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Drivers of litter ingestion by sea turtles: Three decades of empirical data collected in Atlantic Europe and the Mediterranean

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ABSTRACT

Sea turtles are considered as bio-indicators for monitoring the efficiency of restoration measures to reduce marine litter impacts on health. However, the lack of extended and standardised empirical data has prevented the accurate analysis of the factors influencing litter ingestion and the relationships with individual health. Historic data collected from 1988 and standard data collected from 2016 were harmonised to enable such analyses on necropsied loggerhead turtles (*Caretta caretta*) in eight Mediterranean and North-East Atlantic countries. Litter was found in 69.24 % of the 1121 individuals, mostly single-use and fishing-related plastics. Spatial location, sex and life history stage explained a minor part of litter ingestion. While no relationships with health could be detected, indicating that all individuals can be integrated as bio-indicators, the mechanistic models published in literature suggest that the high proportion of plastics in the digestive contents (38.77 % per individual) could have long-term repercussions on population dynamics.

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1. Introduction

Marine litter, mostly consisting of plastics, is ubiquitous in the environment (Andrady, 2011; Barnes et al., 2009) while several million tons of plastic continue to enter the ocean every year (Jambeck et al., 2015) and current densities could triple by 2040 (UNEP, 2021). The damage to the marine environment is alarming and has possible cascading impacts on natural resources (Hardesty et al., 2015; Kühn et al., 2015). Although the factors leading animals to interact with litter are still poorly understood (Santos et al., 2021), the number of species recognised as being affected by marine litter, primarily through ingestion or entanglement, has amplified with the increasing effort for the acquisition of knowledge over the last years (Avery-Gomm et al., 2018; Provencher et al., 2017): From 247 marine species listed to be concerned in 1995 (Laist, 1997), this number more than doubled in two decades (>660 species; Gall and Thompson, 2015; Secretariat of the Convention on Biological Diversity and the Scientific and Technical Advisory Panel - GEF, 2014) and continues to grow (>910 species; Kühn and van Franeker, 2020), being quintupled in the most recent reviews (>1200 species; Santos et al., 2021). Considered as an evolutionary trap, misleading animals into maladaptive choices (Santos et al., 2021; Schlaepfer et al., 2002), marine litter is not only endangering wildlife species and environment but also carries a risk to human health (Werner et al., 2016).

Several international directives attempt to tackle the issue of marine litter (UNEP, 2016). Some rely on sentinel species for assessing environmental health risks posed by marine litter (Fossi et al., 2018). For example, the quantity of litter ingested by the northern fulmar *Fulmarus glacialis* is considered as indicator of the spatial and temporal variations of local pollution levels within the OSPAR Regional Sea Convention (Convention for the Protection of the Marine Environment in the North-East Atlantic) (van Franeker et al., 2011). All seven species of sea turtles have been found to ingest plastic ubiquitously (Duncan et al., 2019b), making them a good candidate taxon for monitoring marine plastic levels. With a larger spatial distribution, including the Mediterranean Sea (Casale et al., 2020), the loggerhead sea turtle (*Caretta caretta*) has been designated as indicator in both, OSPAR and the Barcelona (Convention for the Protection of the Marine Environment and the Coastal Region of the Mediterranean) conventions, as well as the Marine Strategy Framework Directive (MSFD), for evaluating the Good Environmental Status (GES) at the Mediterranean and European scales (Matiddi et al., 2011, 2017; Pham et al., 2017). The species' propensity to ingest marine litter is evidenced at the global scale (Duncan et al., 2019b; Schuyler et al., 2014a, 2014b). The occurrences of litter ingestion are particularly high in the Eastern Atlantic, ranging from 60 up to 80 % (Nicolau et al., 2016; Pham et al., 2017), and across the Mediterranean (Dell'Amico and Gambaiani, 2013), from 14 % in the central sub-basin (Camedda et al., 2014) to >70 % in the Eastern and Western sub-basins (Digka et al., 2020; Domènech et al., 2019; Matiddi et al., 2017) and up to 100 % locally (INDICIT consortium, 2018a). While the GES targets for MSFD criterion for are set at an "*amount of litter and microlitter ingested by marine animals at a level that does not adversely affect the health of the species concerned*" (Commission Decision 2017/848/EC), the understanding of the relationship between litter ingestion and health for the bio-indicator species remains a major issue. Furthermore, the concept of health has many definitions depending on levels and objectives (Frumkin, 2016).

Litter ingestion could cause mortality of sea turtles because of perforation (Nicolau et al., 2016) or obstruction in the digestive tract (Lazar and Gračan, 2011). It can also have sub-lethal effects (Nelms et al., 2016) with possible progressive consequences on an individual's body condition and fitness (Rosolem Lima et al., 2018; Marn et al., 2020), such as dietary dilution (Machovsky-Capuska et al., 2019). By affecting body condition, litter ingestion could cause a slow death, however this is more difficult to evidence. Plastics have the potential to also act as carriers of heavy metals, potentially leading to combined toxic effects (Liu et al., 2021). To understand the relationship between litter ingestion, health and the threshold at which health becomes impacted by litter ingestion, both environmental and intrinsic factors that influence the probability of litter ingestion, must be considered. However, to date, the drivers influencing sea turtles to ingest litter are still not well understood (Santos et al., 2021) and the disparity of methodological approaches employed among studies often prevents influencing factors from being clearly defined (López-Martínez et al., 2021; Provencher et al., 2017).

Litter ingestion could depend on both food and litter availability in the environment, which vary spatially and seasonally (Mansui et al., 2020) and can lead to local high encounter probabilities (Darmon et al., 2017; Schuyler et al., 2014a, 2014b). Although sea turtles migrate according to temperature and food constraints, they may occupy preferential feeding areas (Hochscheid et al., 2007; Schofield et al., 2010) which can overlap with marine litter accumulation areas (Chambault et al., 2019). The loggerhead turtle species mostly occupies surface waters (Narazaki et al., 2013; Patel et al., 2016) where they are highly prone to ingesting buoyant plastics (Domènech et al., 2019; Pham et al., 2017). Moreover, as a generalist carnivorous species (Casale et al., 2008), they could opportunistically ingest litter items intertwined with their natural food or mistake them for their natural prey (Fukuoka et al., 2016; Tomás et al., 2002). For example, plastic bags, torn and fragmented, resemble the bell, tentacles and oral arms of the gelatinous jellyfish (Schuyler et al., 2014a, 2014b). An appeal to the odour released by plastic biofouling (Pfaller et al., 2020), the presence of preys incrusted in the items (Frick et al., 2009) and scavenging behaviours (Andrades et al., 2019) can also influence the probability of litter ingestion. Selectivity of prey is highly related to life history stage, and perhaps to the ability to discriminate between natural and synthetic preys (Duncan et al., 2019a). Being less selective, young turtles occupying oceanic habitats could be more exposed to floating litter when feeding on pelagic organisms, while large turtles could be more selective and able to avoid litter when feeding on benthic organisms (Nelms et al., 2016; Schuyler et al., 2012; Duncan et al., 2021). The body size at which this transitional shift in habitat and feeding diet appears, varies among regions and with food availability (Bjorndal et al., 2000; Casale et al., 2008; Snape et al., 2020). Apart from the availability of plastics in the environment and the overlap of cues from natural foods and plastics perceived by the individual, the individual's acceptance threshold, e.g. related to starvation, may also condition plastic ingestion (Santos et al., 2021). Other individual factors related to energetic requirements, such as for investment in reproduction (Hays et al., 2010; Lutz et al., 2002), or health status before encountering litter, also probably influence the discernment capability and the resulting impacts of litter ingestion on body condition.

The health of robust and long-lived species, such as the loggerhead turtle, is difficult to evaluate and there is no known standard methodology for its assessment. In living turtles, blood chemistry (Fazio et al., 2012), biomarkers, contaminants in the tissues (Fossi et al., 2018) and behavioural factors of reactivity, as well as the ability to feed or float (Li et al., 2015), are clues used to assess individuals' health (Flower et al., 2018; Reséndiz et al., 2018). For individuals found dead, themselves being considered for monitoring litter impacts (INDICIT consortium, 2018a), other parameters must be used to assess the health status before death. Along with physical diagnostics of illness and injuries (Flint et al., 2009; Labrada-Martagón et al., 2010), several health proxies can be used, such as Body Condition Indices (BCI), which are expected to reflect individuals' nutritional status and energy reserves and thus their capacity to reproduce and survive (Labrada-Martagón et al., 2010). More subjectively, body condition is generally scored either from visual assessments (e.g., plastron shape; Flint et al., 2009; Thomson et al., 2009) or from biometric variables (e.g., ratio body mass/carapace length^3; Bjorndal et al., 2000; Clukey et al., 2017).

While health assessment is an issue in itself, the direct and indirect relationships between health parameters and litter ingestion are still poorly understood. Acquiring a better knowledge of the factors favouring litter ingestion is crucial (Santos et al., 2021), both for sea turtle conservation programs and for better evaluating how sea turtles can be used as litter impact indicators (Fossi et al., 2018). In this study, an unprecedented dataset on >1100 necropsied turtles consisting of historic data harmonised with recent standard data collected by >100 institutions distributed in eight countries of the Mediterranean and the European Atlantic waters allows for comparative and powerful assessments to describe litter ingestion and its impacts on turtles. The objective of this study was to attempt to disentangle the environmental and intrinsic factors influencing litter ingestion in order to explore the relationship between litter ingestion and health, assessed by various parameters extracted from the literature. Three groups of hypotheses were tested about the factors influencing plastic ingestion: Both occurrence of litter ingestion and quantities of ingested litter vary with 1) location and season, in relation to marine litter accumulation patterns which may influence the relative availability of litter and food; and biological factors which may influence the individual's acceptance threshold, 2) sex and body size in relation with individuals' energetic needs related to seasons and life history stages; and 3) body condition and health status.

2. Materials and methods

2.1. Sampling method and context

This study is part from the INDICIT ("Indicator Impact Turtle"; 2017–2019) and INDICIT II projects ("Indicator Impact Taxa"; 2017–2022). These projects aimed to support the implementation of indicators of marine litter impacts on sea turtles in MSFD and OSPAR and Barcelona RSCs waters. One of their objectives was to enlarge and empower existing networks for the standard collection of data on litter impacts on sea turtles, in order to analyse the relevance, criteria and biological constraints for using the indicator "Litter ingestion by sea turtles" in these areas, then, later, evaluate GES thresholds. For this, a standard data collection on litter ingestion and body condition of loggerhead sea turtles has been deployed since 2017 by >100 institutions in eight countries of the Mediterranean and European Atlantic: Cyprus, France (Atlantic and Mediterranean coast of the mainland and Corsica), Greece, Italy, Portugal (Azores, Madeira), Spain (Mediterranean waters and Canary Islands), Tunisia and Turkey (INDICIT consortium, 2018). In parallel, historical data collected by these same institutions since 1988, found in existing databases or necropsy reports, has been gathered and harmonised.

2.1.1. Standardised data collection

Professionals and trained volunteers from >100 institutions were mobilised to collect loggerhead turtles, especially stranding networks, rescue centres, fishermen, veterinarians and research laboratories (Darmon et al., 2019), all authorised to handle this protected species under national legislation. Sea turtles were collected opportunistically, found stranded on beaches, bycaught or floating at sea. This study focuses on dead individuals, either already found dead in the field or died afterwards in the rescue centre, while alive individuals are not yet considered as an indicator. A standard protocol was co-built by INDICIT consortium in partnerships with stakeholders involved in data collection on the basis of MSFD guideline (Hanke et al., 2013) and considering stakeholders' feasibility, constraints, skills and experiences (INDICIT consortium, 2018). An external advisory board composed of experts of marine litter and/or sea turtles as well as representatives of MSFD, RSCs and Member states, also made recommendations for data collection outcomes to support the implementation of the bio-indicator and its harmonised deployment among countries and sub-regions in relation with GES definition. The protocol has been published (Matiddi et al., 2019) and shared with local institutions in each of the height countries. Training sessions and collaborations with experts have also been proposed.

2.1.1.1. Quantification and characterization of the ingested litter. Necropsies, litter extraction and characterization were performed as described in Matiddi et al. (2019). The entire digestive tract from mouth to anus (oesophagus, stomach, intestines) was inspected for food and litter. Considering that data collection could be highly time-consuming, some parameters were considered as basic (mandatory for monitoring the impact caused by litter ingestion in the framework of the indicator), the others (specified below) were proposed as "optional" for acquiring more knowledge on the drivers leading to litter ingestion (Appendix-Table S1).

The digestive tracts' contents were washed above a 1 mm mesh sieve and litter pieces were spotted with naked eyes, and binocular precision if necessary. The occurrence of litter (>1 mm) was noted as 1 or 0, depending respectively on presence or absence of litter in the digestive tract. The dry mass (grams) and the abundance (number of fragments) of ingested litter were also recorded. All litter items were then grouped into categories defined according to MSFD guidance (Hanke et al., 2013; Matiddi et al., 2019), differentiating between plastics from industry (pellets) (thereafter noted "IND PLA") and plastics from users' origin as follows: sheet-like (USE SHE, remains of sheet such as bags), hard fragments (USE FRAG, broken pieces of thicker type plastics), threadlike (USE THR, e.g., pieces of nylon wire, fishing line, net-fragments), foams (USE FOA, e.g. polystyrene foam, foamed soft rubber) and other (USE POTH, including elastics, cigarette-filters, balloon-pieces for example). Pieces of litter other than plastics (OTHER), natural food (FOO) and natural non-food items (NFO) were also noted. Litter was dry-weighted (precision 0.01 g) and counted (number of fragments, except FOO which could not be numbered) per category. Contents with a weight below the minimum precision were attributed to 0.001 g. Litter was also differentiated into three colour categories (dark, light, white/transparent; optional) and two size categories by superimposing sieves of 1 and 5 mm (micro-litter, from 1 to 5 mm (Hanke et al., 2013) and upper sizes; optional).

2.1.1.2. Assessment of body condition and ante-mortem health status. First, to correctly interpret the body condition, the body conservation status was considered along the circumstances of discovery (stranding, bycatch, floating at sea), and noted as follow: 1) alive, 2) fresh, 3) partially decomposed, 4) decomposed, 5) severely decomposed. Then, several biometric parameters were measured: In addition to the weight (precision 0.01 g; optional), the curved (CCL) and the straight (SCL) carapace lengths, minimum (Min), maximum (Max) and standard (St), were recorded following the definitions in Matiddi et al. (2019) (precision 0.01 cm; only StCCL and StSCL considered as mandatory). While size at sexual maturity and oceanic/neritic stage may vary among regions (Casale et al., 2008; Tomas et al., 2001), individuals were classified according to five life stages separated every 20 cm StCCL as follow: 1) <20 cm StCCL, 2) [20–40[,3) [40–60[, 4) [60–80[, 5) ≥80 cm. Lastly, the sex (adult female, adult male, not determined; optional) was attributed based on the tail length, gonads shape and the presence of follicles or eggs (Wyneken, 2001).

Based on a visual assessment, the individual's body condition was evaluated as (1) fat, (2) normal or (3) thin, according to the fat reserves (optional) both around the neck and covering the abdomen after opening the plastron (Matiddi et al., 2019). Fat appears coloured from yellow to green depending on body conservation status. It was thick, distributed over the ventral, upper and lower parts of the abdomen for fat individuals and was thin, sparse or almost absent in individuals with poor body condition (Appendix- Fig. S1). In addition, body condition was classified according to the plastron concavity (optional) as (1) convex (good), (2) flat (normal) or (3) concave (thin) (Thomson et al., 2009). Other parameters such as the algal or ectoparasite load, not evidenced to be related with body condition (Stamper et al., 2005), were not considered.

Moreover, a body condition index was considered: While other indices used for mammals were tested and gave similar results (i.e., relative condition, residual index, scaled mass index; Peig and Green, 2010), the Fulton's K index (kg.cm^{-3}) was retained. Calculated as the ratio of body mass (g) and cubic length (cm^3), it is supposed to increase with accumulation of reserves (Bjorndal et al., 2000; Nash et al., 2006). Lastly, the likely causes of morbidity and mortality were evaluated, with a complete description of the external and internal injuries and lesions (optional). A score of injury severity was assigned subjectively, depending on a presumed capacity to move and feed, ranging from severely (amputation, deep cut, fracture, sectioning of carapace), moderately (carapace cut) to not or slightly injured (abrasion of the carapace, delamination of part of the scales, scar).

2.1.2. *Harmonization of historic and recent data*

No historical data was available for Greece and Atlantic Spain where data collection started with the INDICIT project in 2017 as well as for Cyprus where data collection started with INDICIT II project in 2019. For the other involved countries, similar data on litter ingestion (occurrence, dry mass, abundance, category, colour, size) and description of individuals' circumstances of discovery, body conservation status and body condition (body weight, carapaces length, fat reserves, plastron concavity, injuries) collected before the 2017 (INDICIT project) were also gathered, extracted from necropsy reports and existing databases. All parameters (listed in Appendix-Table S1) may not be systematically recorded over time, but the methodologies to measure biometric parameters and the presence and quantities of ingested litter were probably identical. To ensure the comparability of present and past data, the units and categories of qualitative variables were harmonised. When the body conservation status was not explicitly recorded, it was attributed to ‘2’ or ‘3’ when the body condition as noted as being fresh and all digestive sections were known as having been inspected and litter being characterized, ‘4’ when only the presence/absence of ingested litter was recorded or to ‘5’ when the prospection of the digestive tract was impossible. The quantities of ingested litter were considered only when all digestive sections of the digestive tract were prospected. Otherwise, when only a section (oesophagus, stomach or intestines) was analysed, the data was not considered to avoid underestimation. The circumstances of discovery and the causes of mortality and morbidity were sometimes reattributed according to other recorded parameters or comments made by the observer. The units of biometric measures were then unified before attributing individuals to a life history stage. As StCCL was the measure of carapace length the most often recorded by stakeholders, other measures were harmonised for calculating the Fulton's K index following Bjorndal et al. (2000). For this, all missing StCCL values of the entire database (historic and recent data) were completed by converting maxCCL and minCCL values into StCCL thanks to a linear model: Standardised StCCL = 2.01968 + 0.98844 * MinCCL (69 replacements) and 1.511336 + 0.954576 * MaxCCL (205 replacements). The absence of record was noted as “not available” and therefore not included in statistical analyses. A significant amount of time was spent on data verification, first by each author for verification of data collected within each country, then by two authors (GD and JM) for cleaning, harmonization and control of the whole dataset, and finally a feedback check was carried out by all the authors.

2.2. *Data analysis*

Individuals with conservation status ‘5’ were excluded from the analyses, because the severe autolysis of their digestive tract prevented an accurate evaluation of the ingested material and of body condition.

The relationships between body condition indices were tested for significance using analyses of variance. The individuals' health status was determined based on fat reserves, plastron shape and Fulton's K index, and the significance of the relationships with life history stage and the two main circumstances of discovery (stranding and bycatch) was assessed using χ^2 tests. The individuals' causes of death and severity of injuries were also evaluated.

The occurrence of litter and specifically plastic ingestion were calculated as the frequency of individuals found with ingested litter in the digestive tract (all categories except FOO and NFO). The population mean abundance and dry mass of ingested material (litter with natural food FOO and no food items NFO), litter (all categories expect NFO and FOO) and specifically plastics, were calculated considering all individuals, including those with an empty digestive tract or without ingested litter (population means ± standard errors). Variations over years in occurrence, mass and abundance since 1988 were evaluated from linear mixed models, and the differences in occurrence and quantities of ingested litter before and after the dissemination of the MSFD guideline (2013, Hanke et al., 2013) and before and after the INDICIT project (2017) were tested using Student *t*-tests. The mean differences in occurrence and quantities of ingested litter between Atlantic and Mediterranean were tested for significance with Student t-tests. The ingested material was described by differentiating between the mean mass and the mean abundance per litter category. To assess the possible impacts of plastic ingestion on individual's capacity to feed, the ratio of the dry mass of plastics to the dry mass of natural food (category FOO) was calculated.

Subsequently, for evaluating the factors, which may promote litter ingestion, permutational linear models, robust against non-normal distributions of residuals and outlier values, were employed. Different types of models were built, with the occurrence of litter ingestion as response variable (noted as presence (1) /absence (0) for an individual) considering a Binomial error distribution. Other response variables were also modelled using a Normal distribution error: the dry mass of plastics, the abundance of plastic items and the ratios of plastic mass and abundance on StCCL (g.cm^{-1}), as well as plastic mass and abundance on body mass (g.kg^{-1}). The ratio mass plastics/mass FOO was also considered as response variable, by removing the turtles with an empty digestive tract (with neither litter nor food) to avoid a possible bias with individuals who could be chronically ill (Casale et al., 2016). Various explanatory variables were considered for testing each hypothesis. Thus instead of testing all possible combinations of variables in a complete model which in addition, had low statistical power, three categories of models were evaluated according to the three hypotheses:

1) Plastic ingestion is influenced by the spatial and temporal variability of marine litter distribution: The interaction of country/area (Cyprus, France Atlantic and English Channel, France Mediterranean, Greece, Italy, Portugal (Azores), Spain Atlantic (Canaries), Spain Mediterranean, Tunisia, and Turkey) with season (winter: January – March; spring: April–June; summer: July–September; autumn: October–December) was tested. As oceanographic models show variations in litter distribution in the Mediterranean at the sub-regional scale (Mansui et al., 2020), another model was evaluated using the sub-region instead of Country/area specifically for the Mediterranean, the number and distribution of data being insufficient to distinguish sub-regions instead of country for the Atlantic area. Three sub-regions were considered: A) France, Spain, B) Tunisia, Italy and C) Cyprus, Greece, Turkey;
2) Plastic ingestion is influenced by energetic requirements which vary among sexes, life history stages and seasons: The interactions among sex, season and life history stages was considered;
3) Plastic ingestion is influenced by individuals' body condition: Body condition was evaluated either by i) fat reserves, ii) plastron shape, iii) biometric measures (standardised StCCL or body mass), iv) Fulton's K index or v) severity of injuries.

For each hypothesis, the best model was selected with the lowest Akaike’s Information Criterion (AIC) and using backward stepwise selection. Two models with a difference in AIC of less than four were considered as equivalent, and the more parsimonious one was selected. The ability of the model to explain the observed variability in the response variable was then assessed thanks to the correlation coefficient R^2 for measuring its goodness of fit, high R^2 indicating that the explanatory variables explain a large part of the variation in the predictive variable. Analyses were performed with the R software version 4.0.1 (R Core Team, 2020), with the library “lmPerm” (Wheeler and Torchiano, 2016).

3. Results

3.1. Sample description

A total of 1121 loggerhead turtles was necropsied between February 1988 and December 2019. The presence of litter in the digestive tract was evaluated for 1116 individuals. Thirteen individuals with a body condition status of ‘5’ were removed from analyses. Some parameters were not systematically recorded, either because they were proposed as optional in the INDICIT standard protocol or they were not available in historic data (Appendix-Table S2). Therefore, the total numbers reported below do not necessarily equate to 1103 individuals.

Loggerhead turtles were found stranded ($N = 667$), brought back by fishermen after bycatch ($N = 230$), collected when floating at sea ($N = 37$) and one individual was found in a necropsied shark’s digestive tract. The individuals were recovered throughout the year (271 in Spring, 233 in Summer, 161 in Winter, 149 in Autumn). The number of necropsies varied among countries (Table 1) and increased over the years from two (1988) to 274 (2018) (Appendix-Fig. S2). The turtles' mean mass was 21.64 ± 0.54 kg ($N = 494$) and their mean standardised StCCL amounted to 54.36 ± 0.49 cm ($N = 1037$). The turtles were significantly smaller in the Atlantic (standardised StCCL = 37.94 ± 1.34 cm; $N = 180$) compared to the Mediterranean (56.85 ± 0.47 cm; $N = 924$; Student *t*-test = 11.722, $p < <0.001$), with large variations within each area (Table 1). 399 individuals were classified as females, 158 as males and 164 were undetermined (possibly juveniles).

3.2. Ante-mortem health status and causes of mortality

The body condition assessed from plastron concavity was considered flat for 41.71 % individuals ($N = 146$), convex for 36.25 % ($N = 127$) and concave for 22 % ($N = 77$). Fifty percent of individuals were evaluated as normal according to their fat reserves ($N = 554$), 25 % as fat and 25 % as thin ($N = 277$ respectively). Fat reserves and plastron shape varied with life history stage (respectively $\chi^2 = 35.6$; $p < <0.01$; $\chi^2 = 29.5$; $p < <0.01$), stage 2 individuals being more regularly classified as thin compared to stages 3 and 4 individuals, more frequently considered as normal or fat, while stages 1 and 5 were less regularly collected than other stages (Appendix-Tables S3 and S4, Fig. S3). Stranded and bycaught turtles, the numbers of which varied with life history stage (Appendix-Table S5) and country/area (Appendix-Table S6), had a similar body condition, independently of the tested parameter, namely based on Fulton's K index ($t = -1.18$; $p = 0.24$), fat reserves ($\chi^2 = 0.17$, $p = 0.91$) or plastron shape ($\chi^2 = 0.79$, $p = 0.67$) (Appendix-Table S6, Fig. S3).

Assuming a linear relationship between Fulton's K index (0.16 ± 0.02 on average) and body condition, 23.97 % of individuals were classified as poor ($K < 0.097$), 23.97 % as normal (K between 0.097 and 0.11), 25.11 % as good (K between 0.111 and 0.123) and 25.8 % as very good ($K > 0.123$) according to Fulton's K index quartiles. The Fulton's K index did not vary significantly with life history stage ($\chi^2 = 21.06$; $p = 0.049$) or sex ($F = 0.59$; $p = 0.55$) and was not significantly explained either by fat reserves ($R^2 = -0.002$; $F = 0.87$; $p = 0.42$), or plastron shape ($R^2 = 0.002$; $F = 1.28$; $p = 0.28$) and body weight ($R^2 = -0.002$; $F = 0.28$; $p = 0.6$).

The possible cause of death ($N = 973$ available data) was regularly misinterpreted and confused with the circumstances of discovery (stranding, floating at sea) or unidentified (60.33 %, $N = 587$). Death could be attributed to litter in only 14 cases (1.43 %), due to an observed digestive tract occlusion or perforation. In other cases, the cause of death was caused by bycatch (28.05 %, $N = 273$), anthropogenic trauma (5.45 %, $N = 53$, e.g., propeller) or entanglement in litter (2.26 %, $N = 22$).

Table 1

Plastic ingestion by the necropsied loggerheads per area and country (N: sample size with starting date of data collection; mean standard curve carapace length (standardised StCCL); occurrence of plastic ingestion (percentage of turtles found with ingested litter); population means of the dry mass of ingested plastics, the abundance, the relative dry mass per individual's body mass and standardised StCCL, the relative abundance per individual's body mass and standardised StCCL (± standard error)).

	France Atlantic	Portugal (Azores, Madeira)	Spain (Canaries)	Total Atlantic area	France Mediterranean	Cyprus	Greece	Italy	Spain Mediterranean	Tunisia	Turkey	Total Mediterranean area
N (date)	98 (1988)	71 (1996)	10 (2016)	179 (1988)	98 (2007)	24 (2019)	47 (2017)	260 (2008)	207 (1995)	97 (2004)	190 (2016)	757 (1995)
StCCL (cm)	31.31 ± 1.49	41.32 ± 2.2	51.79 ± 5.22	37.94 ± 1.34	49.82 ± 1.45	62.53 ± 3.28	58.28 ± 2.48	56.4 ± 0.83	49.8 ± 0.96	59.2 ± 1.1	66.76 ± 0.72	56.85 ± 0.47
Occurrence (%)	26.53	81.69	100	52.51	77.75	54.17	65.96	52.69	75.36	45.36	38.42	57.42
Dry mass (g)	0.08 ± 0.04	1.25 ± 0.23	0.34 ± 0.13	0.57 ± 0.1	1.45 ± 0.25	0.47 ± 0.26	0.73 ± 0.42	6.2 ± 5.38	1.06 ± 0.19	0.4 ± 0.24	0.2 ± 0.14	2.44 ± 1.56
Abundance (nb pieces)	3.94 ± 1.75	22.93 ± 4	32.6 ± 6.11	11.72 ± 1.89	16.55 ± 2.74	2.62 ± 0.87	6.87 ± 3.01	7.73 ± 1.27	2.63 ± 0.45	0.98 ± 0.4	1.34 ± 0.2	6.76 ± 0.54
Dry mass/ body mass (g/kg)	0.1 ± 0.005	0.16 ± 0.03	0.02 ± 0.01	0.07 ± 0.01	0.01 ± 0.03	0.04 ±0.0002	0.44 ± 0.31	NA	0.08 ± 0.01	NA	0.06 ± 0.04	0.11 ± 0.03
Dry mass/ StCCL (g/ cm)	0.001 ± 7 × 10^{-4}	0.004 ± 0.002	0.03 ± 0.005	0.016 ± 0.002	0.02 ± 0.004	0.007 ± 0.003	0.02 ± 0.01	0.09 ± 0.08	0.02 ± 0.004	0.008 ± 0.003	0.005 ± 0.002	0.04 ± 0.02
Abundance/ body mass (nb pieces/kg)	0.82 ± 0.34	5.69 ± 0.76	1.92 ± 1.6	2.7 ± 2.99	1.03 ± 0.19	0.11 ± 0.006	1.37 ± 0.61	NA	1.25 ± 0.16	NA	1.91 ± 0.78	1.11 ± 2.79
Abundance/ StCCL(nb pieces/ cm)	0.37 ± 0.04	0.11 ± 0.07	0.56 ± 0.11	0.37 ± 0.06	0.24 ± 0.04	0.01 ± 0.007	0.21 ± 0.11	0.13 ± 0.02	0.22 ± 0.02	0.03 ± 0.01	0.04 ± 0.01	0.13 ± 0.01

The death was not related to an anthropogenic cause in only 24 cases (2.46 %, e.g., sickness, predation; $N = 24$). Regarding the severity of injuries, 29.17 % of turtles were considered as very injured ($N = 70$), 4.58 % as moderately injured ($N = 11$) and 66.25 % as not or slightly injured ($N = 159$), with no significant relationship with Fulton's K index ($F = 0.25$; $p = 0.78$), plastron shape ($\chi^2 = 1.19$; $p = 0.88$) or fat reserves ($\chi^2 = 2.3$; $p = 0.68$).

3.3. *Marine litter ingestion*

Among the 1103 individuals, 69.24 % were found with ingested marine litter, 56.62 % with plastics and 30.5 % with more ingested litter than remaining natural food. The individuals ingested on average 31.56 ± 4.61 g of both litter and natural food ($N = 917$). Plastics accounted for 93.89 ± 0.64 % of the dry mass of ingested litter and 38.77 ± 1.3 % of the total dry mass of ingested material including litter, food and natural non-food items. They corresponded to 95.52 ± 0.51 % of the abundance of ingested litter (Table 2). Adjusted to individuals' mass and size, ingested plastics amounted to 0.1 ± 0.033 g plastics / kg turtle ($N = 454$) and 1.6 ± 0.38 pieces/kg turtle ($N = 473$) or 0.03 ± 0.019 g/cm carapace (standardised StCCL) ($N = 1103$) and 0.16 ± 0.013 pieces/cm carapace ($N = 1003$).

3.3.1. *Temporal variations*

Since 1988, the dry mass of ingested plastics did not vary significantly over years ($R^2 = 10^{-4}$; $p = 0.71$), but the occurrence increased ($R^2 = 0.007$; $p = 0.004$, slope $= 0.006$) and the abundance decreased ($R^2 = 0.004$, $p = 0.02$, slope $= -0.21 \pm 0.09$), both slightly but significantly (Appendix-Fig. S4). When comparing the litter ingestion before and after 2013 (publication of MSFD guideline, Hanke et al., 2013), the increase in occurrence was significant (48.17 % and 59.80 % respectively; $p < 0.001$), while the variations in dry mass (0.69 ± 0.09 g and 2.72 ± 1.83 g; $p = 0.28$) and abundance (8.35 ± 1.11 pieces and 7.27 ± 0.62 pieces; $p = 0.41$) were non-significant. When considering data before and after 2017 (INDICIT project start), the occurrence significantly decreased (60.69 % and 52.57 %; $p < 0.01$) as did the abundance (10.52 ± 0.96 pieces and 4.61 ± 0.11 pieces; $p < 0.001$) and the dry mass did not vary significantly (3.62 ± 2.61 g and 0.68 ± 0.11 g; $p = 0.28$).

3.3.2. *Spatial variations*

Considering the entire dataset from 1988, the occurrence of plastic ingestion and the dry mass of ingested plastics did not differ between the Atlantic and the Mediterranean ($t = -1.2$; $p = 0.23$ and $t = 1.16$; $p = 0.24$ respectively; Fig. 1, Table 1), but the abundance appeared significantly higher in the Atlantic compared to the Mediterranean ($t = 2.45$; $p = 0.01$). No significant difference in dry mass of ingested litter appeared when related to neither body mass nor standardised StCCL (respectively $t = -0.78$, $p = 0.44$ and $t = -0.97$, $p = 0.33$) as well as for abundance related to body mass ($t = 1.85$, $p = 0.06$). On the contrary, the number of ingested plastic pieces was significantly higher in the Atlantic compared to the Mediterranean ($t = 3.59$, $p < 0.001$; Table 1).

3.3.3. *Origin of individuals*

The turtles originating from bycatch were more frequently affected by plastic ingestion than turtles found stranded (69.48 % and 47.6 % respectively; $t = 6.24$; $p < 0.001$). The bycaught turtles ingested a greater abundance of plastics than turtles found stranded (12.95 ± 1.24 and 5.81 ± 0.6 pieces respectively; $t = 4.27$; $p < 0.001$) but the difference in dry mass was not significant (respectively 0.89 ± 0.1 and 3.28 ± 2.29 g; $t = -0.91$; $p = 0.36$).

3.4. *Characteristics of ingested litter*

USE SHE, USE FRAG and USE THR were the most important categories in terms of dry mass and abundance (Table 2). The ingested pieces of litter originated from diverse items such as food packaging, bags, cups, caps, cotton buds, lollipop sticks, balloons, finger rinse wipes, sanitary napkins or filters from waste treatment plants (Fig. 1). Litter from fishing activities corresponded mainly to fragments of lines and nets. Micro-plastics (1–5 mm) on average amounted to 0.77 ± 0.12 pieces ($N = 682$; 26 % of the total number of ingested plastics). The majority of plastic pieces was from colour class white -transparent (3.42 ± 0.34 pieces), more rarely dark (1.09 ± 0.12) or light coloured (1.01 ± 0.11).

3.5. *Environmental and intrinsic factors related to litter ingestion*

The models selected were regularly the same regardless of the predictive variable (Appendix-Table S8). All models were either non-significant or the determination coefficients were close to zero regardless of the response variable, underlying that the explanatory variables explained a minor part of the observed variability in the predictive variables (Table 3, Appendix-Table S9).

For Hypothesis 1, the models with Season and Country/area or Sub-region (models at the Mediterranean scale) were generally selected but three models only were significant (Table 3, Appendix-Table S9). They predicted litter ingestion to be higher in sub-region B and lower in sub-region C for occurrence, abundance, as well as abundance/StCCL. Litter ingestion was predicted to be lower in autumn compared to other seasons (Table 4). In the Atlantic, litter ingestion appeared lower in France compared to Portugal and Spain, occurrence and dry mass of ingested plastics being higher in Spain compared to Portugal and vice versa for abundance (Fig. 1).

For Hypothesis 2, the same four models were significant for occurrence, dry mass, abundance and abundance/StCCL (Table 3, Appendix-Table S9): Sex interacted with life history stage in addition to season. Litter ingestion appeared to be higher in winter compared to other seasons, and higher in adult males compared to adult females and undetermined sex (Appendix-Table S10). While, the occurrence of litter

Table 2
Dry mass and abundance of ingested material (litter with natural food and no food items), litter (synthetic material), plastics specifically, and litter categories (population means ± standard errors). The percentages were calculated according to the total ingested litter. The total abundance for all materials was not calculated because it could not be evaluated for food (FOO) and natural no food items (NFO). Total number of data available per parameter from 1988 is specified in brackets.

Category	Total ingested material	Total ingested litter	Total ingested plastics	IND	USE SHE	USE THR	USE FOA	USE FRAG	USE POTH	Non-plastics
Proportion (% of mass)	–	–	–	3.51 ± 0.53	38.63 ± 1.17	17.75 ± 1	4.97 ± 0.53	24.06 ± 1.03	4.97 ± 0.53	6.1 ± 0.64
Proportion (% of abundance)	–	–	–	3.51 ± 0.53	45.75 ± 1.15	22.64 ± 1.05	3.71 ± 0.4	16.86 ± 0.83	3.43 ± 0.41	4.48 ± 0.51
Dry mass (g)	26.52 ± 4.23	2.02 ± 41.27	1.95 ± 1.27	0.03 ± 0.015	0.21 ± 0.03	0.12 ± 0.03	0.04 ± 0.009	1.5 ± 1.26	0.03 ± 0.007	0.07 ± 0.02
Abundance (nb pieces)	–	6.67 ± 0.55	6.27 ± 0.53	0.13 ± 0.03	3.34 ± 0.32	1.19 ± 0.19	0.18 ± 0.03	1.27 ± 0.17	0.16 ± 0.03	0.4 ± 0.11

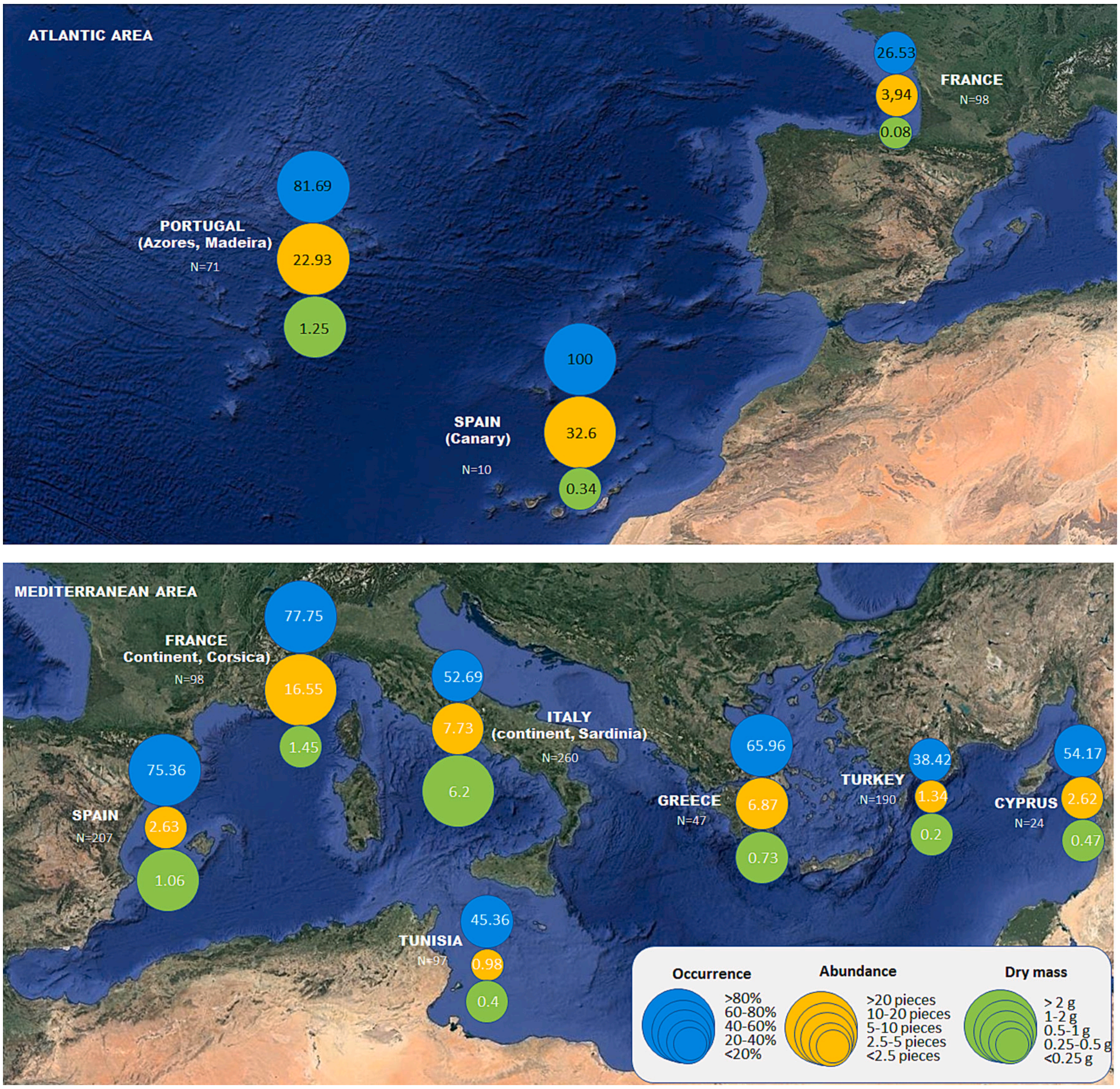

Fig. 1. Litter ingestion in the necropsied loggerhead turtles (1988–2019) in Atlantic (Top) and Mediterranean (bottom) areas: Occurrence (percentage of turtles found with ingested litter, blue) and population means of abundance of plastics (pieces, yellow) and dry mass of ingested plastics (grams, green). The order of magnitude is related to circles' size. Background map Landsat/Copernicus, Google Earth. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

ingestion and the dry mass of ingested plastics increased with life history stages, the abundance and the ratio abundance/StCCL decreased with life history stages, with variations between adult males and females (Fig. 3, Appendix-Table S10).

For Hypothesis 3, fat was selected in the best models as most predictive variable (Appendix-Table S8). While the null models were selected for the ratios dry mass/body weight and abundance/StCCL, the Fulton's K index was retained only for the ratio Dry mass/StCCL. However, none of the selected models was significant, and none of the explanatory variables explained the predicted variables significantly (Table 3, Appendix-Table S9).

4. Discussion

Previously, investigating the drivers of litter ingestion in sea turtles has been prevented by the difficult comparison of local/regional datasets obtained with disparate methodologies (Avery-Gomm et al., 2018; Fossi et al., 2018; Provencher et al., 2017). Owing to the collaboration of over 100 institutions, historical databases were harmonised with new data collection procedures (Matiddi et al., 2019) to obtain a standardised database with information on litter ingestion and individual body condition at unprecedented spatial (2 areas, 8 countries) and temporal (1988–2019) scales.

The very high occurrence of litter ingestion is of concern: Over the study area, almost 70 % of the necropsied turtles were found to ingest litter, and the occurrence was much higher at the country level, especially in France and Spain in the Mediterranean as well as in Portugal (Azores) and Spain (Madeira and Canaries islands) in the Atlantic. The temporal trends are uncertain since variations in occurrence and abundance either increase, decrease or remain stable according to the time period considered (from 1988, 2003 (publication of MSFD guideline, Hanke et al., 2013) or 2007 (INDICIT project start)), while the dry mass remains stable whatever the data period. This could be caused by differences in sample size among countries related to the year the protocol was implemented (Appendix-Table S2). The lack of standard data on plastics concentrations in the environment over a long time period also prevents an accurate analysis of these temporal variations (Cózar et al., 2015). Considering data since 1988, the occurrences were higher than those previously obtained locally, i.e., 40 % on average in the Mediterranean according to Lynch (2018) literature review (including

Table 3
For each hypothesis and each predictive variable (occurrence (%), dry mass (g), abundance (number of pieces)), determination coefficient (R^2) and *p*-value of the models selected. For Hypothesis 1, both country/area (Atlantic and Mediterranean - dark grey) and sub-region (Mediterranean - light grey) were tested. Significant models appear in bold.

	Predictive variable	Selected Model	R^2	p-value
Hypothesis 1. Litter ingestion depends on spatial and seasonal variations in litter accumulation in the environment	Occurrence	Country/Area + Season	**0.14**	**<<0.001**
		Sub-region + Season	**0. 052**	**<<0.001**
	Dry mass	Country/Area + Season	0.03	0.07
		Sub-region + Season	**0.02**	**<<0.001**
	Abundance	Country/Area + Season	**0.11**	**<<0.001**
		Sub-region + Season	**0.09**	**<<0.001**
Hypothesis 2. Litter ingestion depends on individuals' energetic needs	Occurrence	Sex x Stage + Season	**0.03**	**0.002**
	Dry mass	Sex x Stage + Season	**0.03**	**0.002**
	Abundance	Sex x Stage + Season	**0.05**	**<<0.001**
Hypothesis 3. Litter ingestion depends on individuals' body condition and health status	Occurrence	Fat	−0.008	0.8
	Dry mass	Fat	0.01	0.14
	Abundance	Fat	−0.008	0.74

data integrated into this study). Nevertheless, results on occurrence of litter ingestion and quantities of ingested litter do necessarily lead to the same interpretation. While no significant differences between areas in terms of dry mass were found, abundances were higher in the Atlantic area (eleven pieces on average) compared to the Mediterranean (six pieces). This result is similar to reported values in Lynch (2018) findings which classified the Northeast Atlantic and the Mediterranean in the third and fourth ranks at the global scale with about five and ten pieces per turtle respectively. However, when related to animals' size, a higher relative mass was found in the Mediterranean (0.07 g/kg in this study and 0.17 g/kg in Lynch's (2018) meta-analysis) than in the Northeast Atlantic (respectively 0.05 g/kg and 0.11 g/kg).

The litter ingested was diverse and does not necessarily resemble gelatinous prey items as stated by the "jellyfish hypothesis" (Schuyler et al., 2014a, 2014b; Santos et al., 2021). As found in other areas, such as in the Indian ocean (Hoarau et al., 2014) or the South Western Atlantic (Rizzi et al., 2019), litter ingested is generally white or transparent, sometimes coloured, consisting of soft and hard plastics, often single-use items such as those from takeaway restaurants, as well as debris from fishing activities. Based on FTIR (Fourier Transform Infrared Spectroscopy) analyses (GESAMP, 2015), Camedda et al. (2022) evaluated that most ingested items are composed of polyethylene (PE) and polypropylene (PP), both low-density polymers, suggesting that loggerheads are likely to consume plastics in surface and less often in the water column, since denser polymers such as Polyvinyl chloride (PVC) are less frequently found ingested. Potentially turtles could ingest litter in proportion to its availability because the same types of litter are found in the marine environments they occupy (Chambault et al., 2018; Morales-Caselles et al., 2021), and the particularly high plastics concentrations in the Mediterranean could explain the high occurrences of ingestion observed in the sea turtles (Cózar et al., 2015). In line with the first hypothesis, spatial and seasonal variations indeed partly explained the observed variability in occurrence and quantities of litter found ingested in the necropsied loggerhead turtles. Considering hydrographic areas as unit instead of country (directives application scale) for assessing litter pressure on sea turtles is certainly more relevant at the policy level since the probability of litter ingestion varies with litter distribution in the environment (Darmon et al., 2017). In the Mediterranean, Mansui et al. (2020) simulations highlight a homogeneous distribution of litter during the winter period and an accumulation in the north-western basin during the summer period. Our results in the Mediterranean do not corroborate an East-West gradient in the summer period but show a shift in areas of high plastic ingestion from the eastern basin over the western basin to then the central basin. The only boat and aerial surveys on the whole Mediterranean, carried out in summer 2018, highlights the same distribution of litter in the three Mediterranean sub-basins (Lambert et al., 2020). In the Atlantic area, our evaluations (Fig. 2) and those made by Nicolau et al. (2016) on 95 loggerheads (49.8 cm CCL on average) could be related to a possible North-South gradient in floating litter (59 %, 9.68 litter pieces >0.5 cm, 1.35 g on average). However, such simulations at the scale of hydrographic sub-regions are not available in this area to evaluate this hypothesis. Collecting more standardised data in areas that have been poorly or not yet explored, especially in the southern Mediterranean countries (UNEP/MED, 2021) and the mainland coasts of Portugal and Atlantic Spain (OSPAR Commission, 2020), is necessary for testing this hypothesis further, also considering the individual size gradients and migratory roads (Table 1; Casale and Margaritoulis, 2010).

As stated in the second hypothesis, litter ingestion could be influenced by the seasonal variations in individual energetic needs in turn related to sex (Lutz et al., 2002) or size (McCauley and Bjorndal, 1999). Nevertheless, our results appear contrasting: Individuals may have a better ability to avoid litter with age, as the occurrence of litter ingestion and the abundance of ingested litter decrease with life history stage. The amounts of ingested litter could increase according to energy requirements, as the mass of ingested litter increases with life history stage, even more in adult males compared to females. The switching in habitat and trophic niche during life history has been suggested to influence the exposure risks to litter according to individuals' size (Casale et al., 2008). Small individuals, transported relatively passively in upwellings and gyres (Witherington et al., 2012), and pelagic juveniles could be more exposed to litter than large individuals in these

Table 4
Predictions of the significant selected models (Mediterranean scale) for Hypothesis 1. The 3 variables are predicted by Sub-region (A: France, Spain; B: Italy and Tunisia; C: Cyprus, Greece, Turkey) in addition to Season.

Predictive variable	Sub-region			Season			
	A	B	C	Winter	Spring	Summer	Autumn
Occurrence (%)	56.55 ± 0.14	77.87 ± 0.15	46.92 ± 0.14	54.69 ± 0.009	61.14 ± 0.007	56.36 ± 0.007	49.18 ± 0.007
Abundance (nb pieces)	4.92 ± 0.04	10.76 ± 0.03	1.11 ± 0.04	4.25 ± 0.3	4.58 ± 0.22	5.04 ± 0.22	3.42 ± 0.24
Abundance/StCCL (nb pieces/cm^{-1})	0.14 ± 0.001	0.15 ± 0.001	0.14 ± 0.001	0.14 ± /	0.17 ±/	0.13 ± /	0.11 ± /

Fig. 2. Example of litter extracted from the digestive tract of a necropsied loggerhead collected in July 2017 in Corsica, Mediterranean France, 145 pieces of >1 mm weighing a total of 16.17 g extracted (photo: G. Darmon).

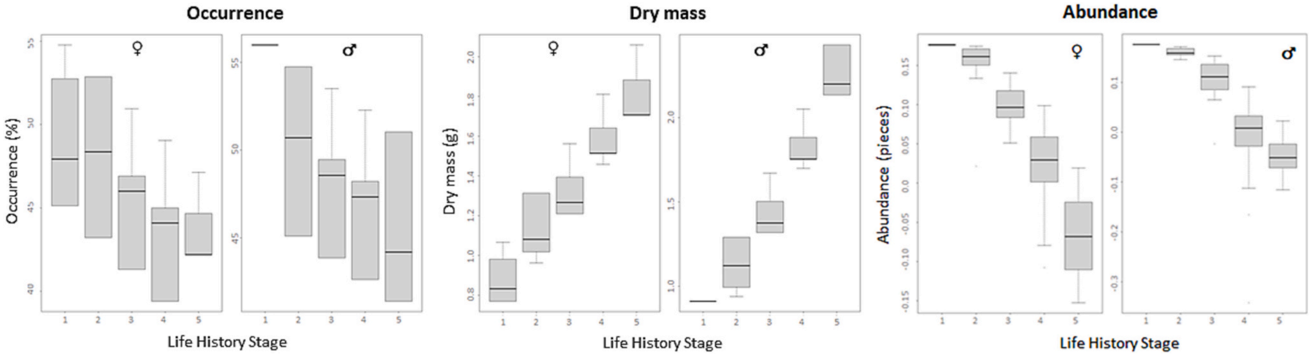

Fig. 3. Models' output for Hypothesis 2 (energetic requirements): Occurrence (Top left), dry mass (Top right) and abundance (bottom) according to Sex (left: adult males and right: adult females) and Life history stage (from 1 to 5).

accumulation zones (Lebreton et al., 2012; Mansui et al., 2020), while adults have the swimming ability and feeding selectivity to avoid litter consumption (Frick et al., 2009). However, although in this study, the tested models are significant, their low correlation coefficients underline that sex, life history stage and season explain only a small part of litter ingestion observed in our sample. The relationship between litter ingestion and individual size also appears to be contrasting among studies. While Schuyler et al. (2015) model based on literature showed life history stage to be the best proxy of litter ingestion at the global scale, other studies as in the Mediterranean, revealed no evidence of a major link between litter ingestion and sex or growth stage (Lazar and Gračan, 2011, in the Adriatic) maybe because of an absence of clear transitional shift between neritic and pelagic habitat during life (Casale et al., 2008). Casale et al. (2008) reported a lower frequency of litter ingestion in smaller individuals bycaught in oceanic areas by longlines (64 %, $N = 13$) compared to larger individuals bycaught by trawlers in neritic areas (22 %, $N = 9$) in the central Mediterranean.

Finally, contrary to our third hypothesis, no significant relationship between litter ingestion and body condition, either assessed by visual scorings (fat reserves, plastron shape), biometric indices (body mass, carapace length, Fulton's K index) or severity of injuries, was found, irrespective of the response variable, even when considering ingested quantities relative to individuals' body mass (Lynch, 2018). Different relationships were found in studies on other species, either negative such in olive ridley turtles *Lepidochelys olivacea* in Hawaii (Clukey et al., 2017) or positive such as in juvenile green turtle *Chelonia mydas* in Brazil (Santos et al., 2015).

In addition to the relative availability of litter and food in the environment, an individual's health status and level of satiety are likely to influence its perception of litter and food cues, thus influencing its acceptance threshold and ability to avoid a low-profit option (Santos et al., 2021). Highlighting impacts of litter ingestion on health, especially of loggerhead turtles, a species with long life expectancy and late reproduction (Omeyer et al., 2017), is challenging. The link between the set of parameters that we considered to assess body condition and health status is not clear. The absence of correlation among the proxies of body condition and the absence of information on the blood chemistry for the dead individuals do not allow for an accurate interpretation and classification of individuals according to health status. Generally, in previous studies, authors focused on determining whether litter ingestion could be the direct cause of mortality. Several items, a single sharp item, or plastic sheets and lines could lead to death by perforation or obstruction of the digestive tract (Wilcox et al., 2018; Santos et al., 2015). Wilcox et al. (2018) evaluated that an ingestion of 14 pieces of litter led to a 50 % probability of mortality in sea turtles. However, most studies reported that the cases of directly caused mortality are relatively rare in loggerhead turtles (Casale et al., 2008; Clukey et al., 2017) while other species such as the green turtle could have a higher frequency of mortality due to litter ingestion (Santos et al., 2016). In the present study, only 1.43 % of direct mortality was attributed with certainty to litter ingestion. However, 97 % of the causes of mortality identified were from anthropogenic origin (bycatch, collision).

Casale et al. (2016) suggests to remove the stranded individuals when assessing litter impacts because they could have died because of poor body condition, supposing that bycaught individuals would be in a better health. However, the occurrence and abundance of ingested litter was lower in the former compared to the latter and they exhibited no difference in body condition according to the proxies that were considered. Furthermore, the differences in litter ingestion observed between bycaught/stranded individuals could be biased by differences in sampling effort (Table S1) and detection probability according to habitat (pelagic/neritic), life history stages (Table S3) and countries (Table S4), also depending on the system linking rescue centres to fishermen.

Studying the sub-lethal effects of litter ingestion is just emerging (Marn et al., 2020; Santos et al., 2020). They are difficult to demonstrate, in particular with biometric or visual parameters only. Matiddi et al. (2017, 2019) proposed the ratio dry mass of ingested litter to food remains as an alternative proxy for evaluating litter impact on individual health. Assuming that the average digestive transit durations of litter and food are comparable (but see Marn et al., 2020), sea turtles that have the capacity to eat normally should ingest either more natural food than litter if they have the ability to discriminate their food, or quantities of litter and food in relation to their respective availability in the environment. In this case, the turtles, which can reduce feeding during period such as the breeding season, should not have ingested neither natural nor synthetic materials. The presence of a greater quantity of litter than natural food should therefore testify the negative impacts of litter, either because litter is more numerous than natural preys in the environment, or because the individual is not able to discriminate against it, due to impaired health (Santos et al., 2020). Therefore, the dilution of ingested nutrients with plastics in the digestive track could influence the feeding behavior, for example because the ingested litter could induce a sensation of satiety (Machovsky-Capuska et al., 2019).

Few studies reported the percentage of litter versus natural food in the digestive content, varying among regions, e.g. 3.4 % in juvenile loggerheads in Azores (Frick et al., 2009), and 7.3 % in the Portuguese coasts with no relationship with body condition (Nicolau et al., 2016). Several authors stressed that the link between litter ingestion, foraging and diet, and the consequences on food acquisition, growth, fitness, lifespan, and possible compensation mechanisms, is barely known. Therefore, there is large need to further study into such cause and consequence relationships (Machovsky-Capuska et al., 2019; Marn, 2016). Marn et al. (2020) mechanistic models showed that even if individuals have the capacity to grow up and become as large as individuals not exposed to plastics, long-term or occasional starvation would decrease reproduction output. Marn et al. (2020) models predict a reduction of energy available for body maintenance from 3 % of plastic in the digestive content, resulting in lower egg production compared to unaffected turtles. The authors' simulations expected that beyond 25 % of litter, the energy left for individuals to ensure the expenditures related to growth, reproduction and reserve accumulation becomes highly weak. Beyond 30 % of plastics in the digestive content, turtles may no longer be able to mature and reproduce, even in apparently good physiological state, then potentially impacting the viability of the population (Marn et al., 2020). As in the present study, the ingested plastics correspond to 38.77 ± 1.3 % of all ingested material on average, according to Marn et al. (2020)'s worst-case scenarios, the quantities ingested could have longer-term repercussions on the loggerhead population dynamics in the Mediterranean and Atlantic Europe.

5. Conclusions

The litter ingestion rates found in this study highlight the urgency of implementing large-scale actions for the reduction of marine litter, especially as other regions and species are possibly much more impacted (Lynch, 2018; Schuyler et al., 2015). The lack of correlation with biological factors could signal that all individuals are of concern, perhaps because of the omnipresence of litter in the marine environment (Barnes et al., 2009; Lambert et al., 2020), which makes interactions with fauna inevitable (Cózar et al., 2015; Darmon et al., 2017). This study shows however, that all individuals, whatever their circumstances of recovery (stranding, bycatch), their body condition or their life history stage, can be included to implement the indicator, without sampling stratification. Due to the loggerhead turtle widespread distribution, a harmonised monitoring, based on the standard data collection of the litter ingested, could be implemented on a wider spatial scale, enabling the influencing factors to be investigated more precisely by increasing sample sizes.

Nevertheless, while the simulations obtained from mechanistic models published in literature (Marn et al., 2020) suggest that the quantities of ingested litter found in this study can jeopardise individuals' reproductive capacities and populations' dynamics, the lack of any link to health proxies underpins the need to better evaluate health (e.g., by systematically collect the so-called "optional" parameters, compare with parameters collected in living individuals) and the cause-and-effect relationships with litter ingestion. The parameters collected to assess health depend on sampling means as well as objectives (e.g., release rehabilitated individuals, evaluation of population dynamics). As the comparison with a reference population, not exposed to litter, is probably impossible, the authors encourage the collection of more standardised data on both litter ingestion and body condition to increase the power of statistical tests to highlight interacting factors acting at such large scales. At the same time, multi-disciplinary approaches could allow for a better understanding of the relationships between litter ingestion, diet, health and population dynamics.

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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

The authors do not have permission to share data.

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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.2022.114364.

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