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ROTAS MIGRATÓRIAS E ANÁLISE GENÉTICA DE POPULAÇÕES DE TARTARUGA DE PENTE (*Eretmochelys imbricata* (Linnaeus 1766))

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Tese apresentada ao Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade da Universidade Estadual de Santa Cruz como parte dos requisitos para obtenção do grau de Doutor em Ecologia e Conservação.

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Orientador: Dr. Mirco Solé

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SUMÁRIO

RESUMO

As tartarugas marinhas apresentam um complexo ciclo de vida caracterizado por grandes migrações entre as áreas de reprodução e alimentação. Os filhotes após a eclosão percorrem os oceanos até serem recrutados como juvenis para as áreas de alimentação, e posteriormente migram quando adultos para áreas de reprodução. Logo, compreender sobre a migração desses animais é fundamental para obter informações ainda desconhecidas do ciclo de vida. Além disso, outros aspectos sobre a vida das tartarugas marinhas ainda precisam ser entendido, visto que permanece grande parte da vida submersa. A aplicação de marcadores moleculares, como mtDNA vem se destacando nos estudos sobre as populações de tartarugas marinhas pelo mundo pois se trata de DNA herdados das fêmeas. Nesse contexto este trabalho teve como objetivo avaliar os estudos de migração de tartarugas marinhas nos últimos 12 anos, e realizar uma análise genética das populações de *Eretmochelys imbricata* que desovam ao longo do nordeste do Brasil. Encontramos 86 artigos sobre migração de tartarugas marinhas. As tartarugas fêmeas se destacaram em 51,16% das pesquisas, e em 39 estudos prevaleceu o continente Americano. Já a técnica de rastreamento que predominou nos trabalhos foi o rastreamento via satélite (68,60%). No entanto análises de haplótipos de mtDNA e a utilização de isótopos estáveis vem crescendo nos estudos sobre migração. A diversidade genética e a composição haplotípica de populações de *E. imbricata* que se reproduzem no Piauí, Rio Grande do Norte, Paraíba, Pernambuco, Alagoas e sul da Bahia foram analisadas e obtivemos seis haplótipos exclusivos para tais locais. Registramos também que o haplótipo H_1 foi compartilhado em todas as áreas de reprodução, e que as populações de *E. imbricata* apresentaram uma baixa diversidade genética. Já a estrutura genética foi composta por cinco grupos diferentes que separaram as populações dos locais reprodutivos dos locais de alimentação, ao mesmo tempo em que apresentaram relações significativas de distância geográfica com os valores do F_{ST} (r= 0.2302, p= 0.007). De modo geral, as informações sobre migração e análise genética desta pesquisa poderão contribuir para a conservação das espécies de tartarugas marinhas ameaçadas de extinção.

Palavras-chaves: Migração, tartaruga marinha, transmissor via satélite, haplótipos, mtDNA, conservação.

ABSTRACT

Sea turtles have a complex life cycle characterized by large migrations between breeding and feeding areas. After hatching, they roam the oceans until they are recruited as juveniles to the feeding areas, and then migrate as adults to breeding areas. Understanding the migration of these animals is essential to obtain information that is still unknown in the life cycle. Also, other aspects of the life of sea turtles still need to be understood, as they remain submerged much of their life. The application of molecular markers, such as mtDNA, has been highlighted in studies on sea turtle populations around the world because it is inherited from females. In this context, this work aimed to evaluate the studies of migration of sea turtles published in the last 12 years and to carry out a genetic analysis of the populations of *Eretmochelys imbricata* that reproduce throughout the northeast of Brazil. We found 86 articles on sea turtle migration. Female turtles stood out in 51.16% of the surveys, and in 39 studies the American continent prevailed. The tracking technique that predominated in the studies was satellite tracking (68.60%). However, analyzes of mtDNA haplotypes and the use of stable isotopes have been growing in migration studies. The genetic diversity and haplotypic composition of *E. imbricata* populations that breed in Piauí, Rio Grande do Norte, Paraíba, Pernambuco, Alagoas, and southern Bahia were analyzed and we obtained six exclusive haplotypes. We also note that the H_1 haplotype was shared in all breeding areas and that the populations of *E. imbricata* had a low genetic diversity. The genetic structure was made up of five different groups that separated populations from breeding sites to feeding sites while showing significant geographical distance relationships with FST values (r= 0.2302, p= 0.007). In general, the information on migration and genetic analysis of this research may contribute to the conservation of endangered sea turtle species.

Keywords: Migration, sea turtle, satellite transmitter, haplotypes, mtDNA, conservation.

1. INTRODUÇÃO GERAL

As tartarugas marinhas são animais longevos e com um complexo ciclo de vida (Pritchard, 1997; Naro-Maciel et al. 2008). No mundo há registro de sete espécies cujas populações são ameaçadas pela destruição dos locais de desova, poluição, roubo dos ovos, desenvolvimento acelerado do litoral, captura incidental por rede de pesca e caça das fêmeas (Marcovaldi et al. 1999). Logo, nos últimos anos esses animais encontram-se classificados em alguma categoria de ameaça de extinção pela *União Internacional para a conservação da Natureza* (IUCN).

Dentre as sete espécies existentes, a *Eretmochelys imbricata* (Linnaeus 1766), conhecida como tartaruga de pente, está categorizada com criticamente ameaçada de extinção (IUCN, 2020). Apresenta distribuição circunglobal, sendo a mais tropical dentre as espécies, e forrageiam principalmente os recifes de corais em busca de esponjas, componente fundamental da sua alimentação (Pritchard & Mortimer 1999). Assim como as demais, a espécie é caracterizada por apresentar um ciclo de vida com grandes migrações entre as áreas de reprodução e alimentação (Plotkin, 2003).

Após o nascimento os filhotes nadam freneticamente até chegar ao habitat oceânico e ali permanecem na fase conhecida como “anos perdido”, sendo guiados pelas correntes oceânicas até serem recrutados quando juvenis para os locais de alimentação (Musick & Limpus 1997). Quando atingem a idade adulta, as fêmeas realizam migrações cíclicas entre áreas de reprodução e alimentação, e provavelmente os machos também seguem o mesmo trajeto (Godley et al. 2008; Casale et al. 2013). Neste contexto, entender sobre a migração das tartarugas marinhas é fundamental para obter informações ainda desconhecidas do ciclo de vida, bem como desenvolver estratégias de conservação mais direcionadas para as espécies ameaçadas de extinção (Luschi & Casale, 2014). Apesar de estudos sobre migração em tais animais serem complexos, visto que passam grande parte da vida em oceanos, vários métodos estão sendo utilizados para elucidar a escassez de informações, como o uso de marcação com anilhas e recaptura, a instalação de transmissores via satélites, análises genéticas e a aplicação de isótopos estáveis (Godley et al. 2008; Ceriani et al. 2012; Putman & Mansfield, 2015).

Além desse comportamento, as tartarugas marinhas permanecem submersas nos mares a maior parte do tempo sendo avistadas poucas vezes. Dessa maneira, vários aspectos da sua vida ainda precisam ser esclarecidos, surgindo à necessidade da aplicação de marcadores genéticos (Bowen & Karl, 2007). Estes últimos vem se destacando em preencher lacunas no conhecimento da biologia e evolução destes animais (Lara-Ruiz et al. 2006), sendo muito utilizados para analisar a genética de populações, o comportamento de filopatria (fidelidade aos locais de desova), relações filogenéticas, migrações e filogeografia (Lara-Ruiz et al. 2006; Bowen & Karl, 2007; Naro-Maciel et al. 2008). Nos últimos tempos a região controle (D-loop) do DNA mitocondrial (mtDNA) se destaca amplamente em estudo de populações de tartarugas marinhas, visto que se trata de DNA herdados das fêmeas, que em conjunto com a alta filopatria materna terminam caracterizando populações geneticamente estruturadas.

Contudo, apesar do mtDNA impulsionar inúmeras pesquisas que descreveram as populações de *E. imbricata* em áreas de reprodução, e a composição destas em locais de alimentação (Vilaça et al. 2013), ainda existem lacunas sobre algumas populações reprodutivas no nordeste do Brasil. A espécie desova principalmente no litoral norte do Estado da Bahia e Sergipe, e no litoral sul do Rio Grande do Norte (Marcovaldi et al. 2007), as quais já tiveram sua composição genética analisada, ao mesmo tempo que os principais locais de alimentação como Arquipélagos e Parques Marinhos brasileiros também tiveram suas populações estudadas (Bass, 1999; Lara-Ruiz et al. 2006; Vilaça et al. 2013; Proietti et al. 2014). Todavia, a espécie também se reproduz em menores quantidades no litoral do Piauí, Paraíba, Pernambuco, Alagoas e sul da Bahia e compreender as características genéticas dessas populações é primordial para a conservação desses animais ameaçados de extinção. Informações genéticas dessas populações podem fornecer subsídios para direcionar melhor estratégias de conservação, como ampliação de áreas prioritárias e medidas mais restritivas em locais de nidificação e alimentação.

Diante do que foi exposto, o capítulo 1 desta tese reuniu informações em uma revisão de literatura sobre os estudos de migração de tartarugas marinhas nos últimos 12 anos, com o intuito de compilar e avaliar as contribuições relacionadas aos padrões de distribuição. Já no capítulo 2 buscamos analisar a diversidade genética e a composição haplotípica de populações de *E. imbricata* que nidificam em praias do nordeste do Brasil, ambos têm como foco contribuir com estratégias de conservação para as espécies.

2. CAPÍTULO 1

MIGRATION OF SEA TURTLES: A REVIEW OF METHODS APPLIED IN RECENT YEARS

Migration of sea turtles: A review of methods applied in recent years

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Resumo

As tartarugas marinhas apresentam uma ampla distribuição entre os oceanos e mares devido ao seu comportamento migratório ao longo do ciclo de vida. As rotas migratórias estão distribuídas desde os locais de nascimento até as áreas de alimentação. Entender a migração desses animais é importante para elucidar aspectos do seu complexo ciclo de vida. Neste contexto, o objetivo dessa revisão foi avaliar os métodos utilizados para estudar padrões de movimentos e rotas de cinco espécies de tartarugas marinhas, avaliando as pesquisas ao longo de 12 anos pelos continentes, quanto ao sexo e faixa etária, bem como, as perspectivas para o futuro, elencando as principais lacunas de conhecimento observadas nos estudos. Foram realizadas buscas nas bases de dados do Google Scholar, Scopus e Web of Science nos últimos 12 anos, nas quais foram obtidos 86 artigos sobre a temática. Entre os estudos as tartarugas fêmeas adultas estiveram presentes em 51,16% das pesquisas, o continente Americano se destacou com 39 estudos sobre migração. A técnica de rastreamento via satélite predominou na maioria dos trabalhos (68,60%). Apesar de ser um método de custo elevado, obteve vantagem em fornecer detalhadamente as rotas desses animais, entretanto as técnicas de rastreamento como análises de haplótipos de mtDNA e dos isótopos estáveis também estão sendo empregadas para esta finalidade, e estão se tornando ferramentas importantes nos estudos sobre migração. Apesar de existirem pesquisas sobre o assunto, observamos que ainda há lacunas quanto à migração de tartarugas marinhas nos primeiros anos de vida, das rotas migratórias dos machos, bem como sobre os métodos de rastreamento, visto que tais conhecimentos são necessários para contribuir com estratégias de conservação efetivas para as espécies ameaçadas de extinção.

Palavras-chaves. Rota migratória, testudines, Transmissor via satélite, mtDNA, isótopos estáveis, conservação.

Abstract

Sea turtles have a wide distribution between oceans and seas due to their migratory behavior throughout their life cycle. Migration routes are distributed from birth areas to feeding areas. Understanding the migration of these animals is important to elucidate aspects of their complex life cycle. In this context, the objective of this review was to evaluate the methods used to study movement patterns and routes of five species of sea turtles, evaluating research over 12 years across continents, regarding sex and age group, as well as the perspectives for the future, listing the main knowledge gaps observed in the studies. Searches were carried out in Google Scholar, Scopus and Web of Science databases in the last 12 years, in which 86 articles on the subject were obtained. Among the studies, adult female turtles were present in 51.16% of the surveys, the American continent stood out with 39 studies on migration. The satellite tracking technique predominated in most studies (68.60%). Despite being a high-cost method, it has gained an advantage in providing detailed routes for these animals, however tracking techniques such as analysis of mtDNA haplotypes and stable isotopes are also being employed for this purpose, and are becoming important tools in studies about migration. Although there is research on the subject, we observe that there are still gaps regarding the migration of sea turtles in the first years of life, the male migration routes, as well as on the tracking methods, since such knowledge is necessary to contribute to strategies of effective conservation for endangered species.

Keywords: Migration route, Testudines, Satellite transmitter, mtDNA, stable isotopes, conservation.

Introduction

Sea turtles migrate between oceans and seas during their life cycle (Pritchard 1997). They use routes during the stages of their life cycles, which still need to be fully understood (Luschi and Casale 2014). Right after birth, most hatchlings follow the course of sea currents until they are "recruited" to their feeding grounds (Musick and Limpus 1997, Hirth 1997). As adults, females migrate from foraging areas to nesting beaches, a migration which is also performed by males for mating (Godley et al. 2008, Casale et al. 2013). Some studies using mark/recapture and satellite transmitters are revealing information about the fidelity to foraging areas (Broderick et al. 2007, Ceriani et al. 2017), their natural history (James et al. 2005a), as well as regarding the distribution of some species of sea turtles in tropical and subtropical waters (Pritchard 1997, Marcovaldi and Marcovaldi 1999).

Among the seven species of sea turtles, two are restricted to specific locations: *Natator depressus* (Garman, 1880), in northeastern Australia and *Lepidochelys kempi* (Garman, 1880) in the Gulf of Mexico (Cheng and Chen 1997). The other five have a circumglobal distribution: *Eretmochelys imbricata* (Linnaeus, 1766); *Chelonia mydas* (Linnaeus, 1758); *Lepidochelys olivacea* (Eschscholtz, 1829); *Caretta caretta* (Linnaeus, 1758); and *Dermochelys coriacea* (Vandelli, 1761) (Marcovaldi and Marcovaldi 1999, Pupo et al. 2006). However, even with wide distributions, the latter species are currently classified as critically endangered (*E. imbricata*), vulnerable (*L. olivacea*, *C. caretta* e *D. coriacea*) and threatened with extinction (*C. mydas*) by the International Union for Conservation (IUCN). Several threats affect the populations of these species (Lutcavage et al. 1997a), turning further knowledge on ecology and behavior during their life cycle crucial for a better planning of conservation strategies and action plans.

To gather information about the migration of sea turtles is pivotal to understand their complex life cycle, temporal and spatial distribution patterns and reproduction (Luschi and Casale 2014, Read et al. 2014). In addition, it is essential to analyze the ability to resist to various anthropic impacts, as well as to know the variation in gene flow between males and females (FitzSimmons et al. 1995, Frankham et al. 2002, Shillinger et al. 2008, Pendoley et al. 2014). However, sea turtles spend a large part of their lives submerged, mostly in areas where they are nearly impossible to capture, thus hampering the collection of information on their migration (Lutcavage and Lutz 1997b). In recent years several tracking technologies and devices have been developed to study the migration patterns of marine animals (Schofield et al. 2013, Luschi and Casale 2014), however, it is worth mentioning that some of these techniques are very expensive (Sutherland et al. 2004, Cooke 2008) while others need to be used properly in order to avoid impacts on the target animals, as is the case of satellite transmitters of varying sizes (Wilson and McMahon 2006, Cooke 2008, Jones et al. 2013).

Among the tracking techniques, the use of metal rings and recapture (Meylan 1982), satellite telemetry providing exact migration routes (Gillespie 2001, Godley et al. 2008), genetic analyses, which indirectly provide data on the contribution of populations from nesting areas to feeding areas (Bowen and Karl 2007), estimating possible migratory patterns in early life stages (Putman and Mansfield 2015) and the use of more specific markers, such as stable isotopes (Ceriani et al. 2012) can be highlighted.

Studies on the different tracking techniques and new methodological approaches are essential to interpret population declines, and to develop effective conservation strategies (Miller et al. 2007, Cooke 2008). Therefore our review aimed to obtain a diagnosis on the studies of sea turtle migrations in order to evaluate the applied methods to study the ocean routes. Other goals were to analyses the distribution of the studies over 12 years on the continents, the influence of sex and age class, in addition to verifying the main knowledge gaps and the perspectives for the future of research in this field.

Material and methods

We conducted systematic searches in the Scopus, Web of Science and Google Scholar databases, restricted to original articles published in journals that contained the terms [sea turtle] AND [“migration” OR “long-distance migration” OR “movement” OR “navigation”] in the title, abstract and/or keywords. In this review, we considered all publications available in the databases in the last twelve years, published until October 2019. After conducting the searches, the articles were evaluated to check if they were within the scope of our research (tracking methods, with no location restriction, targeting the five species of sea turtles with circumglobal distribution (*E. imbricata, C. mydas, C. caretta, L. olivacea* and *D. coriacea*), (Marcovaldi and Marcovaldi 1999, Pupo et al. 2006) and then we analyzed the methods used in these studies.

From the selected articles we extracted the following information: year of publication; study locality (America, Asia, Africa, Europe or Oceania); the species and sex and the method used in the study. We did not consider studies that carried out experiments, nor using methods aimed to study vertical movements, which refers to dives. Moreover, we did not include research on migrations related to magnetic fields since most of them study the fidelity of females to the beaches they were born. Finally, review articles were also left out of our analyses.

We used ArcGis to construct our distribution map using the information from the locations provided in each study, since the geographical coordinates were not available in all surveys. Google Earth was used to obtain the approximate coordinates of each location.

Results

In total, 86 articles were obtained that addressed sea turtle migration (Table 1). We observed that in the last twelve years, research on migration increased in 2012, with ten studies, while in 2015 only four publications were registered (Figure 1A). Regarding the sex of sea turtles, over the years there was a tendency to use only females in 51.16% of the surveys (n=44), followed by juvenile turtles with 10.46% of the data (n=9), males with 6.97% (n=6) and hatchlings with 3.48% (n=3). However, ten studies worked with females and males at the same time (11.62%), five studies mingled females, males and juveniles (5.81%), four chose to analyze females and juveniles (4.65%) and the remaining 5.85% were distributed among surveys that used hatchlings with juveniles or hatchlings with females and also studies of females, males and hatchlings together. The range of monitored individuals in the studies varied from one individual to 2261, however most studies used lower numbers of specimens.

Within the analyzed data set, most research was conducted in the American continent (n=39), with 20.93% being developed in North America (n=18), 12.79% in South America (n=11) and 11.62% in Central America (n=10). The second most studied continent was Europe (n=17), followed by Oceania, Africa and Asia with nine surveys on each continent, and finally, only one survey was recorded that encompassed the three Americas, another that gathered data in Europe and in North America, and one study with information from Asia and Oceania.

We recorded four types of methods used to understand sea turtle migrations. In some studies more than one method for monitoring was used (Figure 2). The use of satellite transmitters was the method that predominated among the studies, being present in 68.60% of the articles (n=59). The use of mtDNA (mitochondrial DNA) haplotype analyzes stood out as the second most used technique, recorded in 16.27% of cases (n=14). Mark/recapture was restricted to 5.81% of the surveys (n=5). Stable isotope analysis was used in only one study (1.16%), however this method was also applied in association with satellite transmitters in four studies (4.65%). The remaining 3.48% corresponds to studies that used mtDNA haplotype analyzes together with satellite transmitters (n=3) (Figure 2).

Discussion

Distribution of research over the 12 years

The increase in studies on sea turtle migration in the last decade, mainly in 2012, may be a consequence of the great advance in tracking techniques that provide more detailed information on the movement of the animals between seas (Godley et al. 2002, López-Mendilaharsu and Rocha 2009, Read et al. 2014). The growing number of scientific productions possibly indicates a greater interest of specialists in sea turtles on the topic. Migratory animals are difficult to study, especially sea turtles that remain 90% of their life cycle submerged. Therefore there is still little available information on the migration of these animals (Lutcavage and Lutz 1997b, Godley et al. 2008) and an intensification of studies in this line of research is necessary.

Most tracking studies have highlighted the distance that sea turtles travel, however we can point out that in some surveys fidelity for the species *C. mydas* and *C. caretta* to their foraging areas in islands of Egypt and Florida was reported (Baudouin et al. 2015, Ceriani et al. 2017). In addition, Arendt et al. (2012) and Becking et al. (2016) reported that males of *C. caretta* and *E. imbricata* in Florida and the Caribbean respectively show similar migration patterns to females.

Sex and migratory movements

The predominance of studies using female turtles (51.16%) is probably related to the fact that they are much more easily captured during their presence on nesting beaches. As these animals spend some time out of the water to dig nests for egg lying, they become more accessible to be marked, equipped with satellite transmitters and susceptible to the collection of biological samples. Thus, they can be tracked during the inter-nesting period and during migrations after nesting (Bjorndal 2000, Hays et al. 2002, Godley et al. 2008). However, this behavior is different for males, hampering the attachment of transmitters (Arendt et al. 2012, Schofield et al. 2013).

In recent years studies with males have also increased to understand the routes they take as adults, as some studies have found out that males of some species also show site fidelity in relation to their breeding areas (Shaver et al. 2005, James et al. 2005b, Van Dam et al. 2008, López-Mendilaharsu and Rocha 2009). Tracking of males of *E. imbricata* in Bonaire in the Caribbean, carried out by Becking et al. (2016), concluded that males remained close to nesting areas approximately three months longer than females. Similar results were obtained for the same species from North America (Van Dam et al. 2008). Additionally, adult males of *C. caretta* tend to stay close to the breeding areas of females on some Greek islands (Schofield et al. 2010), corroborating the previously reported research.

Researcher speculate that the permanence of males in breeding areas may be related to less nutritional urgency to return to feeding areas, since they continue to feed, differently from females (van Dam et al. 2008, Becking et al. 2016). In addition, Becking et al. (2016) suggest that males possibly wait for environmental signals to be able to follow their routes to the feeding areas.

The small number of studies with hatchlings (Casale et al. 2012, Mansfield et al. 2014, Abalo-Morla et al. 2018) is probably associated with the fact that during this life cycle phase they migrate to ocean waters (Bolten 2003, Howel et al. 2010, Mansfield et al. 2014), where they stay until they are recruited to feeding areas. They are also small animals and consequently suffer a much higher predation rate, as well as being characterized by fast growth rates, thus making the use of equipment unfeasible, which varies on average between 5 to 20 cm in length, and can weigh approximately 100 to 500 g (Witherington 2002, Godley et al. 2008, Mansfield et al. 2014).

Garofalo et al. (2013), Chaves et al. (2017) and Prosdocimi et al. (2015) showed that populations of juveniles of *C. caretta* and *C. mydas* inhabiting feeding grounds in Tunisia, Galapagos, and Argentina, were possibly born in Greece, Costa Rica and Brazil respectively. Such results show that it was possible to obtain their migrations indirectly, because they used genetic analyzes, since the animals after hatching travel the oceans and are difficult to be monitored (McLellan and Read 2007). In addition, Swimmer et al. (2002) and Cardona et al. (2005) describe that during the first year of life the hatchlings and juveniles show a lot of habitat variation in oceanic waters, making it impossible to obtain information about their movements.

Migration studies across continents

The presence of large research centers on the American continent may offer an explanation for the concentration of studies in America (n=39) (Figure 3). North America concentrates the main research centers focused on studying the behavior and ecology of sea turtles, such as Sea Turtle Stranding and Salvage Network (STSSN) in México, The Turtle Hospital in Florida, Virginia Institute of Marine Science (VIMS) in Virginia, California Marine Sanctuary Foundation in California, Canadian Sea Turtle Network in Canada, among others. In Costa Rica, there is the Sea Turtle Conservation that has existed since 1959, and in Central America there is also the Fundación Científica Los Roques in Venezuela, and

Fundación Tortugas del mar in Colombia, all developing research aiming to conserve sea turtles. In the south of the continent, some migration studies are being carried out by the TAMAR Project in Brazil (Silva et al. 2011, Marcovaldi et al. 2012), by the Karumbé organization in Uruguay (López-Mendilaharsu and Rocha 2009), in addition to the numerous nongovernmental organizations (NGO) scattered though South American countries. However, this predominance can also be related to financial incentives for research in each region (Godley et al. 2008) since the development of studies on migration is very costly when it comes to animals with large displacement, which can vary from 3,000 to 5,000 USD per animal (Seaturtle, 2020).

Sea turtles show migratory patterns composed of cyclical shifts between feeding and breeding areas (Limpus and Limpus 2001, Luschi et al. 2003). Studies analyzed in our research reveal that there is fidelity to the feeding areas for some species, mainly *C. mydas* (Sales and Luschi 2009, Attum et al. 2014, Read et al. 2014, Ceriani et al. 2017, Hart et al. 2017). However, this pattern was not common in other studies and some specimens of *C. mydas, L. olivacea, E. imbricata* and *C. caretta* migrated to oceanic areas, as reported by Seminoff et al. (2008), Mansfield et al. (2009), Plotkin (2010) and Marcovaldi et al. (2012). The changes may possibly be related to the search for other feeding grounds, or perhaps to seasonal migrations (Zbinden et al. 2008, Reich et al. 2010).

Migrations in oceanic waters are common for the species *D. coriacea*, being recorded in the Indian Ocean (Maslim et al. 2016), in the temperate waters of North America (Benson et al. 2007b), south of the Pacific Ocean (Benson et al. 2007b) and the western South Atlantic (López-Mendilaharsu and Rocha 2009) (Figure 4F and Figure 5G). The migratory movements of *D. coriacea* are mostly related to ocean currents (Lambardi et al. 2008, Shillinger et al. 2008), which end up changing their migratory routes, in addition to dispersing their food sources, such as some pelagic tunicates and coelenterates (Witt et al. 2007).

In the last ten years, some studies using satellite transmitters also documented this relationship (Lambardi et al. 2008, Shillinger et al. 2008, López-Mendilaharsu and Rocha, 2009, Maslim et al. 2016). But there are controversies that the migration of *D. coriacea* is also influenced by the time of year when nesting takes place. According to Benson et al. (2007a,b), females that nest during the northern Summer tend to migrate to the northern hemisphere of the Western Pacific, while those that nest during the southern Summer migrate to the southern hemisphere. As for the other species, our revision suggests that ocean currents do not affect their routes (Cuevas et al. 2008, Girard et al. 2009), with evidence that turtles move against the current (Cheng and Wang 2009).

According to studies that used mtDNA haplotype analysis, stable isotopes, and satellite transmitters, *C. caretta* specimens tend to migrate from Florida to the Bahamas and North Carolina (Girard et al. 2009, Ceriani et al. 2017) and from Greece to North Africa, Turkey, Tunisia, Malta and Adriatic and Aegean Sea islands (Schofield et al. 2010, Zbinden et al. 2011, Garofalo et al. 2013, Patel et al. 2015, Karaa et al. 2016) (Figure 5H and Figure 5I). There are also records of movement between Argentina and Brazil (Prosdocimi et al. 2015), from the Italian Peninsula to Tunisia (Mingozzi et al. 2016), from Japan to the islands in the China Sea and in the Republic of Cape Verde (Varo-Cruz et al. 2013, Saito et al. 2015). Such migrations are revealing several places visited by this species that have not yet been studied, providing valuable data for future conservation strategies, such as, for example, the creation of Conservation Units of Marine Parks in the areas of greatest permanence of these animals.

Like *C. caretta*, *C. mydas* were also monitored over the years (Rees et al. 2008, Blanco et al. 2012, Read et al. 2014, Baudouin et al. 2015, Hart et al. 2017), allowing the identification of areas that can be frequented several times by the same turtles. The analyzed studies showed that this species moved between Suriname, French Guiana, and Brazil (Baudouin et al. 2015), from the Virgin Islands to Antigua and Venezuela (Hart et al. 2017) and between Australia and Caledonia (Read et al. 2014). They also swim in waters in the Caribbean, Nicaragua, Guatemala, Costa Rica, Panama and around the Galapagos Islands (Seminoff et al. 2008, Blanco et al. 2012, Hays et al. 2014, Becking et al. 2016, Jesen et al. 2016, Chaves et al. 2017) (Figure 5J).

The species *L. olivacea* revealed migrations more restricted to Central and South America. According to Plotkin (2010), representatives of the species passed through Costa Rica, Mexico, Guatemala, El Salvador, Honduras, Nicaragua, Panama, Colombia and Ecuador. Migrations occur also on the coast of the northeast region of Brazil, from the state of Sergipe to Alagoas and Paraíba (SILVA et al. 2011) (Figure 4C, 4D and 4E). Such movements corroborate the distribution obtained by Godfrey and Chevalier (2004) and Pupo et al. (2006) demonstrating that the movements of this species are more restricted to some locations.

In our study we observed that *E. imbricata* has a predominance in American waters since it has been monitored during some years, having its presence detected in waters that bathe countries such as Mexico, Nicaragua, Honduras, Venezuela, Dominican Republic, Bahamas and Brazil (Cuevas et al. 2008, Van Dam et al. 2008, Hawkes et al. 2012, Marcovaldi et al. 2012, Becking et al. 2016). Due to the fact that this species is classified as critically endangered (IUCN 2008), it is essential that the seas of the Central American region and northeast Brazil should be considered priority areas for conservation by environmental laws, since in recent years they have been used as migratory routes for this species (Figures 4 and 4B).

Tracking techniques used in migration research

With regard to the methods used in the research, satellite tracking was the one that prevailed in recent years. This method seems to provide more detailed information about the movement of sea turtles, in addition to providing migration routes in real time even over long distances, and to specify the types of movement and speed of these animals (Benson et al. 2007b, Broderick et al. 2007, Cooke 2008, Van Dam et al. 2008). According to James et al. (2005a), satellite transmitters, such as Sirtrack KiwiSat 101, Mk10-PAT, F4G 291A Sirtrack, SPLASH10-BF, Wildlife Computers, among others (Attum et al. 2014, Hays et al. 2014, Patel et al. 2015), allow several scientific studies and represent a good tool for research aimed at ecology and conservation of sea turtles. However, although this method provides important information, it does not have the ability to monitor migratory patterns in the long term, since they have a battery with a limited lifespan, in addition to being a high cost method (James et al. 2005a).

Associated with the satellite trackers, the method of marking with rings and recapture of these animals, allows recognizing migrations in greater proportions, although it requires recapture of sea turtles in nesting sites or in other locations (Limpus et al. 1992, Limpus et al. 2003, Godley et al. 2003). Only two publications on mark/ recapture were recorded in our research, and perhaps this reduction is related to the great advances in tracking techniques, as well as the fact that it takes several years of study to achieve relevant results, since nesting of sea turtle species do not occur every year (Limpus 1992, Miller 1997, Hamann et al. 2003, Thomé et al. 2007). However, it is worth mentioning that this method was essential in the beginning of research on migration of these animals and therefore its importance should not be discarded (Limpus et al. 2003 Read et al. 2014).

Currently, several researchers are directing their efforts towards genetic analysis (Garofalo et al. 2013, Prosdocimi et al. 2015, Maslim et al. 2016, Jensen et al. 2016, Chambault et al. 2018, Labastida-Estrada et al. 2019), for example, the analysis of mtDNA haplotypes, an indirect method used to understand the possible migratory movements of newly hatched turtles. This analysis allows estimating the contributions that different nesting areas have to the formation of groups of sea turtles located in the feeding areas, providing indirect information on the distribution and general movement patterns (Bowen and Karl 2007, Boyle et al. 2009, Jensen et al. 2016). As there is still scarce information on migration and dispersal of hatchlings in oceanic waters (Kobayashi et al. 2008, Boyle et al. 2009, Dethmers et al. 2010, Thomas and Bell 2013), this method is becoming very important for general knowledge on migration, especially in the first years of life. However, studies that apply this method are predominantly undertaken only in feeding areas, and therefore there is still a lack of information from nesting areas.

Recently, stable isotope analyzes are being applied as markers to track feeding behavior and movement of marine animals (Ceriani et al. 2012, Seminoff et al. 2012, Ceriani et al. 2017). This new approach has a lower financial cost than satellite transmitters, and works according to the isotopic composition in the tissues from consumption in feeding areas, therefore, as animals travel through various feeding sites, the tissues provide information on the locations (Reich et al. 2007, Seminoff et al. 2012). We found three studies that used the method to track sea turtles, associated with satellite transmitters. The gradual increase in studies addressing stable isotopes demonstrates that the method is probably an effective tool, and according to Zbinden et al. (2011) the integration of stable isotopes in sea turtle migration researches will have satisfactory answers, however these studies are recent and still need to be deepened to confirm this relationship.

Perspectives for future research and conclusion

The five species of sea turtles studied in our research have a wide distribution around the world (Marcovaldi and Marcovaldi 1999, Pupo et al. 2006) and during their life cycle take several routes through the oceans and seas (Musick and Limpus 1997, Lohman and Lohman 1998). In this context, a research priority should be the expansion of knowledge about migration along the European, Asian, African and Oceanian continents, to better understand the itineraries they carry out, and to direct conservation strategies, since all species are threatened with extinction, and protection is still unsatisfactory of the time they spend migrating (Martin et al. 2007, Boyle et al. 2009, Hamann et al. 2010). During all these years, a large part of the research was carried out using females due to capture logistics in nesting areas, and implantation of transmitters (Kennett et al. 2004, Godley et al. 2008), however there are still large gaps regarding movements of male sea turtles. Some studies argue that just like females, males of some species also show fidelity to breeding areas located close to nesting beaches (Hays et al. 2001, Shaver et al. 2005, James et al. 2005). Thus, complementary studies on male migration can be useful to find out if such behavior is common for all species, in addition to providing more details on the routes they take between the areas of feeding and reproduction.

Most sea turtle populations are formed by juveniles, however anthropic threats are drastically affecting this life stage, reducing survival and harming populations (Huang 2015, Labastida-Estrada et al. 2019). Several conservation actions have been used to reduce such threats, in particular satellite tracking can be a very important tool helping to monitor strandings, in addition to providing information on the ecology of species during this phase of their life cycle. There is still no unified protocol for the use of transmitters, as there is a very large variation in the sample number, with the use of trackers being recorded in at least three turtles, and in other cases in more than 30 animals.

The analysis of mtDNA haplotypes is growing in research mainly with the objective of obtaining indirectly relevant data on the migration of sea turtles, demonstrating the connection that exists between nesting and feeding areas, mainly trying to understand how the groups present in these areas are formed (Bowen and Karl 2007, Garofalo et al. 2013). In these circumstances, this method can serve as an instrument for the development of specific conservation strategies for connected feeding and nesting areas (Maffucci et al. 2006, Martin et al. 2007, Jensen et al. 2016), since existing threats in one region will affect populations in the other, thus contributing to the survival of these animals (Karaa et al. 2016).

The results obtained in our work demonstrate that America stands out in sea turtle migration research (Cuevas et al. 2008, Baudouin et al. 2015), revealing a lack of information from other continents. We also observed that studies with juvenile and male sea turtles are still growing in the scientific field, and that they are important to understand their movements and behaviors. Although there is much research on migration, the five species still need attention, as they are still in some way threatened with extinction. In addition, satellite transmitters, despite having a high cost, are currently considered to be the most useful and effective method for tracking animals, however, advances in tracking techniques are allowing mtDNA haplotype analyzes, and stable isotopes to provide valuable yet unknown data on the migration of sea turtles, and other groups of vertebrates, making it a less expensive alternative in the face of low funding for research. In fact, there are still gaps on migration routes and the use of tracking techniques, and it is essential to intensify the development of more research, due to the need to direct efforts mainly to action plans for the conservation of species.

Oceans are facing unprecedented threats regarding the quality of life of its inhabitants. Migratory species can be influenced by these changes, and the inclusion of more efficient methods in data collection, such as the use of stable isotopes and molecular biology will be fundamental for the conservation of future generations and allow an even better understanding of their life cycles (Boyle et al. 2009, Jensen et al. 2016).

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Figures and Tables

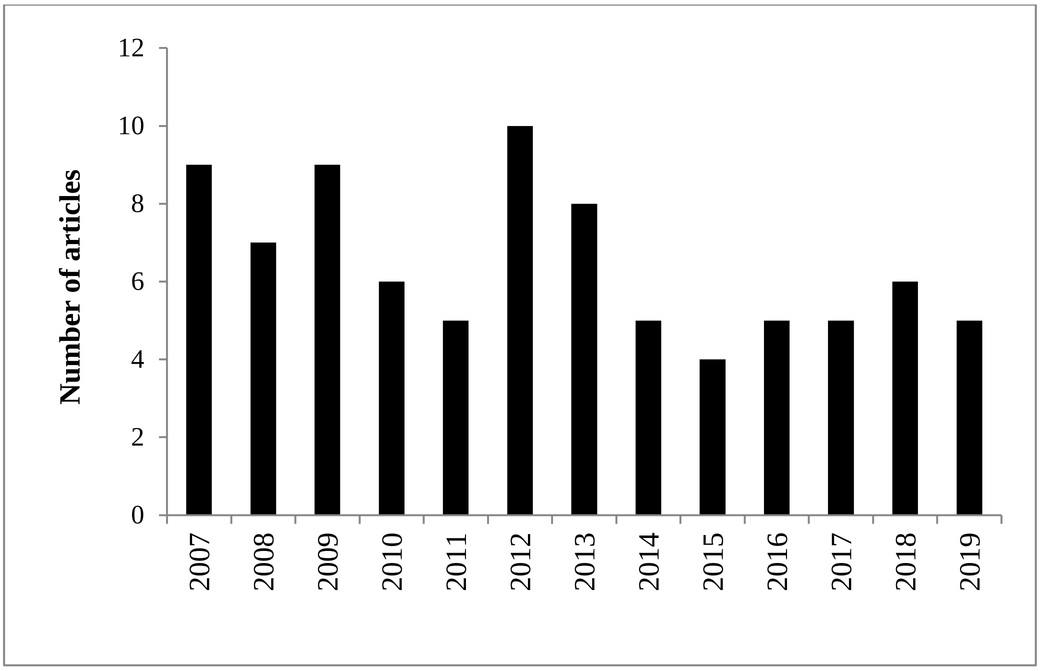

Figure 1. Number of articles on sea turtle migration published between the years 2007 and 2019.

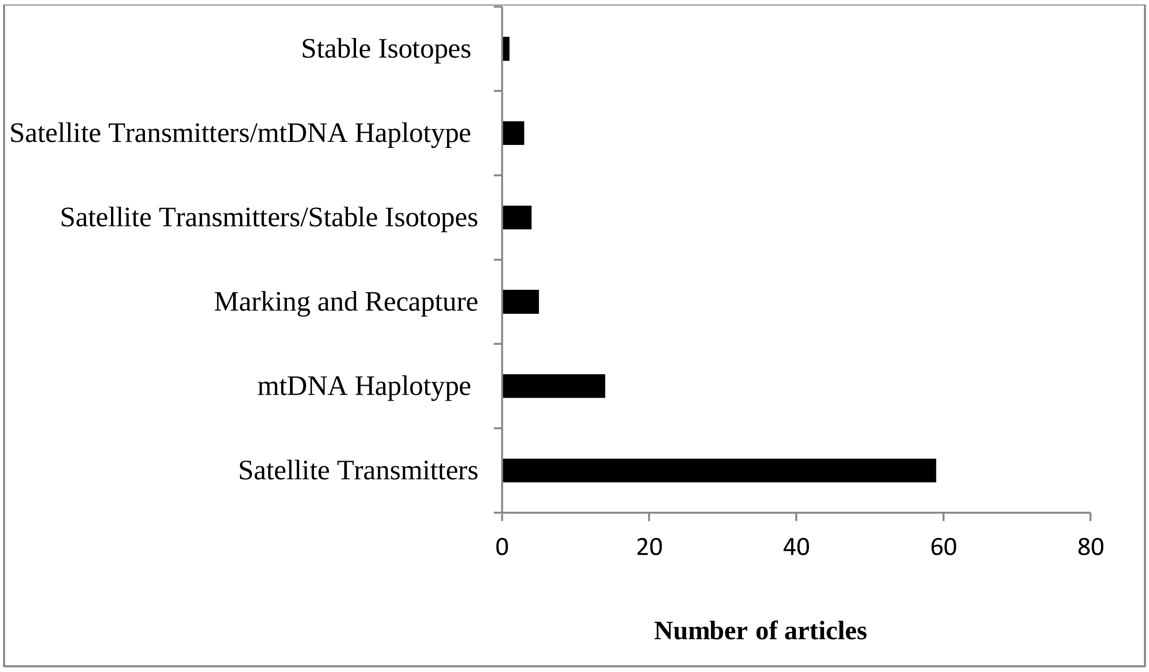

Figure 2. Distribution of the used methods to analyze the migration of sea turtles between the years 2007 and 2019.

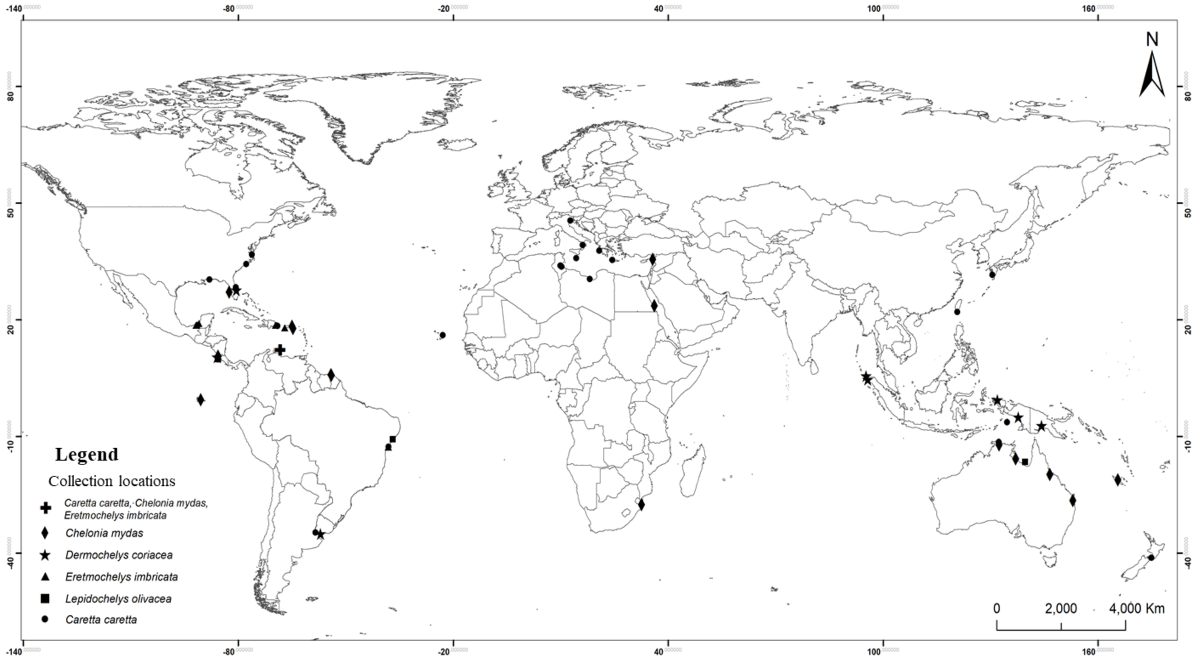

Figure 3. Map of the sampling points of the researches on migration of the five sea turtle species undertaken during the last twelve years.

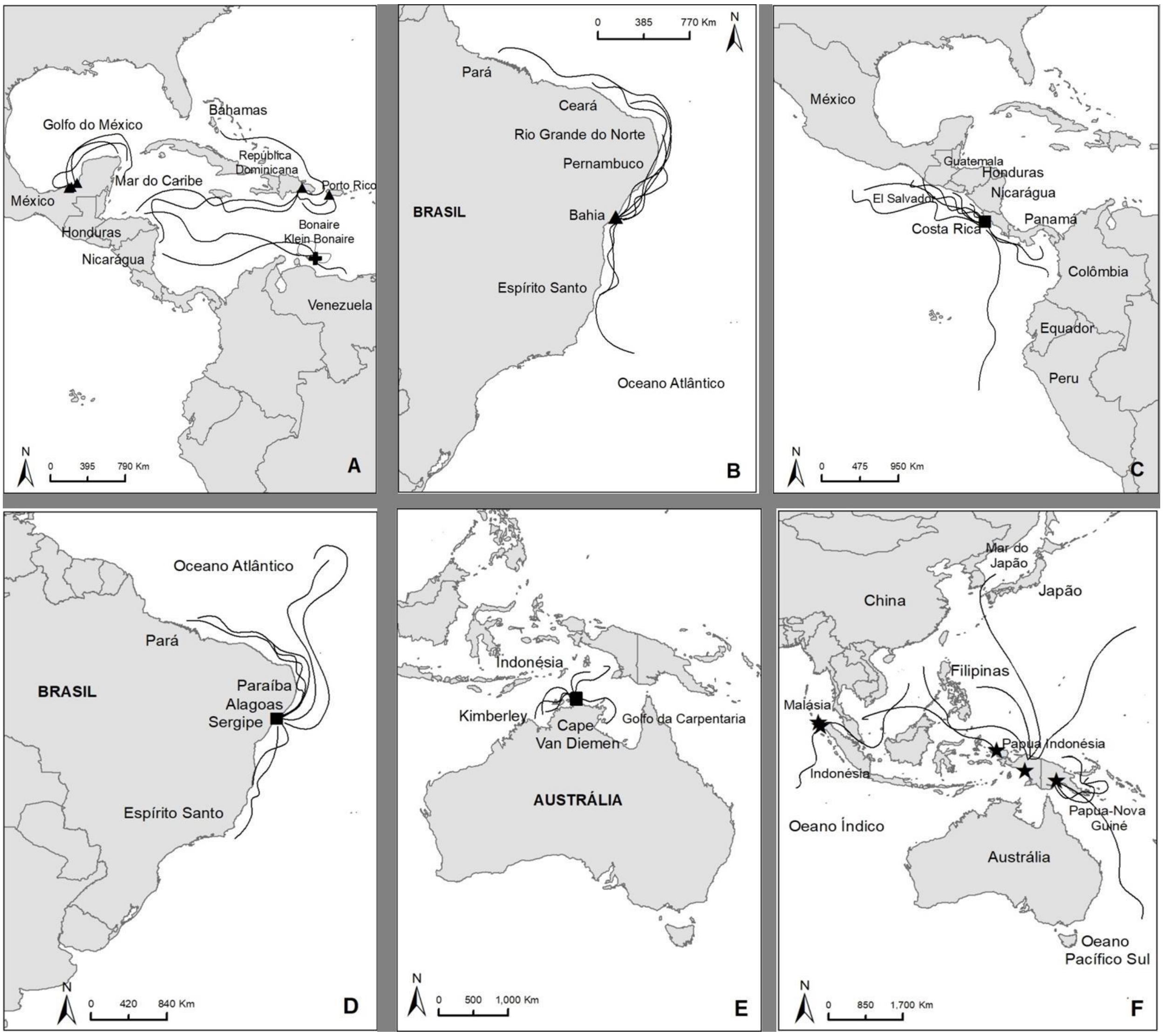

Figure 4. Migratory routes obtained from the researches made during the last ten years for the species *Eretmochelys imbricata* (A; B), *Lepidochelys olivacea* (C; D; E), *Dermochelys coriacea* (F).

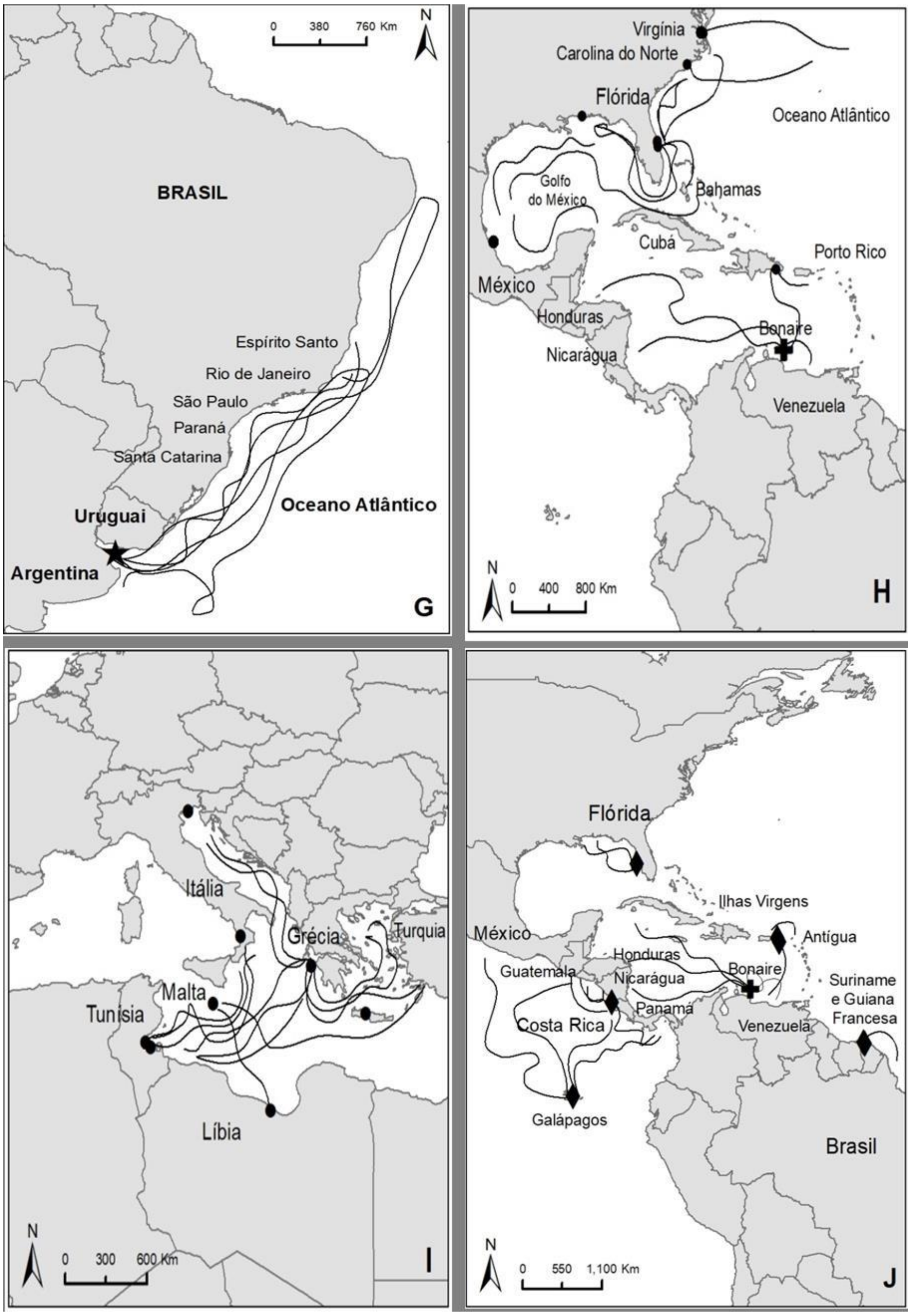

Figure 5. Migratory routes obtained from the researches made during the last ten years for the species *Dermochelys coriacea* (G), *Caretta caretta* (H; I), e *Chelonia mydas* (J).

Table 1. List of studies on sea turtle migration carried out during the last twelve years.

Method	**Species**	**Sex**	**Year of Study**	**Nº of individuals**	**Reference**	**Site**
Satellite Transmitters	*C. mydas*	Female	2010	4	Attum et al. 2014	Africa
	C. mydas	Female	2012	16	Baudouin et al. 2015	South America
	E. imbricata	Female	2006	3	Cuevas et al. 2008	North America
	C. mydas	Female	2011 - 2014	10	Hart et al. 2017	Central America
	C. caretta	Female	2009 – 2011; 2013	8	Mingozzi et al. 2016	Europe
	C. caretta	Female	2010 - 2011	20	Patel et al. 2012	Europe
	C. caretta	Male	2005	3	Saito et al. 2015	Asia
	C. caretta	Male	2006 - 2007	16	Arendt et al. 2012	North America
	C. caretta, *C. mydas* *E. imbricata*	Female Male	2003 - 2013	24	Becking et al. 2016	South America
	D. coreacea	Female	2003	9	Benson et al. 2007a	Oceania
	D. coreacea	Female	2001 e 2003	19	Benson et al. 2007b	Oceania
	C. mydas	Female	2006 - 2009	10	Blanco et al. 2012	Central America
	C. caretta	Juvenile Female	2006 - 2007	7	Casale et al. 2012	Europe
	C. caretta	Male	2006 - 2009	10	Casale et al 2013	Africa
	C. mydas	Female	1996 - 2004	6	Cheng e Wang, 2009	Asia

C. caretta	Female	2005 - 2007	28	Girard et al. 2009	North America
C. caretta	Female	2010 - 2012	39	Hart et al. 2013	North America
E. imbricata	Female	2008 - 2009	10	Hawkes et al. 2012	Central America
C. mydas	Female	2012	8	Hays et al. 2014	Europe
D. coreacea	Female	1996 - 2003	9	Lambardi et al. 2008	Africa
D. coreacea	Female Male Juvenile	2006 - 2008	4	López-Mendilaharsu et al. 2009	South America
C. caretta	Hatchlings	2008 - 2011	17	Mansfield et al. 2017	North America
C. caretta	Juvenile	1986 - 2007	23	Mansfield et al. 2009	North America
E. imbricata	Female	2005	15	Marcovaldi et al. 2012	South America
L. olivacea	Female Male	1990 - 1993	30	Plotkin, 2010	Central America
C. mydas	Female	2006	1	Rees et al. 2008	Ásia
C. caretta	Male	2007 - 2009	9	Schofield et al. 2010	Europe
C. mydas	Female	2003 e 2005	12	Seminoff et al 2008	South America
D. coreacea	Female	2004 - 2007	46	Shillinger et al. 2008	Central America
L. olivacea	Female	2006	10	Silva et al. 2011	South America
E. imbricata	Female Male	2000; 2003 - 2005	15	Van Dam et al. 2008	Central America

C. caretta	Male	1999; 2004 e 2006	5	Varo-Cruz et al. 2013	Africa
L. olivacea	Female	2004 - 2005	8	Whiting et al. 2007	Oceania
E. imbricata	Female	2011 - 2014	31	Hart et al. 2019	Central America
C. caretta	Hatchlings	2015 - 2017	19	Abalo-Morla et al. 2018	Europe
D. coreacea	Female	2005 - 2015	10	Aleksa et al. 2018	Central America
L. olivacea	Female Male	2009 - 2010	14	Behera et al. 2018	Oceania
C. mydas	Female	2018	6	Mettler et al. 2019	Africa
C. caretta	Female Juvenile	2006; 2008; 2009; 2011; 2015 e 2016	8	Luschi et al. 2018	Europe
D. coreacea	Female Male	2002 - 2005	27	Sherrill-Mix et al. 2007	North America
C. caretta	Female	1998 - 2008	68	Griffin et al. 2013	Europe e North America
C. caretta, *C. mydas*	Female Male	2007 - 2012	54	Dujon et al. 2012	Europe
C. caretta	Female Male	2010 - 2011	8	Hays et al. 2014	Europe

C. caretta	Female Male	1995 - 2001	3	Bentivegna et al. 2007	Europe
C. caretta	Male Juvenile	2002 - 2008	34	Kobayashi et al. 2011	Asia
C. caretta	Juvenile	1986 - 2007	23	Mansfield et al. 2009	North America
C. caretta	Female	2004 - 2005	7	Zbinden et al 2007	Europe
C. mydas	Female	2007 - 2008	2	Türkecan &Yerli, 2011	Asia
L. olivacea	Female	2007 - 2009	18	Maxwell et al. 2011	Africa
C. caretta	Female	2006	10	Marcovaldi et al. 2010	South America
C. mydas	Juvenile	2007 - 2008	6	Hart & Fujisaki, 2010	North America
L. olivacea	Juvenile	2001 - 2003	14	Swimmer et al. 2009	Central America
E. imbricata	Female	1995 – 1999; 2004 - 2005	9	Parker et al. 2009	North America
D. coreacea	Female Male	2005 - 2006	2	Doyle et al. 2008	Europe
C. mydas	Female	2000 - 2003	6	Cheng, 2007	Asia
C. caretta	Female Juvenile	2004 - 2005	3	Luschi et al 2013	Europe
C. caretta	Female	2011	42	Foley et al. 2013	North America
E. imbricata *C. mydas*	Female	2005 - 2007	5	Esteban et al. 2015	North America

	C. mydas	Female	1997 – 1998; 2001 - 2009	11	Esteban et al. 2019	Africa
	C. caretta	Female	2008 - 2012	14	Ceriani et al. 2012	North America
Satellite Transmitters/Stable Isotopes	*D. coreacea*	Female Male	2005 – 2007; 2010	78	Seminoff et al. 2012	Oceania
	C. caretta	Female	2010	18	Zbinden et al. 2011	Europe
	C. caretta	Male	2006 - 2007	37	Pajuelo et al. 2012	North America
	D. coreacea	Female	---	14	Maslim et al. 2016	Asia
	C. caretta	Female	2004 - 2010	61	Prosdocimi et al. 2015	South America
	C. caretta	Female Juvenile	1991 -1996; 2005	103	Boyle et al. 2019	Oceania
mtDNA Haplotype	*C. mydas*	Female Male Juvenile	---	133	Chaves et al. 2017	South America
	C. caretta	Female Male Juvenile	2002 - 2009	133	Garofalo et al. 2013	Europe
	C. mydas	Female	1986 – 2015	987	Jensen et al. 2016	Oceania
	C. caretta	Female Male Hatchlings	2007 - 2009	107	Karaa et al. 2016	Africa

Marking and Recapture	*C. mydas*	Female Male Juvenile	1996; 2000; 2002; 2004	463	Dethmers et al. 2010	Oceania e Asia
	E. imbricata	Female	2013 – 2016	227	Labastida-Estrada et al. 2018	North America
	C. caretta	Female, Hatchlings	1991 – 1996; 2005	144	Boyle et al. 2009	Oceania
	C. caretta	Female	1996 -1997; 2003 - 2006	204	Reis et al. 2009	South America
	E. imbricata	Hatchlings	---	30	Tabib et al. 2011	Asia
	E. imbricata	Hatchlings, Juvenile	1992 - 1999	347	Bowen et al. 2007	North America, Central America, South America
	C. caretta	Juvenile	2005 – 2010; 2012	104	Nishizawa et al. 2014	Asia
	C. mydas	Female	1972 - 2011	97	Read et al. 2014	Oceania
	E. imbricata	Juvenile	---	13	Santos et al. 2019	South America
	E. imbricata	Female	2002 - 2009	2261	Horrocks et al. 2011	Central America
	C. caretta	Juvenile	2008 - 2012	1	Casale et al. 2013	Europe
	D. coreacea	Female, Male,	1999 - 2006	152	James et al. 2007	North America

Stable Isotopes	*C. caretta*	Juvenile Female	2007 - 2015	749	Ceriani et al. 2017	North America
	C. mydas	Juvenile	2013 - 2017	425	Chambault et al. 2018	Europe
Satellite Transmitters/mtDNA Haplotype	*C. mydas*	Female, Hatchlings	2001	70	Godley et al. 2010	Africa
	C. caretta	Juvenile	2004 – 2005; 2007	34	Arendt et al 2012	North America

3. CAPÍTULO 2

Structure and genetic composition of *Eretmochelys imbricate* populations in breeding areas in Brazil

Structure and genetic composition of *Eretmochelys imbricate* populations in breeding areas in Brazil

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RESUMO

Os locais de reprodução da tartaruga marinha *Eretmochelys imbricata* são caracterizados por apresentarem informações genéticas do mtDNA que revelam a estrutura e composição genética das populações. Logo, este estudo teve como objetivo analisar com base na região controle do mtDNA, a diversidade genética e a composição haplotípica de populações que se reproduzem no Piauí, Rio Grande do Norte, Paraíba, Pernambuco, Alagoas e sul da Bahia, bem como comparar as informações com dados das áreas de alimentação disponíveis em banco de dados. Os haplótipos das áreas de reprodução foram determinados por sequenciamento do mtDNA e no total foram obtidos seis haplótipos exclusivos para tais locais, e 27 exclusivos para as áreas de alimentação. O haplótipo H_1 foi compartilhado em todas as áreas de reprodução. As populações destas regiões apresentaram uma baixa diversidade e uma estrutura genética composta por cinco grupos divergentes que separaram as populações dos locais reprodutivos dos locais de alimentação. Foram também registradas relações positivas e significativas de distância geográfica com os valores do F_{ST} (r= 0.2302, p= 0.007). Nossos resultados revelaram que as tartarugas de pente dos locais de reprodução compõem uma única população que necessitam de um gerenciamento adequado para proteger a espécie ameaçada, além de fornecer informações que podem contribuir para as futuras ações para a conservação das espécies.

Palavras-chaves: Tartaruga de pente, mtDNA, haplótipos, estrutura populacional, Brasil.

ABSTRACT

The reproductive sites of the sea turtle *Eretmochelys imbricata* are characterized by presenting mtDNA genetic information that reveals the genetic structure and composition of populations. Therefore, this study aimed to analyze, based on the mtDNA control region, genetic diversity and haplotypic composition of populations that reproduce in the Piauí, Rio Grande do Norte, Paraíba, Pernambuco, Alagoas, and southern Bahia, also as to compare the information with data from the feeding areas available in the database. The haplotypes of the reproductive areas were determined by mtDNA sequencing and a total of six haplotypes exclusive to such locations were obtained and 27 exclusives to the feeding areas. The H_1 haplotype was shared in all reproductive areas. The populations of these regions had a low diversity and a genetic structure composed of five divergent groups that separated the populations from the reproductive sites to the feeding sites. Positive and significant geographical distance relationships were also recorded with the F_{ST} values (r= 0.2302, p= 0.007). Our results revealed that hawksbill turtle from reproductive sites comprises a single population that needs adequate management to protect the threatened species, in addition to providing information that can contribute to future actions for the conservation of the species.

Keywords: Hawksbill turtle, mtDNA, haplotypes, population structure, Brazil.

1. INTRODUCTION

Five species of sea turtles can be found along the Brazilian coastline and all of them have been categorized under some level of threat of extinction (Santos et al. 2011). The species *Eretmochelys imbricata* (Linnaeus, 1766), classified as critically endangered (IUCN, 2008) has a circumglobal distribution in tropical and subtropical waters in the Atlantic, Indian and Pacific oceans (Pritchard and Mortimer 1999, Leroux et al. 2012). It feeds preferentially on sponges, shows philopatric behavior, and like other sea turtles, has a life cycle with a migratory habit between birth and feeding areas (Wallace et al. 2010, Putman et al. 2014).

Philopatry, the behavior of females to return to the beaches they were Born to nest, supposes that breeding sites have specific genetic information of maternal inheritance, derived from mitochondrial DNA (mtDNA) (Bowen and Karl 2007), resulting in a genetically structured population that can be seen as Management Units (Hamann et al. 2010). Genetic studies in general, are being increasingly applied in analyzes of the genetic structure and composition of the birth areas, genetic diversity, phylogenetic relationships, migratory behavior, composition of the populations of the feeding areas and philopatry of sea turtles worldwide (Bolten et al. 1998, Bowen et al. 2005, Bjorndal and Bolten 2008; Joseph et al. 2016). In this context, the use of molecular marker as mtDNA (control/D-loop region) stands out for being efficient in verifying the genetic structure among populations in the reproductive areas (Jensen et al. 2013, Reis and Goldberg 2017).

Previous research revealed that the populations of *E. imbricata* are concentrated mainly in the eastern Atlantic Ocean and the Caribbean (Marcovaldi et al. 2007, Vilaça et al. 2013). Mexico, for example, is considered the country hosting the largest breeding population of this species in the Atlantic, in addition to several environments along the coast that are used as feeding areas (Garduño-Andrade 1999, Labastida-Estrada et al. 2019). In Brazil several breeding and feeding areas have already been identified, however only in some genetic analysis have been carried out using mtDNA, such as reproductive sites in Bahia, Sergipe, Rio Grande do Norte and Ceará, and feeding areas such as Archipelago from São Pedro and São Paulo, Archipelago of Fernando de Noronha, Parque Nacional Marinho dos Abrolhos and some regions in southern Brazil (Bass et al. 1996, Bass 1999, Lara-Ruiz et al. 2006, Vilaça et al. 2013, Proietti et al. 2014).

Although such research exists on the Brazilian coast, the genetic characterization of populations in the breeding areas of *E. imbricata* in some regions of Northeastern Brazil, has not yet been carried out. Such information can increase knowledge about the biology of these animals for conservation purposes (Vilaça et al. 2013). Thus, aiming to reduce knowledge gap, this study uses mtDNA to analyze the genetic composition and diversity of populations of *E. imbricate* from their breeding areas (states of Piauí, Rio Grande do Norte, Paraíba, Pernambuco, Alagoas and southern Bahia), and evaluate the genetic structure between the populations of the reproductive and feeding areas of the species.

2. MATERIAL AND METHODS

2.1 Study area and data collection

The study was undertaken on beaches located on the coast of northeastern Brazil, distributed throughout the states of Piauí, Rio Grande do Norte, Paraíba, Pernambuco, Alagoas and Bahia. The coastline is characterized by the presence of sand strips, formation of inlets, some have coral reefs and sandstones, and the vast majority are urban beaches that are under the influence of tourism and anthropic action (Santana et al. 2009, Moura et al. 2012, Oliveira et al. 2016, Melo et al. 2016). The coast of northeastern Brazil stands out for its increased sea turtle nesting activity (Lara-Ruiz et al. 2006). All areas mentioned above have records of nesting of sea turtles of the species *E. imbricata*.

Between 2017 and 2018, six populations of *E. imbricata* breeding areas located in the states of Piauí (PI_BRA), Alagoas (Al_BRA), Bahia (BA_BRA), Rio Grande do Norte (RN_BRA), Pernambuco (PE_BRA) and Paraíba (PB_BRA) (Figure 1 and Table S1) were sampled. In each population, random tissue samples of 3-21 hatchlings/embryos that did not survive were taken for DNA extraction (Table S1). The tissue fragments measuring approximately 3mm were obtained with the aid of a disposable scalpel for each animal during handling of the nests after turtles had hatched. Subsequently the material was placed in microtubes containing absolute alcohol (Proietti et al. 2014), transferred to the laboratory and stored at -20ºC until molecular analysis.

Subsequently, nine populations of feeding areas were included (Atol das Rocas – AR_BRA; Fernando de Noronha – FN_BRA; Costa Rica – CR; Mexico – MEX; Malaysia – MAS; Caribbean – CAR; Australia – AUS; Puerto Rico – PUR; Israel – ISR), using the DNA sequences of the target species available in the GenBank database (Figure 1 and table S1).

Samples were taken under license from SISBIO/ICMBIO nº 56974 and were conducted in accordance with the Ethical Principles of Animal Experimentation adopted by the Ethics Committee on the Use of Animals – CEUA/UESC under nº 038/16.

2.2 Sample processing

The obtained samples of *E. imbricata* were digested with proteinase K (20mg/ml) in a lysis buffer and incubated overnight at 37ºC until complete digestion (Proietti et al. 2012). DNA extraction was performed using the Easy-DNA Kit (Invitrogen) following the manufacturer's protocol. The ~830 pb fragments of the mtDNA D-loop region were amplified by PCR using primers H950 (5'-GTCTCGGATTTAGGGGGTTTG-3') and LCM15382 (5'-GCTTAACCCTAAAGCATTGG-3') (Abreu-Grobois et al. 2006). The amplifications were performed in a total volume of 13µl, containing 5-15 ng of DNA, 10x buffer, 2,25 mM of each deoxynucleoside triphosphate (dNTP), 50 mM of $MgCl_2$, 10 µM of each primer, 0,2 U Taq polymerase. The PCR reactions followed the conditions described by Tabib et al. (2011). Then, the PCR product was purified using ExoSAP-IT®, following the manufacturer's protocol. Sequencing was performed by ABI PRISM® 3500 capillary electrophoresis, using the reverse and forward primers. The final sequences were analyzed and aligned using the BIOEDIT 7.0.9.0 software (Hall 1999).

2.3 Data analysis

To estimate the genetic diversity of populations from breeding and feeding areas, nucleotide diversity (π), haplotypic diversity (h) and the number of haplotypes were calculated using the *DNAsp* v5 program (Librado and Rozas 2009). The relationships between haplotypes and how they are spatially distributed were analyzed by a haplotype network using the median-joining method (Bandelt et al., 1999) in the *NETWORK 4.613* program (www.fluxus-engineering.com). For the genetic structure between populations, the F_{ST} was calculated using the *DNAsp* v5 program (Librado and Rozas 2009). The F_{ST} values were used in the *heatmap* analysis with the populations under study, using the *heatmaply* package (Galili et al. 2017) in software R environment. The number of groups in the *heatmap* was established using the hierarchical clustering algorithm with Euclidean distance and the *average* method, implemented in the *heatmaply* package (Galili et al. 2017) in software R. Then, to assess whether the geographical distance (km) influenced the F_{ST} values obtained between the populations, a Mantel test was performed (Mantel 1967), using the ecodista package (Goslee and Urban 2007) in software R (http://www.r-project.org/).

3. RESULTS

The 15 populations of de *E. imbricate* revealed a total of 33 haplotypes, highlighting the largest number (13) found in PUR. Of the 22 haplotypes, six are exclusive to the breeding areas and the other 27 exclusive to the feeding areas (Figures 1 and 2, Table S1). The most frequent haplotypes in the breeding areas were H_1 (82.35%) followed by H_2 (10.29%), whereas in the feeding areas it were haplotypes H_10 (22.64%) and H_11 (11.32 %) (Figure 1 and Table S1).

As for haplotypic diversity (h), for breeding areas a variation of h = 0.00 (PI_BRA) to h = 0.50 (BA_BRA) was recorded, while nucleotide diversity (π) varied from π = 0.00

(PI_BRA) to π = 0.279 (PE_BRA). In the populations of the feeding areas, MEX showed the lowest diversity (h = 0.00) while the highest indexes were registered in MAS and AUS (h = 1.00 and h = 0.933 respectively), the nucleotide diversity varying between π = 0.00 (MEX) and π = 0.037 (AR_BRA) (Table 1).

Regarding the spatial distribution of haplotypes, H_1 was shared between all breeding areas, H_10 (FN_BRA, CAR, PUR) and H_11 (FN_BRA, MEX, AUS) were shared by three areas and H_2 (PB_BRA and AL_BRA), H_5 (BA_BRA and RN_BRA), H_8 (AR_BRA and CAR), H_9 (AR_BRA and PUR) and H_12 (CR, AUS) were shared by two areas simultaneously (Figures 1 and 2). Exclusive haplotypes were registered in nine of the 15 sampled populations, with emphasis on PUR with 11 exclusive haplotypes (Figures 1 and 2). The haplotype network showed that the *E. imbricata* haplotypes in the breeding areas are more related to each other and are not found in the feeding areas (Figure 2).

Regarding the genetic structure, the *heatmap* analysis based on the F_{ST} values showed that the 14 populations formed five divergent groups (Figure 3 and Figure S1). The first group was formed by the breeding areas (BA_BRA; AL_BRA; PE_BRA; PB_BRA; RN_BRA; PI_BRA) and the other groups restricted to the species' feeding areas, from which we can highlight two main groups: The first gathering the FN_BRA populations; CAR and AR_BRA, and the second by MAS; AUS and MEX (Figure 3). Subsequently, a positive and significant relationship between geographic distance and F_{ST} values was demonstrated through the Mantel test (r = 0.2302, p = 0.007) (Figure 4).

4. DISCUSSION

Our work revealed that breeding areas of *E. imbricata* along the Brazilian coast show low haplotypic diversity, with the presence of exclusive haplotypes. In addition, our data revealed that the breeding areas were formed by only a single genetic group, differing from the other genetic groups in the feeding areas. Thus, we demonstrated that the evaluated breeding areas were made up of only six haplotypes, all of which were registered exclusively for these areas. Thus, the breeding areas are genetically unique, highlighting their importance for the genetic conservation of this endangered species (Santos et al. 2011, Vilaça et al. 2013).

We registered six exclusive haplotypes of *E. imbricata* for the breeding areas, differing from the 27 exclusive haplotypes found in the feeding areas (Figure 1 and Table S1). This predominance of exclusive haplotypes is not uncommon for the hawksbill sea turtle, Reece et al. (2005) and Labastida Estrada et al. (2018) also reported restricted haplotypes from populations in Mexico and the Caribbean, highlighting that this fact may be related to the high degree of female philopatry, that is, fidelity to the places of origin to spawn (natal homing) (Lohman et al. 2001, Almeida et al. 2011). Although the presence of exclusive haplotypes is common for the species, it is worth mentioning that the breeding areas consisted of only six haplotypes and that all were exclusive, showing the importance of these areas for maintaining the genetic diversity of this endangered species.

The breeding areas of hawksbill sea turtles were characterized with low haplotypic diversity (h) when compared to other reproductive areas in northeastern Brazil, such as Arembepe (h = 0.725), Praia do Forte (h = 0.649) and Sauípe (h = 0.643)), as well as being low compared to Islands in the Persian Gulf (h = 0.770 and h = 0.640) and the Caribbean (h = 0.642) (Lara-Ruiz et al. 2006; Tabib et al. 2011; Revuelta et al. 2012). However, there were similarities to the indices previously found for the species in Mexico (h = 0.454 and h = 0.225) (Labastida Estrada et al. 2018). Nucleotide diversity was also similar to the patterns obtained when compared with the data gathered by Labastida Estrada et al. (2018) (ranging from $\pi = 0.0005$ to $\pi = 0.0006$) for Mexico. These data in general emphasize that the haplotypic and nucleotide diversity recorded in our study is low for the breeding areas of the species, but is within the intervals reported in the literature.

Thus, considering that genetic diversity is essential for species persistence over time (Vilaça et al. 2013) and that *E. imbricata* is an endangered species, we highlight the importance of these reproduction areas from the genetic view for species maintenance. Therefore, the need to increase the protected areas, especially the nesting/hatchling points of these animals, is highlighted, since these areas have low genetic diversity. One suggestion would be to expand the protection areas that are close to Conservation Units (UCs), such as breeding sites in the state of Pernambuco that are not part of the Costa dos Corais Environmental Protection Area (APA) and in the state of Paraíba with the APA of Barra do Rio Mamanguape. In addition, greater restrictions are required for those breeding areas that are already part of UCs, mainly during the reproduction of these animals, as in the APA of Delta do Parnaíba / PI and APA Costa dos Corais in Alagoas.

Haplotypic (h) and nucleotidic (π) diversity of the analyzed food areas showed high values following the patterns described in the literature (Lara-Ruiz et al. 2006, Monzón-Arguello 2010, Proietti et al. 2014). Previous studies suggest that those sea turtle populations close to warm ocean currents have greater diversity of haplotypes (Bass et al. 2006), since the dispersion of these animals can occur through ocean currents (Luschi et al. 2003). An example is the Fernando de Noronha archipelago, which due to the influence of the South Equatorial current (north and south of Brazil) has a high genetic diversity (Proietti et al. 2014, Vilaça et al. 2013).

In this context, ocean currents, which occur in the AR_BRA archipelago, could be a possible explanation for the high genetic diversity in this area. At the same time, Caribbean currents with temporal variations can also contribute to the high diversity in PUR and CAR (Blumenthal et al. 2009). As for the diversity of AUS and MAS, we suggest that they are receiving contributions from the Monsoon Drift and south equatorial currents. However, more detailed analyzes need to be carried out to confirm this relationship. Our results support the relationship of ocean currents versus diversity, which was also common for C*helonia. mydas* and C*aretta caretta* (Prosdocimi et al. 2015, Chaves et al. 2017).

Some haplotypes were shared between breeding areas, such as, for example, H_1 and H_2. Although populations demonstrate fidelity to spawning areas, there is a possibility of migrating to nearby areas for nesting (Bowen and Karl, 2007). According to Tabib et al. (2011) the proximity and the strong relationship between haplotypes suggests that these areas behave as a single population from the genetic point of view. This hypothesis is reinforced by the fact that there is no sharing of haplotypes between breeding areas and feeding areas. The feeding grounds of sea turtles are used by several individuals who were recruited as juveniles from various birth places, and those who migrated after reproduction (Reis et al. 2009, Jensen et al. 2013). Therefore, it would be expected that such sites would bring together several distinct haplotypes, as was recorded in our study for the PUR and AUS areas (Figure 1).

However, it is noteworthy that the feeding areas shared haplotypes with different frequencies, suffering the potential influence of ocean currents, which is a factor that influences colonization (Luschi et al. 2003, Prosdocimi et al. 2015). For example, Labastida Estrada et al. (2018) reported that Caribbean currents contributed to the colonization of hawksbill sea turtles of the Caribbean and Mexico. Other results suggest that colonization of Atlantic feeding areas happened due to ocean currents from north to south, suggesting that in the glacial periods breeding and feeding sites expanded at higher latitudes (Encalada et al. 1998, Prosdocimi et al. 2015). Thus, we suggest that the same may have happened for FN_BRA, CAR, MEX and PUR, which represented the highest frequencies of the H_10 and H_11 haplotypes in the haplotypic network. However, future studies of turtles in the feeding areas close to the analyzed breeding areas are necessary to better understand this relationship.

Ocean current patterns are not the only factor that interferes with the wide dispersion of sea turtles. Some populations may be limited to regions due to changes in ocean conditions such as water temperature, geographical distance and physical barriers (Bowen and Karl 2007, Boyle et al. 2009, Prosdocimi et al. 2015). *E. imbricata* has two lineages, one in the Atlantic and one in the Indo-Pacific, with a younger lineage in the east Atlantic (Okayama et al. 1999, Tabib et al. 2011). Our research revealed the presence of five groups (Figure 3), which in general, separated the populations from the breeding areas from the feeding areas, and perhaps the presence of physical barriers explains this fact.

Barriers such as the Amazon Barrier that separates Brazil from the Caribbean, the Central Atlantic Barrier that separates the Americas from Africa and the Benguela Barrier located in the south of the Atlantic (separating the Atlantic Ocean from the Indian Ocean) (Rocha et al. 2005, Rocha et al. 2007, Hahn 2011), may be the reason for the isolation of one group in South America, another in Central America and three more in the Indian Ocean. Such events do not seem to be rare for the species, as according to Reece et al. (2005) populations of Mexico were isolated from the population of the Caribbean after historical processes during the Pleistocene. However, although geographic isolation seems to be an important factor to explain the distribution of genetic variability among populations (Formia et al. 2006, Bowen and Karl 2007), the Mantel test performed in our study, had little explanatory power ($r = 0.2302$, $p = 0.007$). Thus, although geographic isolation influences the genetic structure of the species (F_{ST}), most F_{ST} values among populations may be associated to other factors, such as those mentioned above (ocean currents, physical barriers, among others).

Our results provided genetic information not yet obtained for some breeding areas of *E. imbricata* in Brazil, revealing that these seem to be composed of a single population with low genetic diversity and exclusive to these locations. In addition, as already described in the literature, our data also emphasize that ocean currents can influence the composition of the genetic diversity of populations in the feeding areas, and that the genetic variability of these populations may be a response to the presence of some geographic isolations. Our research suggests that the breeding areas make up a Management Unit that requires a specific management plan for the maintenance of the species. Anthropic threats caused by the development of these locations and local tourism are likely to be threatening the habitat of hawksbill sea turtle populations. Our results also provided unprecedented genetic data relevant to the actions for the conservation of sea turtles.

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Figures and Tables

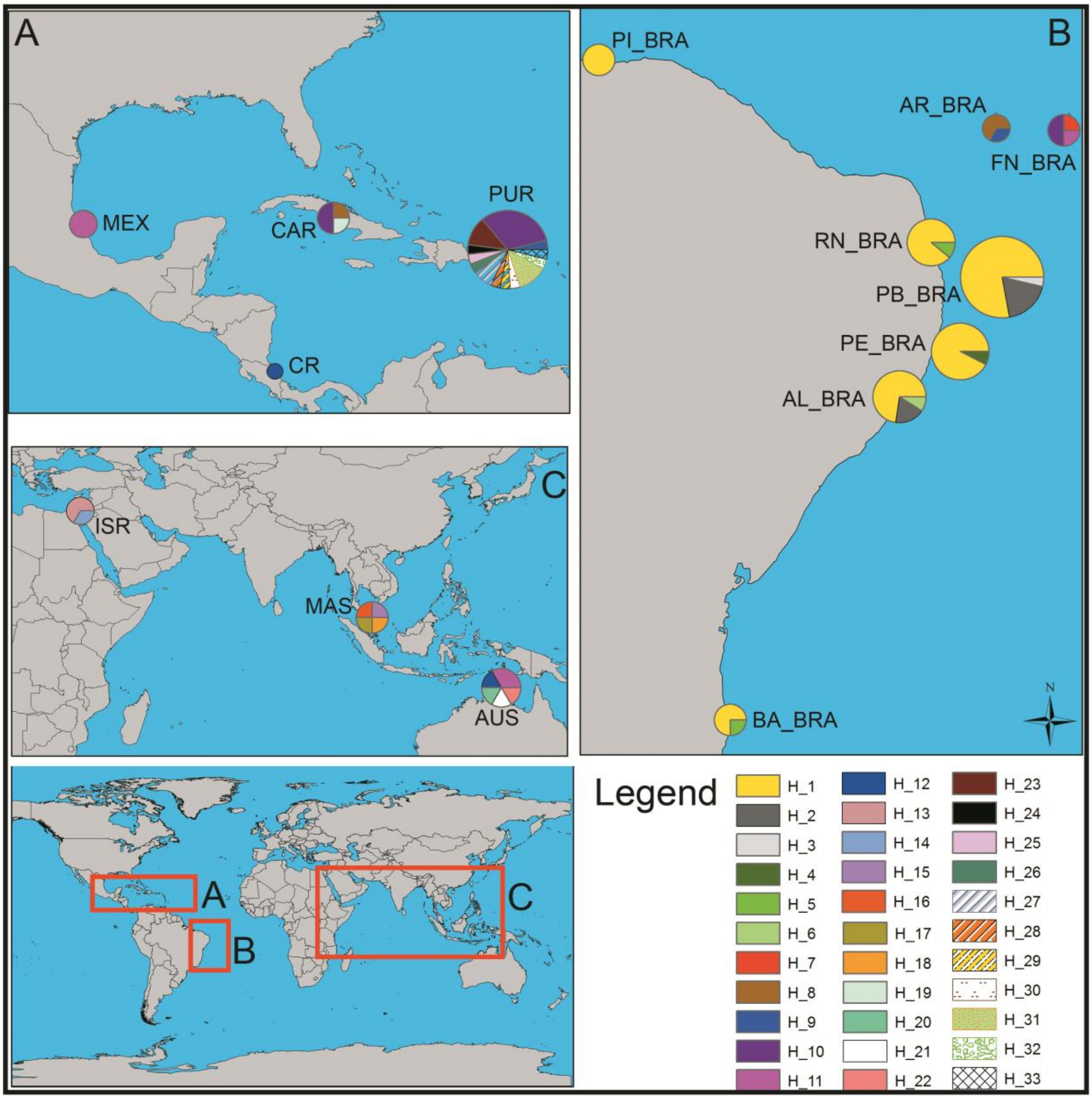

Figure 1: Map showing the location of the 15 populations of *Eretmochelys imbricata* evaluated and the spatial distribution of the 33 haplotypes recorded in the study. Each color represents a haplotype, the thickness being proportional to its frequency in each population. A) Costa Rica - CR; Mexico - MEX; Caribbean - CAR; Puerto Rico - PUR. B) Bahia - BA_BRA; Alagoas - AL_BRA; Pernambuco - PE_BRA; Paraíba - PB_BRA; Rio Grande do Norte - RN_BRA; Piaui - PI_BRA; Atol das Rocas - AR_BRA; Fernando de Noronha - FN_BRA. C) Australia - AUS; Malaysia - MAS; Israel - ISR.

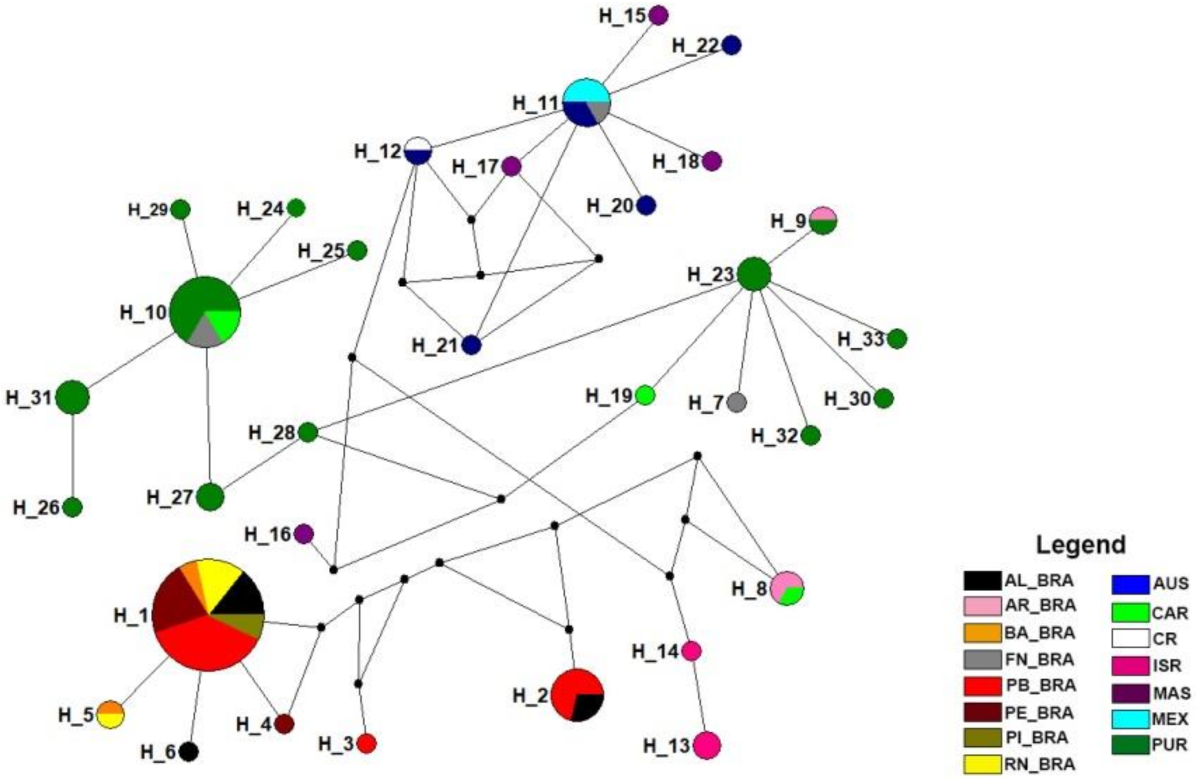

Figure 2: Haplotype network showing the relationships between the 33 haplotypes recorded in the 15 populations of *Eretmochelys imbricata*. Each circle corresponds to a haplotype, the size being proportional to its frequency. The colors represent the occurrence of haplotypes in the evaluated populations and the small black circles represent the mutational steps.

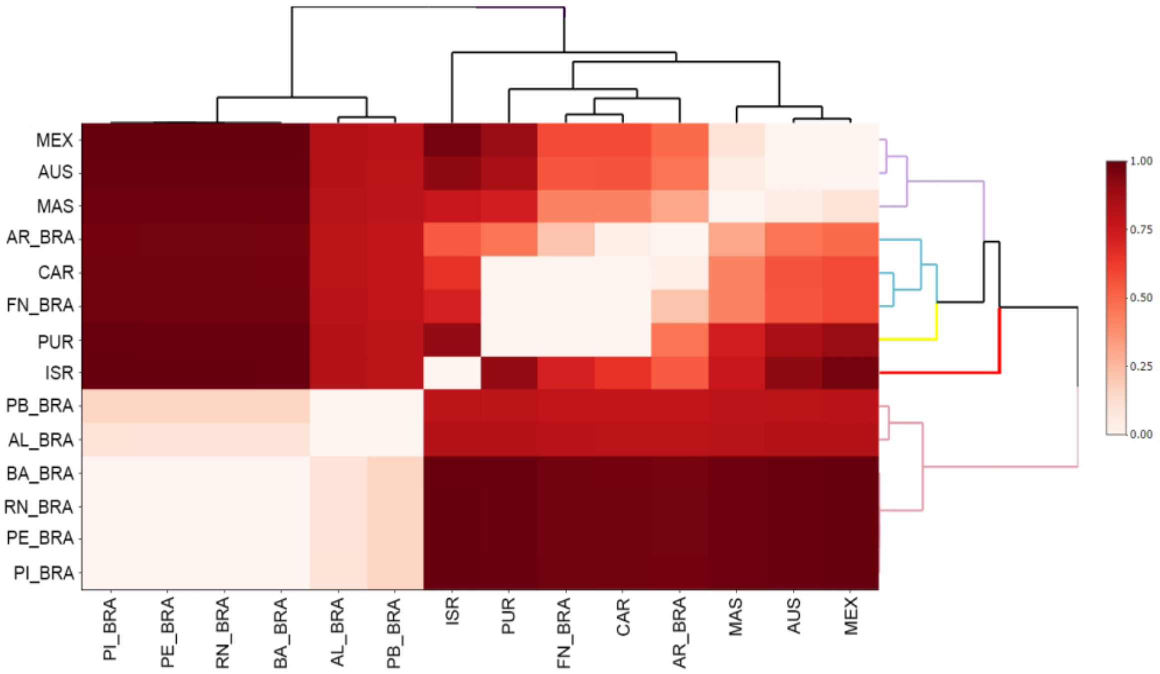

Figure 3: Heatmap of the 14 populations of *Eretmochelys imbricata* with cluster analysis with Euclidean distance and cluster average method using the FST values.

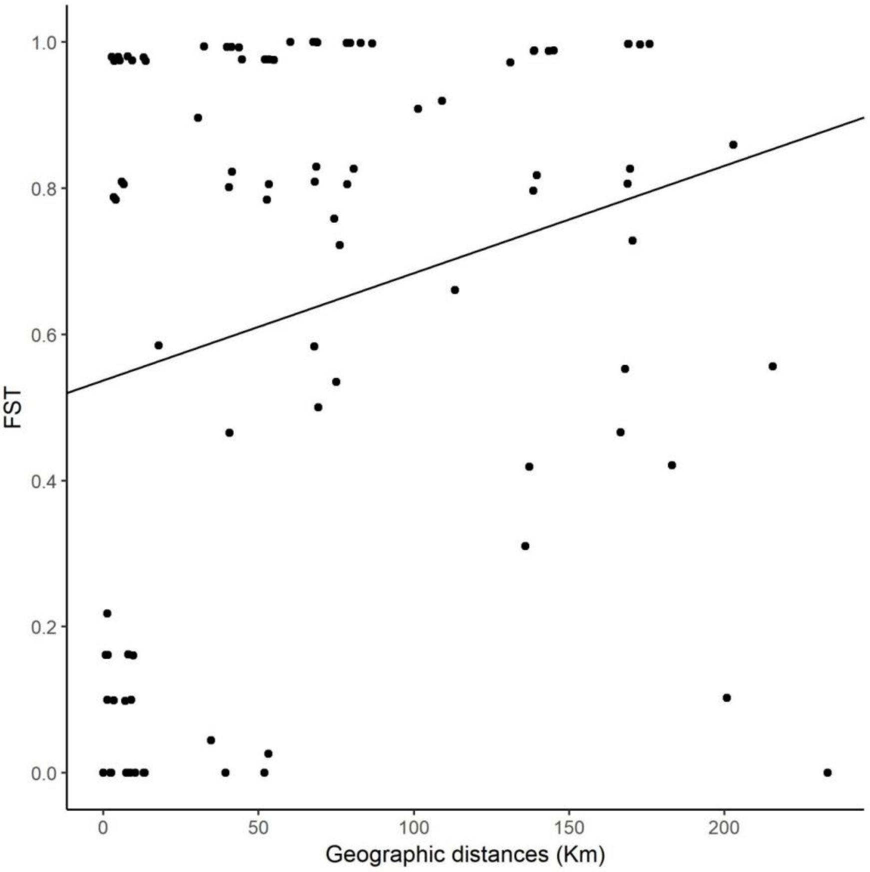

Figure 4: F_{ST} values obtained and geographical distances between the 14 populations of *Eretmochelys imbricata,* with Mantel test (r = 0.2302, p = 0.007).

Table1: Estimates of genetic diversity in the 14 evaluated populations of *E. imbricata*.

Population	Nº	Haplotype Diversity (h)	Nucleotide Diversity (π)
PI_BRA	4	0	0
PB_BRA	27	0.373	0.279
PE_BRA	13	0.153	0.000
BA_BRA	4	0.500	0.001
AL_BRA	11	0.472	0.243
RN_BRA	9	0.222	0.000
FN_BRA	4	0.833	0.029
AR_BRA	3	0.660	0.037

ISR	3	0.666	0.001
MEX	3	0	0
MAS	4	1	0.017
CAR	4	0.833	0.036
AUS	6	0.933	0.003
PUR	25	0.883	0.009
Total Estimates	**120**	**0.768**	**0.418**

Supplemental material

Table S1: Distribution of 33 haplotypes in the 15 populations of *Eretmochelys imbricata* evaluated in breeding and feeding areas.

H	PI_BRA	PB_BRA	PE_BRA	BA_BRA	AL_BRA	RN_BRA	FN_BRA	AR_BRA	CR	ISR	MEX	MAS	CAR	AUS	PUR	**Nº**
H_1	4	21	12	3	8	8	0	0	0	0	0	0	0	0	0	**56**
H_2	0	5	0	0	2	0	0	0	0	0	0	0	0	0	0	**7**
H_3	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**
H_4	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	**1**
H_5	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	**2**
H_6	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	**1**
H_7	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	**1**
H_8	0	0	0	0	0	0	0	2	0	0	0	0	1	0	0	**3**
H_9	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	**2**
H_10	0	0	0	0	0	0	2	0	0	0	0	0	2	0	8	**12**
H_11	0	0	0	0	0	0	1	0	0	0	3	0	0	2	0	**6**
H_12	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	**2**
H_13	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	**2**
H_14	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	**1**
H_15	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	**1**
H_16	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	**1**
H_17	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	**1**
H_18	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	**1**
H_19	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	**1**
H_20	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	**1**
H_21	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	**1**
H_22	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	**1**
H_23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	**3**
H_24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	**1**
H_25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	**1**
H_26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	**1**
H_27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	**2**
H_28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	**1**
H_29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	**1**
H_30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	**1**
H_31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	**3**
H_32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	**1**
H_33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	**1**
Nº/Pop	**4**	**27**	**13**	**4**	**11**	**9**	**4**	**3**	**1**	**3**	**3**	**4**	**4**	**6**	**25**	**-**

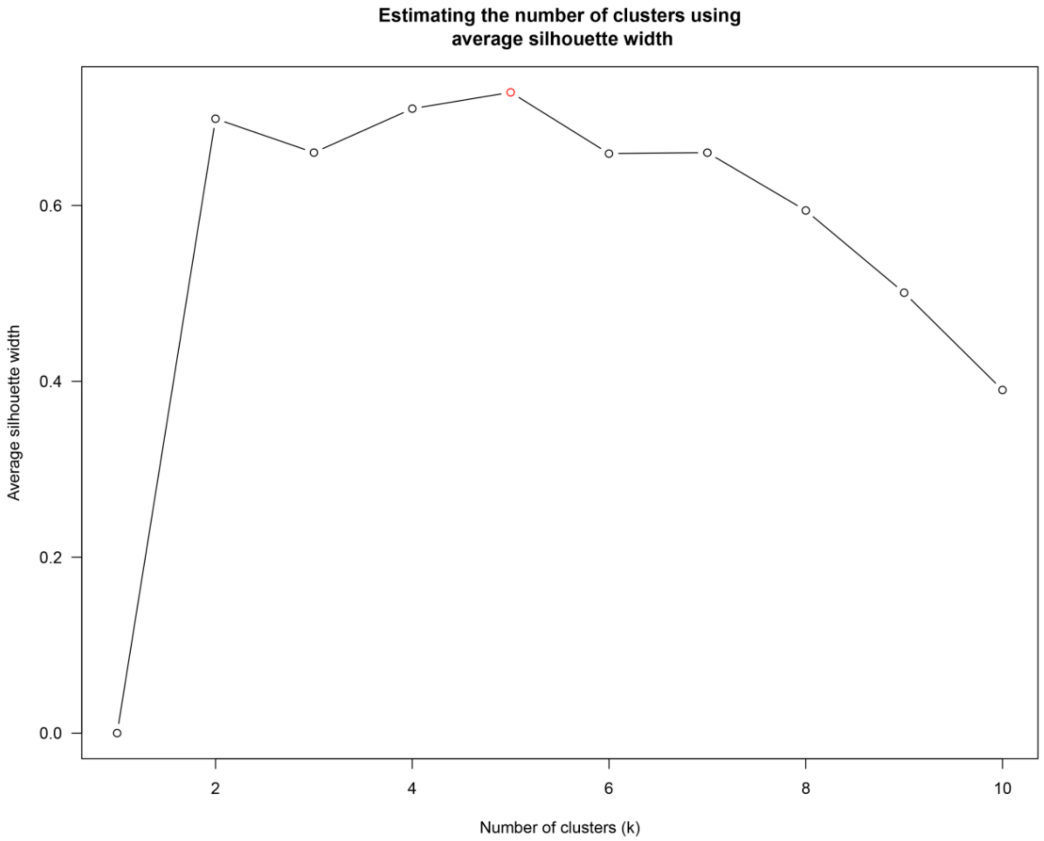

Figure S1: Estimation of the number of groups, using the **average** method for the number of K populations with 120 individuals of *Eretmochelys imbricata* in 14 evaluated populations.

4. CONSIDERAÇÕES FINAIS

Os resultados deste estudo destacaram que as pesquisas sobre migração das cinco espécies de tartarugas marinhas estão mais concentradas no continente americano. Os levantamentos de dados comprovaram que as fêmeas são mais estudadas devido ao comportamento de saírem da água para nidificar, fato o qual facilita a obtenção de dados. Porém, é crescente o número de trabalhos que analisam os trajetos das tartarugas marinhas juvenis e machos, fornecendo rotas migratórias ainda desconhecidas do ciclo de vida desses animais.

Dentre os métodos que são aplicados para rastreá-las, os transmissores via satélite tiveram os maiores registro nos últimos 12 anos de pesquisa, no entanto vale ressaltar que métodos moleculares parecem disponibilizar informações essenciais que os transmissores não conseguem alcançar. Os marcadores moleculares, como isótopos estáveis e mtDNA, são exemplos de métodos eficazes e mais econômicos para esses tipos de estudos, e principalmente para a conservação das futuras gerações. Apesar de tantos esforços conservacionistas as tartarugas marinhas ainda são classificadas como ameaçadas de extinção, ao mesmo tempo em que ainda existem muitas lacunas sobre suas rotas migratórias, havendo a necessidade de aumentar os estudos para direcionar corretamente as estratégias de conservação.

Além disso, as análises genéticas revelaram que as áreas de reprodução estudada no nordeste do Brasil são composta por uma mesma população de *E. imbricata* (geneticamente falando) e com baixa diversidade genética. Esses locais obtiveram seis haplótipos exclusivos, característica que é comum para espécie devido ao comportamento filopatrico. Assim como nas áreas de reprodução, os locais de alimentação e forrageamento apresentaram 27 haplótipos exclusivos, os quais são compartilhados apenas entre estas áreas, além de ter alta diversidade genética que provavelmente pode ser explicada pelas correntes oceânicas que dispersão esses animais. Logo, ficou evidente que não houve compartilhamento de haplótipos entre as áreas de reprodução e alimentação, as análises mostraram a formação de cinco grupos que de maneira geral também separou as áreas de reprodução das de alimentação. Esses resultados indicam que além das corretes oceânicas possíveis isolamentos geográficos podem está justificando a separação dos grupos.

Portanto, os dados desta pesquisa sobre os locais de nascimento de tartaruga de pente no Brasil sugerem que são Unidades de Manejo que precisam de estratégias de conservação adequados, visto que a maioria dos locais sofre interferência humana que ameaçam os animais. A pesquisa também indica que a inclusão e/ou ampliação das Unidades de Conservação próximas a essas regiões podem ser uma alternativa para a manutenção da espécie. De modo geral, os dois capítulos desta tese disponibilizaram informações indispensáveis à conservação das tartarugas marinhas. Salientando que futuras pesquisas precisam ser intensificadas sobre rotas migratórias ainda desconhecidas, como também se faz necessário aumentar o conhecimento genético das populações de *E. imbricata* em áreas de reprodução e alimentação.

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