2008.

GOSS-CUSTARD, J. D.; SUTHERLAND, W. J. Individual behaviour, populations and conservation. *In*: KREBS, J. R.; DAVIES, N. B. (eds.) **Behavioural Ecology.** Oxford: Blackwells, 1997. p. 373-395.

HARPER, J. Y.; SCHULTE, B. A. Social interactions in captive female Florida manatees. **Zoo Biol.**, v. 24, p. 135–144, 2005.

HARRISON, S.; STAHL, A.; DOARK, D. Spatial models and spotted owls: exploring some biological issues behind recent events. **Conserv. Biol**., v. 7, p.950-953, 1993.

HARTMAN, D. S. **Behavior and ecology of the Florida manatee, *Trichechus manatus latirostris* (Harlan), at Crystal River, Citrus County.** Ph.D. dissertation - Cornell University, Ithaca, NY, 1971

HARTMAN, D. S. **Ecology and behavior of the manatee (*Trichechus manatus*) in Florida.** American Society of Mammologists, Special Publications, 1979.

HATT, R. A manatee collected by the American Museum Congo Expedition, with observations on the recent manatees. **Bull. Am. Mus. Nat. Hist**., v. 66, p. 533-566, 1934.

HEDIGER, H. **Wild animals in captivity**. London: Butterworths, 1950. 207 p.

HEDIGER, H. **Man and animal in the zoo.** London: Routledge and Kegan Paul, 1969. 303 p.

HENAUT, Y.; LOPEZ, S. P. B.; MACHKOUR-M'RABET, S.; MORALES-VELA, B.; WINTERTON, P.; DELFOUR, F. Activities and social interactions in captive Antillean manatees in Mexico. **Mammalia**, v. 74, p.141-146, 2010.

HERMAN, L. M.; PEACOCK, M. F.; YUNKER, M. P.; MADSEN, C. J. Bottlenosed dolphin: double-slit pupil yields equivalent aerial and underwater diurnal acuity. **Science**, v. 189, p. 650–652, 1975.

HILL, H.; RAMIREZ, D. Adults play but not like their young: The frequency and types of play by belugas (*Delphinapterus leucas*) in human care. **Anim. Cogn**., v. 1, p. 166-185, 2014

HILL, H. M.; ALVAREZ, C. J.; DIETRICH, S.; LACY, K. Preliminary findings in beluga (*Delphinapterus leucas*) tactile interactions. **Aquat. Mamm.**, v. 42, 2016. Available at: <https://aquila.usm.edu/dissertations/507>.

HUSAR, S. L. The West Indian manatee (*Trichechus manatus*). United States Fish and Wildlife Service, Wildl. **Res. Rept**., v. 7, p. 1-22, 1977.

HYVARINEN, H. Structure and function of the vibrissae of the ringed seal (*Phoca hispida* L.). *In:* KASTELEIN, R. A.; THOMAS, J. A.; NACHTIGALL, P. E. (eds.) **Sensory systems of aquatic mammals**. Woerden, The Netherlands: De Spil Publishers, 1995.

IOC-UNESCO. **Global Ocean Science Report - The current status of ocean science around the world**. L. Valdés et al. (eds.), Paris, UNESCO Publishing, 2017.

JASSO DEL TORO, C.; NEKARIS, K.AI. Affiliative behaviors. *In:* Vonk, J.; Shackelford, T. (eds.) **Encyclopedia of animal cognition and behavior**. Springer, Cham, 2019.

JIANG, Y.; LÜCK, M.; PARSONS, E. C. M. Public awareness, education, and marine mammals in captivity. **Tour. Rev.**, v. 11, p. 237-249, 2007.

JONES, L. A. Tactile communication systems: optimizing the display of information. **Prog. Brain Res**., v. 192, p. 113-128, 2011.

KASTELEIN, R. A.; STEVENS, S.; MOSTERD, P. The tactile sensitivity of the mystacial vibrissae of a Pacific walrus (*Odobenus rosmarus divergens).* Part 2: Masking. **Aquat. Mamm**, v. 16, p. 78-87, 1990.

KENDALL, S.; AHUE, C.; OROZCO, D. L.; PENA, L. H. Conservación y monitoreo de los manatíes en los humedales de Tarapoto. *In:* TRUJILLO, F.; DUQUE, S. (eds.) **Los humedales de Tarapoto. Serie Humedales de la Amazonia y la Orinoquia**. F. Omacha, Corpoamazonía: Universidad Nacional de Colombia, 2014.

KIKUCHI, M.; SUZUKI, M.; UEDA, K.; MIYAHARA, H.; UCHIDA, S. The differences in behavioral responses to a net obstacle between day and night in captive manatees; does entanglement happen at night? **Fish. Sci**., v. 77, p. 795, 2011.

KLEINSCHMIDT, T.; CZELUSNIAK, J.; GOODMAN, M.; BRAUNITZER, G. Paenungulata: a comparison of the hemoglobin sequences from elephant, hyrax, and manatee. **Mol. Biol. Evol**., v. 3, p. 427-435, 1986.

KOELSCH, J. K. **The seasonal occurrence and ecology of Florida manatees (*Trichechus manatus latirostris*) in coastal waters near Sarasota, Florida.** M.Sc. dissertation – University of South Florida, Sarasota, FL, USA, 1997.

KOLCHIN, S. P.; BEL'KOVICH, M. Tactile sensitivity in *Delphins delphis.* **Zool. Zhurnal,** v. 52, p. 620–622, 1973.

KRASNOVA, V. V.; BEL'KOVICH, V. M.; CHERNETSKII, A. D. Formation of behavior in the White Sea beluga calf, *Delphinapterus leucas*, during early postnatal ontogenesis. **Russ. J. Mar. Biol.**, v. 35, p. 53-59, 2009.

LADYGINA, T. F.; POPOV, V. V.; SUPIN, A. Topical organization of somatic projections to the cerebral cortex of the seal *Callorhinus ursius*. **Neurophysiology**, v. 17, p. 344-351, 1985.

LANGBAUER, W. R. Jr. Elephant communication. **Zoo Biol**., v. 19, p. 425-445, 2000.

LAYNE, J. N.; CALDWELL, D. K. Behavior of the Amazon dolphin, *Inia geoffrensis* (Blainville) in captivity. **Zool. Sci. Contrib. N. Y. Zool. Soc.,** v. 49, p. 81-108, 1964.

LEFEBVRE, L.W.; MARMONTEL, M.; REID, J.P.; RATHBUN, G.B.; DOMNING, D.P. Status and biogeography of the West Indian manatee, In: C. A. WOODS, C. A.; SERGILE, F. E. (eds.) **Biogeography of the West Indies: patterns and perspectives**. CRC Press, 2001.

LEHNER, P.N. Sampling methods in behavior research. **Poult. Sci.**, v. 71, p. 643-649, 1992.

LENDE, R. A.; WELKER, W. I. An unusual sensory area in the cerebral neocortex of the bottlenose dolphin, *Tursiops truncatus*. **Brain Res**., v. 45, p. 555–560, 1972.

LILEY, N. R. Chemical communication in fish. **Can. J. Fish. Aquat. Sci**., v. 39, p. 22-35, 1982.

LIMA, R. P. **Peixe-boi marinho (*Trichechus manatus*): Distribuição, status de conservação e aspectos tradicionais ao longo do litoral nordeste do Brasil**. Meio Ambiente em Debate Series, v. 30, Brasília: Ed. IBAMA, 1999.

LING, J. K. The skin and hair of the southern elephant seal, *Mirounga leonina* (Linn.) I. The facial vibrissae. **Aust. J. Zool**., v. 14, p. 855-866, 1966.

LING, J. K. Vibrissa follicles of the Ross seal. **British Antarctica Survey B**, v. 27, p. 19–24, 1972.

LING, J. K. Vibrissae of marine mammals. *In:* HARRISON, R. (ed**.) Functional anatomy of marine mammals.** vol. 3**.** New York, NY: Academic Press, 1977.

LUCCHINI, K.; UMEED, R.; GUIMARAES, L.; SANTOS, P.; SOMMER, I.; BEZERRA, B. The role of touch in captive and semi-captive Antillean manatees *(*Trichechus manatus manatus*).* **Behaviour**, v. 1 (aop), p. 1-23, 2021. Available at: <https://doi.org/10.1163/1568539X-bja10069>

MANN, J. Parental behavior. *In:* **Encyclopedia of marine mammals**. San Diego, CA: Academic Press, 2008. p. 830-836.

MARLER, P ; HAMILTON, W.J. III. **Mechanisms of animal behavior**. New York, NY: Wiley, 1966.

MARSHALL, C. D. Morphology of the bearded seal (*Erignathus barbatus*) muscular–vibrissal complex: A functional model for phocid subambient pressure generation. **Anat. Rec**., v. 299, p. 1043-1053, 2016.

MARSHALL, C. D.; HUTH, G. D.; EDMONDS, V. M.; HALIN, D. L.; REEP, R. L. Prehensile use of perioral bristles during feeding and associated behaviors of the Florida manatee (*Trichechus manatus latirostris*). **Mar. Mamm. Sci**., v. 14, p. 274–289, 1998.

MARSHALL, C. D.; MAEDA, H.; IWATA, M.; FURUTA, M.; ASANO, S.; ROSAS, F.; REEP, R. L. Orofacial morphology and feeding behaviour of the dugong, Amazonian, West African and Antillean manatees (Mammalia: Sirenia): functional morphology of the muscular-vibrissal complex. **J. Zool.**, v. 259, p. 245-260, 2003.

MARSHALL, C. D.; ROZAS, K., KOT, B.; GILL, V.A. Innervation patterns of sea otter (*Enhydra lutris*) mystacial follicle-sinus complexes. **Front. Neuroanat**., v 8, p. 121, 2014.

MASS, A. M.; YA SUPIN, A. Adaptive features of aquatic mammals' eye. **Anat. Rec.,** v. 290, p. 701–715, 2007.

MATTHEWS, D. Polar Bear. San Francisco, CA: Chronicle Books, 1993.

MAUCK, B.; EYSEL, U.; DEHNHARDT, G. Selective heating of vibrissal follicles in seals (*Phoca vitulina*) and dolphins (*Sotalia fluviatilis guianensis*). **J.Exp. Biol**., v. 203, p. 2125-2131, 2000.

MCLAIN, D. K.; MOULTON, M P.; REDFEARN, T. P. Sexual selection and the risk of extinction of introduced birds on oceanic islands. **Oikos**, v. 74, p. 27-34, 1995.

MELLEN, J.; ELLIS, S. Animal learning and husbandry training. *In:* KLEIMAN, D.; ALLEN, M.; THOMPSON, K.; LUMPKIN, S. (eds). **Wild mammals in captivity: principles and techniques.** Chicago: The University of Chicago Press, 1996. p. 88–99.

MELLEN, J.; MACPHEE, M. S. Philosophy of environmental enrichment: past, present, and future. **Zoo Biol**., v. 20, p. 211-226, 2001.

MERCADILLO-ELGUERO, M. I.; CASTELBLANCO-MARTÍNEZ, D. N.; PADILLA-SALDÍVAR, J. A. Behavioral patterns of a manatee in semi-captivity: Implication for its adaptation to the wild. **JMATE**, v. 7, p. 31–41, 2014.

MERCADO III, E. Tubercles: What sense is there? **Aquat. Mamm**., v. 40, p. 95-103, 2014.

MERCADO III, E.; DELONG, C. M. Experiments are the key to understanding socially acquired knowledge in cetaceans. **Behav. Brain Sci**., v. 24, p. 345, 2001.

MILNE, A. O. **Active touch sensing in pinnipeds**. Ph.D. dissertation - Manchester Metropolitan University, Manchester, UK, 2019.

MILNE, A. O.; SMITH, C.; ORTON, L. D.; SULLIVAN, M. S.; GRANT, R. A. Pinnipeds orient and control their whiskers: a study on Pacific walrus, California sea lion and Harbor seal. **J. Comp. Physiol**., v. 206, p. 441-451, 2020.

MOORE, J. C. The status of the manatee in the Everglades National Park, with notes on its natural history. **J. Mammal**, v. 32, p. 22-36, 1951.

MOORE, J. C. Observations on manatees in aggregations. **Amer Mus. Novit**., v. 1811, p. 1-24, 1956.

NAKAI, J.; SHIDA, T. Sinus hairs of the sei-whale (*Balaenoptera borealis*). **Scientific Reports of the Whales Research Institute, Tokyo**, v. 1, p. 41-47. 1948.

NISHIWAKI, M.; MARSH, H. *Dugong dugon* (Müller 1776). *In:* RIDGWAY, H.; HARRISON, R., (eds.) **Handbook of Marine Mammals**. London: Academic Press, 1985.

O'SHEA, T. J.; REEP, R. L. Encephalization quotients and life-history traits in the Sirenia. **J. Mammal**., v. 71, p. 534-543, 1990.

ODELL, D. K. Sirenian life history. *In:* **Encyclopedia of marine mammals.** San Diego, CA, USA: Acedmic Press, 2008. p.1019-1021.

OLIVERA-GÓMEZ, L. D.; MELLINK, E. Distribution of the Antillean manatee (*Trichechus manatus manatus*) as a function of habitat characteristics, in Bahía de Chetumal, Mexico. **Biol. Conserv**., v. 121, p. 127-133, 2005.

PALMER, E.; WEDDELL, G. The relationship between structure, innervation and function of the skin of the bottlenose dolphin (*Tursiops truncatus*). **J. Zool.,** v. 143, p. 553–568, 1964.

PALUDO, D. **Estudos sobre ecologia e conservação do peixe-boi marinho (*Trichechus manatus manatus)* no Nordeste do Brasil.** Brasília: Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis, 1998.

PAUSE, K. C. **Conservation genetics of the Florida manatee, *Trichechus manatus latirostris*.** Ph.D. dissertation - University of Florida, USA, 2007.

PETERSON, S.; BARTHOLOMEW, G. A. The natural history and behavior of the California sea lion. **Special Publication No. 1, The American Society of Mammalogists**. Lawrence, KS, 1967.

POOLE, J. H.; GRANLI, P. Signals, gestures, and behavior of African elephants. *In:* MOSS, C. J.; CROZE, H. J.; LEE, P. C. (eds.) **The Amboseli elephants: A long-term perspective on a long-lived**. Chicago: University of Chicago Press, 2011. p. 109-124.

POOLE, T. B. Senses and Social Communication. *In:* **Social Behaviour in Mammals**. Boston, MA: Springer, 1985.

PRESCOTT, T. J.; MITCHINSON, B.; GRANT, R. A. Vibrissal behavior and function. I*n:* **Scholarpedia of touch**. Scholarpedia, Atlantis Press, Paris, 2015. p. 103-116.

PURVES, D.; AUGUSTINE, G. J.; FITZPATRICK, D.; KATZ, L. C.; LAMANTIA, A-S.; MCNAMARA, J. O.; WILLIAMS, S. M. **Neuroscience.** Sunderland, MA: Sinauer Associates, Inc., 2001.

RAMIREZ-JIMÉNEZ, H. H.; OLIVERA-GÓMEZ, L. D.; CUEVA, H. D. L. Habitat use by the Antillean manatee (*Trichechus manatus*) during an extreme dry season in an urban lake in Tabasco, Mexico. **Therya**, v. 8, p. 19-26, 2017.

REEB, D.; BEST, P. B.; KIDSON S. H. Structure of the integument of southern right whales, *Eubalaena australis*. **Anat. Rec.**, v. 290, p. 596-613, 2007.

REEP, R. L.; BONDE, R. K. **The Florida manatee: biology and conservation.** Gainesville: University Press of Florida, 2006.

REEP, R. L.; GASPARD, J. C. III; SARKO, D.; RICE, F. L.; MANN, D. A.; BAUER, G. B. Manatee vibrissae: evidence for a "lateral line" function. **Ann. N. Y. Acad. Sci**., v. 1225, p. 101-109. 2011.

REEP, R. L.; MARSHALL, C. D.; STOLL, M. L. Tactile hairs on the postcranial body in Florida manatees: A mammalian lateral line? **Brain Behav, Evol**., v. 59, p. 141-154, 2002.

REEP, R. L.; MARSHALL, C. D.; STOLL, M. L.; WHITAKER, D. M. Distribution and innervation of facial bristles and hairs in the Florida manatee (*Trichechus manatus latirostris*). **Mar. Mamm. Sci**., v. 14, p. 257-273, 1998.

REEVES, R. R.; STEWART, B. S.; CLAPHAM, P. J.; POWELL, J. A**. National Audubon Society guide to Marine Mammals of the World.** New York: National Audubon Society, USA, 2002.

REIDENBERG, J. S. Anatomical adaptations of aquatic mammals. **Anat. Rec**., v. 290, p. 507-513, 2007.

REYNOLDS III, J. E. The semisocial manatee. **Nat. Hist**., v. 88, p. 44-53, 1979.

REYNOLDS III, J. E. Aspects of the social behaviour and herd structure of a semi-isolated colony of West Indian manatees, *Trichechus manatus*. **Mammalia**, v. 45, p. 431-452, 1981.

REYNOLDS III, J. E.; ODELL, D. E. **Manatees and dugongs, facts on file.** New York, USA, 1991.

REYNOLDS III, J. E.; ROMMEL, R. **Biology of Marine Mammals**. Washington, DC: Smithsonian Institution Press, 1999.

REYNOLDS III, J. E.; ROMMEL, S. A. Structure and function of the gastrointestinal tract of the Florida manatee, *Trichechus manatus*. **Anat. Rec.,** v. 245, p. 539-558, 1996.

REYNOLDS III, J. E.; POWELL, J. A.; TAYLOR, C. R. Manatees: *Trichechus manatus, T. senegalensis*, and *T. inunguis*. *In:* **Encyclopedia of marine mammals**. San Diego, CA: Academic Press, USA, 2008.

REYNOLDS III, J. E.; POWELL, J. A.; KEITH DIAGNE, L. W.; BARTON, S. L.; SCOLARDI, K. M. Manatees. *In:* WÜRSIG, B; THEWISSEN, J. G. M.; KOVACS, K. (eds.) **Encyclopedia of marine Mammals.** San Diego, CA: Academic Press, 2017.

RICHARDSON, W. J.; GREENE, C. R.; MALME, C. I.; THOMSON, D. H. (eds.) **Marine Mammals and Noise.** New York: Academic Press, 1995.

RIDGWAY, S. H.; CARDER, D. A. Tactile sensitivity, somatosensory responses, skin vibrations, and the skin surface ridges of the bottle-nose dolphin, *Tursiops truncatus*. *In:* **Sensory abilities of cetaceans**. Springer, Boston, MA, 1990.

RIEDMAN, M. L.; ESTES, J. A. The sea otter (*Enhydra lutris*): Behavior, ecology, and natural history. **US Fish Wildlife Serv., Biol. Rep**., v. 90, p. 126, 1990.

RONALD, K.; SELLEY, L. J.; AMOROSO, E. C**. Biological Synopsis of the Manatee.** Faculdade de Ciências Biológicas, Universidade de Guelf, Ontário, 1978.

ROSAS, F. C. W.; PIMENTEL, T. L. Order Sirenia (Manatees, Dugongs, Sea cows). *In:* FOWLER, M. E.; CUBAS, Z. S. (eds.) **Biology, medicine, and surgery of South American wild animals. Iowa:** Blackwell Publishing, 2001.

RUBY, D. E.; NIBLICK, H. A. A behavioral inventory of the desert tortoise: development of an ethogram. **Herpetol. Monogr**., v. 8, p.88-102, 1994.

SAKAI, M.; HISHII, T.; TAKEDA, S.; KOHSHIMA, S. Flipper rubbing behaviors in wild bottlenose dolphins (*Tursiops aduncus*). **Mar. Mammal Sci**., v. 22, p. 966- 978, 2006.

SARKO, D. K.; JOHNSON, J. I.; SWITZER III, R. C.; WELKER, W. I.; REEP, R. L. Somatosensory nuclei of the manatee brainstem and thalamus. **Anat. Rec**., v. 290, p. 1138-1165, 2007a.

SARKO, D. K.; REEP, R. L.; MAZURKIEWICZ, J. E.; RICE, F. L. Adaptations in the structure and innervation of follicle-sinus complexes to an aquatic environment as seen in the Florida manatee (*Trichechus manatus latirostris*). **J. Comp. Neurol.,** v. 504, p. 217-237, 2007b.

SCHULTE, B. A. Social structure and helping behavior in captive elephants. **Zoo Biol**., v. 19, p. 447–60, 2000.

SCOTT, J. P. **Animal Behavior**. Chicago: University of Chicago Press, 1958.

SELF-SULLIVAN, C; MIGNUCCI-GIANNONI, A. *Trichechus manatus* ssp. *manatus*. **The IUCN Red List of Threatened Species 2008**, e.T22105A9359161, 2008. Available at: <http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T22105A9359161.en>.

SILVA Jr., J. M. D. **Ecologia comportamental do golfinho-rotador (*Stenella longirostris*) em Fernando de Noronha.** M.Sc. thesis - Universidade Federal de Pernambuco, 2005.

SILVA, F. J. L. **Manual de métodos de estudo de comportamento de cetáceos**. Natal: Offset Editora, 2014.

SILVA, K. G.; PALUDO, D.; OLIVEIRA, E. M. A.; LIMA, R. P.; SOAVINSKI, R. J. Distribuição e ocorrência do peixe-boi marinho (*Trichechus manatus*) no estuário do rio Mamanguape, Paraíba – Brasil. **Periódico Peixe-boi/ IBAMA – FMM,** v. 1, p. 6-18, 1992.

SILVA, K. G.; PALUDO, D.; OLIVEIRA, E. M. A.; LIMA, R. P.; SOAVINSKI, R. J. Distribuição e ocorrência do peixe-boi marinho (*Trichechus manatus*) no estuário do rio Mamanguape, Paraíba, Brasil. **Nat Resources**, v. 1, p. 5-14, 2011.

SIMPSON, J. G.; GARDNER, M. B. (Comparative microscopic anatomy of selected marine mammals. *In:* RIDGWAY, H. (ed.) **Mammals of the sea. Biology and Medicine.** Springfield, IL: C.C. Thomas, 1972.

SJARE, B.; STIRLING, I. The breeding behavior of Atlantic walruses, *Odobenus rosmarus rosmarus*, in the Canadian High Arctic. **Can. J. Zool.,** v. 74, p. 897-911, 1996.

SLIJPER, E. J. **Whales.** New York: Basic Books, 1962.

SLONE, D. H.; REID, J. P.; KENWORTHY, W. J.; DI CARLO, G.; BUTLER, S. M. Manatees mapping seagrass. **Seagrass-Watch**., v. 46, p. 8–11, 2012.

SOUSA-LIMA, R. S.; PAGLIA, A. P.; FONSECA, G. A. B. Gender, age, and identity in the isolation calls of Antillean Manatees (*Trichechus manatus manatus*). **Aquat. Mamm.,** v. 34, p. 109-122, 2008..

STROBEL, S. M.; SILLS, J. M.; TINKER, M. T.; REICHMUTH, C. J. Active touch in sea otters: in-air and underwater texture discrimination thresholds and behavioral strategies for paws and vibrissae. **J. Exp. Biol.**, v. 221, 2018.

SUTHERLAND, W. J. The importance of behavioural studies in conservation biology. **Anim. Behav**., v. 56, p. 801-809, 1998.

SYNDER, N. F. R.; DERRICKSON, S. R.; BEISSINGER, S. R.; WILEY, J. W.; SMITH, T. M.; TOONE, W. D.; MILLER, B. Limitations of captive breeding in endangered species recovery. **Conserv. Biol**., v. 10, p. 338-348, 1996.

THEWISSEN, J. G. M.; HEYNING, J. Embryogenesis and development in *Stenella attenuata* and other cetaceans. *In:* MILLER, D. L. (ed.) **Reproductive biology and phylogeny in cetacea, whales, dolphins and porpoises.** Florida: CRC Press, 2007.

UMEED, R.; ATTADEMO, F. L. N.; BEZERRA, B. The influence of age and sex on the vocal repertoire of the Antillean manatee (*Trichechus manatus manatus*) and their responses to call playback. **Mar. Mamm. Sci.,** v. 34, p. 577-594, 2017.

WALLS, G. L. **The vertebrate eye and its adaptive radiation.** New York: Hafner Publ. Co., 1963.

WEBER, I. Tactile communication among free-ranging langurs. **Am. J. Phys. Anthropol**., v. 38, p. 481-486, 1973

WELLS, R. S.; BONESS, D. J.; RATHBUN, G. B. Behavior. *In:* REYNOLDS III, J. E.; ROMMEL, S. A. (eds.) **Biology of marine mammals.** Washington, DC: Smithsonian Institution Press, 1999. p. 324–422.

YAMASAKI, F.; KOMATSU, S.; KAMIYA, T. A comparative morphological study on the tongues of Manatee and Dugong (Sirenia). **Sci. Rep. Whales Res. Inst.**, v. 32, p. 127-144, 1980.

YOUNG, C. Agonistic behavior. *In:* VONK, J.; SHACKELFORD, T. (eds.) **Encyclopedia of Animal Cognition and Behavior**. Springer, Cham, 2019.

YOUNG, J. S. **An investigation of captive Florida manatee (*Trichechus manatus latirostris*) behavior and social interactions**. M.Sc. dissertation - Georgia Southern University, Statesboro, USA, 2001.

ZELICK, R.; MANN, D. A.; POPPER, A. N. Acoustic Communication in Fishes and Frogs. *In:* FAY, R. R.; POPPER, A. N. (eds.) **Comparative Hearing: Fish and Amphibians. Springer Handbook of Auditory Research, vol 11.** New York, NY: Springer, 1999.