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Do loggerhead sea turtle (*Caretta caretta*) gut contents reflect the types, colors and sources of plastic pollution in the Southwest Indian Ocean?

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ABSTRACT

We analyzed plastic debris ingested by loggerheads from bycatch between 2007 and 2021 in the Southwest Indian Ocean (SWIO). We also analyzed plastic debris accumulated on beaches of the east coast of Madagascar as a proxy for ocean plastics to compare the characteristics of beached plastics and plastic ingested by turtles. We conducted a "brand audit" of the plastics to determine their country of origin. An oceanic circulation model was used to identify the most likely sources of plastics in the SWIO. In total, 202 of the 266 loggerheads analyzed had ingested plastics. Plastics categorized as "hard" and "white" were equally dominant in loggerheads and on beaches, suggesting no diet selectivity. Both the brand audit and circulation modeling demonstrated that Southeast Asia is the main source of plastic pollution in the region. This study demonstrates that loggerheads can be used as bioindicators of plastic pollution in the SWIO.

1. Introduction

Because of their invaluable physical properties (lightweight, resistant, waterproof, inexpensive, and flexible), plastic products are used worldwide in a large range of applications. Global plastic production has increased tremendously, from 1.5 million metric tons in 1950 to 460 in 2019 (OECD, 2022). It is estimated that 4.8 million to 12.7 million metric tons of plastic waste enter the oceans annually (Jambeck et al., 2015). Terrestrial sources (rivers, land) contribute to 80 % of global ocean plastic pollution, while the remaining 20 % originates from marine activities (fisheries, shipping, Faris and Hart, 1994). Globally, plastics represent 40 to 80 % of coastal debris and 90 % of the debris floating offshore on the surface of the ocean (Galgani et al., 2013; Ryan, 2014). Floating plastics are transported by sea currents and wind along considerable distances (Pruter, 1987; Van Sebille et al., 2020). These debris have deleterious direct effects on many marine species through their ingestion (Schuyler et al., 2014; Senko et al., 2020) or via entanglement (Mann et al., 1995; Laist, 1997). Indirect negative effects may also occur through their toxicity due to endocrine disruptors (Verla et al., 2019). In addition, plastic debris provide floating substrates for "hitchhiking organisms" such as invasive species or pathogens (Therriault et al., 2018).

Plastic debris are found everywhere, including on the sea floor (Ryukyu Trench: Shimanaga and Yanagi, 2016; Marianna Trench: Chiba et al., 2018), in polar environments (Convey et al., 2002), and on beaches of remote islands (Lavers and Bond, 2017; Moy et al., 2018; Lavers et al., 2019). The most persistent fraction of floating plastic debris accumulates on garbage patches within subtropical oceanic gyres in all oceans (Lebreton et al., 2012; Maximenko et al., 2012; Cozar et al., 2014, Litterbase: https://litterbase.awi.de/litter). The North Pacific subtropical gyre, with an accumulation covering an area of at least 1.6 million km^2, has garnered the most attention (Moore et al., 2001; Boerger et al., 2010; Goldstein, 2012; Choy and Drazen, 2013; Chen et al., 2018; Lebreton et al., 2018; Egger et al., 2020; Egger et al., 2021).

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In contrast, the location of the garbage patch in the subtropical Indian Ocean gyre is less studied. One of the possible consequences of this lack of knowledge is that the area of plastic accumulation is not well characterized and located. Some oceanographers have located the patch in the western part of the basin (Maximenko et al., 2012; Van Sebille et al., 2015; van der Mheen et al., 2019; Pattiaratchi et al., 2022) and others in the eastern part (Lebreton et al., 2012; Maes et al., 2018; Peng et al., 2021). Plastic pollution in the Indian Ocean is reported at the surface (Ryan, 2013; Eriksen et al., 2014; Woodall et al., 2015) and on remote islands (Maldives: Imhof et al., 2017; Saliu et al., 2018; Saint Brandon: Bouwman et al., 2016; Seychelles: Duhec et al., 2015, Dunlop et al., 2020; review: Pattiaratchi et al., 2022). Plastic ingestion in the Indian Ocean has been described in seabirds (Ryan, 2008; Cartraud et al., 2019), sea turtles (Hoarau et al., 2014; Ryan et al., 2016), sharks (Cliff et al., 2002), fishes (Fujieda et al., 2008) and deep-sea organisms (Taylor et al., 2016).

Almost 4000 species have been recorded to interact with marine litter all over the world (ingestion, entanglement, impact, Litterbase, 09/03/23: https://litterbase.awi.de/interaction). Some of these species are used as marine litter bioindicators (Van Gestel and Van Brummelen, 1996; GESAMP, 2019). Seabirds (Van Franeker and Law, 2015), sea turtles (Schuyler et al., 2014; Savoca et al., 2022), fishes (Chavarry et al., 2022) and invertebrates (Van Cauwenberghe and Janssen, 2014) provide different information on plastic debris depending on their feeding strategies and body size. Benthic, sessile and filtering species are generally used to monitor coastal pollution, while offshore foragers are used to monitor plastic pollution in the pelagic environment (GESAMP, 2019; Savoca et al., 2022).

As a migratory species, loggerhead sea turtles (*Caretta caretta*, Linnaeus 1758) travel long distances during their lifetime and could be impacted by ingesting plastic debris mistaken for natural prey (Carr, 1986; Bjorndal, 1997; Lazar et al., 2011; Dalleau, 2013; Schuyler et al., 2014; Pham et al., 2017; Pfaller et al., 2020}. Loggerhead sea turtles regularly ingest plastic debris (Bjorndal et al., 1994; Hamann et al., 2010; Lazar et al., 2011; Hoarau et al., 2014; Santos et al., 2016; Savoca et al., 2022). Rizzi et al. (2019) reported that loggerhead sea turtles select red plastics mistaken for red coastal prey such as crabs or mollusks. Schuyler et al. (2012) noted less diet selectivity during the pelagic life stage. As carnivorous turtles, loggerheads have a stronger intestinal wall than herbivorous turtles (such as green turtles, *Chelonia mydas*), which results in better resistance to plastic debris ingestion (Frick et al., 2009), and can defecate ingested plastics (Hoarau et al., 2014). Green turtles and hawksbills (*Erethmochelys imbricata*) are more prone to develop gastrointestinal blockages due to plastic ingestion, and both species have a higher probability of dying (Schumacher et al., 1996; Abreo et al., 2016).

The loggerhead sea turtle is used as a bioindicator of marine plastic pollution in the Mediterranean Sea (Marine Strategy Framework Directive MSFD, Matiddi et al., 2017; GESAMP, 2019) and in the North Atlantic (Pham et al., 2017).

In this study, we explored the possibility of using this species as a bioindicator of plastic pollution in the Southwest Indian Ocean (SWIO).

To do so, we quantified the characteristics of the plastic items found in turtle guts. This included plastic category, color, size and weight. We compared these characteristics with those of plastic items found on beaches of the eastern coast of Madagascar, assuming that this plastic pollution is representative of marine plastic pollution in the known foraging areas of the species in the SWIO (Dalleau et al., 2014). This comparison enabled us to determine whether the turtles "select" a given category or color of plastic or if they ingest them randomly as a function of their abundance (selectivity or opportunism). Finally, we identified the origins of plastics ingested by turtles and beached using a "brand audit" and a dispersal oceanic model.

2. Materials and methods

2.1. Plastic debris ingested by late-juvenile loggerheads

To quantify plastic debris ingested by loggerhead sea turtles, we studied 266 late-juvenile loggerheads from bycatches by longliners operating in the SWIO between 2007 and 2021. Bycaught loggerheads were brought alive to Reunion Island and rehabilitated in a rescue center specialized in sea turtle rehabilitation (hereafter referred to as Kelonia). Loggerheads were caught in oceanic waters, mostly between Reunion Island and the east coast of Madagascar (Fig. 1). The geographical position of each capture was recorded by fishers. After surgery for hook extraction, all sea turtles entering Kelonia received appropriate rehabilitation treatments in individual tanks by caretakers. All turtles were measured (curve carapace length (cm)) and weighed (kg) upon their arrival at Kelonia. We calculated the body condition index (BCI) as BCI = [mass / (length^3) × 100,000] following Bjorndal et al. (2000). Loggerheads defecated plastic debris in the tanks for a mean duration of 2 weeks and a maximum of 6 months during their care. All feces and plastic debris were collected daily with a sieve of 5 mm mesh. Plastic debris were sorted from feces visually, cleaned with alcohol, and left to air dry for 24 h. Loggerheads that did not survive were necropsied following the protocol of Wyneken (2001), and plastic debris were collected from gut contents. For this study, we used the term "ingested" for all plastic debris collected after excretion (feces) or during necropsies. We determined the frequency of occurrence (%FO) of plastic debris ingested by loggerheads annually and globally since 2007 as the ratio between the number of loggerheads having ingested plastic debris and the total number of loggerhead sea turtles analyzed.

2.2. Plastic debris accumulated on beaches

Three beaches were monitored on the east coast of Sainte Marie Island (Madagascar, Fig. 1. A): Albran Est (16°71′38"S, 50°02′11″E), Ambohidena (16°88′89"S, 49°94′69″E) and Ampanihy (16°91′38"S, 49°93′02″E). These sites were chosen because they meet the following criteria of beach selection for plastic debris monitoring (see Henry, 2010; GESAMP, 2019; Barnardo and Ribbink, 2020): they are mostly uninhabited, easy to access, directly exposed to the open ocean and have a moderate slope and small-grain size substrate.

Our studied beaches are located in front of the South Equatorial Current (SEC) that crosses the Indian Ocean from east to west, including the known feeding areas of the loggerheads in the SWIO (Mencacci et al., 2010; Dalleau et al., 2014). All sampling was performed outside the beach clean-up period. Samples were collected in March 2018. For each beach, plastic debris were collected along three belt transects that were 50 m long and 10 m wide, parallel to the coastline and located in the supralittoral zone. The island's main economic activity is located on the west coast, with the nearest village or harbor located >5 km from Ampanihy and 20 km from Albran Est. For this study, we used the word "accumulated" to define plastic debris washed up on beaches.

2.3. Plastic debris characterization

In this study, we analyzed plastic debris over 5 mm long. This includes mesoplastics (>5 to 25 mm) and macroplastics (>25 mm), following the classification proposed by the GESAMP, (2019). Plastic debris ingested by loggerheads and accumulated on beaches were counted, measured (maximum length), weighed (to 0.01 g) and sorted according to category and color. We defined three main categories: (1) hard plastic, (2) soft plastic (i.e., rubber, Styrofoam, foam, plastic bags), and (3) fishing-related debris (i.e., lines, ropes, fishing stoppers, etc.). We considered seven general colors: (1) black, (2) white, (3) blue, (4) red, (5) yellow, (6) green, and (7) colorless.

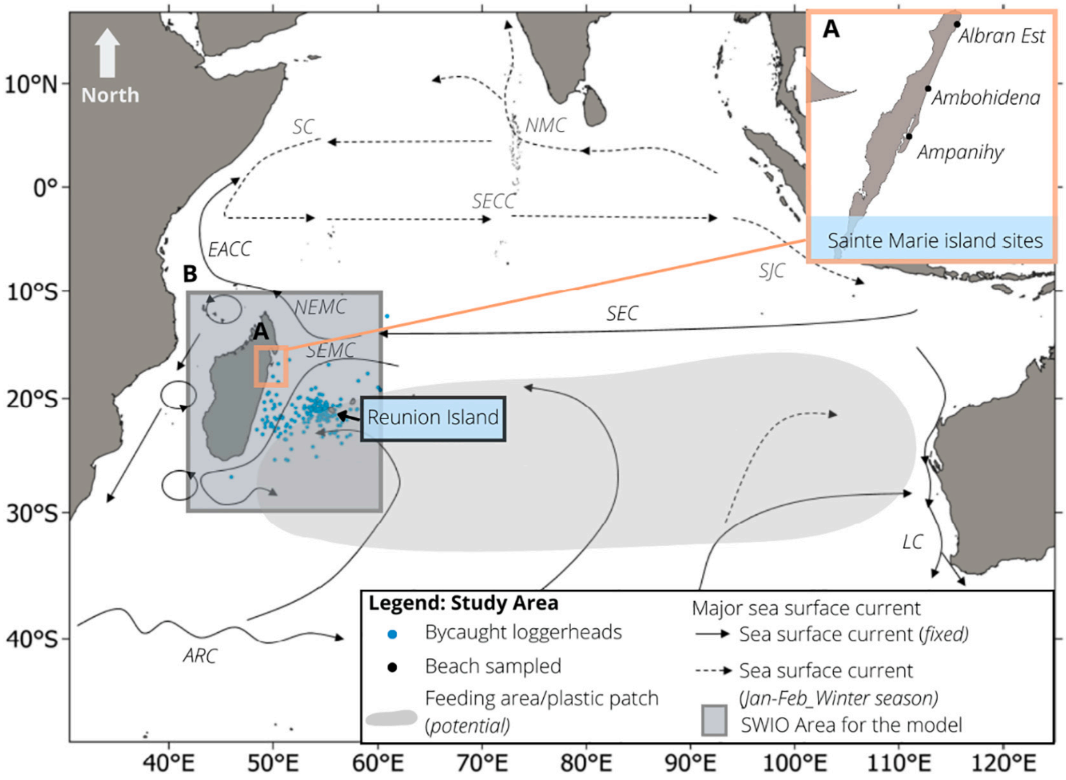

Fig. 1. Study area. Location of 266 juvenile loggerheads sea turtles bycatch; (A) Sampling beach locations in Sainte Marie Island, Madagascar; (B) SWIO area for the inverse dispersal model (between latitudes 10°S and 30°S and the longitude 42°E and 60°E). Arrows represent the major sea surface currents in the Indian Ocean, adapted from Peng et al. (2015); South Equatorial Current (SEC), South Equatorial Counter Current (SECC), Northeast and Southeast Madagascar Current (NEMC and SEMC), East African Coastal Current (EACC), Leeuwin Current (LC), Agulhas Return Current (ARC), Northeast Monsoon Currents (NMC), South Java Current (SJC).

2.4. Statistical analysis

We tested the normality and homoscedasticity of the abundance and weight data of plastic debris ingested by loggerheads and accumulated on beaches with Shapiro–Wilk and Levene's tests, respectively. We tested for differences in the size classes of plastic debris found in the feces of live loggerheads and those found in dead turtles upon necropsy by running Kruskal–Wallis tests with a post hoc analysis using Wilcoxon correction and Bonferroni adjustment. We tested for differences in the abundance and weight of plastic debris beached at each site (Albran Est, Ampanihy, and Ambohidena) using Kruskal–Wallis tests and Kruskal–Wallis multiple comparison nonparametric tests. We tested for differences in abundance and weight between the categories and colors of plastic debris ingested and accumulated on the beach using the same nonparametric tests. Plastic debris abundance is expressed as the number of items per individual (item/ind) and per beach surface (item/m^2) for loggerheads and beaches, respectively. Plastic weight is expressed as the item mass per individual (g/ind) and per beach surface (g/m^2). Data are reported as the mean ± standard error.

2.5. Feeding strategy: selectivity or opportunism?

The correlation between abundance and weight for ingested and accumulated plastic was investigated using pairwise Spearman rank correlation. A selectivity test was conducted using the Manly–Chesson index (Manly, 1974; Chesson, 1978). The selectivity value reflects a preference for ingesting specific plastic debris categories or colors in loggerheads in comparison with the availability of the debris in the environment. Values range from 0 for a complete opportunistic diet to 1 for a complete selective diet:

$$\alpha i = \frac{ri/pi}{\sum_{j=1}^{m}(rj/pj)}, i = 1, 2, \ldots m$$

where αi = selectivity index for plastic category or color i, i = plastic debris category or color, ri = the proportion of plastic debris in the i category or color ingested, and pi = proportion of plastic debris of category/color i in the environment. m is the total number of categories or colors. All analyses were performed in R version 3.2.3 (R Core Team., 2022), with the “selectapref” package applied for calculating the Manly selectivity index (Richardson, 2020).

2.6. Determination of the origin of plastic debris

2.6.1. “Brand audit”

The origin of plastic debris can be inferred with a “brand audit” (Barnardo and Ribbink, 2020). A “brand audit” consists of examining each piece of debris and recording any information such as an incrusted or painted brand name or the language, which may help determine the country of origin (Duhec et al., 2015; Smith et al., 2018). This analysis can be performed only on large debris (macroplastics). When available, for each identified brand, we recorded the manufacturer, the type of product (e.g., food packaging, household product, personal care product), the subtype of the product (e.g., drink, mineral water, oil container), the written polymer code (e.g., high-density polyethylene, HDPE; polyethylene terephthalate, PET; polystyrene, PS), the total number of items ingested by loggerheads and accumulated on beaches, and the website link when available (see the supplementary material). The “brand audit” was reinforced by online investigations (Duhec et al., 2015; Ryan, 2020). First, if the brand name was legible, we searched for the brand by using different search engines (e.g., Google, Yahoo, Ecosia), and we changed the search setting language to Indonesian, Chinese, Japanese, Korean or Thai, depending on the language used for the brand. If we obtained only pictures or logos, we performed a "search by image". We also used keywords to describe our item, for example, brand, drink, bottle, cap, food, or cosmetic, also in different languages. Once the website of the company was found, we noted all information about production and exportation areas. If we did not find the official website, we went through sales sites, press article links or Wikipedia links to collect information. The category "International" was created when the country could not easily be identified, mostly for brands established and sold internationally. This analysis provided the first map of the countries of origin of macroplastics ingested by loggerheads and accumulated on the beaches of Sainte Marie Island.

2.6.2. Reverse dispersal model of plastic debris floating in the SWIO

To complete and validate our analysis of debris origin obtained by the 'brand audit', we used results from an existing global dispersal model for floating marine litter (see Lebreton et al., 2012). In this model, plastic debris is represented by weightless Lagrangian tracers that are released in modeled sea surface currents. For these simulations, sea surface current data were sourced from the HYCOM/NCODA (Hybrid Coordinate Ocean Model/the Navy Coupled Ocean Data Assimilation) global oceanic current reanalysis (Cummings, 2005). Particles were released into the model from estimated source points corresponding to two scenarios:

(i) Terrestrial source: calculated from data on population density in all countries at a global scale (Jambeck et al., 2015),
(ii) Marine source: calculated from data on fishing efforts (Watson et al., 2013) at a global ocean scale. This model does not include maritime traffic.

The model tracks the trajectory of particles from their date of release for a maximum simulation period of 30 years. For this study, we extracted the origin trajectories of all modeled particles arriving in the SWIO area. This area is delimited by latitudes between 10°S and 30°S and longitudes between 42°E and 60°E, corresponding to an area of nearly 4,400,000 km^2 (Fig. 1.B). We extracted the relative contributions of particle inputs by country expressed in numbers of model particles for each scenario. This resulted in 15 subregions and 127 countries and islands being identified. Two other maps with different source scenarios (terrestrial and marine) were created and compared to the 'brand audit' map.

3. Results

3.1. Characterization of plastic debris

3.1.1. Loggerhead Sea turtles

The average curve carapace length of the 266 loggerheads was 70.23 ± 7.31 cm, with a weight of 45.94 ± 9.78 kg and a BCI of 6.36 ± 1.22. In total, 202 (76 %) loggerheads had ingested plastic debris, among which 41 were analyzed by necropsy and 161 were analyzed during their rehabilitation. We found 10,513 plastic particles for a total weight of 3237 g. The frequency of plastic ingestion increased from 25 % in 2007 to 79 % in 2021, corresponding to an average %FO of 70 ± 20 % for the entire period (2007–2021, Fig. 2). The mean duration of plastic debris defecation was 15.5 ± 9.8 days, with a maximum of 179 days during care. On average, loggerheads that had plastics in their feces or guts (N = 202) ingested an abundance of 56.83 ± 4.59 items/ind (mean ± se, minimum = 1 item, maximum = 428 items). This corresponds to a mean weight of 16.69 g ± 17.62 (minimum = 0.01 g, maximum = 111.58 g). Macroplastics represented 32 % of the items in terms of abundance and 69 % in terms of weight. Mesoplastics represented 68 % of the items in terms of abundance and 31 % in terms of weight. There were significantly more macroplastics found in guts than in feces (Wilcoxon Rank, p = 0.044). There was no difference in abundance between categories (hard, soft, and fishing plastic, p.values >0.05) for plastics found in dead loggerheads (gut necropsies) and for plastic found in live loggerheads (feces analysis).

Hard plastic was the most common category ingested ($\chi^2 = 341.89$, df = 2, $p < 0.0001$, Fig. 3.A), representing 80 % of the total plastic debris, with an abundance of 50.1 ± 3.94 items and a weight of 15.5 ± 1.05 g per loggerhead. The soft plastic and fishing plastic categories were less represented, with abundances of 3.14 ± 0.47 and 0.84 ± 0.12 items per loggerhead and weights of 0.56 ± 0.15 g and 0.54 ± 0.11 g per loggerhead, respectively.

Most ingested plastics were white ($\chi^2 = 262.54$, df = 6, $p < 0.0001$, Fig. 4. A), representing 54 % of the total plastic debris, with an abundance of 26.5 ± 2.28 items and a weight of 8.36 ± 0.727 g per loggerhead. The second most abundant color was blue, with an abundance of 6.38 ± 0.727 items and a weight of 3.20 ± 0.332 g per loggerhead. We observed colorless and black plastics with abundances of 4.24 ± 0.775 items and 4.03 ± 0.426 items, respectively, and weights of 0.844 ± 0.203 g and 2.42 ± 0.267 g per loggerhead. Red, yellow and green plastics were rarely found.

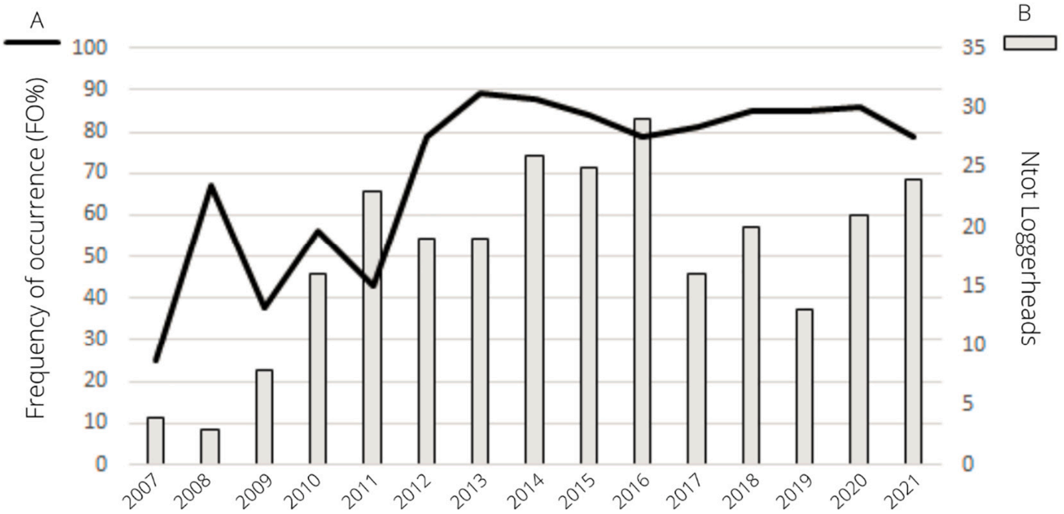

Fig. 2. (A) Frequency of occurrence of plastic debris ingested by loggerheads sea turtles from 2007 to 2021; (B) abundance of loggerheads sea turtles entered in Kelonia rehabilitation center by year.

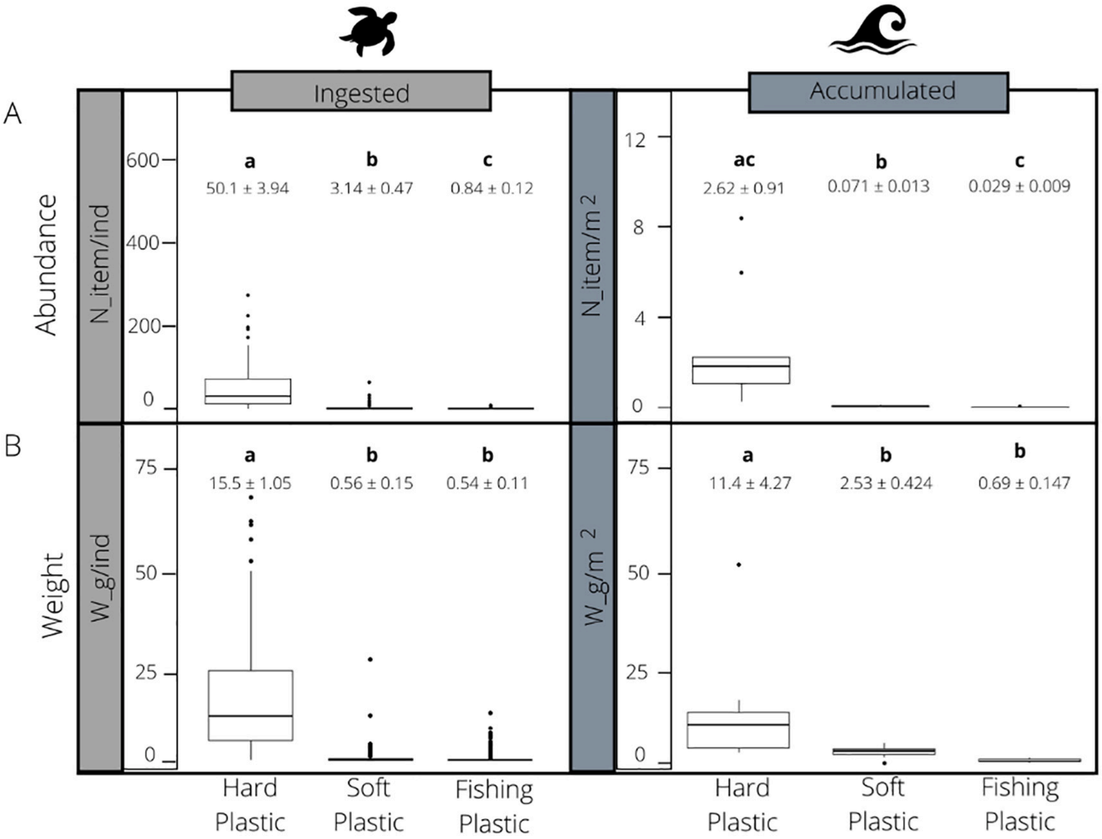

Fig. 3. Boxplot and mean ± se of A) the abundance and B) weight of plastic debris ingested by loggerheads and accumulated on beaches by categories (i.e Hard Plastic, Soft Plastic, and Fishing Plastic). Different letters indicate significant differences between categories ($p < 0.05$).

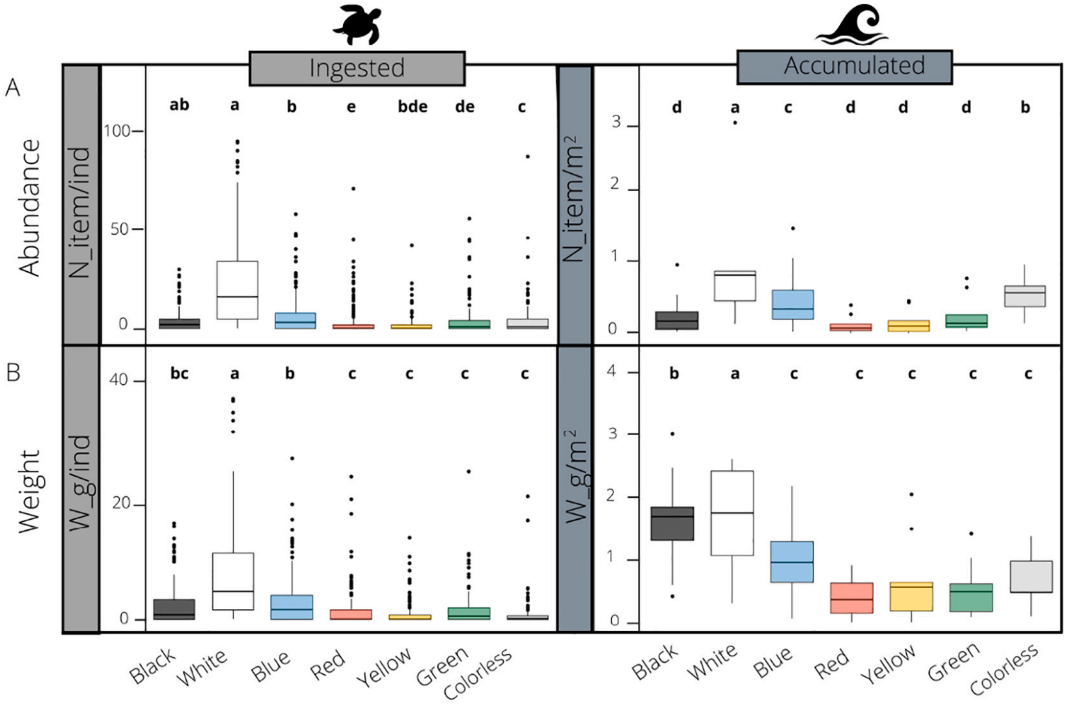

Fig. 4. Boxplot and mean ± se of (A) abundance and B) weight of plastic debris ingested by loggerheads and accumulated on the beaches by colors (i.e Black, White, Blue, Red, Yellow, Green, and Colorless). Different letters indicate significant differences between colors ($p < 0.05$). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.1.2. *Beaches*

A total of 12,244 pieces of plastic debris were collected on the three beaches monitored. For each beach, there were no significant differences between belt transects in terms of abundance and weight ($p > 0.05$). Among the three beaches, Albran Est beach presented more plastic in terms of abundance and weight ($p < 0.05$, abundance: 5.54 ± 3.37 items/m^2; weight: 26.93 ± 18.49 g/m^2) than the beaches at the two other sites, namely, Ampanihy (abundance: 1.43 ± 0.93 items/m^2; weight: 9.79 ± 5.70 g/m^2) and Ambohidena (abundance: 1.19 ± 0.90 items/m^2; weight: 7.29 ± 4.42 g/m^2). Plastic sizes were not significantly different between these three beaches, with an average size of 7.74 ± 8.11 cm for Albran Est, 7.38 ± 5.88 cm for Ampanihy and 7.42 ± 6.25 for Ambohidena.

Hard plastic was the most common category of items accumulated on beaches ($\chi^2 = 18.45$, df = 2, $p < 0.0001$, Fig. 3.B), representing 96 % of the total plastic debris with an abundance of 2.62 ± 0.91 items/m^2 and a weight of 11.4 ± 4.27 g/m^2. The proportion of soft plastic was 3 % by number and 17 % by weight. Fishing gear items were the least abundant items (1 % by number and 5 % by weight).

White plastic debris was the most abundant ($\chi^2 = 19.07$, df = 6, $p = 0.004$), representing 48 % of the total plastic debris with an abundance of 1.30 ± 0.471 items/m^2 and a weight of 1.9 ± 0.464 g/m^2. Blue (abundance: 20 %; weight: 14 %), colorless (abundance: 18 %; weight: 3 %), and black (abundance: 11 %; weight: 23 %) were less often found. Red, yellow and green plastic debris were rare.

3.2. *Selectivity test*

A significant positive correlation between abundance and weight was observed for both plastic debris ingested by loggerheads (rho = 0.91, $p = 0.001$) and plastic debris accumulated on beaches (rho = 0.89, $p < 0.001$). We used the abundance data to investigate loggerhead selectivity. Manly's test indicated no strong selectivity by loggerheads, neither by plastic category nor by color, with all mean index values being below 0.5. The highest selectivity index, which was close to 0.5, was 0.42 ± 0.43 for hard plastic, followed by 0.41 ± 42 for soft plastic and 0.29 ± 0.41 for white plastic. In contrast, the lowest index was observed for fishing gear at 0.18 ± 0.36, followed by colorless plastic at 0.07 ± 0.05, yellow plastic at 0.11 ± 0.24 and green plastic at 0.16 ± 0.32 (Fig. 5).

3.3. *Origin of plastic debris*

3.3.1. *Brand audit: composition and origin*

We determined the country of origin of 980 items ($N_{loggerhead} = 208$; $N_{beach} = 772$). We recovered plastic from 186 different brands, including 31 that were found both in loggerhead sea turtles and on the beaches. The three most common brands were AquaDanone® ($N_{loggerhead} = 39$ %; $N_{beach} = 29$ %), The Coca Cola Company® ($N_{loggerhead} = 2$ %; $N_{beach} = 4$ %) and Sungreen® ($N_{loggerhead} = 4$ %; $N_{beach} = 3$ %; Table 1). Most items were food packaging ($N_{loggerhead} = 68$ %; $N_{beach} = 69$ %). Personal care and household products were less often found. Plastic debris subtypes were mostly plastic caps from mineral water ($N_{loggerhead} = 56$ %; $N_{beach} = 42$ %), followed by caps from other drinking products (soda, juice), food, and oil containers (see the supplementary material). The most abundant polymer type was HDPE ($N_{loggerhead} = 69$ %; $N_{beach} = 59$ %), which is the main component of the caps of plastic bottles (Table 1). Seventy-four percent of the debris of known origin came from Southeast Asia, and 16 % of the items were classified as having “International” sources. The top three source countries were Indonesia (67 % of the items of known origin), China (3 %) and Thailand (3 %) (Fig. 6; see supplementary material: Appendix B).

3.3.2. *Reverse dispersal model of plastic debris in the SWIO*

Dispersal modeling revealed the potential subregion of origin of the plastic debris found in the SWIO. In our model, the main subregion contributing to plastic debris in the SWIO was Southeast Asia for 65 % of the terrestrial sources and 52 % of the marine sources, with a major contribution from Indonesia (Fig. 7). In both source scenarios, Indonesia, China and South Africa were identified as substantial contributors, with 48 %, 13 % and 9 % of inputs for terrestrial sources and 33 %, 10 % and 4 % for marine sources, respectively (Fig. 7; see the supplementary material). The marine source scenario had more plastic debris-emitting subregions for the SWIO than the terrestrial source scenario, highlighting East Asia, Europe, the SWIO, Oceania, Latin America, North America, and South Asia as contributors. Additionally, these marine source scenarios indicated a pathway between the Pacific and Indian Oceans through the Indonesian straits.

4. Discussion

4.1. *Loggerhead sea turtles: opportunistic or selective diet?*

Our study showed that 202 (76 %) of the 266 loggerhead sea turtles from bycatches by Reunion Island longliners in the SWIO had ingested plastic debris. From 2007 to 2021, the frequency of plastic ingestion by loggerhead sea turtles increased from 25 % to 78 %, with a mean of 70 % ± 20 %. This frequency of occurrence is similar to or higher than most of those observed in the Southwest Pacific Ocean (57.1 %, Boyle and Limpus, 2008), in the Gulf of Mexico (51.2 %, Plotkin et al., 1993), and

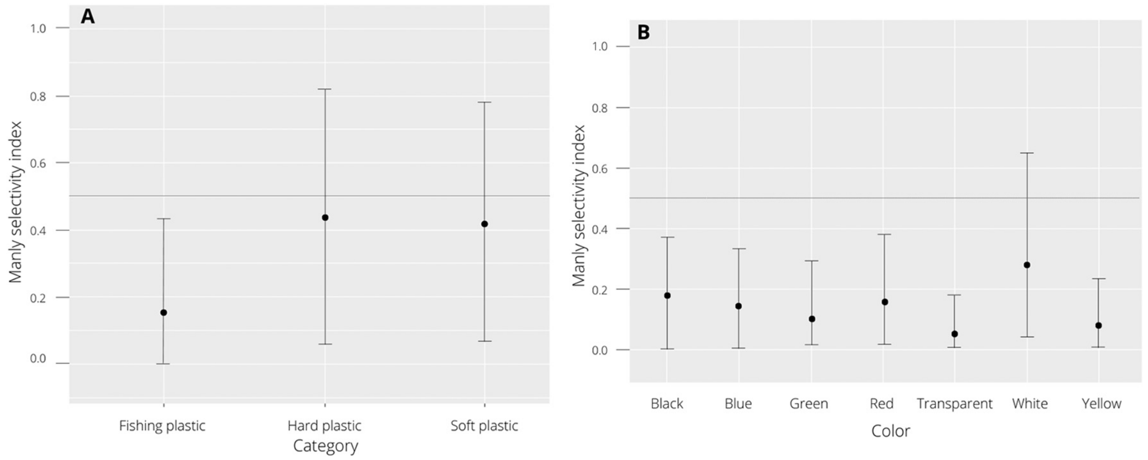

Fig. 5. Manly-Chesson's Selectivity Index for loggerheads sea turtles “diet-related selectivity” in plastic debris ingestion ($N = 202$). Values range from 0 (complete opportunistic diet) to 1 (complete selectivity diet) concerning debris ingested available in the environment for (A) category and (B) color.

Table 1
Most represented brands from macroplastics ingested by sea turtles and stranded on the beaches. Type of product: FP (food packaging); HP (household product); PC (personal care). Type of polymer: HDPE (High-density polyethylene); PS (Polystyrene); PP (Polypropylene). (NA) correspond to undetermined. All 186 brands are represented in the supplementary data with website links.

	Brand	Manufacturer	Type of product	Subtype of product	Type of polymer	Country of production	Country of exportation	Loggerheads sea turtle	Beach
								N = 208	*N* = 772
1	Aqua®	Danone®	FP	Water (cap)	100 % HDPE	Indonesia	Southeast Asia	85	224
2	Teh Gelas®	Orang tua®	FP	Drink	100 % PP	Indonesia	International	18	0
3	Wingsfood®	Wings®	FP	Food	100 % PP	Indonesia	Southeast Asia	9	16
4	Pertamina®	PT Pertamina®	HP	Oil container	100 % HDPE	Indonesia	Southeast Asia	5	24
5	Sungreen®	NA	FP	Drink (cap)	100 % HDPE	Thaïland	NA	9	26
6	Mizone®	Danone®	HP	Drink (cap)	100 % HDPE	China	Southeast Asia	5	10
7	Tingyi®	Tingyi (Cayman Islands) Holding Corp®	FP	Water	67 % HDPE 33 % PS	China	Asia	3	0
8	White-White-Lion®	PT LION Wings®	PC	Toothbrush & toothpaste	100 % HDPE	Japan	Southeast Asia	1	24
9	Kiko®	PT Unifam®	FP	Food	100 % PS	Indonesia	Southeast Asia	2	16
10	Pennzoil®	Shell®	HP	Oil container	100 % HDPE	United States Canada Latin America	United States Canada Latin America	2	14
11	Indofood®	PT.Indofood®	FP	Food	100%PS	Indonesia	Indonesia Middle East of Africa	0	29
12	A product of The Coca Cola Company®	The Coca Cola Company®	FP	Drink (cap)	100 % HDPE	International	International	4	32

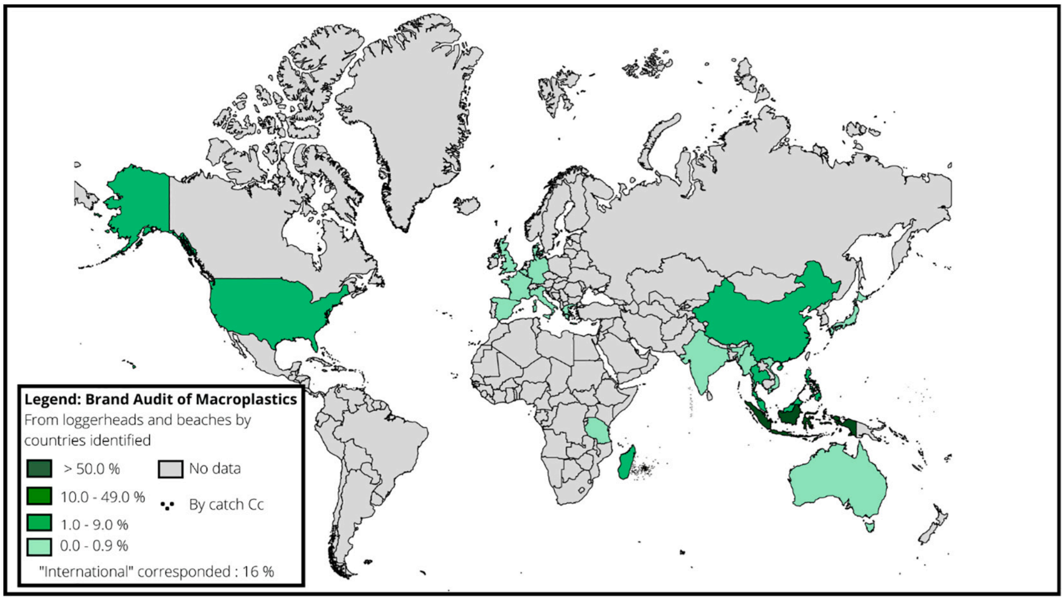

Fig. 6. Proportion of macroplastics in term of abundance identified by country with the 'brand audit', for plastics ingested by loggerhead sea turtles and stranded on beaches in Sainte Marie Island (Madagascar (More detailed information on proportion by sub-region and by country is available in the supplementary data: appendix B).

in the Mediterranean Sea (71 % Campani et al., 2013; 85 % Matiddi et al., 2017; 72 % Digka et al., 2020). All loggerhead sea turtles with plastic ingested an average abundance of 56.83 ± 4.59 plastic debris items per turtle. This level of plastic ingestion is higher than that reported in turtles foraging in the North Atlantic gyre, in the Mediterranean, and in the Southern Atlantic Ocean, where the number of plastic debris items is approximately 30 per turtle on average (Savoca et al., 2022). Our results were similar to the rate of ingestion found in loggerhead sea turtles of the North Pacific, where loggerhead sea turtles ingested an average of 65 ± 30 plastic debris items per turtle (Savoca et al., 2022). This suggests that the plastic accumulation in the western Indian Ocean is nearly as severe as that in the Northern Pacific Ocean.

Despite the ingestion of plastics, most of the loggerhead sea turtles rehabilitated at Kelonia survived (80 %). Loggerhead sea turtles can eliminate plastic items through defecation and demonstrate a high tolerance for plastic ingestion (Tomas et al., 2002; Hoarau et al., 2014; Fukuoka et al., 2016; Nelms et al., 2016; Matiddi et al., 2017). In our study, loggerhead sea turtles defecated plastic debris during a mean

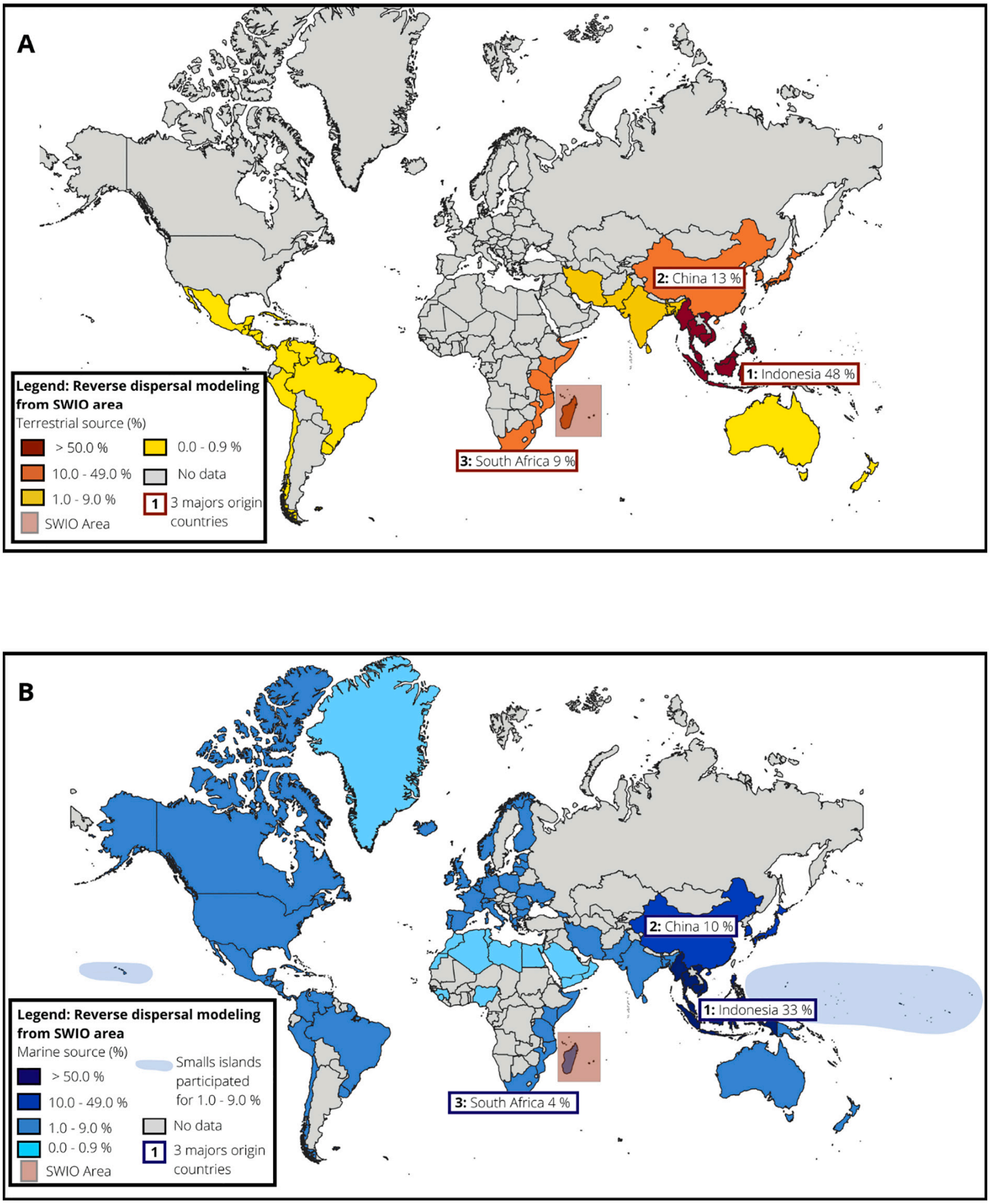

Fig. 7. Proportion of abundance in the sub-region and the three dominant countries of origin of plastic debris (> 5 mm) toward the SWIO area, obtained by the reverse dispersal modeling (> 5 mm) after 30 years, (A) Terrestrial source model, (B) Marine source model (More detailed information on proportion by sub-region and by country is available in the supplementary data: appendix C).

period of 15.5 ± 9.8 days (minimum of 1 day and maximum of 179 days). Solomando et al. (2022) reported a mean of 12.4 ± 2 days, with a minimum of 11 days and a maximum of 151 days, in the Balearic Islands. As macroplastics were mostly found in dead loggerhead sea turtles, we hypothesized that these debris were retained longer than other categories (soft plastic, fishing plastic) for excretion. Necropsies of loggerhead sea turtles at Kelonia revealed that their death was caused by internal hemorrhage (hook) or collision with ships. Our results are in agreement with those of Hoarau et al. (2014), where larger debris were mostly found in the gut contents of dead loggerhead sea turtles.

Loggerhead sea turtles did not appear to select a particular category or color of plastic debris; they adopted an opportunistic diet. Debris from the hard plastic category were primarily ingested, followed by small amounts of soft plastic and fishing debris and no industrial pellets. In other subtropical gyres, the same result was observed for loggerhead sea turtles, with a weaker trend for industrial pellets (North Atlantic, Barreiros and Raykov, 2014, Pham et al., 2017; South Atlantic, Rizzi et al., 2019; North Pacific, Jung et al., 2018), while close to the coastline, loggerhead sea turtles ingested principally soft plastic such as plastic sheet, bags or film (Mediterreannen, Camedda et al., 2014; Campani et al., 2013; Casale et al., 2016; Digka et al., 2020; Solomando et al., 2022). For the environment, we found the same proportions of plastic debris categories accumulated on beaches, with hard plastic debris items representing 96.3 %, followed by soft and fishing plastic debris. The results are also similar for other islands in the Indian Ocean (the Amirantes, Duhec et al., 2015; Saint Brandon, Bouwman et al., 2016; Cocos Islands, Lavers et al., 2019). Hard plastics, including caps, bottles, and toothbrushes, are composed of PET or HDPE polymers (Andrady, 2011; Jung et al., 2018). These items can cross long distances by floating on the surface, whereas soft plastics such as plastic bags are composed of PE polymers, which are more sensitive to degradation and may sink rapidly when fixed biofilms accumulate closer to the coastline (Morét-Ferguson et al., 2010; Ryan et al., 2019; Ryan, 2020; van der Mheen et al., 2020). Digka et al. (2020), noted that adult loggerhead sea turtles ingested more sinking polymers in the form of soft plastic closer to the coastline than late-juvenile loggerhead sea turtles, and their feeding area was more pelagic, with more debris in the hard plastic category. Concerning colors, loggerhead sea turtles ingested mostly white plastic (54 %), followed by blue, colorless and black plastic, and we found the same top colors for the beached plastic debris. These results are in line with previous findings where white was also the predominant color of plastic ingested by loggerhead sea turtles (44 %, Hoarau et al., 2014; 59 %, Clukey et al., 2017; 45 %, Pham et al., 2017), collected on beaches (Duhec et al., 2015; Bouwman et al., 2016) and found at the sea surface (Shaw and Day, 1994; Gregory and Andrady, 2003; Shah et al., 2008; Titmus and Hyrenbach, 2011; Ryan et al., 2016; Martí et al., 2020; Connan et al., 2021).

4.2. Identification of the origin of plastic pollution: Brand audit and reverse dispersal modeling

Both the brand audit and reverse dispersal modeling showed that the main origin of marine plastic pollution in the western Indian Ocean is Southeast Asia, especially Indonesia. We identified the brand and origin of 980 items principally because of bottle caps for mineral water and other drinks. This is in contrast with the findings of Duhec et al. (2015) and Ryan, (2020), who principally identified brands directly on plastic bottles. In our study, we found fewer bottles than caps. Caps are made of HDPE, which has a lower density than seawater, thus increasing their buoyancy. For this reason, caps are transported over long distances. Plastic bottles are made of PET, which has a higher density than seawater; thus, bottles can sink (if not clogged) and therefore accumulate closer to their origin (Brignac et al., 2019; Ryan, 2020).

AquaDanone® was by far the most abundant brand found both in loggerhead sea turtles and on beaches. This brand was also very abundant in Seychelles (Duhec et al., 2015, 10 bottles and 94 caps), in Kenya (Ryan, 2020) and on Reunion Island (Cartraud et al., 2016). Products of this brand are manufactured in Indonesia, and this company is the largest plastic water bottle producer in this country. This is due to its lower production cost, higher quality and a higher level of advertising in comparison to those of other plastic water bottle brands (Andika and Mandang, 2004). Free drinking water in Indonesia is not accessible everywhere, so most people rely on drinking water sold in plastic bottles, resulting in millions of plastic bottles being used every day (Achmad et al., 2016). In the Seychelles, (Duhec et al., 2015; Dunlop et al., 2020; Vogt-Vincent et al., 2022), Saint Brandon (Bouwman et al., 2016), Sri Lanka (Jang et al., 2018) and South Africa (Ryan et al., 2019), plastic debris found on beaches was also identified as originating predominantly from Southeast Asia. The marine source scenario also demonstrated that plastic items originating from the Pacific Ocean islands by fishing efforts (Vanuatu, Fiji, French Polynesia, see Supplementary Data Appendix 2) entered the Indian Ocean through the Indonesian straits. Previous studies have already uncovered this connection (Maes et al., 2018; Miron et al., 2021; Van Sebille et al., 2014; Pattiaratchi et al., 2022). The Indian Ocean is complex, and monsoons have a strong influence on sea currents and therefore directly influence plastic debris accumulation. For example, Vogt-Vincent et al. (2022) observed that debris from terrestrial sources and fisheries are mostly deposited along the coastlines of Seychelles during the northeast monsoon and positive Indian Ocean dipole. This study also confirmed that Seychelles had a very high risk of stranding for plastic marine debris from Chinese, Malaysian or Thai vessels transiting the Indian Ocean. Floating debris are transported by sea currents for years and may finally accumulate on islands (Morishige et al., 2007; van der Mheen et al., 2020; Vogt-Vincent et al., 2022). Islands act as traps of marine debris, the so-called “island scavenging effect” (Bouwman et al., 2016). As plastic pollution in the Indian Ocean is understudied, it is very important to provide a baseline for the abundance and characterization of plastic found in different compartments, such as the shoreline (beaches), ocean (sea surface/water column), deep sea and marine biota (bioindicator species) (GESAMP, 2019; Van Der Mheen, 2020). These observations in situ, combined with dispersal models, can help better understand the circulation and position of the plastic pollution patch in the Indian Ocean.

4.3. Loggerhead sea turtles as bioindicators of plastic marine pollution in the southwest Indian Ocean

We recommend using loggerhead sea turtles as a plastic pollution bioindicator in the Southwest Indian Ocean, as they fill the requirements established by the GESAMP, (2019) and the review of Savoca et al. (2022):

- *Regional representation*

Loggerhead sea turtles are widely distributed in the western Indian Ocean, and late juveniles forage mostly in offshore habitats of the subtropical gyre, where they are in contact with marine plastic pollution (Dalleau, 2013; Dalleau et al., 2014).

- *Ethically sound*

Loggerhead sea turtles are bycaught by longline fishing vessels based around Reunion Island and brought to the Kelonia Center for care. During this period, plastic debris are collected from ejections of live sea turtles until no more ejections occur. Eighty percent of loggerhead sea turtles are rehabilitated and released successfully into their environment.

- *Abundant in the chosen environment and easy, practical analysis*

A memorandum of agreement was established in 2007 between fishers and Kelonia to rehabilitate all turtles caught by longlines. On average, 20 loggerhead sea turtles are included in the analysis per year. The rehabilitation protocol includes care in individual tanks, where feces are collected daily by trained keepers, which is easy and practical. All dead loggerhead sea turtles are necropsied by the veterinarian of Kelonia for gut content analysis and other veterinary investigations. This organization is appropriate for generating a long-term dataset.

- *Already used as a bioindicator species*

Loggerhead sea turtles are already used as plastic pollution bioindicator species in the Mediterranean Sea (Matiddi et al., 2017), in the North Atlantic (Barreiros and Raykov, 2014; Pham et al., 2017), and in the North Pacific (Parker et al., 2005).

- *Species directly linkable to impact and effect and high plastic occurrence in the diet*

Loggerhead sea turtles forage on bottom-dwelling animals but also in oceanic waters. They normally feed on invertebrates such as mollusks, crustaceans, and jellyfish. Plastic particles can easily be mistaken for potential prey, which probably explains the high frequency of plastic ingestion in this species (70 % in our study).

- *Comparable similar species identified worldwide*

The results obtained for loggerhead sea turtles in the western Indian Ocean are comparable to those obtained for the same species in other oceans (Schuyler et al., 2012; Campani et al., 2013; Camedda et al., 2014; Hoarau et al., 2014; Ryan et al., 2016; Matiddi et al., 2017; Pham et al., 2017; Savoca et al., 2022).

5. Conclusion

Our study demonstrates that loggerhead sea turtles of the western Indian Ocean ingest a large amount of plastic debris. The characteristics of this debris are similar to those of the debris found on beaches, suggesting that turtles do not select specific categories or colors of plastics. Both brand audits and reverse dispersal models have shown that the main origin of plastic pollution is Southeast Asia. We recommend using this species as a bioindicator of marine plastic pollution in this region, in addition to already existing monitoring protocols conducted on beaches and other compartments.

CRediT authorship contribution statement

Margot Thibault: Conceptualization, Methodology, Software (Qgis and R), Formal analysis, Investigation, Writing Original Draft, Visualization.

Ludovic Hoarau: Methodology, Validation, Investigation, Review.

Laurent Lebreton: Modeling, Investigation, Review, Funding acquisition.

Matthieu Le Corre: Validation, Review.

Mathieu Barret: Resources (coordinating sampling and providing access to the rehabilitation center for sea turtles), Review.

Emmanuel Cordier: Software (ArcGIS), Review.

Stéphane Ciccione: Review, Funding acquisition.

Sarah-Jeanne Royer: Review.

Alexandra ter Hale: Review.

Aina Ramanampamonjy: Resources (coordinating sampling in Madagascar), Review.

Mayeul Dalleau: Conceptualization, Validation, Funding acquisition, Review, Supervision, Project administration.

Claire Jean: Conceptualization, Validation, Review, Supervision, Project administration.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpolbul.2023.115343.

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