Aquatic Conservation: Marine and Freshwater Ecosystems

WILEY

ARTICLE OPEN ACCESS

Speaking Deads: Sea Turtle Mortality Areas and Fisheries Overlaps Identified Through Backtracking of Stranded Carcasses in the Adriatic Sea

Chiara Agabiti[1] | Elisa Zanetti[1] | Giovanni Quattrocchi[2] | Andrea Cucco[2] | Giulia Baldi[1] | Valeria Angelini[3] | Alice Pari[3] | Martina Monticelli[3] | Vincenzo Olivieri[4] | Anna Angrilli[4] | Pasquale Salvemini[5] | Giovanni Furii[6] | Stefano Lauriola[7] | Daniela Freggi[8] | Paolo Casale[1]

[1]Department of Biology, University of Pisa, Pisa, Pisa, Italy | [2]Institute of Anthropic Impacts and Sustainability in Marine Environment, National Research Council, Oristano, Italy | [3]Fondazione Cetacea Onlus, Riccione, Italy | [4]Centro Studi Cetacei Onlus (CSC), Pescara, Italy | [5]Associazione Panda Molfetta, Molfetta, Italy | [6]Centro Recupero Tartarughe Marine Legambiente, Manfredonia, Italy | [7]Dipartimento di Prevenzione e Servizio Veterinario Area C, Foggia, Italy | [8]Associazione Caretta caretta, Lampedusa and Linosa, Agrigento, Italy

Correspondence: Paolo Casale (paolo.casale@unipi.it)

Received: 14 May 2024 | **Revised:** 4 July 2024 | **Accepted:** 18 July 2024

Funding: The authors received no specific funding for this work.

Keywords: backtracking | fishing effort | mortality areas | sea turtle | strandings

ABSTRACT

1. Interaction with fishing gears represents the main anthropogenic threat at sea for sea turtles worldwide, and identifying the hotspots of turtle bycatch is a priority knowledge gap.
2. Turtle stranding data represent a source of information about mortality areas at sea that are not fully exploited. This study aims to infer turtle mortality areas of turtles stranded along the Italian Adriatic Coast in the period 2019–2021 (1432 records), through backtrack modelling of carcasses. Specifically, the decomposition process of eight loggerhead carcasses was monitored, and the relationship between floating period (FP), turtle size and sea temperature was modelled through a generalized additive model. Oceanographic information was then used to track the routes of floating carcasses back, knowing their size and decomposition stage, and finally estimate the likely area of mortality. A complementary numerical experiment of connectivity between coastal and offshore areas gave indication that areas of potential mortality are relatively close to the coast, particularly in the northern Adriatic.
3. Stranded turtles probably represent just a small fraction (17%–25%) of total at-sea mortalities in the study area (Italian Adriatic waters), with decomposition rates, season and distance from shore influencing their stranding likelihood. Hence, strandings can inform only about spatio-temporal variability of coastal mortality hotspots.
4. Inferred areas of turtle mortality were most likely located in the North and Central Adriatic all over the year and overlap with heatmaps of fishing effort, obtained from vessel monitoring system (VMS) and automatic identification system (AIS) data, in the Gulf of Manfredonia and in the North-West Adriatic in the cold (September–December) and warm (May–August) periods, respectively.

https://doi.org/10.1002/aqc.4236

1 | Introduction

Marine species and ecosystems face a multitude of anthropogenic threats. Fishing represents one of the most important threats to marine animals (i.e., sea birds, Tasker 2000; Lewison et al. 2012; marine mammals, Read et al. 2006; turtles, Wallace et al. 2013; sharks Dulvy et al. 2008; general: Lewison et al. 2014) and the main threat at sea for sea turtle populations worldwide (Hamann et al. 2010; Wallace et al. 2013; Lewison et al. 2014). This impact extends beyond direct interactions, as sea turtles are also threatened by entanglement in abandoned or lost nets and lines (i.e., ghost gears, Duncan et al. 2017).

Assessing the impact of fishing on sea turtle populations is a key for designing appropriate conservation measures but is also challenging due to scarce monitoring of turtle encounters by fishing vessels and the lack of consistent bycatch data, which lead to reporting only bycatch estimates from underreported fishing effort (1%–5%; Wallace et al. 2010, 2013). For instance, identifying marine areas with high interaction between turtles and fishing boats still represents a major knowledge gap (Casale et al. 2018; Fuentes et al. 2023). Various approaches, as well as their combinations (e.g., cumulative pressure intensity, Lucchetti et al. 2016; Dimitriadis et al. 2022), can be employed to infer hotspots of sea turtle death events and areas at high risk of fishing interactions at regional and global levels. The most direct approach is represented by obtaining the location of turtle bycatch events, either from onboard observation (Fortuna et al. 2010; Cambiè et al. 2013) or from fishers (Casale, Simone, et al. 2012; Cambiè et al. 2020; Casale et al. 2020; Baldi et al. 2022). Alternatively, hotspot areas may be inferred by comparing areas frequented by turtles (e.g., through satellite tracking; Roe et al. 2014; Cuevas et al. 2018) and the distribution of fishing effort (Pikesley et al. 2018; Almpanidou et al. 2021; Baldi et al. 2022). Since many stranded turtles are assumed to be the result of bycatch, their distribution can also be used to infer areas with high fishing-induced mortality (Adimey et al. 2014; Tagliolatto et al. 2020; Mihaljević et al. 2024).

Specifically, stranding data were commonly used as an index of turtle abundance and at-sea mortality both quantitatively and spatially (i.e., the extent of distribution ranges and turtle bycatch, Tomás et al. 2008; Casale et al. 2010). Unfortunately, the identification of the cause of death of stranded sea turtles represents a significant challenge due to the decomposition state of the carcasses and the possible absence of evident physical injuries (Hart et al. 2006; Phillott and Godfrey 2019). For instance, trawl fishing (with long haul duration and fast net retrieval) leads sea turtles to drown after forced apnoea (Lutcavage and Lutz 1997) or to a delayed death due to decompression sickness and gas embolism (García-Párraga et al. 2014; Fahlman et al. 2017; Crespo-Picazo et al. 2020; Franchini et al. 2021), leaving no external injuries or marks on animals (Caillouet et al. 1996). Nevertheless, fishing gear interaction is suspected to be a significant factor contributing to sea turtle stranding (Epperly et al. 1996; Casale et al. 2005; Tomás et al. 2008; Casale et al. 2010; Mihaljević et al. 2024). Stranding records can provide additional and valuable information through the approach of backtracking, not fully exploited so far, with just a few studies published (Koch et al. 2013; Nero et al. 2013; Santos, Friedrichs, et al. 2018; Nero et al. 2022). It consists of reconstructing at-sea trajectories of turtle carcasses before stranding and allows to elucidate the mortality spatial distribution and patterns. The numerical method employs oceanographic descriptors (i.e., sea currents) and their spatial and temporal variability to determine the fate of floating bodies at sea (e.g., Quattrocchi et al. 2019). The reliability of this approach is crucially based on the estimates of the floating period (FP) that can be obtained by monitoring movements and/or floating of carcasses either freely drifting at sea (Nero et al. 2013; Santos, Kaplan, et al. 2018; Cook et al. 2021), in delimited space (e.g., plastic or metal nets and cages at sea; Santos, Kaplan, et al. 2018; Cook et al. 2020) or in a controlled environment (e.g., indoor laboratory; Cook et al. 2020).

In the Mediterranean Sea, more than 100,000 turtles are estimated to die annually due to bycatch by several types of fishing gear (one of the highest bycatch rates globally, Lewison et al. 2014), of which bottom trawlers represent the most impacting one (around 40,000 annual deaths) with a high potential to cause mortality (Casale 2011; Lucchetti et al. 2017), particularly in loggerhead sea turtles (*Caretta caretta*, Casale et al. 2018). Specifically, the Adriatic Sea is subjected to one of the highest trawl fishing efforts in Europe (Casale 2011; Eigaard et al. 2016), largely due to the Italian and Croatian fleet, especially in its shallow northern waters (Russo et al. 2020; Mihaljević et al. 2024). On the other hand, the relatively shallow waters of the Adriatic represent important foraging grounds for sea turtles (Haywood et al. 2020) exposing them to a high likelihood of fishery interaction. The matching of size of turtles caught by bottom trawlers and turtles stranded in the same area (Casale et al. 2004, 2010) suggests that stranding data may be a valuable proxy for interactions with trawlers. Thus, for its crucial biological role as developmental and year-round foraging ground (Lazar et al. 2004; Schofield et al. 2010; Zbinden et al. 2011; Baldi et al. 2023), the Adriatic represents a critical area for assessing the impact of trawling on sea turtles, especially on loggerhead turtles originating from Greek rookeries (Clusa et al. 2014; Tolve et al. 2018), and possibly for setting up specific conservation strategies (Lazar and Tvrtkovic 1995; Casale et al. 2015). The relatively small and semi-closed Adriatic Sea with extended sea turtle stranding networks is an excellent candidate to set up and implement a backtracking simulation of trajectories of stranded turtles as a tool for identifying and providing information on potential mortality areas.

The present study aims to implement the backtracking approach in a case study about the Italian coast of the Adriatic Sea where a large dataset of sea turtle stranding records is available. Specific objectives are as follows: (i) infer marine areas within the Adriatic Sea where sea turtle mortality events occur and (ii) identify possible spatio-temporal overlaps with fishing hotspots.

2 | Methods

2.1 | Strandings Data

Data of loggerhead turtles stranded along the Italian Adriatic coast in 2019–2021 were collected from the databases of four organizations (Centro Recupero Tartarughe Marine [CRTM] Molfetta; Fondazione Cetacea; CRTM Manfredonia; Centro

Studi Cetacei). Each stranding record included geographical location and date. For a subset of the records, the following data were also available: size, reported as CCL (i.e., curved carapace length; Bolten 1999), carcass state (reported as freshly dead or decomposed), geographical coordinates and photos.

For records with a photo, a decomposition code (see Section 2.2) was assigned to the record. If missing, geographical coordinates of the stranding location were assigned. Seasonal and latitudinal trends in CCL and total counts of stranded turtles were evaluated by rounding the stranding latitude to the 0.01 decimal degree and running a GAM (generalized additive model, *gamlss* package; Rigby and Stasinopoulos 2005) in R (R Core Team 2023), using Weibull and Poisson distribution, respectively, with the following formulas:

$$\mathrm{CCL} \sim \mathrm{LAT} + \mathrm{pb}\,(\mathrm{MONTH})$$
$$\mathrm{counts} \sim \mathrm{LAT} + \mathrm{pb}\,(\mathrm{MONTH})$$

where counts is the number of strandings, LAT the latitude and MONTH the month of stranding event, smoothed by *pb* function to account for the cyclic nature of months.

2.2 | Modelling the Carcass FP

To obtain the maximum possible displacement of the carcasses at sea and infer their original mortality areas, the maximum FP of a carcass was modelled as a function of the body size and the water temperature, taking into account its decomposition stage at stranding. To model it, the decomposition process of carcasses of loggerhead turtles was monitored with warm and cold environmental conditions to be representative of a wide range of water temperatures. Eight carcasses were deployed in welded mesh cages (1 × 1 cm mesh) of different sizes (≈ 1 m^3; Figure S1): six carcasses from CRTM Molfetta in cold period (November 2021–April 2022) in Bisceglie (Gulf of Manfredonia, Italy) and two carcasses from Lampedusa Rescue Center in warm period (June–July 2022) in Lampedusa (Pelagian Islands Archipelago, Italy). Cages were semi-floating, being laterally equipped with empty tanks, and installed in a sheltered place connected to the sea. Water temperature, carcass floating (yes/no; floating being any portion of the animal surfacing), decomposition state (e.g., tissue degradation) and presence of other organisms (e.g., fish, invertebrates, algae) were periodically monitored. Carcasses were deployed freshly dead in Bisceglie and still frozen in Lampedusa, as the frozen state does not affect the decomposition/floating process (Cook et al. 2020). Once sunk, carcasses were removed and replaced. To increase data regarding the warm period, published data about two carcasses of loggerhead turtles (Santos, Kaplan, et al. 2018), conserved frozen and then thawed in a freshwater bath before deployment in July–September 2015, were added to our dataset. The size of Santos, Kaplan, et al.'s (2018) carcasses, measured as straight carapace length (SCL), was converted into CCL with the equation provided by Bjorndal et al. (2000).

A decomposition stage index was created from carcass monitoring data, ranging from stage 0 (alive) to stage 6 (skeleton; Table S1). The beginning of stage 2 and the end of stage 5 coincided with the start and the end of the carcass floating. Thus, the duration of each stage, the FP reached at the end of each stage and the mean water temperature (mT) relative to FP were calculated, within the 2–5 stage range. Carcasses by Santos, Kaplan, et al. (2018) were classified through the same stage, by comparing photos and descriptions of the reported stages, and relative FP was calculated. The mean temperature reported in the study was considered mT, given the short FP and supported by the small temperature standard deviation (sd). The CCL, FP and mT data were then subset by stage, forming four training subdatasets.

Given mT and CCL as independent variables and FP as the dependent variable, the best fitting model (GAMs; *mgcv* R package, Wood 2011) was selected by (i) selecting the k value of smoothed variables through the GCV.cp method, (ii) smoothing one or both variables, (iii) checking for overfitting by comparing model training error with leave-one-out cross-validation (loocv) error (*loocv_gam* function) and comparing the resulting models through the lowest AIC (*AIC* function). The fittest GAM had the formula $\mathrm{FP} \sim \mathrm{s}\,(\mathrm{mT},\ \mathrm{k}=4) + \mathrm{s}\,(\mathrm{CCL},\ \mathrm{k}=4)$ (Gamma distribution; log linked) and was run on the four training sub-datasets (one for each of the four decomposition stages 2–5). The surface plot derived from the fittest GAM described the relationship between CCL, mT and FP, where FP increases both at the increasing of the CCL and the decreasing of mT (Figure 1; for only decomposition stage 2, as example).

2.3 | Mortality Areas

Mortality areas were identified as the initial locations of carcasses at the start of their FP. Before floating due to the internal decomposition gas (Epperly et al. 1996), dead sea turtles sink and are presumably subjected to limited movements due to the generally low velocities of bottom currents and the possible body interaction with bottom sediments (e.g., displacement of 1.4 km in 4.8 days in the Gulf of Mexico, Nero et al. 2013; Santos, Kaplan, et al. 2018). Consequently, stranded turtles with decomposition stage 1 (freshly dead, obtained from a photo) or turtles with no photo but reported as freshly dead

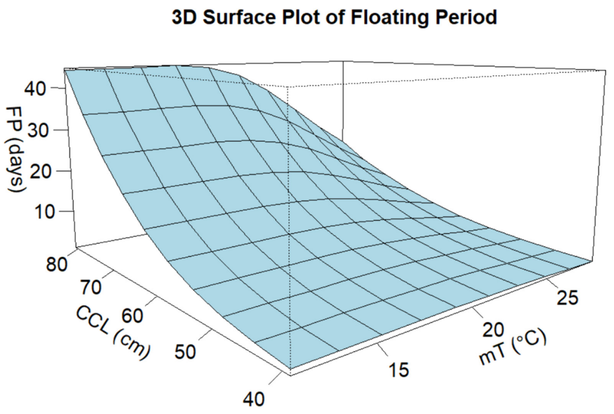

FIGURE 1 | The 3D surface plot derived by the relationship between the carcass floating period (FP), the mean water temperature (mT) and the carcass size (CCL) for the decomposition stage 2, modelled by the best fitting GAM model.

were considered to have died at 2 km off the stranding location, perpendicular to the coast. Stage 6 turtles were supposed to sink and not be moved by currents; therefore, they were excluded from the following analyses. For turtles with decomposition stage 2–5 and within the size range of cage carcasses, the death area was estimated through a backtracking approach, requiring an FP value for each record. FP was estimated through the model outlined above (Section 2.2), where three independent variables are needed: size, decomposition stage and water temperature. While the first two variables were available from the turtle records, water temperature needed to be estimated as follows.

First, daily data on sea surface temperature (SST) were gathered by Copernicus Marine Service (https://data.marine.copernicus.eu/) for the years 2018–2021. Second, a preliminary value of SST was estimated by averaging the SST of the stranding event's month within a 50-km buffer from the stranding point. Third, a preliminary FP was predicted (*predict* function) for each record through the FP model (see Section 2.2.). Fourth, the mean of SSTs (mT) of the period from the floating start date (i.e., stranding date–initial day of FP) to the stranding date, within the same 50-km buffer, was calculated. This temperature was then used to predict a final, more accurate, FP. Records with 5% top FP values were considered outliers and removed. The remaining final FP values were used to identify the location of death, as follows.

Trajectories of stranding records were reconstructed through the adoption of a particle tracking numerical model (North et al. 2008) that runs with stored sea current fields, derived by hydrodynamic modelling. The turtle carcasses were tracked back using a 20-min time step with a 4th-order Runge–Kutta scheme for particle advection and a random displacement model for turbulent motion.

The adopted sea current fields, between 2018 and 2021, refer to the uppermost surface layer of the modelled sea and have horizontal spatial resolution of about 4 km and hourly temporal frequency. They were distributed, along with a quality assessment report, by Copernicus Marine Service (www.copernicus.eu) and produced via the implementation of a coupled wave-current numerical model system including tides, and assimilation of sea observations. European Centre for Medium-Range Weather Forecasts (ECMWF, www.ecmwf.int) provided a complementary hourly dataset of 10-m wind fields, at 12 km of spatial resolution, that was used to estimate the wind-induced drift.

Using these datasets, a drifter path, by chance found in the study area, was compared with the modelled trajectories (see supporting information; Figure S2) through the computation of the trajectory absolute error (TAE; e.g., Cucco et al. 2016). This metric defines the separation distance between the drifter position and the modelled particles trajectories at hourly intervals. The TAE values were found to be below the drifter dispersion length indicating a tolerable divergence between observed and modelled trajectories. Specifically, after 240 h, the TAE is lower than 50 km, which is in line with the results obtained by similar applications (e.g., Amemou et al. 2020; Cucco et al. 2023). The application of a wind-induced drift along the modelled trajectories did not provide homogeneous improvements when compared with the observed trajectory and it was not considered.

Virtual particles representing carcasses were released from two points of the model grid closest to the strandings location (distance range in between 1 and 7 km), at 6-h intervals (00:30, 6:30, 12:30, 18:30) of the stranding day, as strandings were assumed to be registered within 24 h of the stranding event. Particles were backtracked for the predicted FP, likely resulting in overestimating the allowing for the longest possible displacement. The model provided the coordinates of the final position of particles (8 positions per record) that were merged to at sea position of stage 1 strandings and used to generate heatmaps of particle aggregation with 0.1 degree of influence and 0.01 degree of resolution for each fishing period (see Section 2.4) through QGIS (QGIS.org, version 3.24.1-Tisler). The final positions were identified as death locations.

To complement the backtracked reconstruction of stranding trajectories and the relative identification of mortality hotspots, a forward simulation was conducted as follows. Between the latitudes of about 42.0° N and 45.0° N virtual particles were released at 15, 30 and 45 km offshore the Italian Adriatic coast (Figure S3) during a cold (*N* particles: 7038) and a warm (*N* particles: 6072) season, considered as periods with maximum and minimum FP values and displacement, respectively. These FP values for the warm and cold seasons were the median FP values of records belonging to those seasons. Seasons were identified by clustering (***kmeans*** function) records by mT and rounding their cut-off dates to the nearest half-month (15th or 30th day of the month). The proportions of particles reaching the area within 12 km from the coast (i.e., stranding probability) were estimated for each distance of release and for the area comprised between 12 and 45 km (i.e., mean stranding probability), by interpolating the curve through a GAM with Gamma family (*gam* and *predict* function in R).

2.4 | Fishing Effort Hotspots

Distribution of fishing vessels was obtained from two different sources: automatic identification system (AIS) and vessel monitoring system (VMS). VMS has been mandatory in the EU since 2009 (Council Regulation [EC] No 1224/2009) for all fishing vessels with length > 15 m (and for vessels 12–15 m in length fishing outside national waters or for more than 24 h) and provides vessel positions, course and speed with a temporal resolution of 2 h by transmitting information via satellite. AIS is an autonomous tracking system compulsory in the EU in 2014 for fishing vessels with length > 15 m (EU Dir 2011/15/EU), used for exchanging real-time navigation status between equipped stations/ships and for monitoring vessel movements, by transmitting information at regular intervals (2–180 s).

VMS data, represented by 'pings' consisting of vessel coordinates, date, speed, EU ID and heading, were provided by the General Command of Coast Guard for all vessels that in 2018–2021 visited the Adriatic Sea (lat 39.8° N–45.7° N; long 12.3° E–19.4° E), with the gear list for each vessel. Only vessels having trawl as gear were selected. Pings with coordinates on land or near the harbours (≤ 3 nm), heading outside compass range, speed > 20 kn and duplicates were removed by using the *vmstools* R package (Hintzen et al. 2012). Pings with speeds between 0 and 4 knots were then selected, as these speeds are assumed to be indicative of fishing activity. Fishing periods were visually identified by changes over months of the median longitude of VMS pings grouped by a latitudinal range of 0.01 degrees. Heatmaps with 0.1 degrees of influence and 0.1 degrees of resolution were generated for each period through QGIS.

Daily AIS data for years 2018–2020 and the vessel registry were gathered by Global Fishing Watch (GFW). Data consisted of vessel ID (MMSI, Maritime Mobile Service Identity), fishing hours spent in a cell of 0.1 resolution degree and cell coordinates. The gear type used inferred by GFW ('vessel_class_gfw' parameter), and MMSI in the vessel registry allowed the selection of daily AIS data of only trawl fishing boats (vessel_class_gfw = 'trawler'). Only cells within the Adriatic Sea (lat 39.8° N–45.7° N; long 12.3° E–19.4° E) were selected. Fishing periods detected by VMS pings were assigned to AIS data according to the date and the total amount of fishing hours per cell per period was estimated. To identify the distribution of fishing activity, heatmaps with 0.1 degree resolution were generated through QGIS.

3 | Results

3.1 | Strandings

A total of 1432 records of turtle carcasses (Figure 2) stranded on the Adriatic Italian coast were collected (FC: 699; CSC: 513; MOL: 178; MAN: 42), of which 795 with measured CCL (range: 8.1–107 cm; mean: 58.6 ± 16.1). A total of 706 records included photos. Strandings were denser in the North Adriatic Sea (median latitude = 43.73 N; IQR = 2.39 degrees; range: 40.23–44.81 N) with important aggregation also in the Central Adriatic coast and the Gulf of Manfredonia. CCL showed a significant negative correlation with latitude (est: −0.029, $p < 0.01$, $n = 795$), while the number of total strandings per month was significantly positively correlated to the latitude (est: 0.097, $p < 0.01$, $n = 916$). No significant effect of month on both CCL (GAM; $n = 795$) and number of strandings (GAM; $n = 916$) was detected. Turtles stranded with decomposition stage 2 were the most abundant overall and over months (Figure 3).

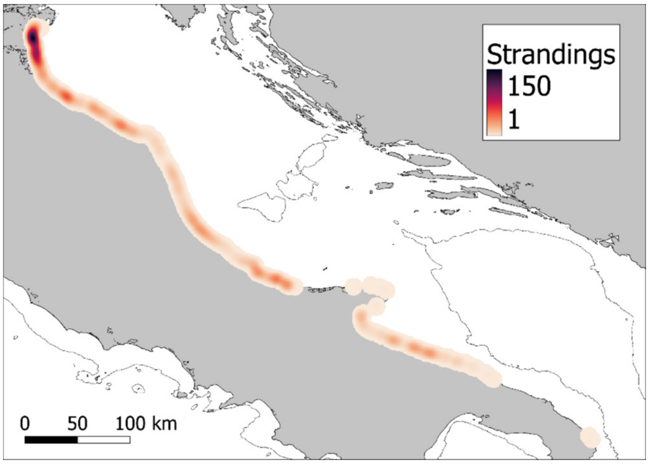

FIGURE 2 | Distribution of 1432 total strandings of loggerhead sea turtles collected in 2019–2021 along the Italian Adriatic coast.

3.2 | Modelling FP of Carcasses

The FP of carcasses monitored in the present study and by Santos, Kaplan, et al. (2018) (total $N = 10$, CCL range: 39.0–80.7 cm) ranged from 0.5 to 140 days within a water temperature interval between 11.61°C and 28.69°C, respectively. The variability of FP values was wider with cold temperatures compared to warm temperatures. Decomposition stage 2 had the longest duration. Duration, FP and temperatures for each decomposition stage (2–5) are reported in Table S2.

3.3 | Mortality Areas

The predicted FP of the 313 stranding records (within the CCL range and with decomposition stages 2–5) ranged from 1.24 to 91.14 days, with a median of 8.25 days. Median FPs for decomposition stage 2–5 were 6.5 (IQR: 14.4; $n = 226$), 17.11 (IQR: 22.95; $n = 63$), 28.03 (IQR: 40.31; $n = 17$) and 6.54 (IQR: 7.69; $n = 7$) days, respectively. A total of 16 records (with FP > 39 days) representing 5% of top outliers were excluded from the backtracking analysis. Mortality areas were estimated for the remaining 297 stranding records. The median FP and the median mT of the three fishing periods identified (A, B, C, see below) were reported in Table 1.

Heatmaps of stranded turtles with decomposition stage 1 and 2–5 combined ($n = 797$; Figure 4) showed that the highest aggregation of backtracked particles occurred in the North and Central Adriatic coasts for all seasons. In particular, particles were concentrated close to the coast (< 30 km) of the Northwest and Central Adriatic Sea with only some spots at > 30 km from the Italian coast in periods B and C. The particles converged to the centre in season C, to a lesser extent in the Gulf of Manfredonia, and dispersed up to 50 km offshore. However, the hotspots of mortality events always occurred within 15 km of the coast. The mortality areas of freshly dead turtles spread all over the coastal area with the highest concentration in the Northwest Adriatic Sea and some spots along the Apulian coast.

The proportion of virtual particles released offshore and reaching the coastal area (0–12 km from the coast) decreased with the distance from the coast, both from 1 December to 15 May (cold season) and from 15 June to 15 October (warm season). Particles released at 15 km reached the coastal area with a proportion > 0.4 in both seasons (warm: 0.451; cold: 0.415). Proportions of particles released at 30 and 45 km were 0.096 and 0.009 in warm season and 0.174 and 0.103 in cold season (Figures 5 and S4). The estimated proportion of turtles dying in the area 12–45 km from the coast and drifting until 12 km from the coast was 0.25 and 0.17 in the cold and warm season, respectively.

3.4 | Fishing Effort Hotspot

A total of 5,631,165 VMS pings were collected. After processing, 2,054,112 pings of 740 trawlers generated seasonal heatmaps. VMS data showed a high occurrence of trawler activity all along the Adriatic Sea (Figure 4). Three fishing periods were visually identified: A (January–April), B (May–August) and C

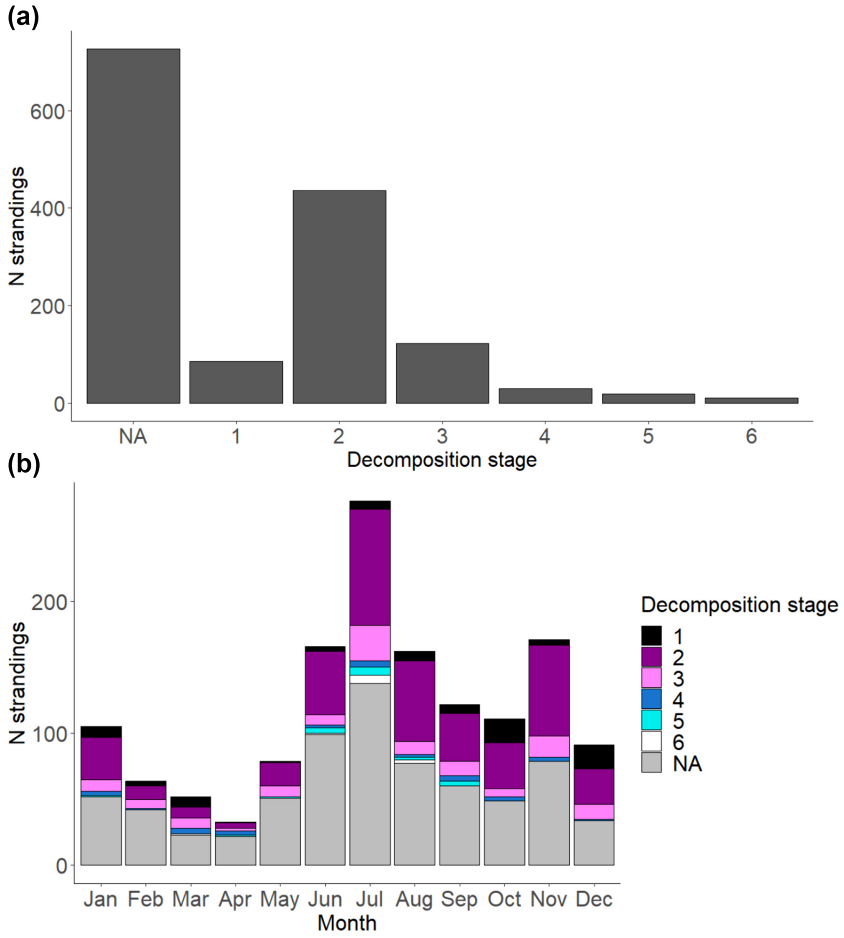

FIGURE 3 | Frequency of decomposition stages (see Table S1 for details) within total stranded loggerhead turtles ($N = 1432$; a) along the Italian Adriatic coast in 2019–2021 and over months (b).

TABLE 1 | Number of backtracked loggerhead turtles stranded along the Italian Adriatic coast in 2019–2021, median floating period (FP), median temperature (mT), and relative interquartile ranges (IQR) of the three fishing periods identified by vessel monitoring system (VMS) data.

Fishing period	Months	*N* strandings	FP (median; IQR)	mT (median: IQR)
A	Jan–Apr	32	30.8; 10.4	14.2; 2.08
B	May–Aug	140	3.68; 3.37	25.9; 2.26
C	Sep–Dec	125	13.7; 13.6	18.1; 6.46

(September–December). High fishing activity occurred in different 30 km offshore areas along the North and South Adriatic Sea in period A and more coastal in the centre, spreading and diluting in medium-high fishing activity areas in the North-East, the Strait of Otranto and the Central Adriatic Sea (up to the neritic edge) in period B. Trawling mainly occurred in more coastal areas (around 15 km offshore) all along the Adriatic Sea in period C, especially in the central part of the basin.

A total of 2,204,180 AIS daily data were gathered about fishing hours of 865 trawlers fishing within the Adriatic Sea. The total fishing hours per season was estimated for 2175 cells (5947 total fishing hours data: 1845, 2118 and 1984 data for period A, B and C, respectively) and ranged from 0–13765.2 h. Areas with high fishing hours showed a shift, as being concentrated in the North and Central Adriatic Sea and the Gulf of Manfredonia in season A and spreading up to the neritic edge and offshore areas in season B. Hotspots of fishing activity were located all along the basin at around 15 km from the coast in season C (Figure 4).

4 | Discussion

This study provides first indications about hotspots of sea turtle mortality, probably determined by fishery interaction, in the Adriatic Sea. Results highlight the challenges in fully determining the extent of offshore deadly interaction with fisheries.

4.1 | Stranding Patterns

Present results show that stranding events occur throughout the year and all along the Italian Adriatic coast, although

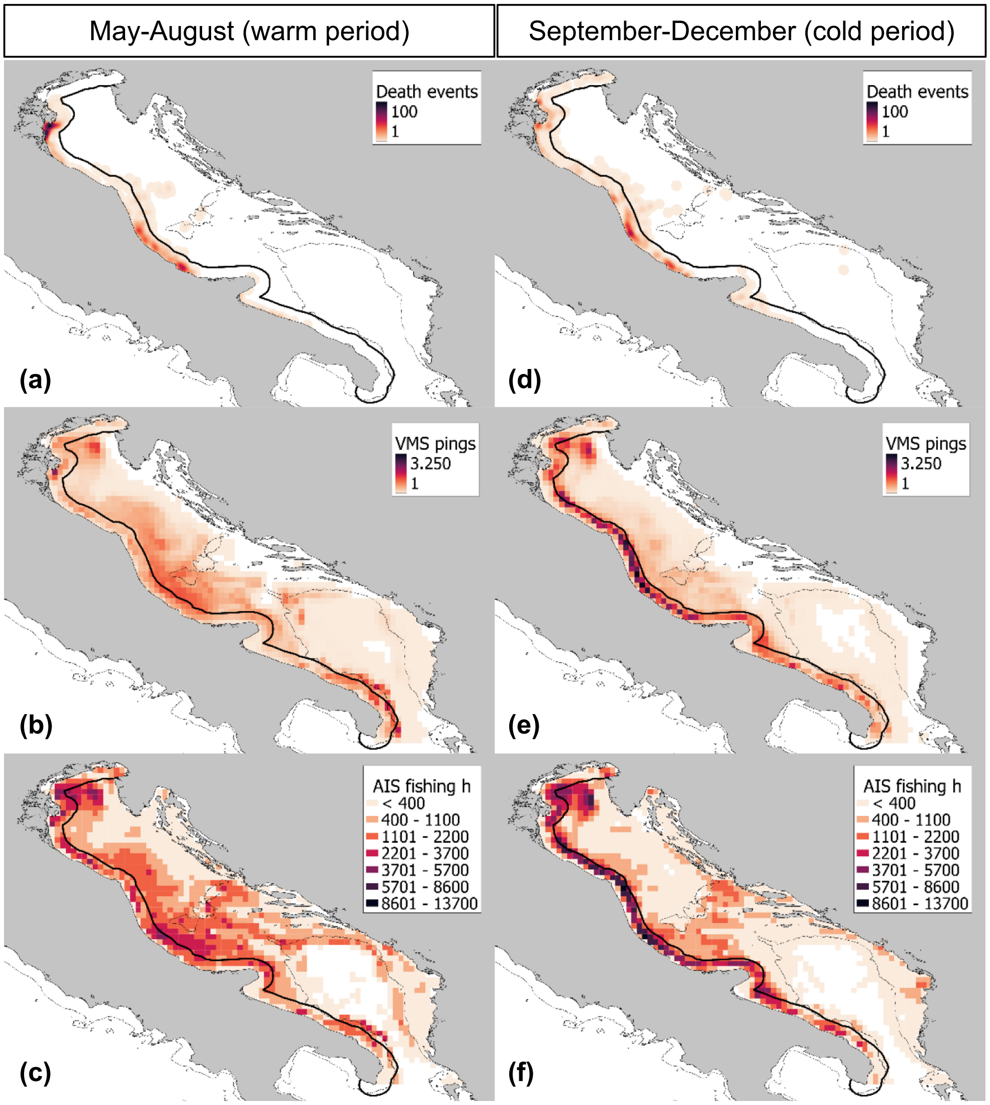

FIGURE 4 | Heatmaps of mortality areas of 797 stranded loggerhead turtles in the Italian coast of the Adriatic Sea (a, d; 0.01 degree resolution), vessel monitoring system (VMS) pings (b, e; 0.1 degree resolution) and automatic identification system (AIS) fishing hour data (c, f; 0.1 degree resolution) in the Adriatic Sea. Only the periods with maximum and minimum extension of the spatial range of fishing effort (considered the most representative) are shown: periods B (May–August, warm period; left side) and C (September–December, cold period; right side). These periods also have the highest and similar number of backtracked turtle strandings (see Table 1). The thicker black line parallel to the shoreline defines a 30-km distance from the Italian Adriatic coast. The thin black line represents 200-m bathymetry.

increasing toward the northern areas where the highest density was observed. This pattern aligns with previous findings that observed a higher density of stranded turtles in the northern part of the Adriatic Sea (Casale et al. 2010), with a high aggregation near the Po River delta (Marisaldi et al. 2023). Assuming that a good part of stranding events is caused by human activity (Casale et al. 2010), the present results confirm the North Adriatic to be the most affected area in Italy and one of the most impacted sub-basins in the Mediterranean Sea (Tomás et al. 2008; Casale et al. 2010; Türkozan et al. 2013; Hama et al. 2020; Dimitriadis et al. 2022). The shallow waters (< 50 m) and the diverse and abundant benthic community make the North Adriatic area an important foraging ground and overwintering area for juvenile and adult sea turtles (Casale et al. 2004; Lazar et al. 2004; Zbinden et al. 2011; Casale and Mariani 2014) that here migrate or reside (Casale, Affronte, et al. 2012; Luschi and Casale 2014; Baldi et al. 2023), and these factors may play a crucial role in aggregation of turtles in the whole area. A similar latitudinal gradient was observed along the Croatian coast (Hama et al. 2020; Mihaljević et al. 2024). However, the coastline morphology and the accessibility of shores may significantly affect the carcass discoverability, impacting the number of strandings observed (Cook et al. 2021).

Turtles with a moderate level of decomposition (stage 2) were the most common, suggesting they have a higher probability of landfall, even in adverse marine conditions, compared to severely decomposed turtles (stages 4–5) and leading to expect a higher presence of mortality areas closer to the coast. The observed turtle size was smaller in the North Adriatic than in the South. This might be due either to a higher susceptibility of small turtles to cold stunning in the colder waters of the North Adriatic or an actual preference for this area

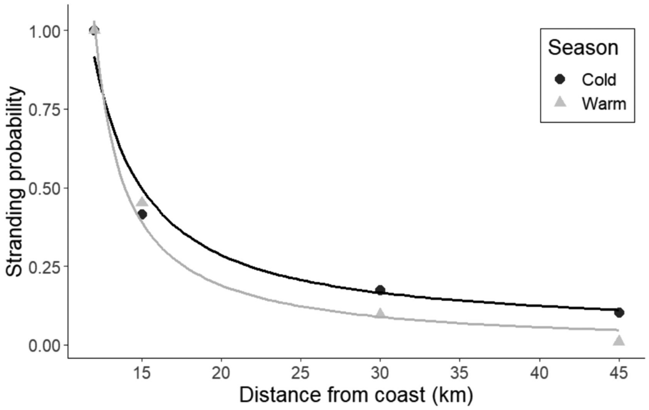

FIGURE 5 | Stranding probability of virtual particles deployed in the forward simulation for warm (15/06–15/10; $N=6072$) and cold (1/12–15/05; $N=7038$) seasons according to distance released from the Italian Adriatic coast, after being floating 3.7 and 27.7 days respectively.

by small turtles. The prevalence of small individuals in the North compared to the South aligns with other findings showing that stranded and floating carcasses of loggerhead turtles in the region are significantly smaller than southern specimens (Hama et al. 2020). Given the presence and fidelity of juvenile individuals in both the North and the South Adriatic (Casale, Affronte, et al. 2012; Casale and Simone 2017; Baldi et al. 2023), the latitudinal difference in stranding size may therefore suggest the concurrence of additional environmental, biological, and behavioural factors (i.e., SST, age, habitat use) to the landfall chances.

4.2 | Mortality Areas

Results indicate that stranded turtles predominantly die close (< 15 km) to the coast, and only during colder periods, turtles dying more offshore can reach the coast. Therefore, the distribution of mortality areas closely reflects the stranding patterns observed along the coast, with relatively short post-mortem displacement, and these areas are notably concentrated in the North-Central Adriatic region. The complementary results of forward tracking show that turtles dying offshore rarely reach the coast, even during the cold period with longer FPs (i.e., higher stranding potential). This implies that stranded turtles represent only a small fraction (17%–25%) of total turtles dying in the wider area. Other factors may reduce the chances that offshore carcasses reach the coast. For instance, Nero et al. (2022), supported by findings in Schultz et al. (2022) elucidated that turtles sinking in water deeper than 30 m are unlikely to resurface due to the pressure effect, further reducing the stranding probability. Seasonal variation also could play a crucial role: turtles dying during warmer periods exhibited higher decomposition rates, decreasing their period of positive buoyancy (FP) and their chances of stranding, compared to turtles dying in colder seasons. The seasonal effect resulting from the present study complements similar observations elsewhere about great variability regarding both season and distance from shore (7%–13%, Epperly et al. 1996; 20%, Hart et al. 2006; 5%–80%, Koch et al. 2013; 4%–90%, Cook et al. 2021). These findings therefore provide quantitative insight into how distance and seasonal variations influence stranding probabilities and emphasize the importance of considering a range of environmental and biological factors when interpreting stranding data.

Due to its inherent limitations, the present approach can provide just general patterns like those described above, while more fine-scale estimates of mortality areas should be regarded with caution. Both the tracking model and the FP model are affected by limitations. For instance, the initial particle distance from the coast/stranding point deployed for simulations is constrained by the resolution grid of the model, and the FP estimation was influenced by several factors, including water temperature data missing for intermediate seasons, a limited sample size of carcasses and logistical constraints related to cage experiments. These experiments may not accurately reflect the natural floating dynamic of the decomposition process as they were not conducted in open sea conditions, not allowing for carcasses to sink to the seabed and enabling the evaluation of whole water column shifts (Santos, Kaplan, et al. 2018; Nero et al. 2022). In addition, organisms-induced decomposition effect, scavenging events, sea state and other parameters potentially affecting and influencing both the decomposition process and the FP (Hart et al. 2006; Cook et al. 2021; Aoki et al. 2023) were not considered. However, it is noteworthy that the estimated FP for high temperatures, as well as the FP predicted by the model, are similar to those reported in previous literature for other turtle species (Cook et al. 2020). Due to the lack of a specific decomposition rate for loggerhead turtles and the general paucity of comparable FP data, mostly expressed as ADH (accumulated degree hours: 'hourly sum of ambient temperatures a carcass experienced'; Nero et al. 2013; Reneker et al. 2018; Cook et al. 2020; Nero et al. 2022), assessing the validity of FP estimates for low temperature is challenging. Nevertheless, the longer cold FPs (up to 140 days) may be explained by the decreasing effect in the decomposition rate of the greater CCL values and the lower SSTs in the present study, compared to the other ones (Nero et al. 2013; Santos, Kaplan, et al. 2018; Cook et al. 2020), as well as the slower decomposition rate of carnivorous species (i.e., *Caretta caretta*) compared to herbivorous turtles (e.g., *Chelonia mydas*) involved in other studies (Santos, Kaplan, et al. 2018; Cook et al. 2020), possibly associated to a different diet and physiology of gut and intestine (Cook et al. 2020).

4.3 | Implications for Conservation: Fishing Effort Pattern and Overlaps With Mortality Areas

VMS and AIS data revealed similar distribution patterns over seasons/time, despite inherent differences in the datasets (i.e., VMS data available only for Italian trawlers; AIS data representing fishing hours of trawlers from several countries). Fishing efforts showed seasonal variations. In the cold period, fishing effort was concentrated along the coastal waters across the Adriatic Sea from the North-West and North-East (adjacent to the Istrian Peninsula) to the Gulf of Manfredonia. In the warmer period, fishing effort was more spread out and extended offshore up to the continental shelf edge (200 m of depth) and concentrated at Otranto Strait. These findings were in accordance with bycatch studies (Fortuna et al. 2010; Casale 2011; Casale et al. 2015; Lucchetti et al. 2016), such as the strong seasonality of bycatch observed in the Gulf of Manfredonia, with a decreasing rate of incidental capture from winter to summer

(Baldi et al. 2022), and the longitudinal and seasonal differences in capture rate by trawl fishery in the North Adriatic (Casale et al. 2004; Lucchetti et al. 2016).

Both fishing activity and mortality events exhibited seasonal patterns. Comparisons between fishing and mortality hotspots are difficult because turtles dying offshore are unlikely to strand to the coast. Thus, comparisons of fishing and turtle stranding data are probably appropriate only in coastal areas ($< 30\,\text{km}$). Overlaps were identified in the Gulf of Manfredonia and in the North-West (Po River delta) in both cold and warm periods, respectively. The marine area offshore to the Po River delta is both a nursery for fishing commercial species and a eutrophic foraging zone for sea turtles especially in warm months, due to Adriatic counter-clockwise circulation (Poulain 2001; Spillman et al. 2007). However, information on stranding events in the Southern Adriatic regions remained scarce, suggesting a potential underestimation of fishing impact on turtle mortality in these areas.

5 | Conclusion and Recommendation

The present study indicates that stranding densities represent a reliable index of coastal hotspots of mortality events, yet revealing limitations in capturing the full scope of mortalities. Strandings cannot provide a comprehensive understanding of the broad impact of offshore fishing, leaving a significant knowledge gap in fishery interactions. Despite these limitations, the application of both backward modelling from stranding events and forward modelling from identified fishing effort hotspots can provide valuable insights. This dual-modelling strategy enhanced the capability to detect mortality events, both in terms of quantity (how many turtles are affected) and spatial distribution (where these events are occurring). Furthermore, the present results combined with novel insights about high-density stranding areas following seasonal patterns along the Croatian coast (Hama et al. 2020; Mihaljević et al. 2024) highlight the potential value of conducting further investigations to assess the spatio-temporal patterns of turtle-fishing interactions, encompassing various gear types and the stranding dynamics of different marine areas.

Improving models and enhancing the accuracy of FP estimates are recommended to increase the detection accuracy of mortality events. Moreover, efforts should be undertaken to collect more comprehensive and valuable stranding data. Improving the quality and completeness of stranding records (especially photos for determining the decomposition stage) as well as post-mortem investigations aimed to assess their death causes are crucial for better analysis and interpretation. Furthermore, decomposition models can be improved by (i) increasing the sample size of carcasses, (ii) testing the decomposition process across a wider range of temperatures and (iii) testing carcasses in open sea environment to account for both temperature and pressure effects on decomposition rates and carcass buoyancy (FP). We recommend replicating similar studies in other areas to take advantage of the available large datasets provided by stranding networks worldwide and the recent availability of open-source AIS data.

Author Contributions

Conceptualization: P.C. Methodology: P.C., G.Q., C.A. and A.C. Formal analysis: C.A. and G.Q. Investigation: E.Z., C.A., P.S. and D.F. Resources: P.S., D.F. and P.C. Data curation: E.Z., C.A. and G.B. Writing – original draft: C.A., P.C. and G.Q. Writing – review and editing: E.Z., G.Q., A.C., G.B., V.A., M.M., V.O., P.S., G.F., S.L. and D.F. Visualization: C.A. Supervision: P.C. Funding acquisition: P.C. and D.F.

Acknowledgements

The authors thank all the fishers and volunteers of the organizations who collaborated with this project, the General Command of the Coast Guard for providing VMS data essential for this study, Bisceglie Approdi for the provision of spaces logistically needed and ASL BT Dip. Prevenzione, Direzione Servizio Veterinario Area ‘C’. C. Agabiti was supported by the PON ‘Ricerca e Innovazione’ 2014-2020 REACT EU program. Open access publishing facilitated by Universita degli Studi di Pisa, as part of the Wiley - CRUI-CARE agreement.

Conflicts of Interest

The authors declare no conflict of interest.

Data Availability Statement

The stranding data used in this study are part of different databases of several private organizations and are not publicly available at the moment. However, data will be provided upon reasonable request.

References

Adimey, N. M., C. A. Hudak, J. R. Powell, et al. 2014. “Fishery Gear Interactions From Stranded Bottlenose Dolphins, Florida Manatees and Sea Turtles in Florida, U.S.A.” *Marine Pollution Bulletin* 81, no. 1: 103–115. https://doi.org/10.1016/j.marpolbul.2014.02.008.

Almpanidou, V., A. Doxa, and A. D. Mazaris. 2021. “Combining a Cumulative Risk Index and Species Distribution Data to Identify Priority Areas for Marine Biodiversity Conservation in the Black Sea.” *Ocean & Coastal Management* 213: 105877. https://doi.org/10.1016/j.ocecoaman.2021.105877.

Amemou, H., V. Koné, A. Aman, and C. Lett. 2020. “Assessment of a Lagrangian Model Using Trajectories of Oceanographic Drifters and Fishing Devices in the Tropical Atlantic Ocean.” *Progress in Oceanography* 188: 102426. https://doi.org/10.1016/j.pocean.2020.102426.

Aoki, D. M., J. R. Perrault, S. L. Hoffmann, et al. 2023. “Forensic Determination of Shark Species as Predators and Scavengers of Sea Turtles in Florida and Alabama, USA.” *Marine Ecology Progress Series* 703: 145–159. https://doi.org/10.3354/meps14214.

Baldi, G., G. Furii, M. Del Vecchio, et al. 2023. “Behavioural Plasticity in the Use of a Neritic Foraging Area by Loggerhead Sea Turtles: Insights From 37 Years of Capture–Mark–Recapture in the Adriatic Sea (Mediterranean Sea).” *ICES Journal of Marine Science* 80: 210–217. https://doi.org/10.1093/icesjms/fsac227.

Baldi, G., P. Salvemini, A. P. Attanasio, et al. 2022. “Voluntary Fishing Logbooks Are Essential for Unveiling Unsustainable Bycatch Levels and Appropriate Mitigating Measures: The Case of Sea Turtles in the Gulf of Manfredonia, Adriatic Sea.” *Aquatic Conservation: Marine and Freshwater Ecosystems* 32, no. 5: 741–752. https://doi.org/10.1002/aqc.3798.

Bjorndal, K. A., A. B. Bolten, and H. R. Martins. 2000. “Somatic Growth Model of Juvenile Loggerhead Sea Turtles *Caretta caretta*: Duration of Pelagic Stage.” *Marine Ecology Progress Series* 202: 265–272. https://doi.org/10.3354/meps202265.

Bolten, A. B. 1999. "Techniques for Measuring sea Turtles." In *Research and Management Techniques for the Conservation of Sea Turtles*, edited by K. L. Eckert, K. A. Bjorndal, F. A. Abreu-Grobois, and M. Donnelly, 110–114. Washington, DC: IUCN/SSC Marine Turtle Specialist Group Publication No. 4.

Caillouet, C. W., Jr., D. J. Shaver, W. G. Teas, J. M. Nance, D. B. Revera, and A. C. Cannon. 1996. "Relationship Between Sea Turtle Stranding Rates and Shrimp Fishing Intensities in the Northwestern Gulf of Mexico: 1986–1989 Versus 1990–1993." *Fishery Bulletin* 94, no. 2: 237–249.

Cambiè, G., I. Jribi, I. Cambera, G. Vagnoli, D. Freggi, and P. Casale. 2020. "Intra-Gear Variation in Sea Turtle Bycatch: Implications for Fisheries Management." *Fisheries Research* 221: 105405. https://doi.org/10.1016/j.fishres.2019.105405.

Cambiè, G., N. Sánchez-Carnero, T. Mingozzi, R. Muiño, and J. Freire. 2013. "Identifying and Mapping Local Bycatch Hotspots of Loggerhead Sea Turtles Using a GIS-Based Method: Implications for Conservation." *Marine Biology* 160, no. 3: 653–665. https://doi.org/10.1007/s00227-012-2120-5.

Casale, P. 2011. "Sea Turtle By-Catch in the Mediterranean." *Fish and Fisheries* 12, no. 3: 299–316. https://doi.org/10.1111/j.1467-2979.2010.00394.x.

Casale, P., M. Affronte, G. Insacco, et al. 2010. "Sea Turtle Strandings Reveal High Anthropogenic Mortality in Italian Waters." *Aquatic Conservation: Marine and Freshwater Ecosystems* 20, no. 6: 611–620. https://doi.org/10.1002/aqc.1133.

Casale, P., M. Affronte, D. Scaravelli, B. Lazar, C. Vallini, and P. Luschi. 2012. "Foraging Grounds, Movement Patterns and Habitat Connectivity of Juvenile Loggerhead Turtles (*Caretta caretta*) Tracked From the Adriatic Sea." *Marine Biology* 159, no. 7: 1527–1535. https://doi.org/10.1007/s00227-012-1937-2.

Casale, P., A. C. Broderick, J. A. Camiñas, et al. 2018. "Mediterranean Sea Turtles: Current Knowledge and Priorities for Conservation and Research." *Endangered Species Research* 36: 229–267. https://doi.org/10.3354/esr00901.

Casale, P., A. Ciccocioppo, G. Vagnoli, et al. 2020. "Citizen Science Helps Assessing Spatio-Temporal Distribution of Sea Turtles in Foraging Areas." *Aquatic Conservation: Marine and Freshwater Ecosystems* 30, no. 1: 123–130. https://doi.org/10.1002/aqc.3228.

Casale, P., D. Freggi, R. Basso, and R. Argano. 2005. "Interaction of the Static Net Fishery With Loggerhead Sea Turtles in the Mediterranean: Insights From Mark-Recapture Data." *Herpetological Journal* 15, no. 3: 201–203.

Casale, P., D. Freggi, G. Furii, et al. 2015. "Annual Survival Probabilities of Juvenile Loggerhead Sea Turtles Indicate High Anthropogenic Impact on Mediterranean Populations." *Aquatic Conservation: Marine and Freshwater Ecosystems* 25, no. 5: 551–561. https://doi.org/10.1002/aqc.2467.

Casale, P., L. Laurent, and G. De Metrio. 2004. "Incidental Capture of Marine Turtles by the Italian Trawl Fishery in the North Adriatic Sea." *Biological Conservation* 119, no. 3: 287–295. https://doi.org/10.1016/j.biocon.2003.11.013.

Casale, P., and P. Mariani. 2014. "The First 'Lost Year' of Mediterranean Sea Turtles: Dispersal Patterns Indicate Subregional Management Units for Conservation." *Marine Ecology Progress Series* 498: 263–274. https://doi.org/10.3354/meps10640.

Casale, P., and G. Simone. 2017. "Seasonal Residency of Loggerhead Turtles *Caretta caretta* Tracked From the Gulf of Manfredonia, South Adriatic." *Mediterranean Marine Science* 18, no. 1: 4–10. https://doi.org/10.12681/mms.1663.

Casale, P., G. Simone, C. Conoscitore, M. Conoscitore, and P. Salvemini. 2012. "The Gulf of Manfredonia: A New Neritic Foraging Area for Loggerhead Sea Turtles in the Adriatic Sea." *Acta Herpetologica* 7, no. 1: 1–12. https://doi.org/10.13128/Acta_Herpetol-9897.

Clusa, M., C. Carreras, M. Pascual, et al. 2014. "Fine-Scale Distribution of Juvenile Atlantic and Mediterranean Loggerhead Turtles (*Caretta caretta*) in the Mediterranean Sea." *Marine Biology* 161: 509–519. https://doi.org/10.1007/s00227-013-2353-y.

Cook, M., J. L. Reneker, R. W. Nero, B. A. Stacy, and D. S. Hanisko. 2020. "Effects of Freezing on Decomposition of Sea Turtle Carcasses Used for Research Studies." *Fishery Bulletin* 118, no. 3: 268–274.

Cook, M., J. L. Reneker, R. W. Nero, B. A. Stacy, D. S. Hanisko, and Z. Wang. 2021. "Use of Drift Studies to Understand Seasonal Variability in Sea Turtle Stranding Patterns in Mississippi." *Frontiers in Marine Science* 8. https://doi.org/10.3389/fmars.2021.659536.

Crespo-Picazo, J. L., M. Parga, Y. Bernaldo de Quirós, et al. 2020. "Novel Insights Into Gas Embolism in Sea Turtles: First Description in Three New Species." *Frontiers in Marine Science* 7. https://doi.org/10.3389/fmars.2020.00442.

Cucco, A., G. Quattrocchi, A. Satta, et al. 2016. "Predictability of Wind-Induced Sea Surface Transport in Coastal Areas." *Journal of Geophysical Research: Oceans* 121, no. 8: 5847–5871. https://doi.org/10.1002/2016JC011643.

Cucco, A., L. Rindi, L. Benedetti-Cecchi, et al. 2023. "Assessing the Risk of Oil Spill Impacts and Potential Biodiversity Loss for Coastal Marine Environment at the Turn of the COVID-19 Pandemic Event." *Science of the Total Environment* 894: 164972. https://doi.org/10.1016/j.scitotenv.2023.164972.

Cuevas, E., V. Guzmán-Hernández, A. Uribe-Martínez, A. Raymundo-Sánchez, and R. Herrera-Pavon. 2018. "Identification of Potential Sea Turtle Bycatch Hotspots Using a Spatially Explicit Approach in the Yucatan Peninsula, Mexico." *Chelonian Conservation and Biology* 17, no. 1: 78–93. https://doi.org/10.2744/CCB-1263.1.

Dimitriadis, C., A. D. Mazaris, S. Katsanevakis, et al. 2022. "Stranding Records and Cumulative Pressures for Sea Turtles as Tools to Delineate Risk Hot Spots Across Different Marine Habitats." *Ocean and Coastal Management* 217: 106017. https://doi.org/10.1016/j.ocecoaman.2021.106017.

Dulvy, N. K., J. K. Baum, S. Clarke, et al. 2008. "You Can Swim but You Can't Hide: The Global Status and Conservation of Oceanic Pelagic Sharks and Rays." *Aquatic Conservation: Marine and Freshwater Ecosystems* 18, no. 5: 459–482. https://doi.org/10.1002/aqc.975.

Duncan, E. M., Z. L. R. Botterell, A. C. Broderick, et al. 2017. "A Global Review of Marine Turtle Entanglement in Anthropogenic Debris: A Baseline for Further Action." *Endangered Species Research* 34: 431–448. https://doi.org/10.3354/esr00865.

Eigaard, O. R., F. Bastardie, M. Breen, et al. 2016. "Estimating Seabed Pressure From Demersal Trawls, Seines, and Dredges Based on Gear Design and Dimensions." *ICES Journal of Marine Science* 73, no. suppl_1: i27–i43. https://doi.org/10.1093/icesjms/fsv099.

Epperly, S. P., J. Braun, A. J. Chester, et al. 1996. "Beach Strandings as an Indicator of At-Sea Mortality of Sea Turtles." *Bulletin of Marine Science* 59, no. 2: 289–297.

Fahlman, A., J. L. Crespo-Picazo, B. Sterba-Boatwright, B. A. Stacy, and D. Garcia-Parraga. 2017. "Defining Risk Variables Causing gas Embolism in Loggerhead Sea Turtles (*Caretta caretta*) Caught in Trawls and Gillnets." *Scientific Reports* 7, no. 1: 2739. https://doi.org/10.1038/s41598-017-02819-5.

Fortuna, C. M., C. Vallini, E. Filidei Jr., et al. 2010. "By-Catch of Cetaceans and Other Species of Conservation Concern During Pair Trawl Fishing Operations in the Adriatic Sea (Italy)." *Chemistry and Ecology* 26, no. S1: 65–76. https://doi.org/10.1080/02757541003627662.

Franchini, D., C. Valastro, S. Ciccarelli, et al. 2021. "Analysis of Risk Factors Associated With Gas Embolism and Evaluation of Predictors of Mortality in 482 Loggerhead Sea Turtles." *Scientific Reports* 11, no. 1: 22693. https://doi.org/10.1038/s41598-021-02017-4.

Fuentes, M. M. P. B., E. McMichael, C. Y. Kot, et al. 2023. "Key Issues in Assessing Threats to Sea Turtles: Knowledge Gaps and Future Directions." *Endangered Species Research* 52: 303–341. https://doi.org/10.3354/esr01278.

García-Párraga, D., J. L. Crespo-Picazo, Y. B. De Quirós, et al. 2014. "Decompression Sickness ('the Bends') in Sea Turtles." *Diseases of Aquatic Organisms* 111, no. 3: 191–205. https://doi.org/10.3354/dao02790.

Hama, F. L., D. Karaica, B. Karaica, et al. 2020. "Sea Turtle Strandings, Sightings and Accidental Catch Along the Croatian Adriatic Coast." *Mediterranean Marine Science* 21, no. 2: 452–459. https://doi.org/10.12681/mms.19490.

Hamann, M., M. H. Godfrey, J. A. Seminoff, et al. 2010. "Global Research Priorities for Sea Turtles: Informing Management and Conservation in the 21st Century." *Endangered Species Research* 11, no. 3: 245–269. https://doi.org/10.3354/esr00279.

Hart, K. M., P. Mooreside, and L. B. Crowder. 2006. "Interpreting the Spatio-Temporal Patterns of Sea Turtle Strandings: Going With the Flow." *Biological Conservation* 129, no. 2: 283–290. https://doi.org/10.1016/j.biocon.2005.10.047.

Haywood, J. C., W. J. Fuller, B. J. Godley, et al. 2020. "Spatial Ecology of Loggerhead Turtles: Insights From Stable Isotope Markers and Satellite Telemetry." *Diversity and Distributions* 26, no. 3: 368–381. https://doi.org/10.1111/ddi.13023.

Hintzen, N. T., F. Bastardie, D. Beare, et al. 2012. "VMStools: Open-Source Software for the Processing, Analysis and Visualisation of Fisheries Logbook and VMS Data." *Fisheries Research* 115: 31–43. https://doi.org/10.1016/j.fishres.2011.11.007.

Koch, V., H. Peckham, A. Mancini, and T. Eguchi. 2013. "Estimating At-Sea Mortality of Marine Turtles From Stranding Frequencies and Drifter Experiments." *PLoS ONE* 8, no. 2: e56776. https://doi.org/10.1371/journal.pone.0056776.

Lazar, B., D. Margaritoulis, and N. Tvrtković. 2004. "Tag Recoveries of the Loggerhead Sea Turtle *Caretta caretta* in the Eastern Adriatic Sea: Implications for Conservation." *Journal of the Marine Biological Association of the United Kingdom* 84, no. 2: 475–480. https://doi.org/10.1017/S0025315404009488h.

Lazar, B., and N. Tvrtkovic. 1995. "Marine Turtles in the Eastern Part of the Adriatic Sea: Preliminary Research." *Oceanographic Literature Review* 12, no. 42: 1106.

Lewison, R., D. Oro, B. J. Godley, et al. 2012. "Research Priorities for Seabirds: Improving Conservation and Management in the 21st Century." *Endangered Species Research* 17, no. 2: 93–121. https://doi.org/10.3354/esr00419.

Lewison, R. L., L. B. Crowder, B. P. Wallace, et al. 2014. "Global Patterns of Marine Mammal, Seabird, and Sea Turtle Bycatch Reveal Taxa-Specific and Cumulative Megafauna Hotspots." *Proceedings of the National Academy of Sciences of the United States of America* 111, no. 14: 5271–5276. https://doi.org/10.1073/pnas.1318960111.

Lucchetti, A., J. Pulcinella, V. Angelini, S. Pari, T. Russo, and S. Cataudella. 2016. "An Interaction Index to Predict Turtle Bycatch in a Mediterranean Bottom Trawl Fishery." *Ecological Indicators* 60: 557–564. https://doi.org/10.1016/j.ecolind.2015.07.007.

Lucchetti, A., C. Vasapollo, and M. Virgili. 2017. "An Interview-Based Approach to Assess Sea Turtle Bycatch in Italian Waters." *PeerJ* 2017, no. 4: e3151. https://doi.org/10.7717/peerj.3151.

Luschi, P., and P. Casale. 2014. "Movement Patterns of Marine Turtles in the Mediterranean Sea: A Review." *Italian Journal of Zoology* 81, no. 4: 478–495. https://doi.org/10.1080/11250003.2014.963714.

Lutcavage, M. E., and P. L. Lutz. 1997. "Diving Physiology." In *The Biology of Sea Turtles, Volume I*, 277–296. Boca Raton, Florida: CRC Press, Inc.

Marisaldi, L., A. Torresan, and A. Ferrari. 2023. "The Area South of the Po River Delta (Italy) is a Hot Spot for Strandings of Loggerhead Sea Turtles." *Journal of the Marine Biological Association of the United Kingdom* 103: e81. https://doi.org/10.1017/S002531542300070X.

Mihaljević, Ž., Š. Naletilić, J. Jeremić, I. Kilvain, T. Belaj, and T. Andreanszky. 2024. "Spatiotemporal Analysis of Stranded Loggerhead Sea Turtles on the Croatian Adriatic Coast." *Animals* 14, no. 5: 703. https://doi.org/10.3390/ani14050703.

Nero, R. W., M. Cook, A. T. Coleman, M. Solangi, and R. Hardy. 2013. "Using an Ocean Model to Predict Likely Drift Tracks of Sea Turtle Carcasses in the North Central Gulf of Mexico." *Endangered Species Research* 21, no. 3: 191–203. https://doi.org/10.3354/esr00516.

Nero, R. W., M. Cook, J. L. Reneker, Z. Wang, E. A. Schultz, and B. A. Stacy. 2022. "Decomposition of Kemp's Ridley (*Lepidochelys kempii*) and Green (*Chelonia mydas*) Sea Turtle Carcasses and Its Application to Backtrack Modeling of Beach Strandings." *Endangered Species Research* 47: 29–47. https://doi.org/10.3354/esr01164.

North, E. W., Z. Schlag, R. R. Hood, et al. 2008. "Vertical Swimming Behavior Influences the Dispersal of Simulated Oyster Larvae in a Coupled Particle-Tracking and Hydrodynamic Model of Chesapeake Bay." *Marine Ecology Progress Series* 359: 99–115. https://doi.org/10.3354/meps07317.

Phillott, A. D., and Godfrey, M. H. (2019) When Is a Stranded Turtle a Bycatch Turtle? Assessing Potential Cause of Stranding in Sea Turtles. *rehabilitation*.

Pikesley, S. K., P. D. Agamboue, J. P. Bayet, et al. 2018. "A Novel Approach to Estimate the Distribution, Density and At-Sea Risks of a Centrally-Placed Mobile Marine Vertebrate." *Biological Conservation* 221: 246–256. https://doi.org/10.1016/j.biocon.2018.03.011.

Poulain, P.-M. 2001. "Adriatic Sea Surface Circulation as Derived From Drifter Data Between 1990 and 1999." *Journal of Marine Systems* 29, no. 1–4: 3–32. https://doi.org/10.1016/S0924-7963(01)00007-0.

Quattrocchi, G., M. Sinerchia, F. Colloca, F. Fiorentino, G. Garofalo, and A. Cucco. 2019. "Hydrodynamic Controls on Connectivity of the High Commercial Value Shrimp *Parapenaeus longirostris* (Lucas, 1846) in the Mediterranean Sea." *Scientific Reports* 9, no. 1: 16935.

R Core Team. 2023. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/.

Read, A. J., P. Drinker, and S. Northridge. 2006. "Bycatch of Marine Mammals in US and Global Fisheries." *Conservation Biology* 20, no. 1: 163–169. https://doi.org/10.1111/j.1523-1739.2006.00338.x.

Reneker, J. L., M. Cook, and R. W. Nero (2018) Preparation of Fresh Dead Sea Turtle Carcasses for At-Sea Drift Experiments. https://doi.org/10.25923/9hgx-fn38

Rigby, R. A., and D. M. Stasinopoulos. 2005. "Generalized Additive Models for Location, Scale and Shape." *Applied Statistics* 54: 507–554. https://doi.org/10.1111/j.1467-9876.2005.00510.x.

Roe, J. H., S. J. Morreale, F. V. Paladino, et al. 2014. "Predicting Bycatch Hotspots for Endangered Leatherback Turtles on Longlines in the Pacific Ocean." *Proceedings of the Royal Society B: Biological Sciences* 281, no. 1777: 20132559. https://doi.org/10.1098/rspb.2013.2559.

Russo, E., M. A. Monti, M. C. Mangano, et al. 2020. "Temporal and Spatial Patterns of Trawl Fishing Activities in the Adriatic Sea (Central Mediterranean Sea, GSA17)." *Ocean & Coastal Management* 192: 105231. https://doi.org/10.1016/j.ocecoaman.2020.105231.

Santos, B. S., M. A. M. Friedrichs, S. A. Rose, S. G. Barco, and D. M. Kaplan. 2018. "Likely Locations of Sea Turtle Stranding Mortality Using Experimentally-Calibrated, Time and Space-Specific Drift Models."

Biological Conservation 226: 127–143. https://doi.org/10.1016/j.biocon.2018.06.029.

Santos, B. S., D. M. Kaplan, M. A. M. Friedrichs, S. G. Barco, K. L. Mansfield, and J. P. Manning. 2018. "Consequences of Drift and Carcass Decomposition for Estimating Sea Turtle Mortality Hotspots." *Ecological Indicators* 84: 319–336. https://doi.org/10.1016/j.ecolind.2017.08.064.

Schofield, G., V. J. Hobson, S. Fossette, M. K. S. Lilley, K. A. Katselidis, and G. C. Hays. 2010. "Fidelity to Foraging Sites, Consistency of Migration Routes and Habitat Modulation of Home Range by Sea Turtles." *Diversity and Distributions* 16, no. 5: 840–853. https://doi.org/10.1111/j.1472-4642.2010.00694.x.

Schultz, E. A., M. Cook, R. W. Nero, et al. 2022. "Point of No Return: Determining Depth at Which Sea Turtle Carcasses Experience Constant Submergence." *Chelonian Conservation and Biology* 21, no. 1: 88–97. https://doi.org/10.2744/CCB-1518.1.

Spillman, C. M., J. Imberger, D. P. Hamilton, M. R. Hipsey, and J. R. Romero. 2007. "Modelling the Effects of Po River Discharge, Internal Nutrient Cycling and Hydrodynamics on Biogeochemistry of the Northern Adriatic Sea." *Journal of Marine Systems* 68, no. 1–2: 167–200. https://doi.org/10.1016/j.jmarsys.2006.11.006.

Tagliolatto, A. B., D. W. Goldberg, M. H. Godfrey, and C. Monteiro-Neto. 2020. "Spatio-Temporal Distribution of Sea Turtle Strandings and Factors Contributing to Their Mortality in South-Eastern Brazil." *Aquatic Conservation: Marine and Freshwater Ecosystems* 30, no. 2: 331–350. https://doi.org/10.1002/aqc.3244.

Tasker, M. L. 2000. "The UK and Ireland Seabird Monitoring Programme—A History and Introduction." *Atlantic Seabirds* 2, no. 3/4: 97–102.

Tolve, L., P. Casale, A. Formia, et al. 2018. "A Comprehensive Mitochondrial DNA Mixed-Stock Analysis Clarifies the Composition of Loggerhead Turtle Aggregates in the Adriatic Sea." *Marine Biology* 165: 1–14. https://doi.org/10.1007/s00227-018-3325-z.

Tomás, J., P. Gozalbes, J. A. Raga, and B. J. Godley. 2008. "Bycatch of Loggerhead Sea Turtles: Insights From 14 Years of Stranding Data." *Endangered Species Research* 5, no. 2–3: 161–169. https://doi.org/10.3354/esr00116.

Türkozan, O., S. Y. Özdilek, S. Ergene, et al. 2013. "Strandings of Loggerhead (*Caretta caretta*) and Green (*Chelonia mydas*) Sea Turtles Along the Eastern Mediterranean Coast of Turkey." *Herpetological Journal* 23, no. 1: 11–15.

Wallace, B. P., C. Y. Kot, A. D. Dimatteo, T. Lee, L. B. Crowder, and R. L. Lewison. 2013. "Impacts of Fisheries Bycatch on Marine Turtle Populations Worldwide: Toward Conservation and Research Priorities." *Ecosphere* 4, no. 3: 40. https://doi.org/10.1890/ES12-00388.1.

Wallace, B. P., R. L. Lewison, S. L. McDonald, et al. 2010. "Global Patterns of Marine Turtle Bycatch." *Conservation Letters* 3, no. 3: 131–142. https://doi.org/10.1111/j.1755-263X.2010.00105.x.

Wood, S. N. 2011. "Fast Stable Restricted Maximum Likelihood and Marginal Likelihood Estimation of Semiparametric Generalized Linear Models." *Journal of the Royal Statistical Society (B)* 73, no. 1: 3–36. https://doi.org/10.1111/j.1467-9868.2010.00749.x.

Zbinden, J. A., S. Bearhop, P. Bradshaw, et al. 2011. "Migratory Dichotomy and Associated Phenotypic Variation in Marine Turtles Revealed by Satellite Tracking and Stable Isotope Analysis." *Marine Ecology Progress Series* 421: 291–302. https://doi.org/10.3354/meps08871.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.