



# Hybridization and genetic characterization of sea turtles in Alagoas, northeastern Brazil

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Received: 1 April 2022 / Accepted: 22 December 2022 / Published online: 5 January 2023  
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## Abstract

Sea turtles are migratory species with wide geographical distributions, usually spanning multiple countries. This characteristic, along with their complex life cycle, makes sea turtle conservation challenging. In Brazil, continued monitoring and recent studies have advanced the knowledge of sea turtle genetic composition and population structure. Some of these studies have shown that hybridization is highly frequent in certain regions along the Brazilian coast, despite being relatively rare globally. Here, we investigate the hybridization and genetic diversity of sea turtles in nesting and feeding grounds in the state of Alagoas, northeastern Brazil, using the control region of mitochondrial DNA and three nuclear loci. We were able to identify hybrids between four sea turtle species, but mainly between *Caretta caretta* and *Eretmochelys imbricata* and *C. caretta* and *Lepidochelys olivacea*. Most hybrids were readily identified using morphology and mitochondrial DNA, but some were only detected with nuclear DNA. Apart from hybrids, the genetic profile of each species was congruent with previous studies in Brazil. However, one stranded *E. imbricata* had a haplotype (Ei-IP17) and nuclear allele typically found in the Indo-Pacific, suggesting long distance migration for this species. Our results indicate that hybridization events might be even more geographically spread along the coast of Brazil and provide evidence of the connection between *E. imbricata* from the Atlantic and Indo-Pacific Ocean basins.

**Keywords** Population genetics · Hawksbills · Loggerheads · Olive ridleys · Green turtles · Hybrids

## Introduction

Sea turtles are migratory species with complex life cycles. Five of the seven sea turtle species have wide distributions across different regions of the globe with distinctive habitat changes throughout their lifespan (Bolten 2003). This migratory behavior can make conservation planning challenging,

particularly when sea turtle movement patterns span different countries, thereby requiring collaborative conservation efforts (Wallace et al. 2010). To address this challenge and guide conservation planning at smaller scales, regional management units (RMUs) have been suggested for sea turtles based on distributional and ecological data (Wallace et al. 2010). Among these RMUs, the Southwest Atlantic Ocean (SWA) exhibited considerable threat levels for sea turtle populations (Wallace et al. 2011). Nevertheless, recent studies have reported population recovery at some nesting sites in the region, likely due to continuing conservation efforts in recent decades (Marcovaldi et al. 2007; Colman et al. 2019).

In Brazil, efforts on sea turtle conservation have been historically conducted by TAMAR institute (Marcovaldi and Marcovaldi 1999). Additionally, a National Action Plan for Sea Turtle Conservation (PAN Tartarugas Marinhas) was established in 2010 and it is currently in its second phase (ICMBio 2017). Research priorities established by the PAN Tartarugas Marinhas include the identification and monitoring of nesting and feeding grounds of the five sea turtle species known to occur along

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Responsible Editor: Christophe Eizaguirre .

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Tamí Mott and Robson G. Santos have contributed equally to this study.

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the Brazilian coast: *Caretta caretta* (loggerhead turtles), *Chelonia mydas* (green turtles), *Dermochelys coriacea* (leatherback turtles), *Eretmochelys imbricata* (hawksbill turtles) and *Lepidochelys olivacea* (olive ridley turtles) (Marcovaldi et al. 2007), as well as the evaluation of genetic profiles, population dynamics and hybridization between these species (ICMBio 2017). Research on sea turtle genetic diversity in nesting and feeding grounds in Brazil has increased in recent years (Reis et al. 2010b; Naro-Maciel et al. 2012; Proietti et al. 2014a; Jordão et al. 2015). Some studies have reported a high hybridization frequency in a few nesting sites in northeastern Brazil (Lara-Ruiz et al. 2006; Reis et al. 2010a) however, this seems to be rare in sea turtle populations worldwide (Brito et al. 2020). In Brazil, hybridization rates can reach up to 42% between hawksbills and loggerheads on the coast of the state of Bahia (Lara-Ruiz et al. 2006), and 27% between loggerheads and olive ridleys on the coast of the state of Sergipe (Reis et al. 2010a).

A high hybridization rate in wild populations may lead to several evolutionary outcomes, including the enhancement of genetic diversity and adaptative divergence (Abbott et al. 2013). However, it can also compromise small populations by limiting their growth rate through the production of inviable offspring (Todesco et al. 2016). The consequences of these processes in sea turtles are not yet completely understood, but a few studies have observed some differences in behavior and reproductive success between hybrids and parental species (Proietti et al. 2014b; Soares et al. 2017; Arantes et al. 2020a). For instance, while the clutch size of loggerhead and hawksbill hybrids has been reported as intermediate, emergence success was lower in hybrids (Soares et al. 2017; Arantes et al. 2020a). Likewise, post-emergence behavior can also be slightly divergent. Some hybrids, morphologically identified as one parental species, may adopt the migration patterns of the other (Proietti et al. 2014b). Furthermore, these hybrids are not likely to be completely inviable since genetic studies using mitochondrial DNA (mtDNA) and nuclear DNA (nDNA) have detected crosses between F1 hybrids and parental species (e.g., Vilaça et al. 2012; Brito et al. 2020; Arantes et al. 2020c).

Factors promoting this high hybridization frequency in Brazil require further investigation, but the broad spatial and temporal overlapping in sea turtle breeding activities, particularly in northeastern Brazil, certainly favors hybridization (Vilaça et al. 2012). Loggerhead and hawksbill breeding activities overlap along the northern coast of Bahia (Fig. 1), which is the largest nesting site for both species in the SWA (Lara-Ruiz et al. 2006; Marcovaldi et al. 2007). Loggerhead nests extend north along the coast of Sergipe State, where they now coincide with olive ridley nests and several hybrids between the two species have been reported in this area (Reis et al. 2010a). Olive ridley nests extend to the southern coast

of Alagoas State, where loggerhead nests become sparse, but still occur.

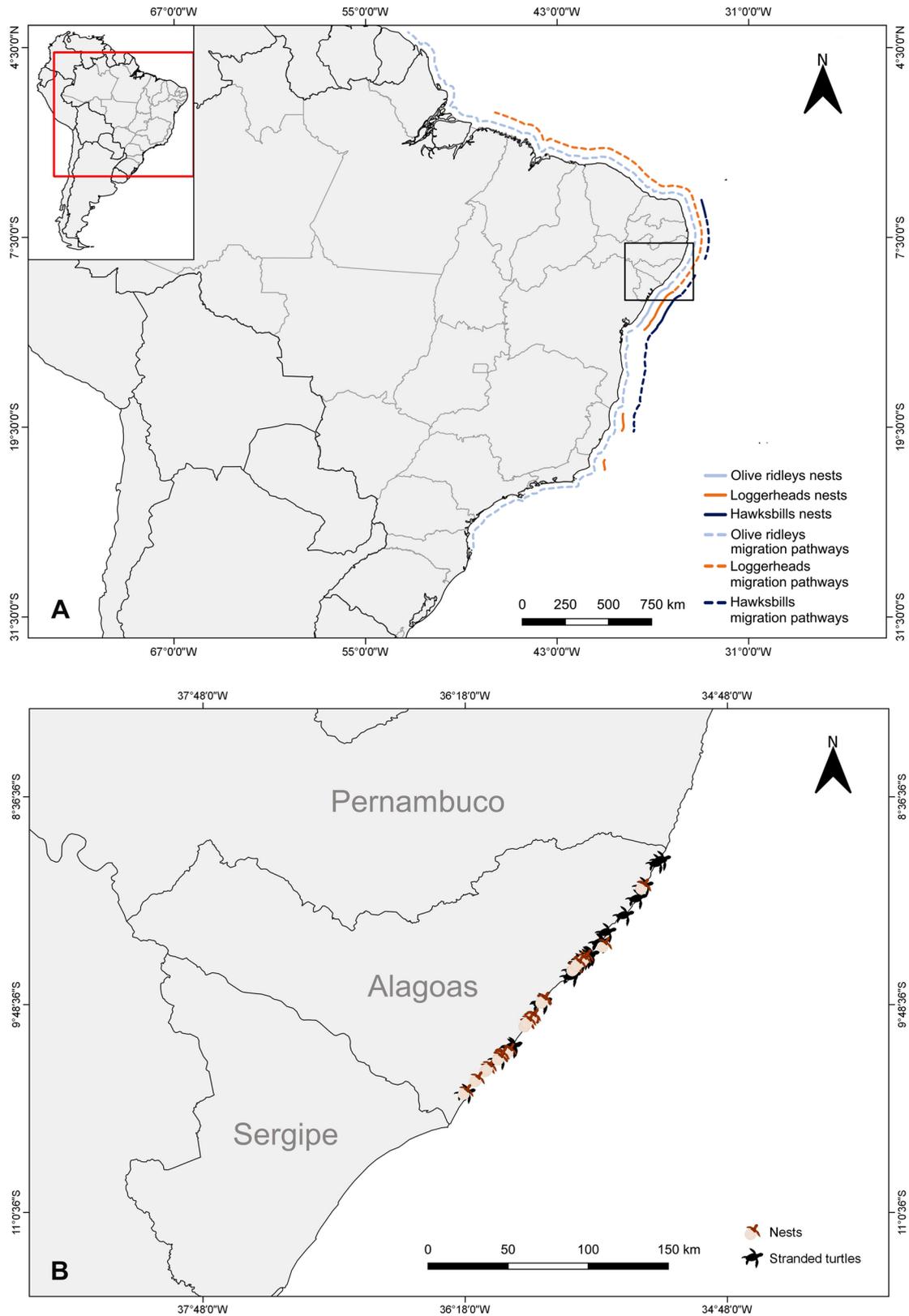
The coast of Alagoas is an important area for sea turtles, harboring extensive coral reefs that act as feeding and development grounds. Currently, five sea turtle species can be found in this region: loggerheads, green turtles, hawksbills, leatherbacks and olive ridleys; although leatherback sightings are rare (Oliveira et al. 2016; Bonfim et al. 2022). Olive ridley nests are frequent in the southernmost portion of Alagoas, while nests of the other species are present throughout the coast of this state. Green turtle nests are rare, but this species uses the coast of Alagoas as a feeding ground extensively. Furthermore, satellite tracking studies have shown that hawksbills and loggerheads from Bahia, as well as olive ridleys from Sergipe nesting sites, usually feed in Alagoas or pass through while migrating to northern feeding grounds (Fig. 1A, Marcovaldi et al. 2012).

These conditions may enable interactions among sea turtle species in Alagoas, facilitating hybridization, but so far only one stranded hybrid (between a hawksbill and loggerhead) has been reported in the region (Brito et al. 2020). Based on the conditions presented above, our hypothesis is that the presence of hybrids in the region is highly possible. Therefore, our main goal was to assess hybridization among sea turtle species occurring along the coast of Alagoas using morphology, mtDNA and nDNA data.

## Methods

We used 53 muscle samples collected along the coast of Alagoas (Fig. 1B) by the *Instituto Biota de Conservação* between May 2019 and April 2021. Samples were taken from stranded turtles, as well as from hatchlings found dead after emergence events. Our sampling focused mainly on hawksbills and loggerheads as more nest samples were available for these species, but we also included olive ridley and green turtle samples for comparative purposes. Twenty-four samples were taken from turtles that were morphologically identified as hawksbills (15 hatchlings and nine stranded turtles), 23 from loggerheads (14 hatchlings and nine stranded turtles), three from olive ridleys (one hatchling and two stranded turtles) and three from green turtles (all stranded turtles). The morphology of stranded turtles and hatchlings was assessed in the field upon sample collection by staff of *Instituto Biota de Conservação* and hatchling morphology was also examined in the laboratory. Species were morphologically identified through the examination of scutes on the carapace, inframarginal scutes on the plastron and prefrontal scales on the head (Pritchard and Mortimer 1999). Each hatchling sample was collected from a different nest.

Total genomic DNA was extracted using the phenol–chloroform method (Sambrook et al. 1989), and a fragment of



**Fig. 1** Approximate distribution of the main nesting sites and movement pathways of loggerhead, hawksbill and olive ridley turtles on the coast of the SWA (A). Solide lines indicate nesting sites and dashed lines indicate movement pathways based on sattelite tracking

studies (Marcovaldi et al. 2010, 2012; Santos et al. 2019; Soares et al. 2021). Sea turtles sampling along the coast of Alagoas State, SWA (B)

621 base pairs (bp) of the mtDNA control region was recovered through polymerase chain reaction (PCR) using the primers LCM15382 and H950 (Abreu-Gobrois et al. 2006). To better evaluate putative hybrids we also employed three nuclear loci: the oocyte maturation factor *mos* (CMOS) using the primers LIZ-CMOS and HCMOS-III (Kearney and Stuart 2004) and two anonymous loci, 3061 and 109472 using the primers described by Arantes et al. (2020c). We chose these nuclear loci because they have been shown to present informative variability between loggerhead, hawksbill and olive ridley sea turtles (Vilaça et al 2012; Arantes et al. 2020c). In addition to the primers we used, for the CMOS fragment, we also ran tests with primers developed for sea turtles. We ultimately chose these primers because they provided higher amplification success. We then aligned our CMOS sequences with sequences from GenBank, generated with primers developed for sea turtles, to make sure the fragments overlapped. The CMOS fragment was approximately 550 bp while 3061 and 109472 were approximately 320 bp each. While mtDNA was sequenced for all samples, nDNA was only amplified for a subset of samples. This subset included all hybrids identified through morphology and mtDNA (see results) and a few representatives of each species (confirmed by morphology and mtDNA) for comparative purposes (Online Resource 1). PCR reactions consisted of 20.8 µl of 1X Master Mix PCR Buffer with 0.4 mM of each dNTP and 3 mM of MgCl<sub>2</sub>, 1.0 µl of each primer (10 pmol); 0.2 µl of Taq DNA polymerase (5 U/µl) and 2 µl of DNA template (10–100 ng/µl). Control region fragments were amplified using the following conditions: initial denaturation at 94 °C for 7 min followed by 40 cycles of denaturation at 94 °C for 30 s, annealing at 50 °C for 30 s, extension at 72 °C for 1 min and a final extension at 72 °C for 5 min. Nuclear loci fragments were amplified using the same protocol, except for 109472 annealing temperature which was 58 °C. Negative controls were included to check for contamination. Successfully amplified samples were purified with isopropanol and sequenced through Sanger sequencing using the forward primer.

All sequences were checked for contamination using the BLAST tool in GenBank and for some samples we repeated DNA extraction, PCR and sequencing to double check our results. We edited the sequences using Bioedit v7.1.3.0 (Hall 1999) and aligned them with MAFFT v7 using the L-INS-i algorithm (Katoh and Standley 2013). Mitochondrial haplotypes were identified using the Archie Carr Center for Sea Turtle Research database (<https://accstr.ufl.edu/resources/mtdna-sequences/>) and nuclear sequences were identified using the GenBank database (<https://www.ncbi.nlm.nih.gov/genbank/>). Nuclear alleles were reconstructed using the PHASE algorithm implemented in DNAsp v5 (Librado and Rozas 2009). For the purposes of this study, we considered a specimen to be a hybrid when it had the morphology

of one species and mtDNA or nDNA of a different species. Additionally, we used nDNA to perform an assignment analysis to determine the most likely association and generation of hybrids. We performed this analysis using three different species pairs: hawksbills and loggerheads, loggerheads and olive ridleys, and hawksbills and olive ridleys. The remaining species were not considered because of their small sample size (see results and Online Resource 1). The analysis was performed using *snappclust* as implemented in the R package *adegenet* (Jombart 2008; R Core Team 2021). For each analysis, we set the number of expected clusters to two ( $k=2$ ), indicated the presence of hybrids between each species pair (hybrids = TRUE) and specified the hybridization coefficient for F1 and first-generation backcross (hybrid.coef = c(0.5, 0.25)). All other parameters were run as default.

## Results

Overall, it was possible to identify all specimens based on the morphological characteristics of each species. However, some specimens were degraded or exhibited morphological characteristics of more than one species (see detailed results below). Mitochondrial haplotypes of all 53 samples were successfully identified according to the Archie Carr Center database, meaning that no new haplotypes were found (Online resource 1). Amplification of nDNA was less effective than mtDNA, particularly for stranded turtles, likely due to the lower abundance of nDNA coupled with sample degradation caused by long environmental exposure. Consequently, we were only able to recover one locus for most samples (Online Resource 1). In total, we identified nine hybrids out of 53 samples, three (5.6%) with only one source of evidence (weakly supported) and six (11.3%) with more than one source of evidence (strongly supported). Five hybrids were hatchlings from local nests and four were stranded turtles (Table 1). Details on hybridization and overall genetic characterization are given below.

## Hybridization

We identified four hybrids from nest samples based solely on morphology and mtDNA. One sample was a hatchling identified as a hawksbill (T6R40), which had the CC-A4 haplotype, typical of loggerheads. The three remaining hybrids (T4R14, T9R1-2019 and MIR1) had loggerhead morphology and the haplotype-F, unique to olive ridleys. Specimen T9R1-2019 was from an olive ridley nest but exhibited malformations and asymmetry of lateral scute counts, five on the right side and seven on the left side (Online resource 2). Regarding the nuclear dataset, we successfully recovered sequences from the three analyzed loci for all four hybrids. The hawksbill x loggerhead hybrid (T6R40) had alleles of

**Table 1** Sea turtle hybrids found on the coast of Alagoas, Brazil between 2019 and 2021

Field number	Type	Morphology				mtDNA	nDNA			Hybridization evidence
		Lateral scutes	Inframarginal scutes	Pairs of prefrontal scales	Id		3061	109472	CMOS	
T9R1/20	Nest	4/6*	4	–	Ei	Ei	Ei	Ei/Lo	Ei	Weak
MIR1	Nest	5	3	2	Cc	Lo	Cc	Cc/Lo	Cc	Strong
T9R1/19	Nest	5/7*	4	2	Cc	Lo	Lo	Lo	Lo	Weak
T6R40	Nest	4	4	–	Ei	Cc	Ei/Cc	Ei/Cc	Ei	Strong
T4R14	Nest	5	4	2	Cc	Lo	Cc	Cc/Lo	Cc/Lo	Strong
T3T68	Stranded turtle	4	4	–	Ei	Ei	–	–	Ei/Cc	Weak
T4T8	Stranded turtle	4	–	–	Cm	Cc	–	–	Cc	Strong
T4T363	Stranded turtle	4	4	–	Ei	Cc	Ei	–	–	Strong
T5T279	Stranded turtle	5	3	2	Cc	Cm	Cc	–	Cc	Strong

\*indicate specimens with malformations. Details on morphology, haplotypes and alleles can be found in Online Resource 1

both species at the 3061 and 109472 loci, but only hawksbill alleles at CMOS. One of the three loggerhead x olive ridley hybrids (T9R1-2019) only had olive ridley alleles at the three nuclear loci. The second (T4R14) only had loggerhead alleles at 3061, but alleles of both parental species at 109472 and CMOS. The last sample (MIR1) only had loggerhead alleles at 3061 and CMOS, and alleles of both species at 109472.

Using nDNA, we were also able to identify one more hybrid from nests (T9R1-2020), not detected with mtDNA or morphology. The new hybrid had hawksbill morphology and mtDNA (Ei-BR16) but exhibited an olive ridley allele at the 109472 locus while having only hawksbill alleles at 3061 and CMOS (Table 1). This specimen was classified as a hybrid with weak evidence because it had a single olive ridley allele, while morphology and all other genetic evidence indicated that it was a hawksbill. Nevertheless, this specimen also exhibited dorsal scute malformations (Online resource 2). Membership probabilities of nest hybrids indicated that T6R40 was likely an F1 hybrid (46.9%), T4R14 was likely a loggerhead (41.8%) or a backcross of a F1 hybrid and a loggerhead (40.4%), MIR1 likely a loggerhead (58.1%) and that T9R1-19 was likely an olive ridley (75.6%, Fig. 2). Membership probabilities of T9R1-2020 were higher for hawksbills (55.8%) and for a backcross between an F1 hybrid and a hawksbill (35.7%, Fig. 2).

Among stranded turtles, one of the four hybrids was identified as a hawksbill (T4T363), but had the loggerhead CC-A4 haplotype. The second hybrid had loggerhead morphology, and the CM-A8 haplotype (T5T279), typical of green turtles. The third hybrid had green turtle morphology and the CC-A4 haplotype (T4T8) from loggerheads. The last hybrid (T3T68) was only identified by nDNA. While this specimen had hawksbill morphology and mtDNA, it presented a loggerhead allele at CMOS. Nuclear data from the other hybrids revealed that the hawksbill x loggerhead

hybrid (T4T363) only had hawksbill alleles at 3061. One green turtle x loggerhead hybrid (T5T279) only had loggerhead alleles at both 3061 and CMOS loci, while the other sample (T4T8) also only had loggerhead alleles at CMOS (Online Resource 1).

Membership probabilities of T3T68 and T4T363 were higher for loggerheads (42.5%) and hawksbills (52.9%), respectively (Fig. 2). Membership probabilities of green turtle x loggerhead hybrids were not estimated due to the low recovery of green turtle alleles.

## Genetic characterization

Except for the five hybrids, all remaining nest samples ( $n = 25$ ) exhibited haplotypes from their respective species. Eleven hatchlings, identified as hawksbills, exhibited the Ei-A01 haplotype, one had the Ei-BR16 haplotype and one had the Ei-BR10 haplotype, all typical of the species. All 11 non-hybrid loggerhead hatchlings had the CC-A4 haplotype, typical of the species. The single hatchling identified as olive ridley had the haplotype-F, which is also unique to this species (Online Resource 1). All non-hybrid samples evaluated for 3061 (total  $N = 16$ ), 109472 (total  $N = 11$ ) and CMOS (total  $N = 6$ ) had alleles compatible with their morphological identifications (Online Resource 1).

The eight stranded turtles with hawksbill morphology had haplotypes typical of the species: Ei-A01 (4), Ei-BR10 (2), Ei-BR16 (1) and Ei-IP17 (1). The latter is commonly found in hawksbills from Indo-Pacific nesting sites in the Seychelles Islands and Chagos archipelago. To corroborate the identification of this sample, we performed DNA extraction, PCR and sequencing a second time and the same haplotype was recovered. All eight non-hybrid stranded turtles identified as loggerheads had the CC-A4 haplotype, characteristic of this species. The two turtles identified as olive ridley had

**Fig. 2** Membership probabilities of hawksbill, loggerhead and olive ridley specimens and their hybrids as recovered using nuclear loci 3061, 109472 and CMOS. Probabilities were estimated for three pairs of species: hawksbills and loggerheads **A** olive ridleys and loggerheads **B** and hawksbills and olive ridleys **C** Hybrids are indicated in bold

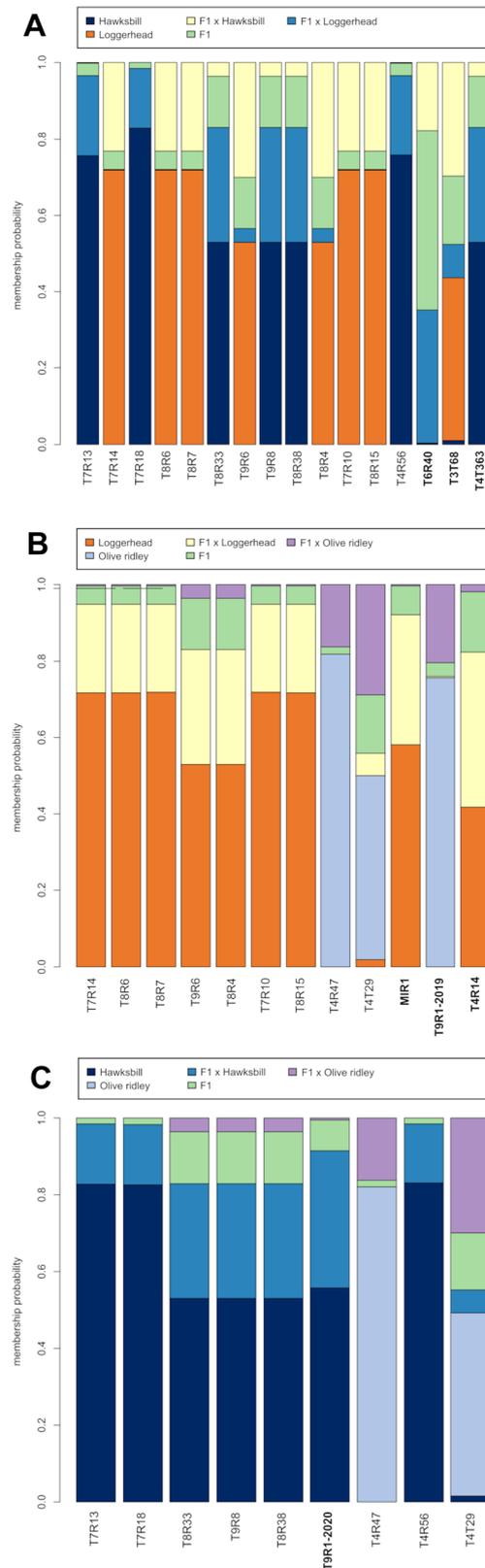
the haplotype-F and the two green turtles had the CM-A8 haplotype, both unique to each species (Online Resource 1).

### Discussion

In this study, we contribute to the current knowledge on sea turtle hybridization in the SWA. Here, we found hybrids among four sea turtle species: loggerheads, hawksbills, green turtles and olive ridleys. We also expanded sampling on loggerheads and hawksbills in understudied nesting areas in Alagoas and observed that the genetic profile of these species is very similar to what is found in other nesting sites in the SWA (Lara-Ruiz et al. 2006; Reis et al. 2010b). Remarkably, we observed a hawksbill haplotype typical of the Indo-Pacific in the Alagoas feeding ground. This is not the first time an Indo-Pacific haplotype has been observed in the Atlantic, which reinforces the connection between these regions (Arantes et al. 2020b). Below we discuss these topics in detail.

### Hybridization

Hybrids among sea turtle species have already been reported in the SWA (Fig. 3), where loggerhead x hawksbill and loggerhead x olive ridley hybrids are particularly more frequent (Lara-Ruiz et al. 2006; Reis et al. 2010a; Proietti et al. 2014a; Brito et al. 2020). Although the causes for the high hybridization frequency between these species are still not completely clear, the temporal and spatial overlapping of their breeding activities likely facilitates this process (Reis et al. 2010a). While breeding activities of these species are still understudied in Alagoas, it is possible to find nests of these three species along the coast of this state (Oliveira et al. 2016), which may facilitate hybridization between them. In fact, all hybrids between loggerheads and olive ridleys (3) found here were from nests. All of these samples had loggerhead morphology and olive ridley mtDNA, the same pattern observed in hybrids from Sergipe nesting site (Reis et al. 2010a). The two remaining hybrids from Alagoas nests had hawksbill morphology. One had loggerhead mtDNA (CC-A4, T6R40), the same pattern found in most hybrids from Bahia (Lara-Ruiz et al. 2006), and the other had an olive ridley allele in the 109472 nuclear locus (T9R1-2020). Hybridization between hawksbills and olive ridleys have been reported in the SWA before, but this appears to



**Fig. 3** Known reports of sea turtle hybrids in the Southwest Atlantic Ocean. *ARG* Argentina, *URU* Uruguay, Brazilian States: *AL* Alagoas, *BA* Bahia, *ABR* Abrolhos Archipelago, Bahia, *CE* Ceará, *RS* Rio Grande do Sul, *SE* Sergipe. Source of hybrid records: Arantes et al. (2020a): *ABR*, Brito et al. (2020): *AL*, *BA*, *CE*, *ES*, *RS*, *URU*; Karl et al. (1995): *BA*; Lara-Ruiz et al. (2006): *BA*; Proietti et al. (2014b): *CE*, *RS*; Prodocimi et al. (2014): *ARG*; Reis et al. (2010a): *SE*; This study: *AL*



be much less frequent (Lara-Ruiz et al. 2006; Brito et al. 2020). Nuclear data from nest samples also revealed that these hybrids are likely F1 or backcrosses with parental species (Fig. 2), which indicates that hybridization may be an ongoing process in the region.

Among the stranded turtle hybrids, two had hawksbill morphology. One specimen had loggerhead mtDNA (T4T363) while the other (T3T68) had loggerhead nDNA that matched an Indo-Pacific loggerhead allele (as did its hawksbill mtDNA). The only other hybrid previously reported from Alagoas was a hybrid between these species, a stranded turtle with hawksbill morphology and loggerhead mtDNA (CC-A4) (Brito et al. 2020). However, both species use the Alagoas coastline as both feeding and reproductive grounds, thus it is difficult to determine how these stranded specimens were using this area. It is plausible that the T4T363 specimen could have originated from the Bahia nesting site, since a particularly high frequency of hawksbill x loggerhead hybrids have been reported there (Lara-Ruiz et al. 2006) and individuals from this nesting site are also reported to migrate through Alagoas (Marcovaldi et al. 2012). On the other hand, the loggerhead Indo-Pacific allele we found in the T3T68 specimen, seems to reinforce that this

specimen was indeed from that region (see detailed discussion below).

The remaining stranded hybrids (2) identified through mtDNA were crosses between green and loggerhead turtles. Hybrids between these species are less common in the SWA, probably due to the low overlapping in their nesting activities. While loggerhead nests are mainly found on the Brazilian mainland coast, green turtle nests are mostly concentrated on oceanic islands, such as Rocas Atoll and Trindade, and are sparse on continental areas within the SWA (Marcovaldi and Marcovaldi 1999; Marcovaldi and Chaloupka 2007). Nevertheless, some green turtle nests can be found along the Brazilian coast, mainly in the northern region of Bahia, the main nesting site for loggerheads in Brazil (Lara-Ruiz et al. 2006). So, it is plausible that this region is the probable origin of these hybrids.

Understanding the role hybrids play in sea turtle population structure is particularly important given their status as threatened species (IUCN 2022), especially when we take climate change effects into consideration. Many sea turtle populations are already reported to have strong female bias (Hays et al. 2014; Jensen et al. 2018), which tends to be even more exacerbated with the predicted

rise of global temperatures (IPCC 2021). Higher nesting beach temperatures could not only promote higher female output, and consequently higher female proportions in natural populations, but also increase hatchling mortality (Hays et al. 2017). Furthermore, the decrease in beaches available for nesting due to sea level rise and coastal urbanization can potentially cause shifts in habitat use (Fuentes et al. 2010, 2011), which can promote further overlapping of breeding and nesting activities of these species. If these environmental and anthropogenic factors act synergistically, we may likely observe an increase in hybridization frequency over time. Thus, the continuous monitoring of ecological and genetic aspects of these populations is fundamental.

The use of a multilocus approach to investigate hybridization in these populations has been shown to be essential for improving our understanding of the hybridization process (Vilaça et al. 2012; Brito et al. 2020; Arantes et al. 2020c). Here, we were only able to use three nDNA loci, which precludes us from reaching more conclusive results, particularly on hybrid generation. The lower success rate in the amplification of these loci in stranded specimens, likely due to sample deterioration, also limited our interpretation of these data. The use of nonspecific primers for the CMOS gene also warrants caution in the interpretation of these data. However, all but one allele observed in this locus have been identified before using sea turtle primers. Only one hybrid was defined by CMOS data, all other hybrids can be identified using mtDNA or the other two nDNA loci (Table 1, Online Resource 1). Despite these limitations, the inclusion of nDNA allowed us to identify hybrids that would otherwise not have been observed solely using mtDNA and morphology. Nevertheless, as suggested by previous studies, a better comprehension of hybrid ecology is required to understand how this high hybridization frequency along the Brazilian coast can affect population dynamics (Vilaça et al. 2012; Arantes et al. 2020c).

Studies on the spatial distribution of nesting and feeding grounds, as well as genetic diversity are initial in Alagoas. Consequently, information on breeding periodicity, sex ratios and comprehensive genetic characterizations are still unavailable. Nevertheless, sex ratio studies on loggerhead and hawksbill nesting on the Brazilian coast indicate high female bias (Marcovaldi et al. 1997; Godfrey et al. 1999), thus it is likely that future studies will reveal a similar pattern for Alagoas. Therefore, constant monitoring of this population, regarding shifts in habitat use and population parameters, is extremely important to better understand the consequences of hybridization and thereby, improve conservation actions.

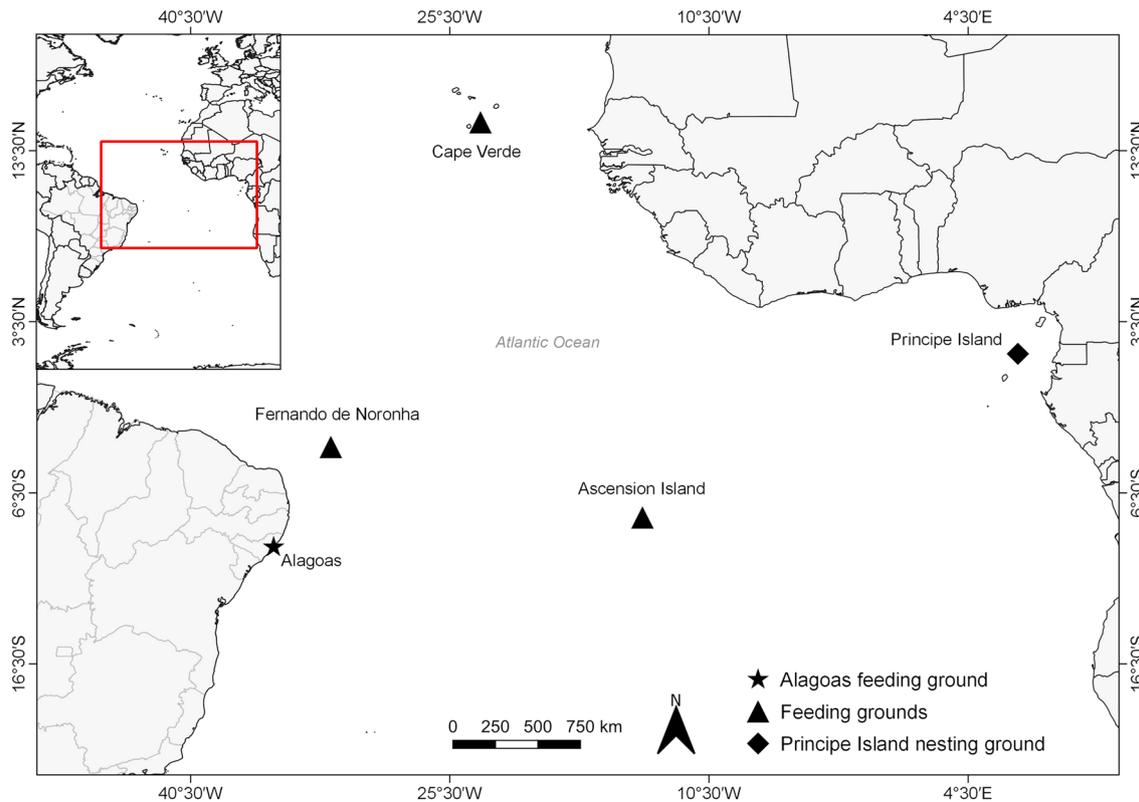
## Genetic characterization

The genetic diversity of hawksbill and loggerhead nests in the study area was similar to other reproductive areas in the SWA. The CC-A4 haplotype, observed in all non-hybrid loggerhead nests (11), is widely found in loggerhead nesting sites in Brazil (Reis et al. 2010b). Likewise, among the three haplotypes we identified in non-hybrid hawksbill nests (14), the Ei-A01 is widely distributed throughout feeding grounds in the SWA and in the two major hawksbill nesting sites in Brazil: Bahia and Rio Grande do Norte (Proietti et al. 2014a; Simões et al. 2021). The two other haplotypes, Ei-BR16 and Ei-BR10, are both exclusive to Brazilian nesting sites (Lara-Ruiz et al. 2006). Additionally, the single olive ridley nest sample had the haplotype-F, which is the only haplotype observed for olive ridleys in the SWA to date (Bowen et al. 1997).

We observed that all stranded loggerheads (9) had the same CC-A4 haplotype found in the nests. As mentioned above, this haplotype is the most commonly observed in loggerhead nesting and feeding sites in Brazil and is also exclusive to this region (Reis et al. 2010b). This low haplotype diversity is also in accordance with previous studies and the presence of this exclusive Brazilian haplotype reinforces that the specimens analyzed here likely originated from Brazilian nesting sites (Reis et al. 2010b). We observed a similar genetic profile in stranded hawksbills with haplotypes commonly found in Brazilian nesting sites: Ei-BR10 (2), Ei-BR16 (1) and Ei-A01 (1) (Lara-Ruiz et al. 2006; Proietti et al. 2014a; Simões et al. 2021). Finally, the presence of the Ei-IP17 haplotype was surprising since this haplotype is only found in Indo-Pacific nesting sites (Vargas et al. 2016), implications of which are discussed below.

In general, the genetic profile we observed for both species suggests that feeding grounds are mostly occupied by individuals from local nesting sites. Satellite tracking studies also suggest that the study area is within a migratory corridor for loggerheads and hawksbills migrating from their main nesting area in Bahia to feeding grounds farther north, but it is also the final destination for some of these individuals (Marcovaldi et al. 2010, 2012).

The occurrence of the Ei-IP17 haplotype among our stranded samples was a surprising and novel result, since this haplotype is typical for Indo-Pacific nesting sites in the Seychelles Islands and Chagos Archipelago (Vargas et al. 2016), suggesting a connection between the Atlantic and Indo-Pacific Oceans. To our knowledge, this is the first time the Ei-IP17 haplotype has been reported in an Atlantic feeding ground. Two other Indo-Pacific haplotypes, Ei-IP16 and Ei-IP33, have been previously reported in feeding grounds in Fernando de Noronha and Ascension Island (Fig. 4, Arantes et al. 2020b). Additionally, three orphan haplotypes



**Fig. 4** Known occurrences of hawksbill Indo-Pacific haplotypes in south Atlantic feeding and nesting sites. Star denotes the study site in the state of Alagoas, northeastern Brazil

(Ei-A49, Ei-A70 and Ei-A75) observed in the Atlantic feeding grounds of Ascension Island, Fernando de Noronha, Cape Verde and Principe Island, group together with haplotypes from the Indo-Pacific (Arantes et al. 2020b). The same occurs with the EATL haplotype observed in the Principe Island nesting site in Africa (Monzón-Argüello et al. 2011; Arantes et al. 2020b).

Haplotype sharing between Atlantic and Indo-Pacific Oceans can also be seen in loggerhead, green and leatherback turtles (Dutton et al. 1999; Bourjea et al. 2007; Shamblin et al. 2014), and migrations in both directions through southern Africa have been suggested. For instance, the CM-A8 haplotype, widely found in green turtle nesting sites in the Atlantic, can also be found in the Mozambique nesting site (Bourjea et al. 2007), a similar pattern to that of the loggerhead CC-A2 haplotype (Shamblin et al. 2014). Loggerhead haplotypes from the Indo-Pacific have also been observed in the Atlantic, suggesting that westward migrations may also occur (Shamblin et al. 2014). Colonization of the Atlantic by olive ridleys is suggested to have occurred through southern Africa (Bowen et al. 1997). Likewise, haplotype sharing between hawksbill nesting sites in Principe Island and in

the Indo-Pacific led Monzón-Argüello et al. (2011) to suggest the colonization of this east African nesting site by hawksbill migrants from the Indo-Pacific. Thus, although it seems plausible that the Ei-IP17 haplotype found here could have originated directly from the Indo-Pacific, we cannot disregard putative unsampled nesting sites in east Africa as a possible origin, since hawksbill haplotypes from such sites have already been found in SWA feeding grounds (Proietti et al. 2014a).

The hawksbill sample analyzed here was from a juvenile male (curved carapace length of 42.1 cm), which could indicate an occasional incursion. We also observed Indo-Pacific alleles in the CMOS locus of seven additional hawksbill, loggerhead and olive ridley samples (Online Resource 1). Due to the generally slower evolutionary rates of nuclear genes, these alleles may have persisted at low frequencies in Atlantic sea turtle populations after their separation from Indo-Pacific lineages. On the other hand, this may evidence that at least some gene flow between Atlantic and Indo-Pacific sea turtles still exists. Nevertheless, wider sampling of feeding and nesting grounds in the Atlantic is required to help elucidate hawksbill and other sea turtle population structure and migration pathways.

## Concluding remarks

Although relatively rare in sea turtles, hybridization seem to be very common in Brazilian nesting and feeding grounds (Lara-Ruiz et al. 2006; Brito et al. 2020, our study). Although our total sample size was relatively small, we were still able to detect hybrids in Alagoas nests, as well as in stranded animals (11.3% of our total sampling), including putative crosses between hybrids and parental species. This suggests that hybridization events may be common in the region, as seen in other sites in the SWA, such as Sergipe and Bahia (Lara-Ruiz et al. 2006; Reis et al. 2010a). Most hybrids were readily identified using only morphology and mtDNA, however the use of nuclear data revealed new hybrids that would otherwise remain unidentified, which highlights the importance of using an integrative approach when studying hybridization (Vilaça et al. 2012; Brito et al. 2020).

The use of mtDNA and nDNA also revealed a possible connection between feeding grounds in the study area and nesting sites in the Indo-Pacific. Understanding these connections and migratory pathways is essential to the development of appropriate conservation strategies and is one of the main priorities in sea turtle research (Hamann et al. 2010). Although a more comprehensive research effort is required to clarify the connections between sea turtles in the Atlantic and Indo-Pacific, our findings represent the fifth hawksbill locality in the South Atlantic with Indo-Pacific haplotypes (Arantes et al. 2020b), reinforcing the connection between these regions.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s00227-022-04168-y>.

**Acknowledgements** JPFAA thanks FAPEAL for providing PhD scholarship (#23038.023347/2016-74). TM thanks Conselho Nacional de Desenvolvimento Científico e Tecnológico—CNPq (309904/2015-3 and 312291/2018-3) for financial support. We thank Camila Domitt, Maíra Proietti and Kim Barão for kindly read and comment on an earlier version of the manuscript. We also thank the editor and two anonymous reviewers for constructive comments on the manuscript.

**Author contributions** JPFAA, TM and RGS contributed to the study conception and design. OKLM participated in sample collection and material preparation. Sample processing and data analysis were performed by JPFAA. The first draft of the manuscript was written by JPFAA and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

**Funding** This study was partially funded by Fundação Grupo Botânico de Proteção da Natureza (#1143/20182) and PADI Foundation (#47777/2020). Beach monitoring and sample collection was partially supported by Long Term Ecological Research–Brazil site PELD-CCAL funded by the Brazilian National Council for Scientific Research and Technological Development (CNPq–#441657/2016-8, #442237/2020-0) and the Research Support Foundation of the State of Alagoas (FAPEAL–#60030.1564/2016, #PLD2021010000001).

**Data availability** All data generated in this study is provided in the article and online resources or was described previously and is already available at the GenBank database.

## Declarations

**Conflict of interest** The authors declare no conflict of interest.

**Ethical approval** All applicable national guidelines for sampling of organisms for the study have been followed and all necessary approvals have been obtained from local authorities (SISBIO 57705–12).

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