



# Incidental capture of sea turtles in the Northeast Atlantic Portuguese pelagic longline fishery

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## ABSTRACT

Incidental catch or bycatch of sea turtles by pelagic longline fisheries is a major concern worldwide. The Northeast Atlantic hosts key foraging and developmental areas for oceanic juvenile loggerhead sea turtles (*Caretta caretta*) originating mainly from the Southeastern USA and Cape Verde. This region may be one of the most heavily fished areas by pelagic longline for which no recent assessments of fisheries interactions exist. We analysed fishery observer data collected between 2015 and 2020 to assess sea turtle bycatch by Portuguese commercial longliners targeting swordfish (*Xiphias gladius*) and blue shark (*Prionace glauca*) in the Northeast Atlantic. A total of 177 sea turtles interacted with the gear during the 896 fishing sets (887,641 hooks) monitored. Loggerheads ( $n = 139$ ) ranging between 32 and 78 cm curved carapace length (CCL) were caught at a rate of 0.152 turtles per 1000 hooks, and leatherbacks (*Dermodochelys coriacea*;  $n = 38$ ) between 100 and 210 cm estimated length at a rate of 0.043 turtles per 1000 hooks. Loggerhead and leatherback bycatch shows a clear seasonal pattern in the region. At haul-back mortality rates of oceanic-stage juvenile loggerheads was estimated at 26% whereas no at haul-back mortality was registered for leatherback turtles. Model estimates, based on AIS derived fishing effort from Global Fishing Watch, indicate a total of 1439 interactions (552–3069 BCI) for loggerhead, and 604 interactions (262–1129 BCI) for leatherback turtles between 2016 and 2020. Information from this study is essential to support effective management strategies for sea turtle conservation in the Northeast Atlantic.

## 1. Introduction

Incidental capture or bycatch of sea turtles by pelagic longline fisheries is a well-known issue (Lewison et al., 2004a; Lewison and Crowder, 2007; Wallace et al., 2010a, 2013a). Pelagic longlines targeting swordfish, sharks and tunas are commonly used throughout the world, with fishing effort extending across the Pacific, Indian and Atlantic oceans (Lewison et al., 2004a; Watson and Kerstetter, 2006). Because their horizontal and vertical distributions overlap with those of pelagic longline fishing gear, sea turtles are vulnerable to hooking or entanglement that may cause serious injuries and/or mortality. Bycatch in pelagic longline fisheries is one of the greatest anthropogenic sources of mortality for sea turtles in open waters of the Northeast Atlantic (Bolten et al., 1994; Ferreira et al., 2001; Lewison et al., 2004a, TEWG 2009, Bolten et al., 2010, Wallace et al., 2011, NMFS and USFWS 2020).

Six of the seven species of sea turtles interact with longline gear in the International Commission for the Conservation of Atlantic Tunas-ICCAT Convention area (i.e. Atlantic, Mediterranean Sea, Caribbean Sea and Gulf of Mexico). The six species are loggerhead (*Caretta caretta*), leatherback (*Dermodochelys coriacea*), green (*Chelonia mydas*), hawksbill (*Eretmodochelys imbricata*), olive ridley (*Lepidochelys olivacea*) and Kemp's ridley (*Lepidochelys kempii*) sea turtles (Coelho et al., 2013; Gray and Diaz, 2017). Loggerhead and leatherback turtles are the most frequently captured species by longline gear in the North Atlantic (Gardner et al., 2008; Mejuto et al., 2008; Angel et al., 2014; Gray and Diaz, 2017) and worldwide (Lewison et al., 2004a, 2004b).

Loggerhead sea turtles found in pelagic habitats of the Northeast Atlantic are mostly oceanic juveniles (Bolten, 2003a) undertaking developmental migrations that span several years, followed by a neritic stage during which they inhabit coastal areas for further maturation

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(Bjorndal et al., 2000; Bolten, 2003b). They originate from the North-west and Northeast Atlantic Ocean subpopulations or Regional Management Units (RMU; Wallace et al., 2010b). Major breeding areas of loggerheads in the Northwest Atlantic Ocean RMU are in the south-eastern USA and Yucatan peninsula of Mexico (Bolten et al., 1998; Ceriani and Meylan, 2017). Abundance assessments based on nests counts on Florida core index beaches show a pronounced decline between 1998 and 2006 followed by an increasing trend in annual number of nests over the past decade, likely as a result of increases in the number of nesting females estimated from nests, and clutch frequency (Bolten et al., 2019). A corresponding trend was observed in oceanic in-water habitats in the Northeast Atlantic (Vandeperre et al., 2019). However, the lack of significant changes in the overall trend of the number of annual nests for 30 years (1989–2018) raises concern about the recovery of the loggerhead Northwest Atlantic subpopulation (Bolten et al., 2019; Ceriani et al., 2019) which is currently considered of “Least Concern” under the IUCN Red List criteria (Ceriani and Meylan, 2017). In the Northeast Atlantic Ocean RMU loggerheads breed mainly in Cape Verde Archipelago and are currently considered “Endangered” under the IUCN Red List criteria because of limited nesting habitat area and continued anthropogenic pressure on nesting beaches (Casale and Marco, 2015).

The leatherback sea turtle is widely distributed in the Atlantic Ocean and belongs to the Northwest Atlantic RMU (Wallace et al., 2010b). Leatherbacks originate from tropical and subtropical beaches and undertake long range migrations to foraging grounds in temperate and sub-polar latitudes to live as oceanic foragers throughout their lives (Eckert et al., 2012). This species is currently considered “Vulnerable” under the IUCN Red List criteria (Wallace, 2013b), and most of the global population occurs in the Atlantic Ocean after a severe decline of these individuals in the Pacific in the past 30 years (Spotila et al., 2000; Fossette et al., 2014). The Northwest Atlantic subpopulation exhibited a decreasing nest trend between 2008 and 2017, and nesting female abundance at several nesting sites with previously high density, have declined drastically (NMFS and USFWS 2020).

The Portuguese pelagic longline fishery targeting swordfish (*Xiphias gladius*) and blue shark (*Prionace glauca*) in the Northeast Atlantic shows a pronounced and asynchronous seasonal pattern, where by swordfish captures are higher during autumn and blue shark catches dominate during spring (Aires, da, Silva and Pereira, 1999, Santos et al., 2002, Aires-da-Silva et al., 2008, Vandeperre et al., 2014, Roxo et al., 2017, Parra et al. under review). This fishery is managed by ICCAT providing stock assessments, determining Total Allowable Catch (TAC) and attributing fishing quotas to each contracting party (e.g. Portugal), as well as making recommendations for management actions. The Portuguese pelagic longline fleet was composed of 39 vessels that were identified as regularly fishing with drifting longline gear in the North Atlantic during 2020 (Parra et al. under review). Vessel size ranged between 15 and 46 m, with a gross tonnage capacity of > 50 t, and an unknown portion of the fleet with frozen fish storage capacity (Parra et al. under review). These vessels operate mostly within the 200 nm EEZs of mainland Portugal, Azores, Madeira and Canary Islands, and in international waters in the Northeast Atlantic.

Several studies have evaluated and quantified sea turtle bycatch by pelagic longline in the Northeast Atlantic. Bolten et al. (1994), Martins et al. (2001) and Ferreira et al. (2001) reported bycatch rates, size frequency, physical condition and position of the hooks in turtles bycaught by pelagic longline in the Azores. Huang et al. (2015) reported sea turtle bycatch characteristics and distribution by the Taiwanese longline fleet operating in the region. Other studies have reported sea turtle bycatch while testing different hook types/sizes or hook-and-bait combinations during experimental pelagic longline sets (Bolten and Bjorndal, 2005; Mejuto et al., 2008; Santos et al., 2012; Coelho et al., 2015; Huang et al., 2016). The Northeast Atlantic region hosts important foraging and developmental grounds for juvenile loggerhead turtles (Bolten et al., 1993; Bjorndal et al., 2000; Bolten, 2003a), and is a main fishing area for the Portuguese and Spanish pelagic longline fleets (Queiroz et al., 2016;

Anonymous, 2019, Parra et al. under review), yet little contemporary information on sea turtle bycatch is available for this area. This study provides an assessment of sea turtle bycatch in the Portuguese pelagic longline fishery operating in the Northeast Atlantic between 2015 and 2020, in terms of species and size composition, spatial and temporal variability of bycatch rates and the relationship with operational characteristics of the fishery. We further report on the physical condition after capture, direct or at-haul-back mortality, hook location, and provide model derived estimates of the total number of interactions with sea turtles for the Portuguese fleet during the study period. Current policy on sea turtle bycatch by pelagic longline, as well as mitigation opportunities, are also discussed.

## 2. Methods

### 2.1. Fisheries data

Data was collected under the Azores Fisheries Observer Program (POPA – Programa de Observação das Pescas dos Açores; [www.popaobservers.org](http://www.popaobservers.org)) and COSTA project (Consolidating Sea Turtle Conservation in the Azores; [www.costaproject.org](http://www.costaproject.org)) on-board Portuguese commercial longline fishing vessels between September 2015 and December 2020. The fleet was sampled based on an opportunistic sampling design in which observers embarked on vessels that provided suitable accommodation for the observer, and with the cooperation of vessels owners and captains. A total of 896 sets was monitored by 6 different observers during 72 fishing trips performed by 18 different longline vessels between 18 and 33 m in length, resulting in 887,641 hooks deployed in the area between 10°–42° W and 20–46° N (Fig. 1). The number of sets and vessels observed per year are summarized in Table 1. The fishing gear used was the “American style” longline which consisted of a monofilament nylon mainline approximately 100 Km in length and weighted branchlines suspended by two types of buoys: large (LB) and small buoys (SB). LB are used to locate the gear at the surface and, together with SB, provide stability to the gear (Ferreira et al., 2011). The number of LB per set varied between 7 and 29, resulting in sets with 6–28 sections, respectively. Each section had 8–19 SB and between each SB, 3–5 hooks. Hooks were separated by intervals of 60–120 m. Branchlines measured from 12 to 18 m and had a wire or monofilament leader. Light-sticks were used in all sets. Hook types used were the Ancora (16/0 and 17/0) offset J (75% of all sets), the straight J (22%) or a combination of both (3%). Hooks were mainly baited with mackerel (*Scomber* spp.), squid (*Loligo* spp.), and occasionally shark meat (*Prionace glauca*). The number of hooks per section varied from 36 to 80, with a total number of hooks per set ranging from 360 to 1792 (mean:  $990 \pm 127$  S.D.). The gear was typically deployed between 17:30 and 23:00 h and retrieved between 7:15 and 16:50 h. Set duration, estimated by the difference between the beginning of gear deployment and the end of gear retrieval, ranged between 12.7 and 42.8 h (mean:  $23.8 \pm 2.5$  S.D.). Soaking time, calculated as the difference between the starting time of gear deployment and starting time of retrieval, ranged between 9.1 and 32.6 h (mean:  $13.9 \pm 1.8$  S.D.).

### 2.2. Sea turtle bycatch

For each turtle interaction with the gear, observers identified the species, recorded hook location or entanglement and physical condition after capture. Turtles were brought on board using a dip-net whenever possible, while larger turtles were immediately released using line cutters to remove as much fishing line possible. Curved carapace length (CCL) was measured to the nearest lower 0.1 cm when turtles were hauled in. Hook location was divided into three categories: external (entangled or foul-hooked on the body), mouth, and deep-hooking (internally hooked in the throat, oesophagus, or deeper). Physical condition was evaluated based on the procedures and resuscitation techniques described in NMFS SEFSC (2019) and classified as follows: strong

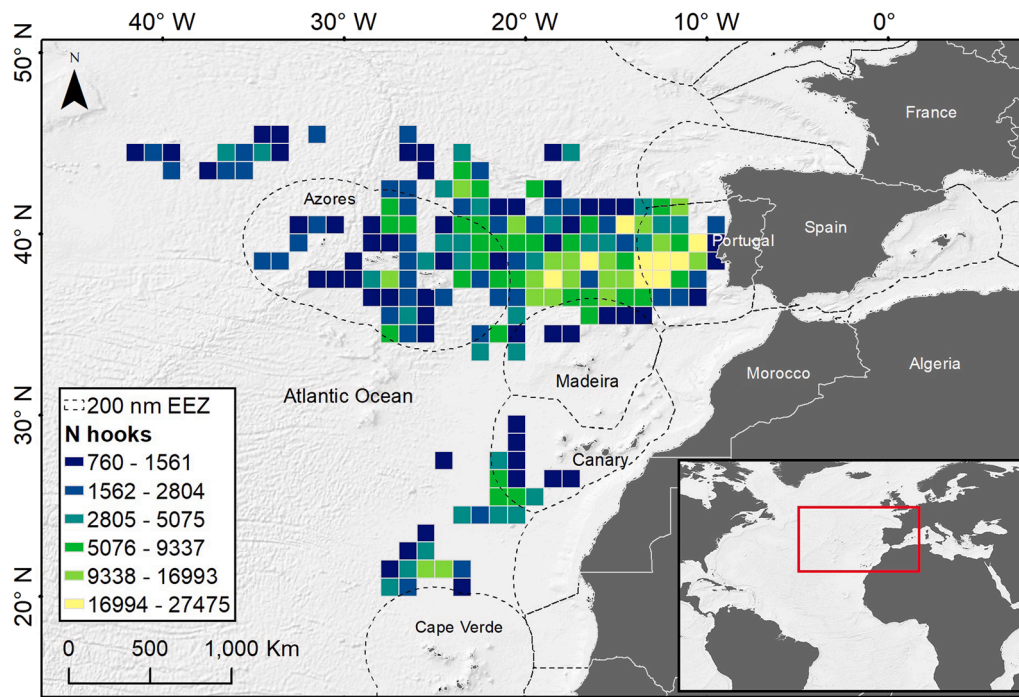


Fig. 1. Observed fishing effort (i.e. number of hooks) by Portuguese longliners operating in the Northeast Atlantic between 2015 and 2020. Data is presented over a 1-degree cell grid. Dashed lines represent the 200 nautical mile exclusive economic zone (EEZ).

Table 1

Observed number of fishing trips, vessels, sets, hooks, and captured sea turtles, and proportion of sets that captured sea turtles per year by Portuguese pelagic longline vessels operating in the Northeast Atlantic.

Year	N trips	N vessels	N sets	N hooks	N loggerheads	N leatherbacks	% sets
2015	7	4	78	79,266	4	10	16.7
2016	16	8	220	226,074	33	5	12.8
2017	12	9	145	143,984	17	4	12.4
2018	14	10	192	187,477	9	5	6.8
2019	12	7	129	119,426	48	4	14.7
2020	11	7	133	131,414	28	10	17.3

(active/with movement), weak (sluggish or inactive but react to eye and cloaca touching) and dead (no movement or reaction to eye and cloaca touching). Hooks were removed when possible and if not, the line was removed as much as possible prior to release. Weak or inactive turtles were kept on board for a few hours in the shade and when possible with the posterior part of the body elevated. Turtles recorded as dead were discarded at sea. The aforementioned procedure was performed in the presence of the observer and served as a reference to disseminate best handling practices among fishers.

### 2.3. Data analysis

All analyses were conducted within the R statistical environment v4.2.2 (R Core Team, 2022). Generalized linear mixed models (GLMM) were used to relate sea turtle catch per unit of effort (CPUE; in number of individuals per 1000 hooks) with operational and spatio-temporal variables in order to estimate the number of sea turtles caught by the Portuguese pelagic longline fleet between 2016 and 2020. Such approach is commonly used to derive standardized catch rates that account for differences in fishing operations and/or variability in temporal and spatial distribution of the resources (Maunder and Punt, 2004). Candidate predictor variables for inclusion in the model as fixed terms were month, vessel length, leader type, hook type, soaking time, bait type, and target species CPUE. Leader type was either wire, mono-filament nylon or the use of both. Hook type was either straight J or

offset J. Because bait type was recorded as a proportion for each fishing set, we considered two categories: more than or equal to 80% of mackerel ( $m \geq 80$ ), and less than 80% of mackerel ( $m < 80$ ), where a mixture of squid (mean:  $13.7 \pm 20\%$  S.D.) and blue shark meat (mean:  $4.4 \pm 7.7\%$  S.D.) were used. Target species consisted of swordfish and blue shark nominal CPUE (Parra et al. under review). Although target species captures are likely to have no influence on sea turtles bycatch, they were included in the modelling process to investigate the level of association between them. The size of the hook (16/0 or 17/0) could not be included in the analysis because only 22% of all sets had this information.

Preliminary data exploration included boxplots, density plots and histogram to visualize potential outliers and distribution frequencies (Zuur et al., 2010). Spearman's rank correlation and Variance Inflation Factor (VIF) were used to test for collinearity between variables. Sea turtle CPUE was investigated for spatial autocorrelation using the Moran's I (morantest function from the "spdep" package v1.2-7; Bivand, 2022). Because loggerhead and leatherback CPUE in our data had a significant positive spatial correlation, indicating a clustered pattern in space, geographic coordinates were included in the models to account for spatial effects. Sea turtle counts were modelled assuming a Poisson distribution and a log link function using the glmer function from the "lme4" package v1.1-31 (Bates et al., 2015). The logarithm of the number of hooks was included as an offset term and vessel ID as a random effect to account for dependence among observations from the

same vessel. Models were fitted to the data in a backward stepwise selection process to select significant variables ( $p < 0.05$ ) based on the Akaike's information criterion corrected for small sample sizes (AICc) (Zuur et al., 2009). Model residuals and the dispersion parameter were evaluated in each step. Because Pearson and deviance residuals do not typically follow a normal distribution in Poisson models (Feng et al., 2020 and references therein), residual analysis was performed using a simulation-based approach to compute scaled (quantile) residuals for investigating model misspecification, over/under-dispersion, outliers and zero-inflation ("DHARMA" package; Hartig, 2022). Final model coefficients were expressed in terms of incident rate ratios (IRR), and significant variables were plotted against fitted values using the "sjPlot" package v2.8.12 (Lüdtke, 2022).

The next step involved the preparation of the Global Fishing Watch data (GFW; available at <https://globalfishingwatch.org>) for model prediction. GFW provides daily AIS-derived (automated identification system) fishing effort data (measured in hours of fishing) gridded at 0.01 degrees, and grouped by flag state and gear type, and also by individual vessels identified by the maritime mobile service identity number (MMSI) (Kroodsma et al., 2018). Under the Portuguese jurisdiction, the obligation of the carriage of AIS is restricted to fishing vessels with more than 15 m in length (Decree-Law 52/2012 March 7th 2012). A total of 60 vessels carrying AIS were identified for the Portuguese drifting longline fleet with sizes ranging between 15 and 46 m (mean 24 m), and a total gross capacity of 7220 t (mean 164 t) (Parra et al. under review). For the purpose of this study, GFW data was extracted for the Portuguese fleet with drifting longline gear type and for the period between 2016 and 2020. Subsequently, it was spatially cropped by the extent of the observer data, and aggregated by 0.1° cells and by month, resulting in a dataset with 140,137 entries. For significant variables retained in the final models, each entry of the GFW dataset was assigned to the median value for numerical variables (i.e. vessel length and soak time) and to the most frequent category for categorical variables (i.e. leader, hook and bait types) of the observer data (Table S1). For target species we used the monthly standardized CPUE estimated with the same observer data used in this study, and presented in Parra et al. (under-review). To convert GFW fishing effort expressed in fishing hours into number of hooks, it was assumed that the mean duration of a fishing set of 23.8 h, from the beginning of gear deployment until the end of gear retrieval, corresponded to the mean of 990 hooks per set that was observed.

In order to investigate the level of representativeness of the observed compared to the GFW estimated effort data, we used Pearson's correlation coefficient to measure the degree of seasonal and spatial correlation between both datasets over the studied period and within cells of a 1-degree grid in which we had observed effort. Moreover, and in order to obtain a measure of the accuracy of the GFW effort data, matching GFW data were extracted for the observer dataset, and correspondence was assessed in terms of daily effort and spatial coordinates of individual vessels.

A parametric bootstrap method was used to derive estimates of the number of sea turtles bycaught by the Portuguese pelagic longline fleet based on the GLMM model (Knowles and Frederick 2020). The final GLMM was refitted for each of 1000 new datasets which were resampled from the GFW dataset with replacement, using the bootMer function from the "lme4" package v1.1–31 (Bates et al., 2015). Yearly estimates of the number of sea turtles caught were calculated from the median of the bootstrap sample (i.e. 0.5 quartile), while the 95% confidence intervals (BCI) corresponded to the 0.025 and 0.975 quartiles, making no assumptions about the underlying distribution. Seasonal maps of sea turtles nominal and bootstrapped CPUE, and predicted number of interactions were produced using the "ggplot2" package (v3.4.0, Wickham, 2016). Seasonal quarters were considered as follows: spring (March-May), summer (June-August), autumn (September-November) and winter (December-February).

### 3. Results

#### 3.1. Fishing effort

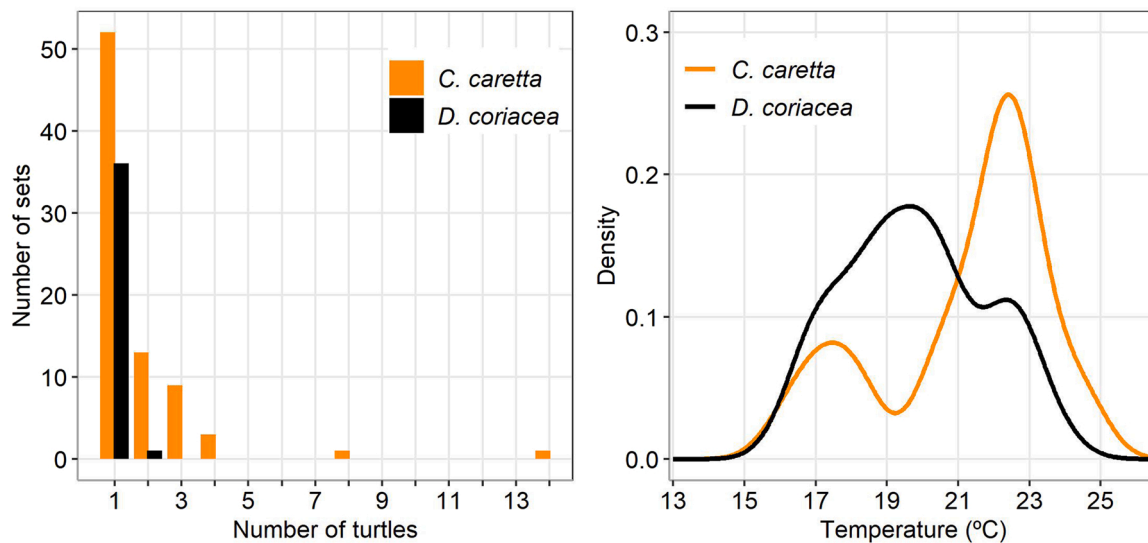
From 2015–2020, a total of 887,641 hooks from 896 fishing sets deployed by Portuguese longline vessels in the Northeast Atlantic was observed. According to the GFW data, a total of 15,995 fishing days were estimated for the fleet operating in the region and during the same period, and the observer data covered 5.5% (884 fishing days) of this total. Moreover, our data covered 46% of the fleet in number of vessels (i.e. 39 vessels identified to have swordfish fishing quotas during 2020 and that regularly fish with pelagic longlines; Parra et al. under review). A significant spatial correlation ( $p < 0.001$ ) was found between the observed and GFW estimated fishing effort for all seasons except during summer months ( $p = 0.34$ ; Supplementary Fig. S1), where the lowest number of fishing sets were observed (Supplementary Fig. S2). Details of the seasonal distribution of fishing effort, operational characteristics and target species captures are presented in Parra et al. (under review). In general, most of the fleet fishing effort occurred between Portugal mainland and the Azores EEZs, between 10°–24° W and 36–42° N, congregated west off Portugal mainland during autumn when vessels targeted mostly swordfish, and gradually moved away westwards towards the Azores region during winter and spring, when vessels targeted mainly blue shark. During summer, fishing effort appears dispersed over the region, between 10°–40° W and 25–50° N, with vessels targeting both swordfish and blue shark. A total of 25,341 blue sharks and 15,560 swordfish were caught during the study period, both species representing 88.3% of the total catch in numbers.

#### 3.2. Sea turtle bycatch

For the observed effort, a total of 177 sea turtles were incidentally caught between 2015 and 2020 (Table 1). Loggerhead ( $n = 139$ ) and leatherback ( $n = 38$ ) turtles were the only sea turtle species recorded to interact with the longline gear and both species were recorded caught in the same fishing set in two occasions. The density of bycaught sea turtles according to sea surface temperature recorded on board vessels further showed different patterns between species, with a higher proportion of incidental captures recorded between 22 and 23 °C for loggerhead and 19–20 °C for leatherback turtles (Fig. 2). Sea turtles were recorded to interact with the gear in 114 fishing sets, 12.7% of all sets. A single loggerhead was caught on 52 sets, 2–4 were caught on 25 sets, and 8 or 14 were caught on 2 sets (Fig. 2). Ninety-one percent (91%) of all sets showed zero loggerhead turtles recorded. A single leatherback was caught on 36 sets, and 2 were caught on 1 set (Fig. 2). Ninety-six percent (96%) of the sets showed zero leatherback turtles recorded. Loggerhead nominal CPUE per fishing set ranged from 0 to 13.9 individuals per 1000 hooks, with an overall mean  $\pm$  S.D. of  $0.152 \pm 0.712$ , whereas leatherback CPUE per set ranged from 0 to 2.08, with an overall mean of  $0.043 \pm 0.216$ .

##### 3.2.1. Loggerhead

Of the 139 loggerhead turtles bycaught, 45% were hooked in the mouth, 37% were deeply hooked (swallowed hook), 17% were recorded hooked externally (entangled or foul-hooked) and one had no information (Table 2). For the 133 turtles with known gear leader type, 61% were caught on hooks with monofilament nylon and 39% with wire leaders. Of the 135 turtles with hook type recorded, 73% were caught with the offset J hook and 27% with the straight J hook. For the 135 turtles with known hook fate, the hook was removed from 105 (78%) turtles before release, while 30 (22%) were released with the hook still in place. For the 131 turtles with recorded physical condition after capture, 62% were considered strong, 12% were weak, and 26% were dead. Most of the turtles recorded dead were hooked in the mouth or deeply hooked (Fig. 3). The size of the turtles ranged between 32 and 72 cm CCL (mean  $\pm$  S.D. =  $52.1 \pm 8.7$  cm; Fig. 4).



**Fig. 2.** Distribution of the number of sets by the number of turtles (sets with zero turtles caught not included), and proportion of loggerhead and leatherback bycatch in relation to the sea surface temperature recorded on-board Portuguese pelagic longline vessels between 2015 and 2020.

**Table 2**  
Number of loggerhead and leatherback turtles bycaught by Portuguese longline vessels between 2015 and 2020 in the Northeast Atlantic according to hook location, gear leader and hook types, and physical condition after capture.

		Sets		Loggerhead		Leatherback	
		N	%	N	%	N	%
Leader type	Wire	225	26.5	52	39.1	9	27.3
	Nylon	624	73.5	81	60.9	24	72.7
Hook type	Straight J	196	22.6	36	26.7	2	0.1
	Offset J	670	77.4	99	73.3	29	99.9
Bait	Mackerel (≥ 80%)	614	68.5	7	0.1	7	0.2
	Mackerel (< 80%)	282	31.5	132	99.9	28	99.8
Physical condition	Strong			81	61.8	35	100
	Weak			16	12.2	0	0
	Dead			34	26	0	0
Hook location	External			24	17.4	25	80.6
	Mouth			62	44.9	5	16.1
	Deep-hooking			52	37.7	1	3.3

Loggerhead monthly CPUE showed higher rates in June (1.05 individuals/1000 hooks) followed by July (0.31 individuals/1000 hooks), coinciding with the period when both swordfish and blue shark catch rates were low (Fig. 5). Seasonal CPUE ranged from 0.03 during winter and 0.59 during summer. Seasonal spatial distribution of loggerhead CPUE was not uniform throughout the study area but rather clustered in space (Fig. 6). Of the 139 recorded loggerhead turtles, 84 (60%) were caught from spring to autumn, west of Canary Islands between 15°–25° W and 20–30° N, where only approximately 10% of the observed fishing effort was recorded. Twenty-one turtles (15%) were caught during summer and autumn, mostly in international waters west of mainland Portugal between 10°–20°W and 35–40°N, where the highest observed fishing effort was recorded. A significant positive correlation was found between loggerhead CPUE and the number of hooks deployed over cells of a 1-degree grid (Spearman’s rank correlation  $R = 0.17$ ,  $n = 188$ ,  $p = 0.03$ ).

### 3.2.2. Leatherback

Of the 38 leatherback turtles that were recorded to interact with the gear, the type of interaction was recorded for 35 turtles. For the 31 turtles that had information on hook location, 25 (81%) were hooked externally or foul-hooked mostly in the flippers, 5 (16%) were hooked in

the mouth and one was deeply hooked (Table 2). For the 33 captures with known gear leader type, leader was monofilament nylon for 24 turtles (73%) and wire for 9 (27%). From 35 leatherback turtles recorded to interact with the gear, hook type was the offset J for 32 (91%) turtles and straight J for the remaining 3 (Table 2). Physical condition after capture was inferred to be strong since all individuals were active after capture and were immediately released due to their large size. Leatherback CCL was visually estimated for 23 individuals and undetermined for the remaining 12, and ranged between 100 and 210 cm (mean  $\pm$  S.D. =  $167 \pm 30$  cm).

Leatherback monthly CPUE was highest during November (0.11 individuals/1000 hooks), followed by September (0.088 individuals/1000 hooks), coinciding with the period when swordfish captures were higher (Fig. 5). Leatherback bycatch was not observed during January, February and July. Seasonal CPUE varied between 0.015 during winter and 0.089 during autumn. Seasonal spatial distribution of leatherback nominal CPUE appears clustered in space during autumn within the EEZ of mainland Portugal and adjacent international waters, between 10°–22°W and 37–41°N, where higher observed fishing effort was recorded (Fig. 6). Throughout the rest of the year, leatherback CPUE appears scattered in the area. A significant positive correlation was found between leatherback CPUE and the number of hooks over cells of a 1-degree grid (Spearman’s rank correlation  $R = 0.34$ ,  $n = 188$ ,  $p < 0.001$ ).

### 3.3. Bycatch estimates

For loggerhead, significant variables retained in the final model were month, soaking time, leader type, swordfish CPUE, bait type and the interaction between longitude and latitude, while for leatherback only longitude and season were retained (Table S2). Because month was found to be not-significant for leatherback CPUE, we aggregated months into seasons. The variance of the random effect vessel ID was zero in both models. The final model for loggerheads explained 33.8% of the variance and the dispersion parameter was 1.05, whereas for leatherbacks, the model explained only 7.6% of the variance and the dispersion parameter was 0.97. For both species, residual analysis showed a linear QQ plot and non-significant test results for the presence of dispersion and/or outliers (Fig. S3 and S4). The distribution of the residuals against predicted values and against all predictors showed a uniform pattern with no significant quantile deviations, indicating that models were correctly specified. Overall, both final models were considered adequate in terms of their fit to the data, and model assumptions considered to be

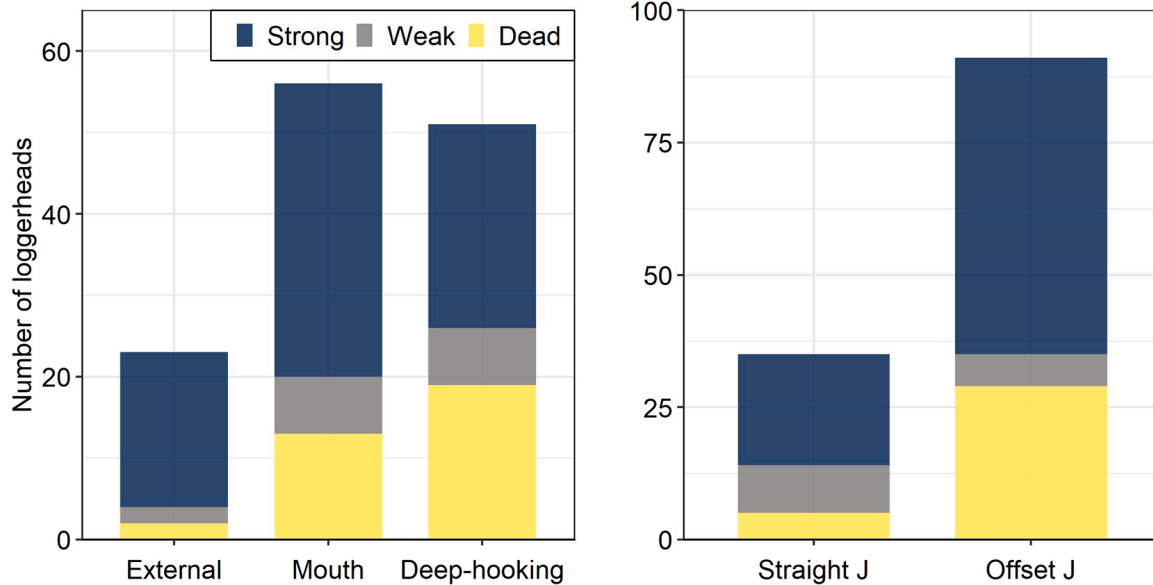


Fig. 3. Number of bycaught loggerhead turtles by hook location (left panel) and hook type (right panel), and by physical condition after capture.

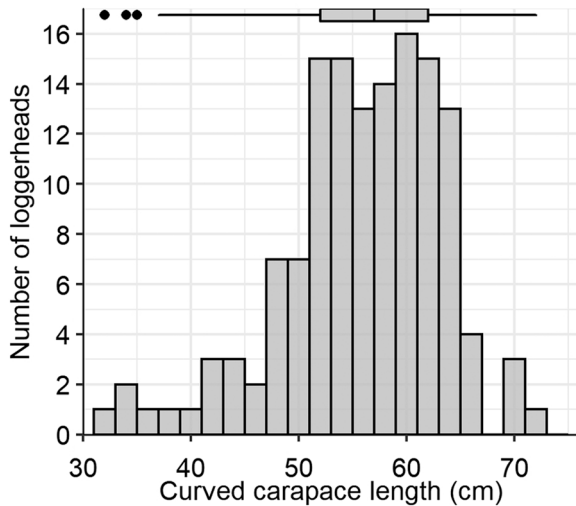


Fig. 4. Size frequency of loggerhead turtles bycaught by Portuguese longline vessels between 2015 and 2020. On the top boxplot, dots indicate outliers, bar indicate first and third quartiles and line indicate median.

met.

Predictor plots showed that loggerhead bycatch rates were relatively higher between July and September, when swordfish catches were higher in the region, and increased at lower longitudes and latitudes (Fig. 7). Results further indicated that for each one percent increase in soaking time, loggerhead CPUE is expected to increase by a factor of 1.16 (1.07–1.25 95% CI), given the other variables retained in the final model held constant (Table S2). Furthermore, the use of nylon leaders compared to wire leaders is expected to decrease loggerhead CPUE by a factor of 0.46 (0.27–0.79 95% CI), yet these results are biased towards fishing sets deployed south of 30° N latitude during summer that used wire leaders and caught 3–14 turtles per set (Fig. 6). For leatherback turtles, the model showed that catch rates were higher during autumn and increase eastwards, in particular east of 20° W (Fig. 7).

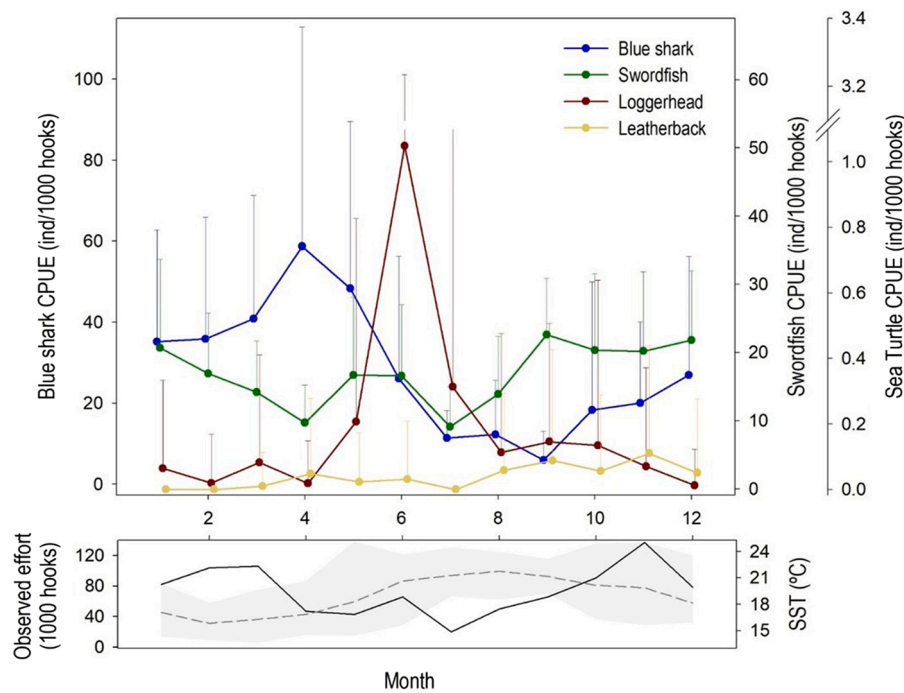
Comparing the GFW and the observer datasets, between 2016 and 2020 the GFW data only identified 948 from a total of 952 days in which fishing events occurred and that were recorded in our data. The total number of fishing hours in the GFW data was higher by a factor of 1.12

compared to the observer data (13,925 vs 12,357 fishing hours), and with a slightly higher average number of fishing hours per day (i.e. 14.7 ± 8.7 S.D. vs 13.3 ± 3.4 S.D.) for the GFW and observer data, respectively. The correlation between the daily effort, longitude and latitude was significant ( $p < 0.001$ ), yet was found weak for the daily effort ( $R = 0.24$ ; Fig S5). The total number of sea turtle interactions for the Portuguese pelagic longline fleet operating in the Northeast Atlantic between 2016 and 2020 was estimated at 1439 (552–3069 BCI) for loggerhead, and 604 (262–1129 BCI) for leatherback turtles. Yearly estimates for loggerhead varied between 148 (53–313 BCI) and 496 (195–1049 BCI) interactions during the years of 2017 and 2019, respectively, and for leatherback turtles between 97 (39–194 BCI) and 139 (64–251 BCI) interactions during the years of 2018 and 2019, respectively (Table 3).

Loggerhead and leatherback seasonal maps of the predicted number of interactions with the Portuguese pelagic longline fleet between 2016 and 2020 are presented in Fig. 8. These maps were derived from the bootstrapped median CPUEs (shown in Fig. S6 and Fig. S7, respectively) and applied to the GFW fishing effort converted to number of hooks. Overall, results show that the area within the EEZ mainland Portugal and adjacent international waters during autumn has a relatively higher susceptibility to sea turtle’s interactions with the fleet.

#### 4. Discussion

The recorded bycatch rates of loggerhead and leatherback turtles by Portuguese longline vessels in the Northeast Atlantic from 2015 to 2020 showed evidence of seasonal and spatial patterns. Temporal overlap of higher loggerhead and leatherback bycatch rates only occurred during autumn, when vessels targeted mostly swordfish in the region. This pattern in sea turtle bycatch is consistent with what has been previously reported for the U.S. pelagic longline fishery operating in the Northwest Atlantic, with higher bycatch of loggerhead and leatherback turtles occurring between July and December in sets dominated by swordfish captures (Gardner et al., 2008; Kot et al., 2010; Swimmer et al., 2017). The Portuguese pelagic longline fishery targeting swordfish and blue shark in the Northeast Atlantic is markedly seasonal and likely reflecting species abundances in the region. Swordfish, blue shark, and loggerhead and leatherback turtles are highly migratory, widely distributed and with different temporal and spatial niches that overlap differently depending on habitat preferences and requirements of each species. Spatial overlap of loggerhead and leatherback bycatch occurred



**Fig. 5.** Monthly mean nominal CPUE for sea turtle and target species, observed fishing effort (number of hooks; solid line, lower panel) and mean sea surface temperature (SST; dashed line, lower panel) recorded on board Portuguese longline vessels operating in the Northeast Atlantic from 2015 to 2020. Bars (upper panel) are Standard Deviation of the Mean (S.D.). Shaded grey area (lower panel) represent SST maximum and minimum values.

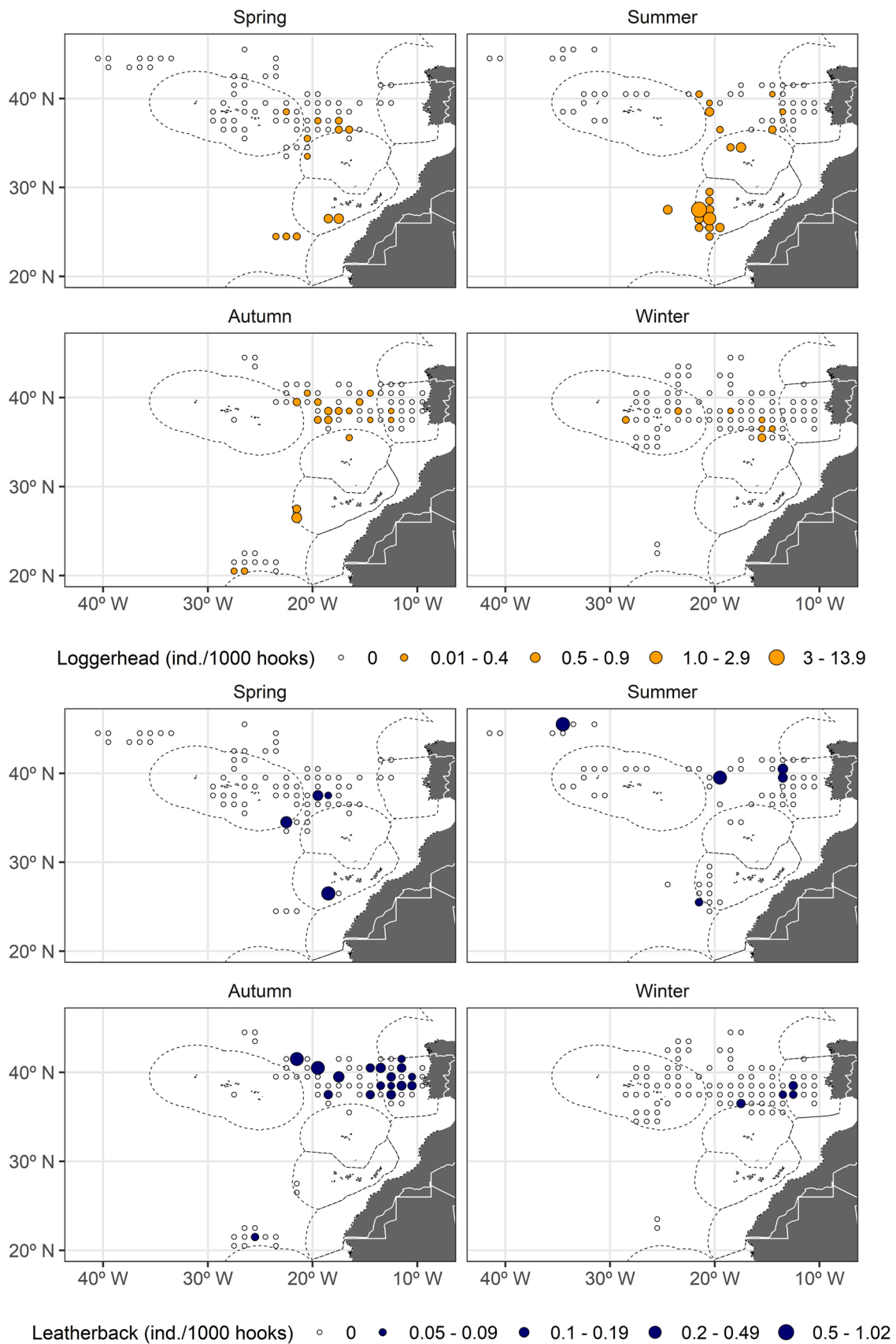
marginally within Portugal mainland EEZ during autumn. Despite bycatch of both species occurred in a similar range of surface water temperatures ( $\sim 16\text{--}23\text{ }^{\circ}\text{C}$ ), the interval in which higher bycatch was recorded differed between species (loggerhead:  $22\text{--}23\text{ }^{\circ}\text{C}$ ; leatherback:  $19\text{--}20\text{ }^{\circ}\text{C}$ ; Fig. 2), reflecting differences in physiological constraints and habitat preferences between the two species. Sea turtles are poikilotherms, and temperature is known to influence their distribution (Kobayashi et al., 2008; Mansfield et al., 2009; Polovina et al., 2000; Benson et al., 2011; Varo-Cruz et al., 2016; Chambault et al., 2019). As shown in previous studies, temperature is also known to affect sea turtle bycatch, and the ranges here presented lie within those previously reported (Brazner and Mcmillan, 2008; Gardner et al., 2008; Howell et al., 2008, 2015, Donoso and Dutton, 2010, Swimmer et al., 2017).

From the observed operational characteristics of the fishery here considered, the GLMMs revealed that soaking time, leader and bait type had a significant influence on loggerhead bycatch, whereas none of the factors appeared to have influenced leatherback bycatch. Similar to other studies (Echwikihi et al., 2011 and references therein) bait type was demonstrated to have a strong influence on sea turtles bycatch, with considerably higher rates of loggerhead bycatch recorded in hooks baited with squid compared to hooks baited with mackerel. Our results showed that fishing sets baited mostly with mackerel and without or little use of squid or shark meat are expected to decrease loggerhead CPUE by a factor of 0.57 (0.36–0.91 95% CI; Table S2). Hook type was found not significant for sea turtles bycatch, which is in agreement with Lima et al. (unpublished manuscript). That study, based on data collected in an experiment to evaluate the influence of different hook types on sea turtle bycatch in the Azores (Bolten and Bjørndal, 2005), also found no significant differences in loggerhead CPUE between the use of 9/0 straight J or 9/0 offset J hooks. Furthermore, our study found that vessel size (based on vessels longer than 18 m) did not have a significant effect on loggerhead and leatherback bycatch. Pons et al. (2010) also found no significant effect of vessel size (ranging from about 14–48 m) on loggerhead bycatch rates for the Brazilian fleet operating in the Southwest Atlantic.

#### 4.1. Loggerhead

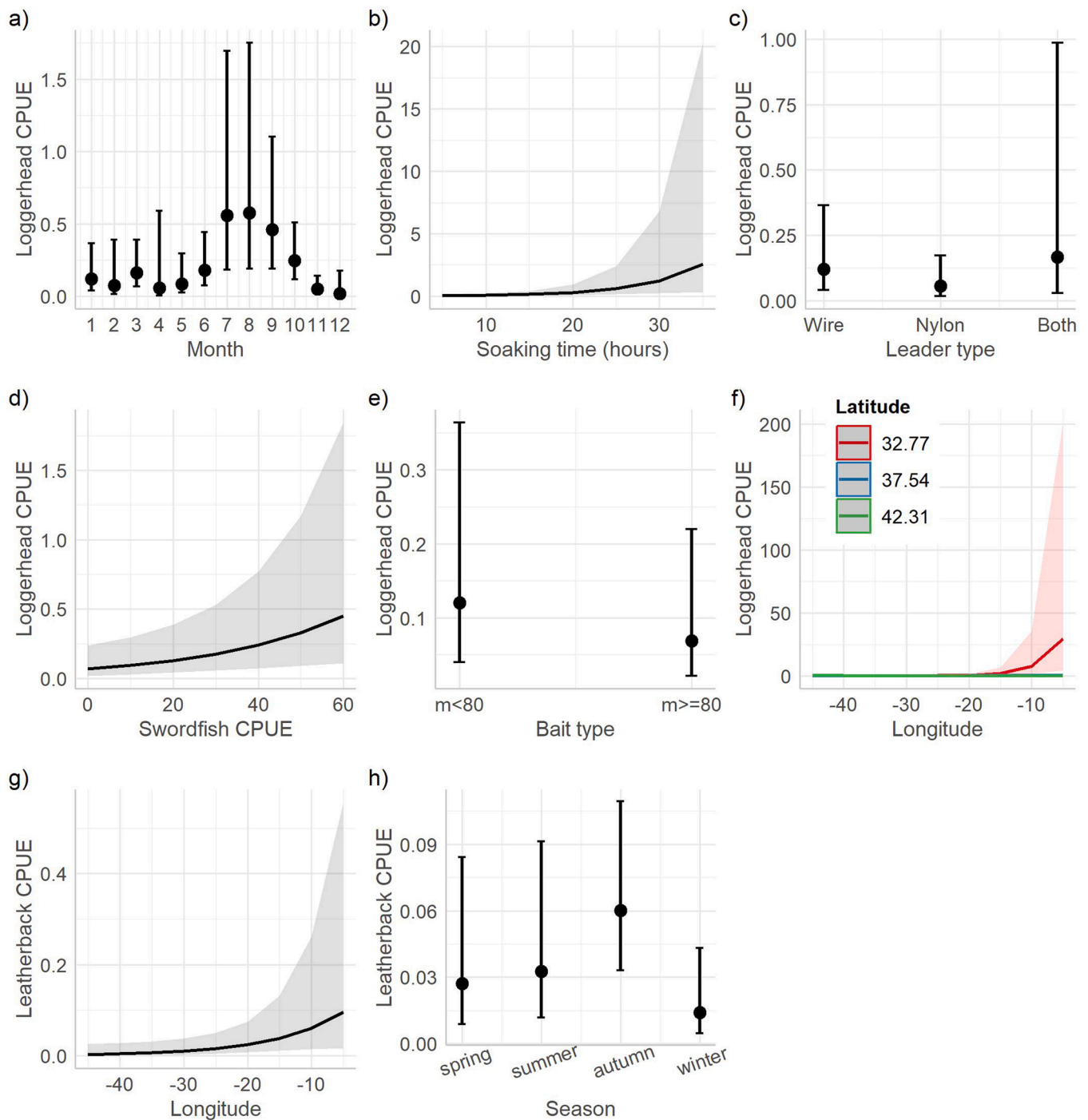
Loggerhead bycatch was clustered in space west off the Canary Islands during summer and in international waters between mainland Portugal and the Azores during autumn (Fig. 6). This clustered rather than uniform distribution of loggerhead bycatch was previously reported in the Atlantic (Bolten and Bjørndal, 2005; Gardner et al., 2008; Lewison et al., 2009; Pons et al., 2010; Ferreira et al., 2011; Swimmer et al., 2017) and elsewhere (Petersen et al., 2009; Donoso and Dutton, 2010). This indicates that other factors influence loggerhead distribution and bycatch in the region. Satellite telemetry studies have shown that loggerhead distribution is associated with oceanic mesoscale features such as eddies and frontal systems (e.g. Polovina et al., 2000, 2004, 2006, Kobayashi et al., 2008, Mansfield et al., 2009, Chambault et al., 2019). The Canary Island region, where considerably higher bycatch was recorded in this study, constitutes a major pathway for long-lived island-induced eddies (life span  $> 3$  months), located between  $22^{\circ}$  and  $29^{\circ}\text{N}$ , and with a clear dominance of anticyclone eddies over cyclonic eddies propagating westward to at least  $32^{\circ}\text{W}$  (Sangrá et al., 2009, 2015). This distinctive feature plays an important role in transporting cold nutrient-rich upwelling waters from the eastern boundary towards the interior ocean, with increased productivity through vertical mixing processes. Several studies have demonstrated that satellite tracked juvenile loggerhead turtles associated more with the inner core of anticyclonic eddies (Howell et al., 2010; Gaube et al., 2017), preferentially with life spans  $> 2$  months (Chambault et al., 2019). This could explain the high bycatch rates recorded south of  $30^{\circ}\text{N}$ , west off Canary Islands, especially during early summer.

In this study, the overall mean loggerhead CPUE by Portuguese pelagic longline vessels was slightly higher than those reported for the Spanish pelagic longline fishery operating in central North Atlantic (Mejuto et al., 2008), and considerably higher compared to those reported by Coelho et al. (2015) and Santos et al. (2012) for the Portuguese longline fleet operating in the tropical Northeast Atlantic and in the Equatorial Atlantic, respectively (Table 3). Overall CPUE reported by Mejuto et al. (2008) for the subtropical Northeast Atlantic is also



**Fig. 6.** Seasonal maps of loggerhead and leatherback mean nominal CPUE (individuals per 1000 hooks) bycaught by Portuguese longline vessels operating in the Northeast Atlantic between 2015 and 2020. Data is presented over a 1-degree cell grid. spring: March-May, summer: June-August, autumn: September-November, and winter: December-February.





**Fig. 7.** Loggerhead (a-f) and leatherback (g-h) final GLMMs term plots based on observer data collected on-board Portuguese pelagic longline vessels from 2015 to 2020. Catch per unit effort (CPUE) expressed in number of individuals per 1000 hooks. Grey and colour shading, and error bars represent the 95% confidence interval.

notably higher compared to the overall estimate here presented, yet it is less than half of the 1.03 here estimated for the subtropical subregion (20–30°N) alone. While these differences in bycatch rates likely reflect differences in abundance and distribution of loggerhead turtles between areas of the North Atlantic, other reasons could be attributed to operational factors such as the period of the year when these rates were recorded, which is not specified in [Mejuto et al. \(2008\)](#), and/or probably because the areas between studies overlap slightly, with the rates presented by [Mejuto et al. \(2008\)](#) recorded southwest of Canary Island, closer to the area where [Coelho et al. \(2015\)](#) reported relatively lower

loggerhead bycatch rates ([Table 4](#)).

In contrast, the overall rate here reported was considerably lower than those previously reported for the Azores. The Azores archipelago is an important foraging and developmental ground for oceanic-stage loggerhead turtles originating mostly from the southeastern USA ([Bolten et al., 1998, 2003a, Bjørndal et al., 2003, Okuyama and Bolker, 2005](#)). In this study, observer coverage within the Azores EEZ accounted for 16% of the total observed effort and only 3 loggerheads were caught during winter and spring. Fishing effort by the Portuguese pelagic longline fleet in the Azores appears quite low during autumn, when

**Table 3**

Bootstrapped median estimates ( $\pm$  95% bootstrapped confidence interval; BCI) of the number of sea turtle interactions by the Portuguese pelagic longline fleet based on the final GLMMs and the GFW effort data estimated in number of hooks.

Year	GFW effort	Loggerhead			Leatherback		
		Median	Lower BCI	Upper BCI	Median	Lower BCI	Upper BCI
2016	3141,521	208	80	429	125	55	229
2017	3469,774	148	53	313	120	49	231
2018	3193,942	331	123	743	97	39	194
2019	3263,806	496	195	1049	139	64	251
2020	2696,801	256	101	535	123	55	224
Total	15,765,844	1439	552	3069	604	262	1129

higher loggerhead catch rates would be expected (Ferreira et al., 2001), yet considerably higher during spring when vessels target blue shark (Parra et al. under review). Furthermore, the size distribution of loggerhead turtles incidentally caught by the Portuguese longline fishery in the Northeast Atlantic here presented are in line with those reported for pelagic longline fisheries in the Atlantic (35–77 CCL; Bolten et al., 1994; Ferreira et al., 2001; Kotas et al., 2004; Bolten and Bjørndal, 2005; Santos et al., 2012; Coelho et al., 2015).

At haul-back or direct mortality of loggerheads was estimated at 26%. Turtles that were found dead were mostly hooked in the digestive tract (i.e. mouth and deep-hooking), similar to what has been reported for pelagic longline swordfish fisheries in the Atlantic (Ferreira et al., 2001; Watson et al., 2005; Santos et al., 2012; Coelho et al., 2015), and in the Pacific Ocean (Gilman et al., 2007). The direct mortality rate here reported likely represents a fraction of the total fishing induced mortality because loggerhead turtles caught by the pelagic longline fishery are also susceptible to hook injuries (Parga, 2012), and/or decompression sickness (García-Párraga et al., 2014) which can result in delayed or post-release mortality. Post-hooking sublethal effects include reduced fitness, altered diving behaviour and orientation loss leading to negative consequences for foraging and survival (Ryder et al., 2006). Delayed-mortality of sea turtles captured and released from longline has been estimated within the range of 5% and 85%, depending on whether the gear is removed from the turtle, turtles have ingested hooks, or the line is left trailing (Bolten et al., 1994; Chaloupka et al., 2004; Ryder et al., 2006; Lewison and Crowder, 2007; Sasso and Epperly, 2007; Swimmer and Gilman, Álvarez de Quevedo et al., 2012, 2013; Swimmer et al., 2014).

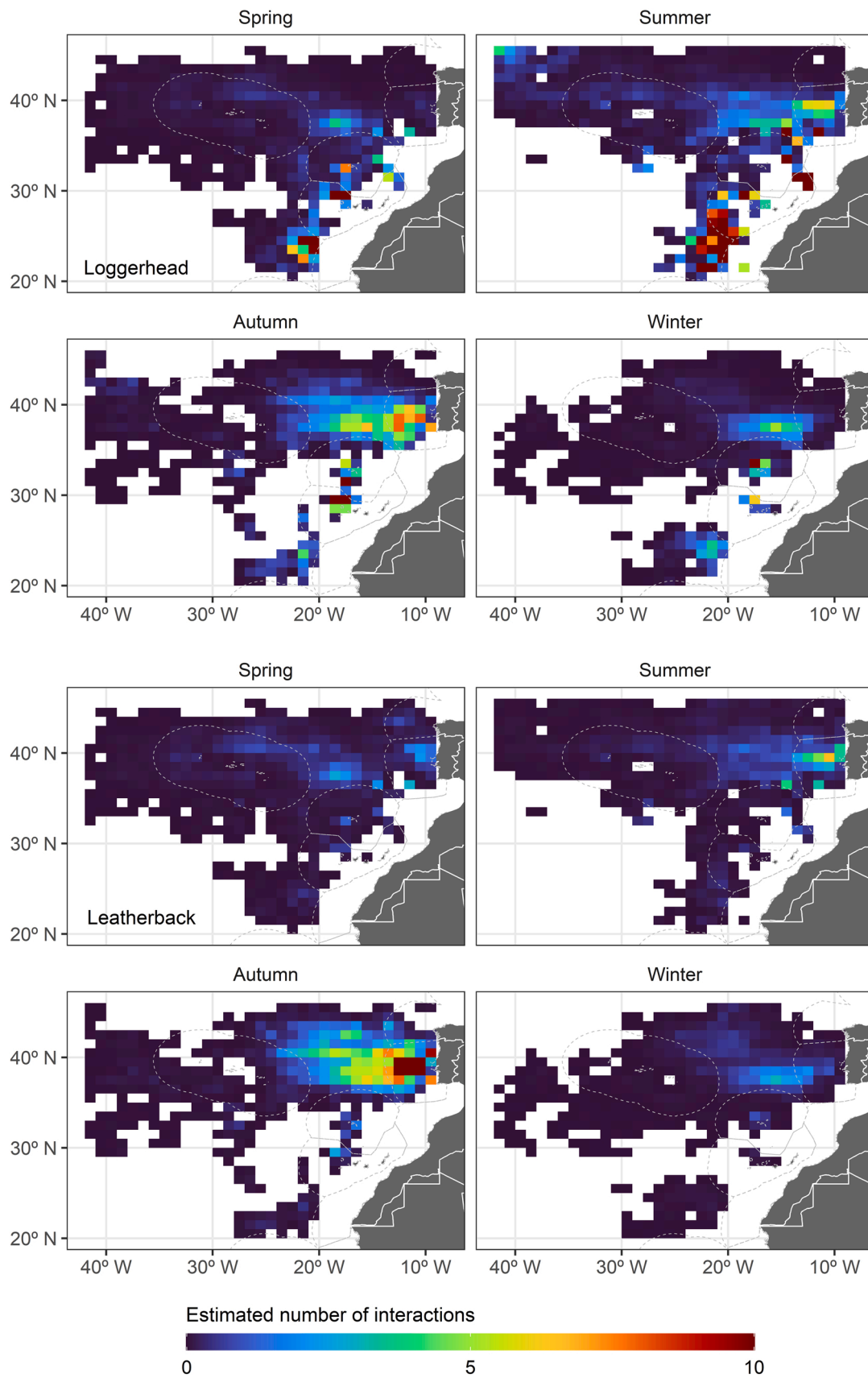
#### 4.2. Leatherback

Leatherback bycatch from Portuguese pelagic longline vessels operating in the Northeast Atlantic between 2015 and 2020 appeared clustered in space during autumn, mostly within Portugal mainland 200 nm EEZ (Fig. 6). The spatial clustering of leatherback bycatch in pelagic longline fisheries has been previously reported in other studies (Gardner et al., 2008; Lewison et al., 2009; Petersen et al., 2009). In this study, the spatial clustering of leatherback bycatch occurred within the area and period of higher observed fishing effort and when vessels targeted mostly swordfish (Parra et al. under review). During the rest of the year, bycatch is low and appeared scattered in the region, reflecting the overall spatial patterns of fishing effort by the fleet. Donoso and Dutton (2010) similarly concluded that leatherback bycatch in the southeast Pacific longline fishery generally reflected patterns of fishing effort. Although significant, the correlation between leatherback CPUE and the observed fishing effort in number of hooks per 1-degree grid square was weak ( $R = 0.34$ ). This suggests that the relationship may not be linear and likely influenced by other environmental, operational, and/or demographic factors.

The overall mean leatherback bycatch rate here estimated is similar to those reported for the Azores, yet it is considerably lower than those reported for areas of the Northeast Atlantic (Table 4). This could be attributed to the different periods when these bycatch rates were

recorded, and likely reflect seasonal patterns of leatherback distribution and abundance in the North Atlantic. Studies based on satellite telemetry data collected on leatherbacks of the Northwest Atlantic subpopulation showed high-use areas in the waters offshore Western Europe, namely within Portugal mainland EEZ, and in the subtropical East and Central North Atlantic (Eckert, 2006; Fossette et al., 2014), specifically around Cape Verde all year-round and in the Azores from October to March, respectively (Fossette et al., 2014). Between October and March, the observed fishing effort in this study was mostly concentrated in mainland Portugal EEZ and adjacent international waters, and leatherback bycatch was not recorded in the Azores during the entire study period. The area where most of the bycatch was recorded off the Portuguese west coast is characterized by the occurrence of coastal upwelling that extends 100–300 km offshore, with more active and persistent conditions from April to September, and consequent increase in productivity (Santos et al., 2001; Lemos and Pires, 2004). This feature likely provides favourable foraging conditions for leatherbacks in the region. Furthermore, relatively high leatherback bycatch by pelagic longline was also reported by Mejuto et al. (2008) for the subtropical Northeast Atlantic, which was not observed in this study. Leatherback bycatch south of 30°N was relatively low and occurred mostly during spring (Fig. 6). Moreover, the low leatherback CPUE recorded during winter may indicate that turtles are distributed probably to the south to avoid colder waters (~17 °C). Leatherback turtles experience a wide range of temperatures (9–33 °C) yet they do not spend time in surface waters cooler than 20 °C, and only experience lower temperatures briefly during deep dives (McMahon and Hays, 2006).

Leatherback turtles with < 145 cm CCL are generally considered juveniles (Eckert, 2002), although reproductive females as small as 105–125 cm CCL have been reported (Stewart et al., 2007). The mean size here reported of 167 cm CCL suggests that bycaught turtles were mostly adults, yet caution should be taken when classifying animals as adults or juveniles based on size alone (Stewart et al., 2007). Additionally, leatherbacks were generally recorded hooked in the flipper or entangled in the gear, similar to what has been reported by other studies (Bolten and Bjørndal, 2005; Watson et al., 2005; Santos et al., 2012; Coelho et al., 2015). Despite the apparent absence of leatherback mortality here observed, most of bycatch overlapped in space and time with the highest fishing effort recorded, namely within mainland Portugal EEZ and adjacent international waters during autumn, which is reason for concern given the recent decrease in female nesting of the Northwest Atlantic subpopulation (NMFS and USFWS 2020). Furthermore, most of the leatherbacks recorded to interact with the gear were released with some line trailing and their fate remains unknown. Research has shown that, when released carefully and completely from fishing gear, many leatherbacks survive entanglement without apparent long-term effects, yet post-release mortality rates remain logistically challenging to quantify (Bond and James, 2021). This underlines the need for further monitoring of pelagic longline fisheries in the Northeast Atlantic to ascertain the long-term magnitude of leatherback bycatch by this fishery.



**Fig. 8.** Seasonal distribution of the predicted number of loggerhead and leatherback interactions with the Portuguese pelagic longline fishery between 2016 and 2020. Interaction estimates were produced based on the bootstrapped median CPUE and the spatial explicit GFW fishing effort, and summarized over a 1-degree cell grid.

**Table 4**

Summary of published studies of sea turtle bycatch (CPUE in number of individuals per 1000 hooks) by pelagic longline fisheries in the North Atlantic (NA), and specifically for the Northeast Atlantic (NeA).

Area	Extent	N hooks	Loggerhead CPUE	Leatherback CPUE	Source
Temperate and subtropical NeA	10–42°W, 20–46°N	887,641	0.152	0.043	This study
Azores	Unclear	Unclear	0.27	-	Ferreira et al. (2001)
Azores	23–31°W, 36–36°N	416,199	0.23–1.68	0.011–0.043	Bolten and Bjørndal (2005)
Central NA	25–35°W, 30–45°N	38,385	0.104	0.391	Mejuto et al. (2008)
West NA	20–60°W, 35–55°N	Unclear	0.39–0.88	0.16–0.44	Swimmer et al. (2017)
North Atlantic	0–65°W, 15–50°N	2215,150	0–0.0128	0–0.0104	Huang (2015)
Subtropical NeA	17–30°W, 15–30°N	38,028	0.421	0.631	Mejuto et al. (2008)
Tropical NeA	20–38°W, 11–22°N	254,520	0.086	0.337–0.990	Coelho et al. (2015)
Equatorial Atlantic	42°W–9°E, 7°S–7°N	305,352	0.033	0.189	Santos et al. (2012)

#### 4.3. Bycatch estimates

The number of sea turtle interactions here estimated was based on models that quantified sea turtle bycatch in terms of spatio-temporal variability and in relation to operational factors, and therefore rely heavily on the assumptions underlying the chosen approach. Loggerhead and leatherback models explained 33.8% and 7.6% of the variance, respectively, pointing to a significant amount of unexplained variance that could be attributed to unaccounted environmental and demographic parameters that likely influence sea turtle presence and density in the region, and the interaction with the fishing gear. The relatively wide confidence interval estimated by the bootstrap procedure further exacerbate the level of uncertainty associated with our estimates (Table 3). Additional error can also be expected from the effort data, notwithstanding the overall results suggest that the GFW data is a fairly accurate representation of the observer data. GFW data appears to have overestimated the observer data in terms of the total amount of fishing hours between 2016 and 2020 by a factor of 1.12, yet we consider this to be acceptable for the purpose of this study. GFW daily data gaps longer than 24 h (Fig. S5) can result when a vessel turns off its AIS or travels in a region with exceptionally poor satellite coverage, such as the area off the coast of Europe where most of the observed fishing effort occurred in this study (Kroodsma et al., 2018). Despite the aforementioned limitations, these estimates represent an improvement of previously published preliminary sea turtle interaction estimates for the Portuguese pelagic longline fleet operating in the Northeast Atlantic (Gray and Diaz, 2017).

The sea turtle bycatch estimates here presented are exclusively related to Portuguese drifting longline vessels with more than 15 m in length and operating mostly offshore, and do not account for vessels of coastal artisanal fisheries. These fisheries comprise a polyvalent multi-gear fleet (demersal longlines, purse seines, trawls, and gill/trammel nets) with over 3200 licenced boats with less than 12 m, that operate within 2–10 nm off the coast (INE 2021). The actual impact of these fisheries on loggerhead and leatherback sea turtles remains uncertain, yet the main cause of stranding for both species along the Portuguese coast was attributed to interaction with fisheries, namely set gill or trammel nets followed by longlines (Nicolau et al., 2016).

Our results suggest that from a total of 1439 juvenile loggerheads estimated to interact with the longline gear between 2016 and 2020, 374 have likely perished during fishing operations (i.e. 26% at haul-back mortality rate here estimated), with an average of 75 deaths per year. From the remaining 1065 interactions, it is likely that 53–905 loggerheads will have potentially succumbed to post-release mortality (5–85%), depending on the type of interaction (i.e. external, mouth or deeply hooked), release procedure and amount of gear removed (Bolten et al., 1994; Chaloupka et al., 2004; Ryder et al., 2006; Lewison and Crowder, 2007; Sasso and Epperly, 2007; Swimmer and Gilman, Álvarez de Quevedo et al., 2012, 2013; Swimmer et al., 2014). These estimates represent a fraction of the annual mean number of

loggerhead interactions estimated for the US pelagic longline fishery in the Northwest Atlantic (530–840 interactions and 2–62 estimated mortalities; Finkbeiner et al., 2011), for the Canadian fleet operating in Canadian waters (1199 interactions; Brazner and Mcmillan, 2008), and for countries operating in the Mediterranean Sea (up to 20,200 interactions; Casale, 2011). Regarding leatherback turtles, at haul-back mortality was not observed in our study, however Finkbeiner et al. (2011) reported an average leatherback mortality of 17–27 turtles from 707 to 901 estimated interactions per year in the Northwest Atlantic pelagic longline fishery, resulting in a ca. 3% mortality rate. Under this assumption, we could expect that from a total of 604 estimated interactions between 2016 and 2020, 18 leatherbacks may have resulted in bycatch deaths, with an average of less than 4 deaths per year.

Overall, these estimates provide a well-founded perspective on the threat of the industrial Portuguese pelagic longline fleet for sea turtles populations inhabiting the Northeast Atlantic, and contribute to the estimation of the cumulative effects of all large and small-scale fleets operating in North Atlantic (Lewison et al., 2004b; Wallace et al., 2010a; Finkbeiner et al., 2011; Kroodsma et al., 2018), together with other anthropogenic sources of mortality in the open ocean such as litter ingestion and entanglement (Schuyler et al., 2014) that may be hindering the recovery and conservation of these populations.

#### 4.4. Mitigation opportunities

Reduction of sea turtle bycatch and mortality by pelagic longline fisheries can be achieved by time-area closures to regulate fishing effort, changes in fishing gear and operations (e.g. bait, hook shape and size, depth of the gear, time of gear retrieval and deployment) and/or handling and release practices to increase survival of captured turtles (see Gilman et al., 2006a and Swimmer et al., 2020 for a review). A combination of these regulatory measures has been implemented since 2004 in the U.S.-managed pelagic longline fisheries targeting swordfish and tunas, and were demonstrated to be highly effective in reducing sea turtle capture and mortality in the Pacific and Atlantic oceans (Gilman et al., 2006b; Swimmer et al., 2017). In this study, we identified areas and periods of clustered sea turtle bycatch in the Northeast Atlantic where the implementation of mitigation measures, such as effort limitations, the use of large circle hooks and/or the use of whole finfish bait (Gilman et al., 2006a and Swimmer et al., 2020 for a review) could be prioritized. In the Azores region, the mandatory use of circle hooks and a prohibition to use wire leaders (Ordinance n° 116/2018 October 25th 2018) have recently been implemented, while the adoption of additional sea turtle bycatch mitigation measures at the ICCAT level currently remains under discussion ([https://www.iccat.int/com2021/ENG/PA4\\_811\\_ENG.pdf](https://www.iccat.int/com2021/ENG/PA4_811_ENG.pdf)).

The application of appropriate safe handling techniques increases sea turtle post-capture survival chances and alleviates the impacts of longline fishing on these populations (Zollett and Swimmer, 2019). Therefore, additional regulations in the U.S. swordfish longline fishery

in the Northwest Atlantic include requirements for education and outreach efforts focusing on sea turtles, and increased on-board scientific observer coverage (Swimmer et al., 2017). While a broad implementation of existing guidelines (ICCAT Rec. 10–09 and 13–11, EC Regulation 2017/2017) appears slow, the COSTA project has promoted better practices and resuscitation techniques through workshops and its on-board observers, and has provided adequate release equipment such as long-handled line cutters and clippers to the participating Portuguese fleet. Nevertheless, international cooperation is required to move forward and significantly reduce sea turtle bycatch and mortality in the Northeast Atlantic.

## 5. Conclusions

The present study provides information that is useful to support management efforts for sea turtle conservation, namely for the Recovery Actions (specifically, Actions 6245 and 6246) considered of highest priority for implementation and/or continuing under the Recovery Plan for the loggerhead Northwest Atlantic population (Bolten et al., 2019). Furthermore, it provides data to respond to the criterion D1C1, as defined in the Good Environment Status (GES) Descriptor 1 of the European Marine Strategy Framework Directive (MSFD; 2008/56/EC), referring to sea turtle mortality rates from bycatch for the Northeast Atlantic region (Girard et al., 2022). Future work will focus on the refinement of bycatch estimates with the inclusion of environmental variables into the models to account for the variability in sea turtle distribution and abundance, and test alternative modelling approaches. The quantification of the impact of this fishery on sea turtle populations should be further investigated using demographic models, as demonstrated for sea turtle populations in the Mediterranean (Casale and Heppel 2016), to determine populations abundance and the potential biological removal by longline fisheries in the region.

## CRedit authorship contribution statement

**Hugo Parra:** Writing – review & editing, Formal analysis, Writing – original draft. **Miguel Machete:** Methodology, Writing – review & editing. **Marco Santos:** Conceptualization, Methodology. **Karen A. Bjorndal:** Conceptualization, Writing – review & editing, Funding acquisition. **Frederic Vandeperre:** Conceptualization, Methodology, Validation, Writing – review & editing, Project administration, Funding acquisition.

## 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. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fishres.2023.106673.

## References

- Aires-da-Silva, A., Ferreira, R.L., Pereira, J.G., 2008. Case study: Blue Shark catch-rate patterns from the Portuguese swordfish longline fishery in the Azores. In: Camhi, M.D., Pikitch, E.K., Babcock, E.A. (Eds.), *Sharks of the Open Ocean: Biology, Fisheries & Conservation*. Fish and Aquatic Resources Series 13, Blackwell Publishing, Oxford, U.K., pp. 230–235.
- Aires-da-Silva, A., Pereira, J.G., 1999. Catch rates for pelagic sharks taken by the Portuguese swordfish fishery in the waters around the Azores, 1993–1997. *Col. Vol. Sci. Pap. ICCAT* (49), 300–305. ([https://www.iccat.int/Documents/CVSP/CV049\\_1999/n\\_4/CV049040300.pdf](https://www.iccat.int/Documents/CVSP/CV049_1999/n_4/CV049040300.pdf)).
- Álvarez de Quevedo, I., San Félix, M., Cardona, L., 2013. Mortality rates in by-caught loggerhead turtle *Caretta caretta* in the Mediterranean Sea and implications for the Atlantic populations. *Mar. Ecol. Prog. Ser.* 489, 225–234. <https://doi.org/10.3354/meps10411>.
- Angel, A., Nel, R., Wanless, R.M., Mellet, B., Harris, L., Wilson, I., 2014. Ecological risk assessment of sea turtles to tuna fishing in the ICCAT region. *Col. Pap. ICCAT Vol. Sci* (70), 2226–2259. ([https://www.iccat.int/Documents/CVSP/CV070\\_2014/n\\_5/CV070052226.pdf](https://www.iccat.int/Documents/CVSP/CV070_2014/n_5/CV070052226.pdf)).
- Anonymous, 2019. International Commission for the Conservation of Atlantic Tunas (ICCAT) - Report of the Standing Committee on Research and Statistics (SCRS). Madr., Spain, 30 Sept. 4 Oct. 2019, Coraz. De. Maria, 8-28002 Madr., Spain 454. ([https://www.iccat.int/Documents/Meetings/Docs/2019/REPORTS/2019\\_SCRS\\_ENG.pdf](https://www.iccat.int/Documents/Meetings/Docs/2019/REPORTS/2019_SCRS_ENG.pdf)).
- Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67, 1–48. <https://doi.org/10.18637/jss.v067.i01>.
- Benson, S.R., Eguchi, T., Foley, D.G., Forney, K.A., Bailey, H., Hitepuuw, C., Samber, B.P., Tapilatu, R.F., Rei, V., Ramohia, P., Pita, J., Dutton, P.H., 2011. Large-scale movements and high-use areas of western Pacific leatherback turtles, *Dermochelys coriacea*. *Ecosphere* 2, 1–27. <https://doi.org/10.1890/ES11-00053.1>.
- Bivand, R., 2022. R packages for analyzing spatial data: a comparative case study with areal data. *Geogr. Anal.* 54, 488–518. <https://doi.org/10.1111/gean.12319>.
- Bjorndal, K.A., Bolten, A.B., Martins, H.R., 2000. Somatic growth model of juvenile loggerhead sea turtles *Caretta caretta*: duration of pelagic stage. *Mar. Ecol. Prog. Ser.* 202, 265–272. <https://doi.org/10.3354/meps202265>.
- Bjorndal, K.A., Bolten, A.B., Martins, H.R., 2003. Estimates of survival probabilities for oceanic-stage loggerhead sea turtles (*Caretta caretta*) in the North Atlantic. *Fish. Bull.* 101, 732–736.
- Bolten, A.B., 2003a. Active swimmers – passive drifters: the oceanic juvenile stage of loggerheads in the Atlantic system. *Loggerhead Sea Turtles*. Smithsonian Books, Wash. DC 63–78.
- Bolten, A.B., 2003b. Variation in sea turtle life history patterns: neritic vs. oceanic developmental stages. In: Lutz, P.L., Musick, J.A., Wyneken, J. (Eds.), *The Biology of Sea Turtles*, vol. II. Boca Raton, FL, pp. 243–257.
- Bolten, A.B., Bjorndal, K.A., 2005. Experiment to Evaluate Gear Modifications on Rates of sea Turtle Bycatch in the Swordfish Longline Fishery in the Azores – Phase 4. Final Project Report submitted for publication to the National Marine Fisheries Service. Southeast Fisheries Science Center. National Oceanic and Atmospheric Administration Award Number NA03NMF4540204, 20 pp.
- Bolten, A.B., Martins, H.R., Bjorndal, K.A., Gordon, J., 1993. Size distribution of pelagic-stage loggerhead sea turtles (*Caretta caretta*) in the waters around the Azores and Madeira. *Arquipél. Life Mar. Sci.* 11, 49–54.
- Bolten, A.B., Bjorndal, K.A., Martins, H.R., 1994. Life history model for the loggerhead sea turtle (*Caretta caretta*) population in the Atlantic: potential impacts of a longline fishery. In: Balazs, G.H., Pooley, S.G. (Eds.), *Research plan to assess marine turtle hooking mortality: results of an expert workshop held in Honolulu, Hawaii, 16–18 November 1993*, 201. NOAA Technical Memorandum NMFS-SWFSC, pp. 48–55.
- Bolten, A.B., Bjorndal, K.A., Martins, H.R., Dellinger, T., Bischoff, M.J., Encalada, S.E., Bowen, B.W., 1998. Transatlantic Developmental Migrations of Loggerhead Sea Turtles Demonstrated by mtDNA Sequence Analysis. In: *Ecol. Appl.* 8, pp. 1–7. <https://doi.org/10.2307/2641306>.
- Bolten, A.B., Crowder, L.B., Dodd, M.G., MacPherson, S.L., Musick, J.A., Schroeder, B.A., Witherington, B.E., Long, K.J., Snover, M.L., 2010. Quantifying multiple threats to endangered species: an example from loggerhead sea turtles. *Front. Ecol. Environ.* 9, 295–301. <https://doi.org/10.1890/090126>.
- Bolten, A.B., Crowder, L.B., Dodd, M.G., Lauritsen, A.M., Musick, J.A., Schroeder, B.A., Witherington, B.E., 2019. Recovery plan for the Northwest Atlantic population of the

- loggerhead sea turtle (*Caretta caretta*). Second revision (2008). Assessment of progress toward recovery. National Marine Fisheries Service, U.S. Fish and Wildlife Service.
- Bond, E.P., James, M.C., 2021. Post-release movements of leatherback turtles (*Dermodochelys coriacea*) following incidental capture in fishing gear in the Atlantic Ocean. *Fish. Bull.* 119, 255–260. <https://doi.org/10.7755/FB.119.4.5>.
- Brazner, J.C., Mcmillan, J., 2008. Loggerhead turtle (*Caretta caretta*) bycatch in Canadian pelagic longline fisheries: Relative importance in the western North Atlantic and opportunities for mitigation. *Fish. Res.* 91, 310–324. <https://doi.org/10.1016/j.fishres.2007.12.023>.
- C.E. Ryder T.A. Conant B.A. Schroeder Report of the Workshop on Marine Turtle Longline Post-Interaction Mortality. Bethesda, Maryland USA, 15–16 January 2004. US Dept Commer., NOAA Tech. Memo. NMFS-OPR- 29 2006 40.
- Casale, P., 2011. Sea turtle by-catch in the Mediterranean. *Fish Fish* 12, 299–316. <https://doi.org/10.1111/j.1467-2979.2010.00394.x>.
- Casale, P., Marco, A., 2015. Caretta caretta (North East Atlantic subpopulation). The IUCN Red List of Threatened Species 2015: e.T83776383A83776554. (<https://doi.org/10.2305/IUCN.UK.2015-4.RLTS.T83776383A83776554.en>).
- Ceriani, S.A., Meylan, A., 2017. Caretta caretta (North West Atlantic subpopulation), (amended version of 2015 assessment). The IUCN Red List of Threatened Species 2017, e.T84131194A119339029. (<http://www.iucnredlist.org/details/84131194/0>).
- Casale, P., Heppel, S., 2016. How much sea turtle bycatch is too much? A stationary age distribution model for simulating population abundance and potential biological removal in the Mediterranean. *Endang. Species Res* 29, 239–254. <https://doi.org/10.3354/esr00714>.
- Ceriani, S.A., Casale, P., Brost, M., Leone, E.H., Witherington, B.E., 2019. Conservation implications of sea turtles nesting trends: elusive recovery of a globally important loggerhead population. *Ecosphere* 10, e02936. <https://doi.org/10.1002/ecs2.2936>.
- Chaloupka, M., Parker, D., Balazs, G., 2004. Modeling post-release mortality of pelagic loggerhead sea turtles exposed to the Hawaii-based longline fishery. *Mar. Ecol. Prog. Ser.* 280, 285–293. <https://doi.org/10.3354/meps280285>.
- Chambault, F., Baudena, A., Bjorndal, K.A., Santos, M.A., Bolten, A.B., Vandeperre, F., 2019. Swirling in the ocean: Immature loggerhead turtles seasonally target old anticyclonic eddies at the fringe of the North Atlantic gyre. *Prog. Oceanogr.* 175, 345–358. <https://doi.org/10.1016/j.pocean.2019.05.005>.
- Coelho, R., Fernandez-Carvalho, J., Santos, M.N., 2013. A review of fisheries within the ICCAT convention area that interact with sea turtles. *Coll. Pap. ICCAT Vol. Sci* (69), 1788–1827. ([https://www.iccat.int/Documents/CVSP/CV069\\_2013/n\\_4/CV069041788.pdf](https://www.iccat.int/Documents/CVSP/CV069_2013/n_4/CV069041788.pdf)).
- Coelho, R., Santos, M.N., Fernandez-Carvalho, J., Amorim, S., 2015. Effects of hook and bait in a tropical northeast Atlantic pelagic longline fishery: Part I-Incidental sea turtle bycatch. *Fish. Res.* 164, 302–311. <https://doi.org/10.1016/j.fishres.2014.11.008>.
- Donoso, M., Dutton, P.H., 2010. Sea turtle bycatch in the Chilean pelagic longline fishery in the southeastern Pacific: opportunities for conservation. *Biol. Conserv.* 143, 2672–2684. <https://doi.org/10.1016/j.biocon.2010.07.011>.
- Echwikhi, K., Jribi, I., Bradai, M.N., Bouain, A., 2011. Effect of bait on sea turtles bycatch rates in pelagic longlines: an overview. *Amphib. Reptil.* 32, 493–502. <https://doi.org/10.1163/156853811x601924>.
- Eckert, K.L., Wallace, B.P., Frazier, J.G., Eckert, S.A., Pritchard, P.C.H., 2012. Synopsis of the biological data on the leatherback sea turtle (*Dermodochelys coriacea*). U.S. Department of Interior, Fish and Wildlife Service, Biological Technical Publication BTP-R4015–2012. Washington, DC.
- Eckert, S.A., 2002. Distribution of juvenile leatherback sea turtle *Dermodochelys coriacea* sightings. *Mar. Ecol. Prog. Ser.* 230, 289–293. <https://doi.org/10.3354/meps230289>.
- Eckert, S.A., 2006. High-use oceanic areas for the Atlantic leatherback sea turtles (*Dermodochelys coriacea*) as identified using satellite telemetered location and dive information. *Mar. Biol.* 149, 1257–1267. <https://doi.org/10.1007/s00227-006-0262-z>.
- Feng, C., Li, L., Sadeghpour, A., 2020. A comparison of residual diagnosis tools for diagnosing regression models for count data. *BMC Med. Res. Methodol.* 20, 175. <https://doi.org/10.1186/s12874-020-01055-2>.
- Ferreira, R.L., Martins, H.R., Silva, A.A., Bolten, A.B., 2001. Impact of swordfish fisheries on sea turtles in the Azores. *Arquipél. Life Mar. Sci.* 18, 75–79.
- Ferreira, R.L., Martins, H.R., Bolten, A.B., Santos, M.A., Erzini, K., 2011. Influence of environmental and fishery parameters on loggerhead sea turtle by-catch in the longline fishery in the Azores archipelago and implications for conservation. *J. Mar. Biol. Assoc. UK* 91, 1697–1705. <https://doi.org/10.1017/S0025315410000846>.
- Finkbeiner, E.M., Wallace, B.P., Moore, J.E., Lewison, R.L., Crowder, L.B., Read, A.J., 2011. Cumulative estimates of sea turtle bycatch and mortality in USA fisheries between 1990 and 2007. *Biol. Conserv.* 144, 2719–2727. <https://doi.org/10.1016/j.biocon.2011.07.033>.
- Fossette, S., Witt, M.J., Miller, P., Nalovic, M.A., Albareda, D., Almeida, A.P., et al., 2014. Pan-Atlantic analysis of the overlap of a highly migratory species, the leatherback turtle, with pelagic longline fisheries. *P. Roy. Soc. B-Biol. Sci.* 281, 20133065. <https://doi.org/10.1098/rspb.2013.3065>.
- García-Párraga, D., Crespo-Picazo, J.L., de Quirós, Y.B., Cervera, V., Martí-Bonmati, L., Díaz-Delgado, J., Arbelo, M., Moore, M.J., Jepson, P.D., Fernández, A., 2014. Decompression sickness (“the bends”) in sea turtles. *Dis. Aquat. Org.* 111, 191–205. <https://doi.org/10.3354/dao02790>.
- Gardner, B., Sullivan, P.J., Morreale, S.J., Epperly, S.P., 2008. Spatial and temporal statistical analysis of bycatch data: patterns of sea turtle bycatch in the North Atlantic. *Can. J. Fish. Aquat. Sci.* 65, 2461–2470. <https://doi.org/10.1139/F08-152>.
- Gaube, P., Barceló Jr, C.D.J.M., Domingo, A., Miller, P., Giffoni, B., Marcovaldi, N., Swimmer, Y., 2017. The use of mesoscale eddies by juvenile loggerhead sea turtles (*Caretta caretta*) in the southwestern Atlantic. *PLOS ONE* 12, e0172839. <https://doi.org/10.1371/journal.pone.0172839>.
- Gilman, E., Kobayashi, D., Swenarton, T., Dalzell, P., Kinan, I., Brothers, N., 2006b. Efficacy and commercial viability of regulations designed to reduce sea turtle interactions in the Hawaii-based longline swordfish fishery. Western Pacific Regional Fishery Management Council, Honolulu, HI, USA.
- Gilman, E., Zollett, E., Beverly, S., Nakano, H., Davis, K., Shiode, D., Dalzell, P., Kinan, I., 2006a. Reducing sea turtle by-catch in pelagic longline fisheries. *Fish Fish* 7, 2–23. <https://doi.org/10.1111/j.1467-2979.2006.00196.x>.
- Gilman, E., Kobayashi, D., Swenarton, T., Brothers, N., Dalzell, P., Kinan-Kelly, I., 2007. Reducing sea turtles interactions in the Hawaii-based longline swordfish fishery. *Biol. Conserv.* 139, 19–28. <https://doi.org/10.1016/j.biocon.2007.06.002>.
- Girard, F., Girard, A., Monsinjon, J., Arcangeli, A., Belda, E., Cardona, L., et al., 2022. Toward a common approach for assessing the conservation status of marine turtle species within the European marine strategy framework directive. *Front. Mar. Sci.* 9, 1–22. <https://doi.org/10.3389/fmars.2022.790733>.
- Gray, C.M., Diaz, G.A., 2017. Preliminary estimates of the number of sea turtle interactions with pelagic longline gear in the ICCAT convention area. *Collect. Pap. ICCAT Vol. Sci* (73), 3128–3151. ([https://www.iccat.int/Documents/CVSP/CV073\\_2017/n\\_9/CV073093128.pdf](https://www.iccat.int/Documents/CVSP/CV073_2017/n_9/CV073093128.pdf)).
- Hartig, F., 2022. DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version (v0.4.6). (<https://CRAN.R-project.org/package=DHARMA>).
- Howell, E.A., Kobayashi, D.R., Parker, D.M., Balazs, G.H., Polovina, J.J., 2008. TurtleWatch: a tool to aid in the bycatch reduction of loggerhead turtles *Caretta caretta* in the Hawaii-based pelagic longline fishery. *Endang. Species Res.* 5, 267–278. <https://doi.org/10.3354/esr00096>.
- Howell, E.A., Dutton, P.H., Polovina, J.J., Bailey, H., Parker, D.M., Balazs, G.H., 2010. Oceanographic influences on the dive behavior of juvenile loggerhead turtles (*Caretta caretta*) in the North Pacific Ocean. *Mar. Biol.* 157, 1011–1026. <https://doi.org/10.1007/s00227-009-1381-0>.
- Howell, E.A., Hoover, A., Benson, S.R., Bailey, H., Polovina, J.J., Seminoff, J.A., Dutton, P.H., 2015. Enhancing the TurtleWatch product for leatherback sea turtles, a dynamic habitat model for ecosystem-based management. *Fish. Oceano* 24, 57–68. <https://doi.org/10.1111/fog.12092>.
- Huang, H.-W., 2015. Conservation hotspots for the turtles on the high seas of the Atlantic Ocean. *PLOS ONE* 10, e0133614. <https://doi.org/10.1371/journal.pone.0133614>.
- Huang, H.-W., Swimmer, Y., Bigelow, K., Gutierrez, A., Foster, D.G., 2016. Influence of hook type on catch of commercial and bycatch species in an Atlantic tuna fishery. *Mar. Policy* 65, 68–75. <https://doi.org/10.1016/j.marpol.2015.12.016>.
- INE 2021. Estatísticas de Pesca - 2020. Instituto Nacional de Estatística, I.P., Lisboa, Portugal.
- Knowles, J., Frederick, C., 2020. Prediction intervals from merMod objects. ([https://cran.r-project.org/web/packages/merTools/vignettes/Using\\_predictInterval.html](https://cran.r-project.org/web/packages/merTools/vignettes/Using_predictInterval.html)) (accessed 9 December 2022).
- Kobayashi, D.R., Polovina, J.J., Parker, D.M., Kamezaki, N., Cheng, I.-J., Uchida, I., Dutton, P.H., Balazs, G.H., 2008. Pelagic habitat characterization of loggerhead sea turtles, *Caretta caretta*, in the North Pacific Ocean (1997–2006): Insights from satellite tag tracking and remotely sensed data. *J. Exp. Mar. Biol. Ecol.* 356, 96–114. <https://doi.org/10.1016/j.jembe.2007.12.019>.
- Kot, C.Y., Boustany, A.M., Halpin, P.N., 2010. Temporal pattern of target catch and sea turtle bycatch in the US Atlantic pelagic longline fishing fleet. *Can. J. Fish. Aquat. Sci.* 67, 42–57. <https://doi.org/10.1139/F09-160>.
- Kotas, J.E., dos Santos, S., de Azevedo, V.G., Gallo, B.M.G., Barata, P.C.R., 2004. Incidental capture of loggerhead (*Caretta caretta*) and leatherback (*Dermodochelys coriacea*) sea turtles by the pelagic longline fishery off southern Brazil. *Fis. Bull.* 102, 393–399.
- Kroodsma, D.A., Mayorga, J., Hochberg, T., Miller, N.A., Boerder, K., Ferretti, F., Wilson, A., Bergman, B., White, T.D., Block, B.A., Woods, P., Sullivan, B., Costello, C., Worm, B., 2018. Tracking the global footprint of fisheries. *Science* 361, 6378. <https://doi.org/10.1126/science.aao5646>.
- Lemos, R.T., Pires, H.O., 2004. The upwelling regime off the west Portuguese Coast. *Int. J. Clim.* 24, 511–524. <https://doi.org/10.1002/joc.1009>, 1941–2000.
- Lewison, R.L., Crowder, L.B., 2007. Putting longline bycatch of sea turtles into perspective. *Conserv. Biol.* 21, 79–86. <https://doi.org/10.1111/j.1523-1739.2006.00592.x>.
- Lewison, R.L., Freeman, S.A., Crowder, L.B., 2004a. Quantifying the effects of fisheries on threatened species: The impact of pelagic longlines on loggerhead and leatherback sea turtles. *Ecol. Lett.* 7, 221–231. <https://doi.org/10.1111/j.1461-0248.2004.00573.x>.
- Lewison, R.L., Crowder, L.B., Read, A.J., Freeman, S.A., 2004b. Understanding impacts of fisheries bycatch on marine megafauna. *Trends Ecol. Evol.* 19, 598–604. <https://doi.org/10.1016/j.tree.2004.09.004>.
- Lewison, R.L., Soykan, C.U., Franklin, J., 2009. Mapping the bycatch seascape: multispecies and multi-scale spatial patterns of fisheries bycatch. *Ecol. Appl.* 19, 920–930. <https://doi.org/10.1890/08-0623.1>.
- Lima, F., Alves, R.B., Parra, H., Machete, M., Santos, M., Bjorndal, K.A., Vandeperre, F., Bolten, A.B., unpublished manuscript. Effects of gear modifications on target and bycatch species megafauna: a multi-year experiment in the pelagic longline fisheries of the Azores.
- Lüdecke, D., 2022. sjPlot: Data Visualization for Statistics in Social Science. R package version (v2.8.12). (<https://CRAN.R-project.org/package=sjPlot>).
- Mansfield, K.L., Saba, V.S., Keinath, J.A., Musick, J.A., 2009. Satellite tracking reveals a dichotomy in migration strategies among juvenile loggerhead turtles in the

- Northwest Atlantic. *Mar. Biol.* 156, 2555–2570. <https://doi.org/10.1007/s00227-009-1279-x>.
- Martins, H.R., Bolten, A.B., Ferreira, R.L., 2001. Impact of longline fisheries on sea turtles in the archipelago of the Azores. pp.76-77. In: Ciccione, S., Ross, D., Jean-Yves Le Gall (Eds.), *Advance in Knowledge and Conservation of Sea Turtles in South- West Indian Ocean. La Reunion 28 Nov.- 2 dec. 1999*, 1. Etudes et Colloques du Editions du Centre d'Etude et de Découverte des Tortues Marine de La Réunion (CEDTM), p. 135.
- Maunder, M.N., Punt, A.E., 2004. Standardizing catch and effort data: a review of recent approaches. *Fish. Res.* 70, 141–159. <https://doi.org/10.1016/j.fishres.2004.08.00>.
- McMahon, C.R., Hays, G.C., 2006. Thermal niche, large-scale movements and implications of climate change for a critically endangered marine vertebrate. *Glob. Change Biol.* 12, 1330–1338. <https://doi.org/10.1111/j.1365-2486.2006.01174.x>.
- Mejuto, J., García-Costés, B., Ramos-Cardelle, A., 2008. Trials using different hook and bait types in the configuration of the surface longline gear used by the Spanish swordfish (*Xiphias gladius*) fishery in the Atlantic Ocean. *Col. Pap. ICCAT Vol. Sci* (62), 1793–1830. ([https://www.iccat.int/Documents/CVSP/CV062\\_2008/n\\_6/CV062061793.pdf](https://www.iccat.int/Documents/CVSP/CV062_2008/n_6/CV062061793.pdf)).
- National Marine Fisheries Service and U.S. Fish and Wildlife Service, 2020. Endangered Species Act status review of the leatherback turtle (*Dermochelys coriacea*). Report to the National Marine Fisheries Service Office of Protected Resources and U.S. Fish and Wildlife Service.
- National Marine Fisheries Service Southeast Fisheries Science Center, Stokes, L., Bergmann, C., 2019. Careful release protocols for sea turtle release with minimal injury. NOAA Tech. Memo. NMFS-SEFSC 735, 74. <https://doi.org/10.25923/mrj-e506>.
- Nicolau, L., Ferreira, M., Santos, J., Araújo, H., Sequeira, M., Vindaga, J., Eira, C., Marçalo, A., 2016. Sea turtle strandings along the Portuguese mainland coast: spatio-temporal occurrence and main threats. *Mar. Biol.* 163, 1–13. <https://doi.org/10.1007/s00227-015-2783-9>.
- Okuyama, T., Bolker, B.M., 2005. Combining genetic and ecological data to estimate sea turtle origins. *Ecol. Appl.* 15, 315–325. <https://doi.org/10.1890/03-5063>.
- Parga, M., 2012. Hooks and sea turtles: A veterinarian's perspective. *B. Mar. Sci.* 88, 1–12. <https://doi.org/10.5343/bms.2011.1063>.
- Parra, H., Pham, C.K., Machete, M., Santos, M., Bjørndal, K.A., in preparation. The Portuguese industrial pelagic longline fishery in the Northeast Atlantic: catch composition, spatio-temporal dynamics of fishing effort, and target species catch rates.
- Petersen, S.L., Honig, M.B., Ryan, P.G., Nel, R., Underhill, L.G., 2009. Turtle bycatch in the pelagic longline fishery off southern Africa. *Afr. J. Mar. Sci.* 31, 87–96. <https://doi.org/10.2989/AJMS.2009.31.1.8.779>.
- Polovina, J.J., Kobayashi, D.R., Parker, D.M., Seki, M.P., Balazs, G.H., 2000. Turtles on the edge: Movement of loggerhead turtles (*Caretta caretta*) along oceanic fronts, spanning longline fishing grounds in the central North Pacific, 1997–1998. *Fish. Oceanogr.* 9, 71–82. <https://doi.org/10.1046/j.1365-2419.2000.00123.x>.
- Polovina, J.J., Balazs, G.H., Howell, E.A., Parker, D.M., Seki, M.P., Dutton, P.H., 2004. Forage and migration habitat of loggerhead (*Caretta caretta*) and olive ridley (*Lepidochelys olivacea*) sea turtles in the central North Pacific Ocean. *Fish. Oceano* 13, 36–51. <https://doi.org/10.1046/j.1365-2419.2003.00270.x>.
- Polovina, J.J., Uchida, I., Balazs, G., Howell, E.A., Parker, D., Dutton, P., 2006. The Kuroshio extension bifurcation region: a pelagic hotspot for juvenile loggerhead sea turtles. *Deep-Sea Res. Pt II* 53, 326–339. <https://doi.org/10.1016/j.dsr2.2006.01.006>.
- Pons, M., Domingo, A., Sales, G., Fiedler, F.N., Miller, P., Giffoni, B., Ortiz, M., 2010. Standardization of CPUE of loggerhead sea turtle (*Caretta caretta*) caught by pelagic longliners in the Southwestern Atlantic Ocean. *Aquat. Living Resour.* 23, 65–75. <https://doi.org/10.1051/alr/2010001>.
- Queiroz, N., Humphries, N.E., Mucientes, G., Hammerschlag, N., Lima, F.P., Scales, K.L., Miller, P.L., Sousa, L.L., Seabra, R., Sims, D.W., 2016. Ocean-wide tracking of pelagic sharks reveals extent of overlap with longline fishing hotspots. *Proc. Natl. Acad. Sci. USA* 113, 1582–1587. <https://doi.org/10.1073/pnas.1510090113>.
- R Core Team, 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: (<https://www.R-project.org/>).
- Roxo, A., Mendes, S., Correia, J., 2017. Portuguese commercial fisheries of Swordfish, *Xiphias gladius*. *Rev. Fish. Sci. Aquac.* 25, 150–157. <https://doi.org/10.1080/23308249.2016.1251879>.
- Sangrà, P., Pascual, A., Rodríguez-Santana, A., Machín, F., Mason, E., McWilliams, J.C., Pelegrí, J.L., Dong, C., Rubio, A., Aristegui, J., Marrero-Díaz, A., Hernández-Guerra, A., Martínez-Marrero, A., Auladell, M., 2009. The Canary Eddy Corridor: A major pathway for long-lived eddies in the subtropical North Atlantic. *Deep-Sea Res. Pt I* 56, 2100–2114. <https://doi.org/10.1016/j.dsr.2009.08.008>.
- Sangrà, P., 2015. Canary Islands eddies and coastal upwelling filaments off North-west Africa. In: Valdés, L., Déniz-González, I. (Eds.), *Oceanographic and biological features in the Canary Current Large Marine Ecosystem*. IOC-UNESCO, No. 115. Paris. IOC Technical Series, pp. 105–114.
- Santos, A.M.P., Borges, M.F., Groom, S., 2001. Sardine and horse mackerel recruitment and upwelling off Portugal. *ICES J. Mar. Sci.* 58, 589–596. <https://doi.org/10.1006/jmsc.2001.1060>.
- Santos, M.N., Garcia, A., Pereira, J.G., 2002. A historical review of the by-catch from the Portuguese surface long-line swordfish fishery: observations on blue shark (*Prionace glauca*) and short-fin mako (*Isurus oxyrinchus*). *Col. Vol. Sci. Pap. ICCAT* (54), 1333–1340. ([https://www.iccat.int/Documents/CVSP/CV054\\_2002/n\\_4/CV054041333.pdf](https://www.iccat.int/Documents/CVSP/CV054_2002/n_4/CV054041333.pdf)).
- Santos, M.N., Coelho, R., Fernandez-Carvalho, J., Amorim, S., 2012. Effects of hook and bait on sea turtles bycatch in an equatorial Atlantic pelagic longline fishery. *B. Mar. Sci.* 88, 683–701. <https://doi.org/10.5343/bms.2011.1065>.
- Sasso, C.R., Epperly, S.P., 2007. Survival of pelagic juvenile loggerhead turtles in the open ocean. *J. Wildl. Manag.* 71, 1830–1835. <https://doi.org/10.2193/2006-448>.
- Schuyler, Q., Hardesty, B.D., Wilcox, C., Townsend, K., 2014. Global analysis of anthropogenic debris ingestion by sea turtles. *Conserv. Biol.* 28, 129–139. <https://doi.org/10.1111/cobi.12126>.
- Spotila, J.R., Reina, R.D., Steyermark, A.C., Plotkin, P.T., Paladino, F.V., 2000. Pacific leatherback turtles face extinction. *Nature* 405, 529–530. <https://doi.org/10.1038/35014729>.
- Stewart, K., Johnson, C., Godfrey, M.H., 2007. The minimum size of leatherbacks at reproductive maturity, with a review of sizes for nesting females from the Indian, Atlantic and Pacific Ocean basins. *Herpetol. J.* 17, 123–128.
- Swimmer, Y., Gilman, E., 2012. Report of the Sea Turtle Longline Fishery Post-release Mortality Workshop, November 15–16, 2011. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-PIFSC-34, 31 pp.
- Swimmer, Y., Campora, C.E., McNaughton, L., Musys, M., Parga, M., 2014. Post-release mortality estimates of loggerhead sea turtles (*Caretta caretta*) caught in pelagic longline fisheries based on satellite data and hooking location. *Aquat. Conserv.: Mar. Freshw. Ecosyst.* 24, 498–510. <https://doi.org/10.1002/aqc.2396>.
- Swimmer, Y., Gutierrez, A., Bigelow, K., Barceló, C., Schroeder, B., Keene, K., Shattenkirch, K., Foster, D.G., 2017. Sea turtle bycatch mitigation in the U.S. longline fisheries. *Front. Mar. Sci.* 4, 260. <https://doi.org/10.3389/fmars.2017.00260>.
- Swimmer, Y., Zollett, E.A., Gutierrez, A., 2020. Bycatch mitigation of protected and threatened species in tuna purse seine and longline fisheries. *Endang. Species Res* 43, 517–542. <https://doi.org/10.3354/esr01069>.
- Turtle Expert Working Group, 2009. An assessment of the Loggerhead Turtle Population in the Western Northern Atlantic Ocean, NMFS-SEFSC-575.
- Vandeperre, F., Aires-da-Silva, A., Santos, M., Ferreria, R., Bolten, A.B., Santos, R.S., Afonso, P., 2014. Demography and ecology of blue shark (*Prionace glauca*) in the central North Atlantic. *Fish. Res.* 153, 89–102. <https://doi.org/10.1016/j.fishres.2014.01.006>.
- Vandeperre, F., Parra, H., Pham, C., Machete, M., Santos, M., Bjørndal, K., Bolten, A., 2019. Relative abundance of oceanic juvenile loggerhead sea turtles in relation to nest production at source rookeries: implications for recruitment dynamics. *Sci. Rep.* 9, 13019. <https://doi.org/10.1038/s41598-019-49434-0>.
- Varo-Cruz, N., Bermejo, J.A., Calabuig, P., Cejudo, D., Godley, B., López-Jurado, L.F., Pikesley, S.K., Witt, M.J., Hawkes, L.A., 2016. New findings about the spatial and temporal use of the Eastern Atlantic Ocean by large juvenile loggerhead turtles. *Biodivers. Res* 22, 481–492. <https://doi.org/10.1111/ddi.12413>.
- Wallace, B.P., Lewison, R.L., McDonald, S.L., McDonald, R.K., Kot, C.Y., Kelez, S., Bjorkland, R.K., Finkbeiner, E.M., Helmbrecht, S., Crowder, L.B., 2010a. Global patterns of marine bycatch. *Conserv. Lett.* 3, 1–12. <https://doi.org/10.1111/j.1755-263X.2010.00105.x>.
- Wallace, B.P., DiMatteo, A.D., Hurley, B.J., Finkbeiner, E.M., Bolten, A.B., Chaloupka, M.Y., et al., 2010b. Regional management units for marine turtles: a novel framework for prioritizing conservation and research across multiple scales. *PLoS ONE* 5, e15465. <https://doi.org/10.1371/journal.pone.0015465>.
- Wallace, B.P., DiMatteo, A.D., Bolten, A.B., Chaloupka, M.Y., Hutchinson, B.J., Abreu-Grobois, F.A., et al., 2011. Global conservation priorities for marine turtles. *PLoS ONE* 6, e24510. <https://doi.org/10.1371/journal.pone.0024510>.
- Wallace, B.P., Kot, C.Y., DiMatteo, A.D., Lee, T., Crowder, L.B., Lewison, R.L., 2013a. Impacts of fisheries bycatch on marine turtle populations worldwide: toward conservation and research priorities. *Ecosphere* 4, 1–49. <https://doi.org/10.1890/ES12-00388.1>.
- Wallace, B.P., Tiwari, M., Girondot, M., 2013b. The IUCN red list of threatened species. *Dermochelys coriacea*, T6494A43526147. <https://doi.org/10.2305/IUCN.UK.2013->
- Watson, J.W., Kerstetter, D.W., 2006. Pelagic longline fishing gear: a brief history and review of research efforts to improve selectivity. *Mar. Technol. Soc. J.* 40, 5–10. <https://doi.org/10.4031/002533206787353259>.
- Watson, J.W., Epperly, S.P., Shah, A.K., Foster, D.G., 2005. Fishing methods to reduce turtle mortality associated with pelagic longlines. *Can. J. Fish. Aquat. Sci.* 62, 965–981. <https://doi.org/10.1139/f05-004>.
- Wickham, H., 2016. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York, 2016. (<https://ggplot2.tidyverse.org/>).
- Zollett, E.A., Swimmer, Y., 2019. Safe handling practices to increase post-capture survival of cetaceans, sea turtles, seabirds, sharks and billfish in tune fisheries. *Endang. Species Res.* 38, 115–125. <https://doi.org/10.3354/esr00940>.
- Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. *Mixed effects models and extensions in ecology with R*. Berlin, Germany: Springer Science & Business Media.
- Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* 1, 3–14. <https://doi.org/10.1111/j.2041-210X.2009.00001.x>.