



**SCIENTIFIC COMMITTEE
TWENTY-SECOND REGULAR SESSION**

11-19 August 2026

Apia, Samoa (Hybrid)

**Identifying seasonal bycatch hotspots using longline observer data:
a case study of leatherback turtles in the Atlantic Ocean**

WCPFC-SC22-2026-EB-IP08

10 July 2026

M. Nishimoto, S. Ueno, K. Okamoto, H. Ijima, and D. Ochi

Seasonal hotspots of leatherback turtle bycatch in the Atlantic Ocean: Insights from longline observer data

Makoto Nishimoto

m.nishimoto103@gmail.com

Fisheries Research Agency

Shintaro Ueno

Fisheries Research Agency

Kei Okamoto

Fisheries Research Agency

Hiroataka Ijima

Fisheries Research Agency

Daisuke Ochi

Fisheries Research Agency

Research Article

Keywords: Marine ecosystems, fishery management, conservation strategy, seasonal migration, spatiotemporal model, hotspot analysis

Posted Date: May 13th, 2025

DOI: <https://doi.org/10.21203/rs.3.rs-6545094/v1>

License:   This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Additional Declarations: No competing interests reported.

Abstract

Bycatch from pelagic longline fisheries poses a serious threat to the endangered leatherback turtle in the Atlantic Ocean. However, the spatiotemporal distribution of bycatch risk remains poorly understood, largely due to data limitations such as sparse observer coverage, zero-inflation, and inconsistent temporal sampling. Here, we analyze 18 years (2002–2019) of Japanese longline observer data to identify seasonal high-risk areas for turtle bycatch, using a zero-inflated binomial model based on stochastic partial differential equations (SPDE) combined with hotspot analysis. This framework allows us to extract meaningful spatial patterns from data-poor situations and generate spatially explicit estimates of relative leatherback density and bycatch risk. Our results reveal that bycatch hotspots occur predominantly near the African coast in the first quarter and expand across both the African coast and the broader North Atlantic in the fourth quarter. Seasonal differences in risk were more pronounced than interannual fluctuations, aligning with known migratory behaviors of leatherbacks. These findings underscore the importance of season-specific conservation strategies such as time-area closures or dynamic bycatch avoidance measures, providing actionable spatial and seasonal risk maps that could inform the design and timing of mitigation measures. More broadly, our approach offers a practical solution for assessing risk in other threatened marine taxa under data-limited conditions and enhances evidence-based conservation planning in marine ecosystems.

Introduction

The conservation of vulnerable species has become increasingly urgent as human activities and environmental disturbances push many to the brink of extinction (Sutherland et al. 2014; Hanson et al. 2020). Despite this urgency, critical knowledge gaps remain for numerous species, particularly regarding their spatial and seasonal density distributions (Thompson 2004). Most sea turtle species, which are highly affected by human activities and environmental changes, are classified as endangered and listed in the IUCN red list of threatened species (Seminoff & Shanker 2008). Due to their wide-ranging migratory patterns, obtaining density distribution for this species is challenging, leaving basic density distributions largely unknown (Bolten 2003; Hays 2004). Among these, the leatherback turtle (*Dermochelys coriacea*) is considered a critically endangered species in the IUCN Red List due to dramatic declines in some populations, caused by anthropogenic factors including fisheries interactions and habitat disturbance (Bolten 2003; Wallace et al. 2013). The highly migratory ecology and extensive habitat of this species contributes to the occurrence of bycatch in coastal and pelagic fisheries including longline, purse seine, and gillnet, which has been a major concern due to its negative impacts on populations (Ross 1995; Lewison et al. 2004; Lewison & Crowder 2007). Understanding the density distribution of leatherback turtles and the mechanism of bycatch is crucial for devising effective conservation measures (Fossette et al. 2014).

Bycatch related fisheries operational data represents a valuable resource for identifying high-risk areas of interaction between sea turtles and fisheries. These datasets contain spatial and temporal ecological observations that have enabled major advancements in bycatch risk analysis, such as hotspot

identification and studies on the influence of prey availability and environmental factors on interaction rates (Ferreira et al. 2011; Cambié et al. 2013; Lucchetti et al. 2017; Nordstrom et al. 2020; Lopez et al. 2024). For instance, Fossette et al. (2014) used broad-scale tracking and fisheries operational data to uncover seasonal and spatial variations in bycatch risk across the Atlantic, while Roe et al. (2014) demonstrated the potential of spatially separated management zones in reducing bycatch risk in the Pacific. Despite these advances, most studies have primarily addressed static or localized patterns, constrained by the spatial overlap between tracking data and longline vessel operations. Consequently, dynamic, large-scale spatiotemporal trends in leatherback turtle density and bycatch risk remain poorly understood. Moreover, historical shifts in these patterns are seldom explored, hindering the development of conservation strategies responsive to evolving environmental and fisheries conditions.

Addressing these challenges requires advanced statistical approaches that can simultaneously handle issues such as zero-inflated data, spatiotemporal sampling biases, and missing observations. The SPDE (Stochastic Partial Differential Equations) framework, a highly accurate method for modeling spatial correlations in continuous domains, has been successfully applied in various ecological studies to address such issues (Munoz et al. 2013; Thorson et al. 2017; Thorson et al. 2019; Lezama-Ochoa et al. 2020; Jaksons et al. 2022). In this study, we apply an SPDE-based zero-inflated binomial distribution model to analyze bycatch data for Atlantic leatherback turtles. This approach accounts for spatiotemporal autocorrelation and missing data by leveraging information from neighboring observations, enabling robust estimation of turtle density distributions and bycatch risk. In addition, by integrating SPDE analysis with hotspot analysis, we can identify high-priority conservation areas after addressing data gaps (Evans et al. 2021). While this combined approach has not yet been applied in a biological conservation context, it holds great promise for analyzing bycatch data and understanding spatial population dynamics.

The Atlantic Ocean represents a key habitat for leatherback turtles, with longline fisheries operating extensively across this region (Fossette et al. 2008; Witt et al. 2011). Although some nesting sites in the Atlantic have remained stable or even increased in contrast to the declines seen in the Pacific (Fossette et al. 2008), bycatch from large-scale longline fisheries remains a persistent threat (Wallace et al. 2013; Fossette et al. 2014). Bycatch information for Atlantic leatherback turtles, collected from Japanese observer data since 1997, includes records of bycatch numbers and fishing effort (total hooks). Despite challenges such as zero-inflation and spatiotemporal biases, the application of advanced statistical methods to these datasets can shed light on previously unidentified Atlantic-wide leatherback turtle density distributions and bycatch hotspots. Additionally, this study will identify cold spots—areas with consistently low bycatch occurrence—which are equally important for understanding spatial risk heterogeneity. By examining seasonal and annual changes in these hot/cold spots, we can better understand the ecological drivers of bycatch risk and contribute to more effective conservation management.

In this study, we applied a spatiotemporal model combining SPDE and zero-inflated binomial distribution to Japanese longline observer data to analyze fluctuations in bycatch occurrence for Atlantic

leatherback turtles. Using quarterly fishing records and sea surface temperature (SST) data, we estimated relative turtle density across the Atlantic, identified hot/cold spots of bycatch risk, and examined their annual and seasonal dynamics. By addressing these gaps, our research aims to provide actionable insights into the ecological drivers of bycatch risk and support the development of more effective and adaptive conservation strategies for this critically endangered species.

Materials and Methods

Study area and data

This study focuses on the Atlantic Ocean, encompassing both the Northern and Southern Hemispheres (Fig. 1). Various fisheries, including longline and purse seine operations, are active in the Atlantic, with longline fishing being particularly extensive. The nesting sites of the Atlantic leatherback turtle are located in several tropical regions, such as Costa Rica, Panama, Puerto Rico, Colombia, Trinidad and Tobago, French Guiana, Suriname, U.S. Virgin Islands, the mainland United States and Gabon (Dow et al. 2007; Giron dot 2015; Horrocks et al. 2016). They are a highly migratory species and their distribution range extends from the North Atlantic to the South Atlantic (Bolten 2003). The migratory pattern of this species shows seasonality, with North Atlantic populations known to migrate from high to low latitudes for nesting during the summer (Doyle et al. 2008).

Data on fishing operations and sea turtle bycatch within the ICCAT convention area have been collected since 1997 through Japan's scientific observer program. This study uses data collected from 2002 to 2019, a period with a relatively large number of observed operations and sufficient spatial coverage. The data used include the year of capture, latitude and longitude of the fishing start point, the number of hooks observed, the number of leatherback turtle bycatches, and recorded sea surface temperature (SST) by vessel. Given that the behavior and ecology of the leatherback turtle may vary seasonally, the data were divided into quarters (Q1: January-March, Q2: April-June, Q3: July-September, Q4: October-December). Of these, Q1 and Q4, which had sufficient observation points and relatively high bycatch frequency, were selected for analysis. Data were filtered according to known distribution limits, ranging from 60°N to 45°S, based on suitable thermal environments for leatherback turtles (Doyle et al. 2008; Fossette et al. 2010).

SPDE approach

Continuous spatial process modeling is generally computationally intensive. However, the stochastic partial differential equation (SPDE) approach proposed by Lindegren et al. (2011) allows for an efficient approximation of spatial processes, making such modeling more feasible. Specifically, it reduces the continuous spatial correlations in a Gaussian random field (GRF) to a discrete Gaussian Markov random field (GMRF) by using a sparse precision matrix based on neighboring relations, thereby avoiding the computationally demanding estimation of the inverse covariance matrix (see Lindegren et al. 2011 for

details). In the SPDE approach, a Delaunay triangulation mesh is created to define neighboring relationships and represent spatial correlations. The entire process, from constructing the graphical model to performing fast computations using Laplace approximations, is implemented in the R package INLA (<https://www.r-inla.org>) (Lindgren and Rue 2015; Rue et al. 2017), making it a useful tool for implementing spatial statistical models that are often computationally demanding. In this study, we used INLA version 23.04.24 to create a mesh of the study area based on the location information of the observation points (Fig. 1) and conducted the estimation using the spatiotemporal statistical model described in the subsequent modeling section.

Modeling for bycatch event

Leatherback turtle bycatch risk was calculated as the number of bycatches per 1,000 hooks (considering an offset term for fishing effort). The geographic distribution of observed hooks, leatherback turtle bycatch counts, and observed SST was aggregated into 5° x 5° square grids. For SST data, we used HadISST data with combined spatial resolution in the absence of onboard observation records (i.e., areas without fishing effort) (HadISST v1.1; Rayner et al. 2003). All the above data were compiled for each of the quarters 2002–2019, and monthly data were averaged to make quarterly data.

The leatherback turtle bycatch data exhibited greater variance than the mean, along with a high frequency of zero observations. We modeled the bycatch count data using a zero-inflated negative binomial distribution, which appropriately handles overdispersed discrete data with many zeros. The zero-inflated negative binomial distribution consists of two models: one for whether the observed count is zero, and another for sampling the non-zero discrete observations. Following the notation of Ross et al. (2012), we describe the negative binomial model below. Let $y_{s,t}$ ($i = 1, 2, \dots, N$) denote the bycatch count at location s and time t (year), which is assumed to follow the following negative binomial distribution:

$$y_{s,t} = \begin{cases} 0 & \text{with probability } \psi_{s,t} \\ \text{NegBinom}(\mu_{s,t}, \phi) & \text{with probability } 1 - \psi_{s,t} \end{cases}$$

1

Here, $\psi_{s,t}$ is the parameter determining whether the data is zero, $\mu_{s,t}$ represents relative density, and ϕ is the parameter indicating the probability of bycatch not occurring. Using $\mu_{s,t}$ in from Eq. (1), we constructed the following model, considering SST as an environmental factor affecting relative density (Catch per unit effort: CPUE), with fishing effort (total number of hooks) as an offset term:

$$z_{s,t} = \log(\mu_{s,t}) = a + bSST_{s,t} + \eta_s + x_{s,t} + \log(E_{s,t})$$

2

where a is the intercept, b is the coefficient for SST, η_s is spatial random field, $x_{s,t}$ is the spatiotemporal effect, and $\log(E_{s,t})$ is the offset term for fishing effort. The spatial random field η_s represents the random effect for spatial autocorrelation, approximated as a discrete GMRF based on neighborhood relations using the SPDE approach. The spatiotemporal version $x_{s,t}$ represents the combined spatial and temporal autocorrelation (expressed as the Kronecker product of the precision matrices for spatial correlation and AR (1); Cameletti et al. 2013). Incorporating these terms into the model allows for considering unknown environmental factors and their temporal variations as stochastic fluctuations affecting relative density. In this study, the average effect of environmental factors such as habitat suitability and prey density were represented by the latent variable η_s , while the other variation including temporal factors was represented by the latent variable $x_{s,t}$. These autocorrelation terms are also useful in missing data estimation, enabling the investigation of relative density changes from spatiotemporally limited observation data.

For the prior distribution, we applied PC-priors (Fuglstad et al. 2018), which effectively penalize deviations from the prior and help control model flexibility, thereby reducing the risk of overfitting. We used these priors for the spatial correlation parameters, specifically the range and marginal standard deviation, as well as for the temporal correlation strength parameter. We set a weakly informative prior with a median range of 2,500 km (UTM), a median marginal standard deviation of 0.5, and a 0.7 probability that the temporal autocorrelation (ρ) exceeds 0.5 (where $0 < \rho < 1$). For all other parameters, we used the default priors provided by INLA.

Hot spot analysis

To identify potential bycatch hotspots for leatherback turtles, we calculated the Getis-Ord G_i^* statistic (Ord and Getis 1995) using the estimated relative density values to detect local spatial patterns in each neighboring region. The statistic is calculated as the ratio of a spatial lag for a given feature to the sum of neighboring feature values. A positive G_i^* value indicates that the feature and its neighbors have high values, while a negative value indicates low values. Based on this statistic, we calculated p-values and classified hotspots and cold spots into seven categories (very hot: $G_i^* > 0$ and p-value < 0.01 , hot: $G_i^* > 0$ and p-value < 0.05 , somewhat hot: $G_i^* > 0$ and p-value < 0.1 , very cold: $G_i^* < 0$ and p-value < 0.01 , cold: $G_i^* < 0$ and p-value < 0.05 , somewhat cold: $G_i^* < 0$ and p-value < 0.1 , insignificant: other cases). These analyses were performed using R version 4.2.2 and the R package *spdep* version 1.2-8.

Results

In the 2002–2019 Atlantic longline fishery, operating effort was located over a wide swath of the Atlantic Ocean, with localized areas of high leatherback bycatch (Fig. 1). In Q1, we found that bycatch occurs near the west coast along the African continent, but less so in the North Atlantic. On the other hand, in Q4, bycatch events were observed along the west coast of Africa as well as in the North Atlantic.

Analysis of leatherback bycatch events using long-term data from the Atlantic longline fishery yielded estimated parameters such as environmental factor coefficients and spatiotemporal latent effects (Table S1). The posterior distribution of fixed effects confirmed the normality of the distribution, and the positive effect of SST on the relative density of leatherback turtles was statistically detected with 95% credible intervals for both Q1 and Q4 (Figure S1).

The estimated values for the latent spatial field η showed positive effects in the eastern Atlantic during Q1 and in the northern Atlantic and southern regions near the African continent during Q4 (Fig. 3). The estimated temporal correlation parameters of the latent spatial field x were close to 1, with values of 0.7 and 0.85 for Q1 and Q4, respectively, indicating the presence of temporal autocorrelation (Table S1). Furthermore, dynamic changes in the spatial distribution of the latent field x were observed in both Q1 and Q4 (Figure S2): During Q1, positive effects were evident near the eastern coast of Africa from 2002 to 2013, but shifted to negative effects in the same region thereafter. For Q4, positive effects were noted across the Atlantic until around 2006, with a subsequent shift to negative effects primarily south of 20°N after 2007.

Temporal changes in estimated relative density were generally consistent with the trend in relative density's variability observed at the monitoring sites in each year (Fig. 4). Estimates were consistently higher than observed values in most years for both Q1 and Q4, demonstrating the advantage of using a zero-inflated model to address false negatives in bycatch data (Fig. 4, Figure S3). Note that except for the zero data, the observed and predicted values were approximately consistent, indicating a good model fit. Furthermore, there is a notable trend that estimates for the fourth quarter are generally higher than those for the first quarter. This indicates a high risk of bycatch in Q4 and that not properly accounting for missing bycatch data and excess 0 data can lead to underestimation of risk.

The spatial patterns of predicted relative density varied by season (Fig. 5). In Q1, high-density areas were concentrated along parts of the African coast, whereas in Q4, the distribution expanded to include regions in the North Atlantic and Central America. Moreover, there was a trend of shrinking high-density areas in Q1 between 2014 and 2019, while no notable temporal changes were observed in Q4 (Figure S4).

Potential bycatch hotspots and cold spots for each year and season were identified by calculating local G_i^* statistics for the predicted relative densities (Fig. 6, Figure S5). The spatial distribution of leatherback turtle bycatch risk did not change much over time as an overall trend, but changed greatly with season. In Q1, hotspots tended to concentrate near the coast of Africa, whereas in Q4, hotspots were more broadly distributed. Cold spots appeared near the distribution boundaries of leatherback turtles, specifically around 60°N and 45°S, with Q1 showing extensive cold spots in high-latitude regions.

Discussion

This study employed a spatially explicit statistical approach to long-term bycatch records, maximizing the information content of leatherback turtle bycatch data in the Atlantic Ocean. Our analysis revealed

seasonal hotspots and cold spots of bycatch risk with greater seasonal than interannual variability. To our knowledge, this is the first study to statistically delineate these risk areas across seasons, offering valuable insights for implementing spatially and seasonally adaptive conservation measures. Elucidating these seasonal differences in risk is important for understanding the ecology of conservation species and devising management policies (Lewison & Crowder 2007). In addition, the results of this study, which showed large seasonal differences in bycatch risk, support the effectiveness of season-specific conservation measures (e.g., bycatch avoidance measures), similar to previous studies (Kot et al. 2010; Fossette et al. 2014; Roe et al. 2014; Blades et al. 2019).

Our findings are consistent with known drivers of leatherback turtle distribution, including sea surface temperature, jellyfish abundance, nesting seasonality, and proximity to nesting sites (Bolten 2003; Witt et al. 2011; Bailey et al. 2012; Nordstrom et al. 2020; Lopez et al. 2024). For example, the high relative density observed in Q1 along the western coast of Africa (Fig. 5), particularly near Gabon—one of the world’s largest nesting sites—may reflect post-nesting foraging activity in nutrient-rich areas. During this period, turtles tend to forage vertically in jellyfish-dense waters (Heaslip et al. 2012), potentially explaining the spatial concentration in warm coastal zones (Figure S6). In contrast, the broader distribution of high CPUE in Q4, spanning the Caribbean and North Atlantic, likely reflects long-distance migratory movements following nesting events in South America (Hays et al. 2006; James et al. 2005; Fossette et al. 2014). Although this study's density estimates are based on longline bycatch data, the high-density regions identified for each quarter generally align with previous studies that estimated distribution using satellite tag tracking (Fossette et al. 2014).

Bycatch risk for leatherback turtles varies considerably by season due to their migratory behavior, as shown in previous studies (Fossette et al. 2014; Roe et al. 2014), and our findings support this pattern (Fig. 6). Notably, our results also reveal that within each season, the locations of both hotspots and cold spots remain relatively consistent across years (Figure S5). This suggests that the behavior of Atlantic leatherback turtles is strongly driven by seasonal cues. The bycatch risk maps developed in this study could help inform targeted conservation strategies. For instance, in Q1, when turtle distributions are more concentrated, temporary fishing closures in areas with high hotspot values could be effective. In contrast, during Q4, when hotspots are more widely dispersed, promoting the use of circle hooks—which are known to reduce mortality in longline bycatch—may serve as a useful seasonal mitigation measure. Identifying cold spots is equally important, as these areas can help prioritize zones for focused conservation efforts (Spear & Storfer 2010; Cobos et al. 2023). To date, few studies have statistically examined cold spots for sea turtles. This study is the first to spatially identify areas of lower bycatch risk for leatherback turtles in the Atlantic based on longline fishery data. These insights may also assist in balancing conservation and fisheries objectives. For example, because bycatch risk north of 30°N in Q1 is relatively low, fishers could intensify efforts to target commercial species in this region with minimal concern about leatherback bycatch. While any changes would require careful consensus-building, such findings may support the reconsideration or adjustment of certain fishing restrictions aimed at leatherback turtle conservation in specific areas.

This study has several limitations. First, the data on leatherback turtles are limited to the longline fisheries of only Japanese vessels. Including data from other countries' longline fisheries, such as Taiwan, China, and Brazil, could cover a broader area and yield more reliable estimates of individual density and bycatch risk. Moreover, it may also become possible to elucidate the relative density and hotspots for Q2 and Q3, which were excluded from the analysis due to insufficient data. Second, the analysis does not include other fishing methods. While this study focused on longline fisheries due to their extensive geographic coverage, leatherback turtles are also bycaught by trawl and purse-seine fisheries, with reports indicating that the mortality rates in these fisheries may exceed those of longline vessels (Wallace et al. 2013). Considering multiple fishing methods when assessing the impact on leatherback turtle populations could lead to more concrete management recommendations.

A promising direction for future research is the analysis of population models. In this study, although no clear decreasing trend in relative density was observed at the observation sites (Fig. 4), it was found that the density distribution may be locally fluctuating across the Atlantic Ocean (Figure S4). The Atlantic population is considered more stable than that of the Pacific (Fossette et al. 2008; Witt et al. 2011). However, the extensive range and high fishing effort of longline vessels necessitate careful monitoring to ensure that the population does not shift into decline due to major fishing impacts (Lewison et al. 2004). The effects of fishing on the population and the population growth rate can only be clarified through population dynamics analysis, making the development of a population model essential in future research. Additionally, examining other environmental factors is a topic for future study. In this study, environmental factors other than SST that affect relative density were aggregated into two latent spatial fields, η and x (Fig. 3, Figure S2). Incorporating jellyfish distribution into the model could enhance predictive power (Nordstrom et al. 2020). Additionally, as has been done in previous studies, analyzing tracking survey data could be valuable for further improving bycatch risk assessments (Fossette et al. 2014). This would deepen our understanding of the relationship between seasonal migration routes and hotspot/cold spot distributions.

Conserving rare and highly mobile species remains a major challenge, particularly due to the difficulty of obtaining reliable population data and the scarcity of direct observations (Thompson 2004; Runge et al. 2014). These limitations often hinder our ability to accurately map density distributions and identify conservation hotspots—key components for effective management (Cepic et al. 2022). In this study, we addressed these challenges by combining spatial density estimation using the SPDE framework with hotspot analysis to assess both density distribution and bycatch risk for Atlantic leatherback turtles. Our modeling approach explicitly accounts for spatial and temporal autocorrelation, data heterogeneity, and zero-inflation, enabling the interpolation of density in areas with limited or no observations. This statistical framework is particularly suited to the realities of conservation biology, where data gaps are common but management decisions cannot wait for perfect information. By borrowing strength from neighboring locations and time periods, our method offers a practical tool for generating data-informed insights into spatiotemporal risk patterns. As such, it contributes not only to the species-specific management of leatherback turtles but also to broader efforts in data-limited fisheries and marine

megafauna conservation. This work helps bridge the gap between data-limited conservation science and actionable management by offering a scalable framework for reducing bycatch in pelagic ecosystems.

Conclusion

This study presents a flexible statistical framework for assessing spatiotemporal bycatch risk, which we applied to leatherback turtles in the Atlantic. By leveraging longline fishery data, we estimated relative density and identified seasonal hotspots and cold spots. These spatial distributions of seasonally fluctuating bycatch risk then reflect the life history ecology of leatherback turtles. Our approach provides key insights into areas of elevated risk—even beyond direct observation zones—and offers practical guidance for implementing targeted mitigation measures within ICCAT-managed waters. While developed in the context of sea turtles, this framework is broadly applicable to other taxa affected by bycatch, such as seabirds and non-target fish species. By analyzing hotspot overlap among species (e.g., Lewison et al. 2009), it becomes possible to explore ecological trade-offs and inform ecosystem-based management. This is especially relevant when balancing conservation priorities with the economic imperatives of pelagic fisheries. For example, identifying areas where high commercial yield overlaps minimally with bycatch hotspots can inform spatial zoning that supports both biodiversity and sustainable fishing. Future applications of this approach hold particular promise for multi-species risk assessments, integrative conservation planning, and the refinement of dynamic ocean management strategies.

Declarations

CRedit authorship contribution statement

Makoto Nishimoto: Conceptualization, Formal analysis, Methodology, Writing – original draft, Writing – review & editing. **Shintaro Ueno:** Conceptualization, Writing – original draft, Writing – review & editing. **Kei Okamoto:** Conceptualization, Writing – original draft, Writing – review & editing. **Hiroataka Ijima:** Methodology, Writing – original draft, Writing – review & editing. **Daisuke Ochi:** Conceptualization, Data curation, Methodology, Supervision, Writing – original draft, Writing – review & editing.

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.

Funding

This research was conducted as a part of the research and assessment program for internationally managed fisheries resources, the Fisheries Agency of Japan.

Acknowledgement

We would like to thank Sachico Tsuji for his advice on analysis in writing this paper. We also thank Naoto Matsubara for his comments on the content of the earlier version of the manuscript.

Data availability

Data will be made available on request.

References

1. Bailey, H., Benson, S.R., Shillinger, G.L., Bograd, S.J., Dutton, P.H., Eckert, S.A., Morreale, S.J., Paladino, F.V., Eguchi, T., Foley, D.G., Block, B.A., Piedra, R., Hitipeuw, C., Tapilatu, R.F., Spotila, J.R., 2012. Identification of distinct movement patterns in Pacific leatherback turtle populations influenced by ocean conditions. *Ecol. Appl.* 22(3), 735–747. <https://doi.org/10.1890/11-0633>.
2. Blades, D.C., Walcott, J., Horrocks, J.A., 2019. Leatherback bycatch in an eastern Caribbean artisanal longline fishery. *Endanger. Species Res.* 40. <https://doi.org/10.3354/ESR01000>.
3. Bolten, A.B. 2003. Variation in sea turtle life history patterns: neritic vs. oceanic developmental stages. In (Lutz PL, Musick JA, Wyneken J, eds.) *The Biology of Sea Turtles Vol. II* Pp. 243-257. CRC Press, Boca Raton.
4. Cambié, G., Sánchez-Carnero, N., Mingozi, T., Muiño, R., Freire, J., 2013. Identifying and mapping local bycatch hotspots of loggerhead sea turtles using a GIS-based method: Implications for conservation. *Mar. Biol.* 160(3), 653–665. <https://doi.org/10.1007/s00227-012-2120-5>.
5. Cepic, M., Bechtold, U., Wilfing, H., 2022. Modelling human influences on biodiversity at a global scale—A human ecology perspective. *Ecol. Modell.* 465. <https://doi.org/10.1016/j.ecolmodel.2021.109854>.
6. Cobos, M.E., Nuñez-Penichet, C., Campbell, P.D., Cooper, J.C., Machado-Stredel, F., Barve, N., Ashraf, U., Alkiske, A.A., Ng'eno, E., Nair, R.R., Atauchi, P.J., Adeboje, A., Peterson, A.T., 2023. Effects of occurrence data density on conservation prioritization strategies. *Biol. Conserv.* 284. <https://doi.org/10.1016/j.biocon.2023.110207>.
7. Dow, W., Eckert, K., Palmer, M., Kramer, P. 2007. An atlas of sea turtle nesting habitat for the wider Caribbean region. The Wider Caribbean Sea Turtle Conservation Network and The Nature Conservancy, Beaufort, North Carolina.
8. Doyle, T.K., Houghton, J.D.R., O'Suilleabháin, P.F., Hobson, V.J., Marnell, F., Davenport, J., Hays, G.C., 2008. Leatherback turtles satellite-tagged in European waters. *Endanger. Species Res.* 4(1–2), 23–31. <https://doi.org/10.3354/esr00076>.
9. Evans, R., English, P.A., Anderson, S.C., Gauthier, S., Robinson, C.L., 2021. Factors affecting the seasonal distribution and biomass of *E. pacifica* and *T. spinifera* along the Pacific coast of Canada: A spatiotemporal modelling approach. *PLoS One* 16(5), e0249818.
10. 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

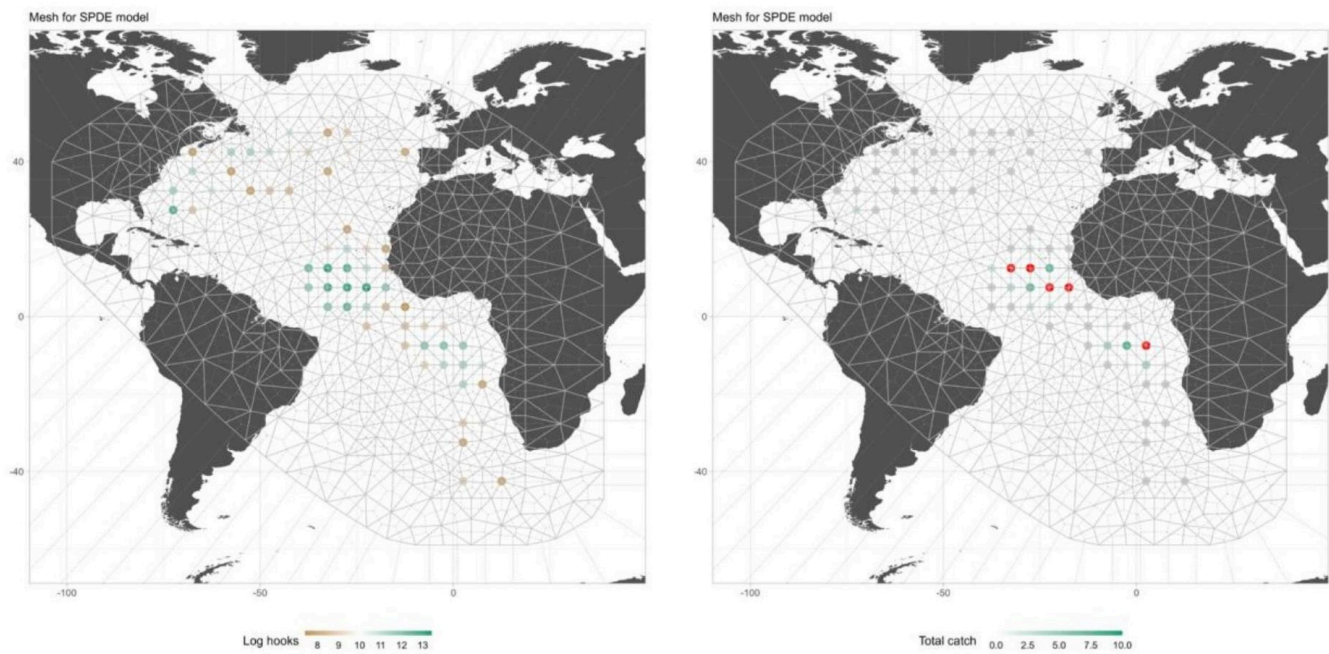
- archipelago and implications for conservation. *J. Mar. Biol. Assoc. U. K.* 91(8), 1697–1705.
<https://doi.org/10.1017/S0025315410000846>.
11. Fossette, S., Girard, C., López-Mendilaharsu, M., Miller, P., Domingo, A., Evans, D., Kelle, L., Plot, V., Prosdocimi, L., Verhage, S., Gaspar, P., Georges, J.Y., 2010. Atlantic leatherback migratory paths and temporary residence areas. *PLoS ONE* 5(11). <https://doi.org/10.1371/journal.pone.0013908>.
 12. Fossette, S., Kelle, L., Girondot, M., Goverse, E., Hilterman, M.L., Verhage, B., de Thoisy, B., Georges, J.Y., 2008. The world's largest leatherback rookeries: A review of conservation-oriented research in French Guiana/Suriname and Gabon. *J. Exp. Mar. Biol. Ecol.* 356(1–2), 69–82.
<https://doi.org/10.1016/j.jembe.2007.12.024>.
 13. Fossette, S., Witt, M. J., Miller, P., Nalovic, M. A., Albareda, D., Almeida, A. P., ... & Godley, B. J. (2014). Pan-Atlantic analysis of the overlap of a highly migratory species, the leatherback turtle, with pelagic longline fisheries. *Proceedings of the Royal Society B: Biological Sciences*, 281(1780), 20133065.
<https://doi.org/10.1098/rspb.2013.3065>
 14. Girondot, M. 2015. Leatherback turtle population in the Atlantic Ocean. In Spotila and Tomillo [eds.], *The Leatherback Turtle: Biology and Conservation*, pp.97-109. Johns Hopkins University Press, Maryland.
 15. Hanson, J.O., Rhodes, J.R., Butchart, S.H.M., Buchanan, G.M., Rondinini, C., Ficetola, G.F., Fuller, R.A., 2020. Global conservation of species' niches. *Nature* 580(7802), 232–234.
<https://doi.org/10.1038/s41586-020-2138-7>.
 16. Hays, G.C., Hobson, V.J., Metcalfe, J.D., Righton, D., Sims, D.W., 2006. Flexible foraging movements of leatherback turtles across the North Atlantic ocean. *Ecology* 87(10), 2647–2656.
[https://doi.org/10.1890/0012-9658\(2006\)87\[2647:FFMOLT\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[2647:FFMOLT]2.0.CO;2).
 17. Hays, G.C., 2004. Good news for sea turtles. *Trends Ecol. Evol.* 19(7), 349–351.
<https://doi.org/10.1016/j.tree.2004.05.009>.
 18. Heaslip, S.G., Iverson, S.J., Bowen, W.D., James, M.C., 2012. Jellyfish support high energy intake of leatherback sea turtles (*Dermochelys coriacea*): Video evidence from animal-borne cameras. *PLoS ONE* 7(3). <https://doi.org/10.1371/journal.pone.0033259>.
 19. Horrocks, J.A., Stapleton, S., Guada, H., Lloyd, C., Harris, E., Fastigi, M., Berkel, J., Stewart, K., Gumbs, J., Eckert, K.L. 2016. International movements of adult female leatherback turtles in the Caribbean: results from tag recovery data (2002-2013). *Endang. Species Res.* 29, 279-287.
 20. Jaksons, R., Bell, P., Jaksons, P., Cook, D., 2022. Fish biodiversity and inferred abundance in a highly valued coastal temperate environment: the inner Queen Charlotte Sound, New Zealand. *Mar. Freshw. Res.* <https://doi.org/10.1071/MF21247>.
 21. James, M.C., Ottensmeyer, C.A., Myers, R.A., 2005. Identification of high-use habitat and threats to leatherback sea turtles in northern waters: New directions for conservation. *Ecol. Lett.* 8(2), 195–201. <https://doi.org/10.1111/j.1461-0248.2004.00710.x>.
 22. Lezama-Ochoa, N., Pennino, M.G., Hall, M.A., Lopez, J., Murua, H., 2020. Using a Bayesian modelling approach (INLA-SPDE) to predict the occurrence of the Spinetail Devil Ray (*Mobular mobular*). *Sci.*

- Rep. 10, 1–11. <https://doi.org/10.1038/s41598-020-73879-3>.
23. Lewison, R. L., Freeman, S. A., & Crowder, L. B., 2004. Quantifying the effects of fisheries on threatened species: The impact of pelagic longlines on loggerhead and leatherback sea turtles. *Ecology Letters*, 7(3), 221–231. <https://doi.org/10.1111/j.1461-0248.2004.00573.x>.
24. Lewison, R.L., Crowder, L.B., 2007. Putting longline bycatch of sea turtles into perspective. *Conserv. Biol.* 21(1), 79–86. <https://doi.org/10.1111/j.1523-1739.2006.00592.x>.
25. 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(4), 920–930. <https://doi.org/10.1890/08-0623.1>.
26. Lindgren, F., Rue, H., Lindström, J., 2011. An explicit link between Gaussian fields and Gaussian Markov random fields: the SPDE approach (with discussion). *J. R. Stat. Soc. B* 73, 423–98.
27. Lindgren, F., Rue, H., 2015. Bayesian spatial modelling with R-INLA. *J. Stat. Softw.* 63, 1–25. <https://doi.org/10.18637/jss.v063.i19>.
28. Lopez, J., Griffiths, S., Wallace, B., Cáceres, V., Helena Rodríguez, L., Abrego, M., Alfaro-Shigueto, J., Andracka, S., José Brito, M., Camila Bustos, L., Cari, I., Carvajal, J., Clavijo, L., Cocas, L., de Paz, N., Herrera, M., Mangel, J., Pérez-Huaripata, M., Piedra, R., ... Zárate, P. (2024). Vulnerability of the Critically Endangered leatherback turtle to fisheries bycatch in the eastern Pacific Ocean. I. A machine-learning species distribution model. *Endangered Species Research*, 53, 271–293. <https://doi.org/10.3354/esr01288>
29. Lucchetti, A., Vasapollo, C., Virgili, M., 2017. Sea turtles bycatch in the Adriatic Sea set net fisheries and possible hot-spot identification. *Aquat. Conserv.: Mar. Freshw. Ecosyst.* 27(6), 1176–1185. <https://doi.org/10.1002/aqc.2787>.
30. Munoz, F., Pennino, M. G., Conesa, D., López-Quílez, A., & Bellido, J. M. (2013). Estimation and prediction of the spatial occurrence of fish species using Bayesian latent Gaussian models. *Stochastic Environmental Research and Risk Assessment*, 27, 1171–1180. <https://doi.org/10.1007/s00477-012-0652-3>
31. Nordstrom, B., James, M.C., Worm, B., 2020. Jellyfish distribution in space and time predicts leatherback sea turtle hot spots in the Northwest Atlantic. *PLoS ONE* 15(5). <https://doi.org/10.1371/journal.pone.0232628>.
32. Ord, J.K., Getis, A., 1995. Local spatial autocorrelation statistics: distributional issues and an application. *Geogr. Anal.* 27, 286–306.
33. Rayner, N.A., Parker, D.E., Horton, E.B., Folland, C.K., Alexander, L.V., Rowell, D.P., Kent, E.C., Kaplan, A., 2003. Global analyses of sea surface temperature, sea ice, and night marine air temperature since the late nineteenth century. *J. Geophys. Res.* 108(D14), 4407. <https://doi.org/10.1029/2002JD002670>.
34. Roe, J. H., Morreale, S. J., Paladino, F. V., Shillinger, G. L., Benson, S. R., Eckert, S. A., ... & Spotila, J. R. (2014). Predicting bycatch hotspots for endangered leatherback turtles on longlines in the Pacific

- Ocean. Proceedings of the Royal Society B: Biological Sciences, 281(1777), 20132559.
<https://doi.org/10.1098/rspb.2013.2559>
35. Ross J.P., 1995. Historical decline of loggerhead, ridley, and leatherback sea turtles. in: Bjorndal K.A. Biology and Conservation of Sea Turtles. Smithsonian Institution Press, 189-195.
 36. Ross, B.E., Hooten, M.B., Koons, D.N., 2012. An accessible method for implementing hierarchical models with spatio-temporal abundance data. PLoS ONE 7(11).
<https://doi.org/10.1371/journal.pone.0049395>.
 37. Rue, H., Riebler, A., Sørbye, S.H., Illian, J.B., Simpson, D.P., Lindgren, F.K., 2017. Bayesian computing with INLA: a review. Annu. Rev. Stat. Appl. 4, 395–421. <https://doi.org/10.1146/annurev-statistics-060116-054045>.
 38. Runge, C. A., Martin, T. G., Possingham, H. P., Willis, S. G., & Fuller, R. A. (2014). Conserving mobile species. Frontiers in Ecology and the Environment, 12(7), 395-402. <https://doi.org/10.1890/130237>
 39. Seminoff, J. A., & Shanker, K. (2008). Marine turtles and IUCN Red Listing: a review of the process, the pitfalls, and novel assessment approaches. Journal of Experimental Marine Biology and Ecology, 356(1-2), 52-68. <https://doi.org/10.1016/j.jembe.2007.12.007>
 40. Spear, S.F., Storfer, A., 2010. Anthropogenic and natural disturbance lead to differing patterns of gene flow in the Rocky Mountain tailed frog, *Ascaphus montanus*. Biol. Conserv. 143(3), 778–786. <https://doi.org/10.1016/j.biocon.2009.12.021>.
 41. Sutherland, W. J., Aveling, R., Brooks, T. M., Clout, M., Dicks, L. v., Fellman, L., Fleishman, E., Gibbons, D. W., Keim, B., Lickorish, F., Monk, K. A., Mortimer, D., Peck, L. S., Pretty, J., Rockström, J., Rodríguez, J. P., Smith, R. K., Spalding, M. D., Tonneijck, F. H., & Watkinson, A. R. (2014). A horizon scan of global conservation issues for 2014. In Trends in Ecology and Evolution (Vol. 29, Issue 1, pp. 15–22). <https://doi.org/10.1016/j.tree.2013.11.004>
 42. Thompson, W. L., editor. 2004. Sampling rare or elusive species: concepts, designs and techniques for estimating population parameters. Island Press, Washington, D. C.
 43. Thorson, J. T., J. N. Ianelli, and S. Kotwicki., 2017. The relative influence of temperature and size-structure on fish distribution shifts: A case-study on Walleye pollock in the Bering Sea. Fish and Fisheries 18:1073-1084.
 44. Thorson, J. T., G. Adams, and K. Holsman., 2019. Spatio-temporal models of intermediate complexity for ecosystem assessments: A new tool for spatial fisheries management. Fish and Fisheries 20:1083-1099.
 45. Wallace, B.P., Tiwari, M., Girondot, M. 2013. *Dermochelys coriacea*. The IUCN Red List of Threatened Species 2013: e.T6494A43526147. <https://dx.doi.org/10.2305/IUCN.UK.2013-2.RLTS.T6494A43526147.en>. Accessed on 04 October 2024.
 46. Witt, M. J., Bonguno, E. A., Broderick, A. C., Coyne, M. S., Formia, A., Gibudi, A., Mounguengui, G. A. M., Moussounda, C., Nsafou, M., Nougessono, S., Parnell, R. J., Sounguet, G. P., Verhage, S., & Godley, B. J., 2011. Tracking leatherback turtles from the world’s largest rookery: Assessing threats across

Figures

(a)



(b)

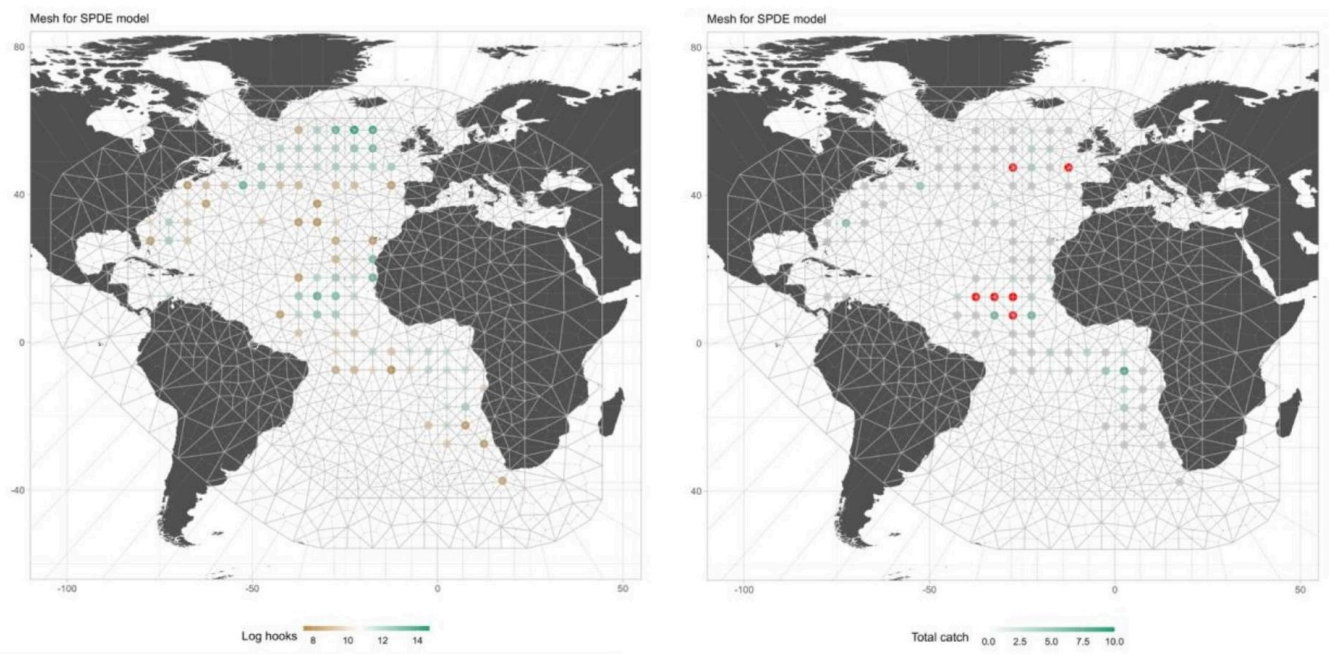
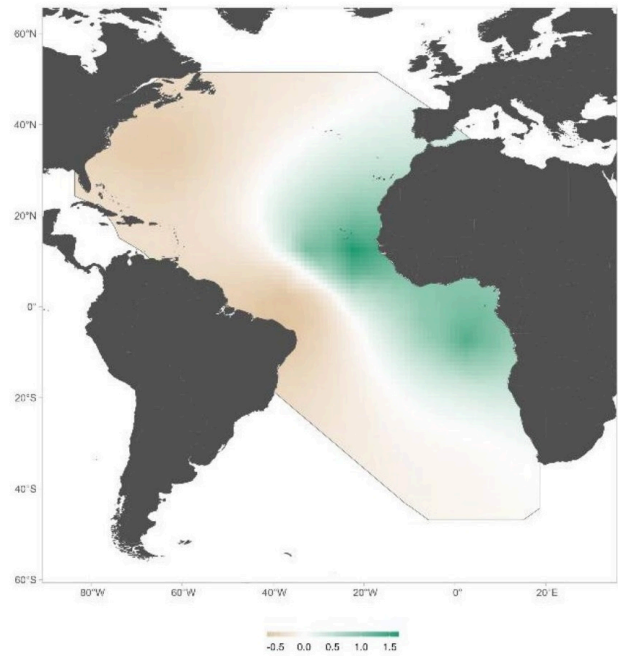


Figure 1

Distribution map of a total number of observed hooks (log scale) and the total number of captures for (a) Q1 and (b) Q4. The triangular area inside the figure is the triangulation used to calculate the Gaussian Markov random field in the SPDE approach. When applying the SPDE approach, the estimation is extended to a larger area than the observation points in order to properly handle spatial correlations near the boundary. For the total number of captures, locations with no capture history are shown in gray, and locations with a total number of captures greater than 10 are shown in red.

(a)



(b)

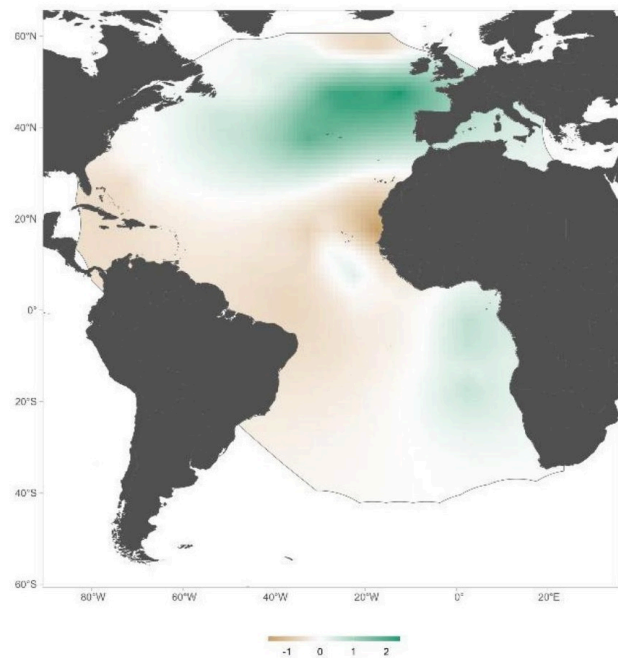


Figure 2

Figure 3. Spatial distribution of latent spatial fields η in (a) Q1 and (b) Q4. Here, annual averages are shown, respectively.

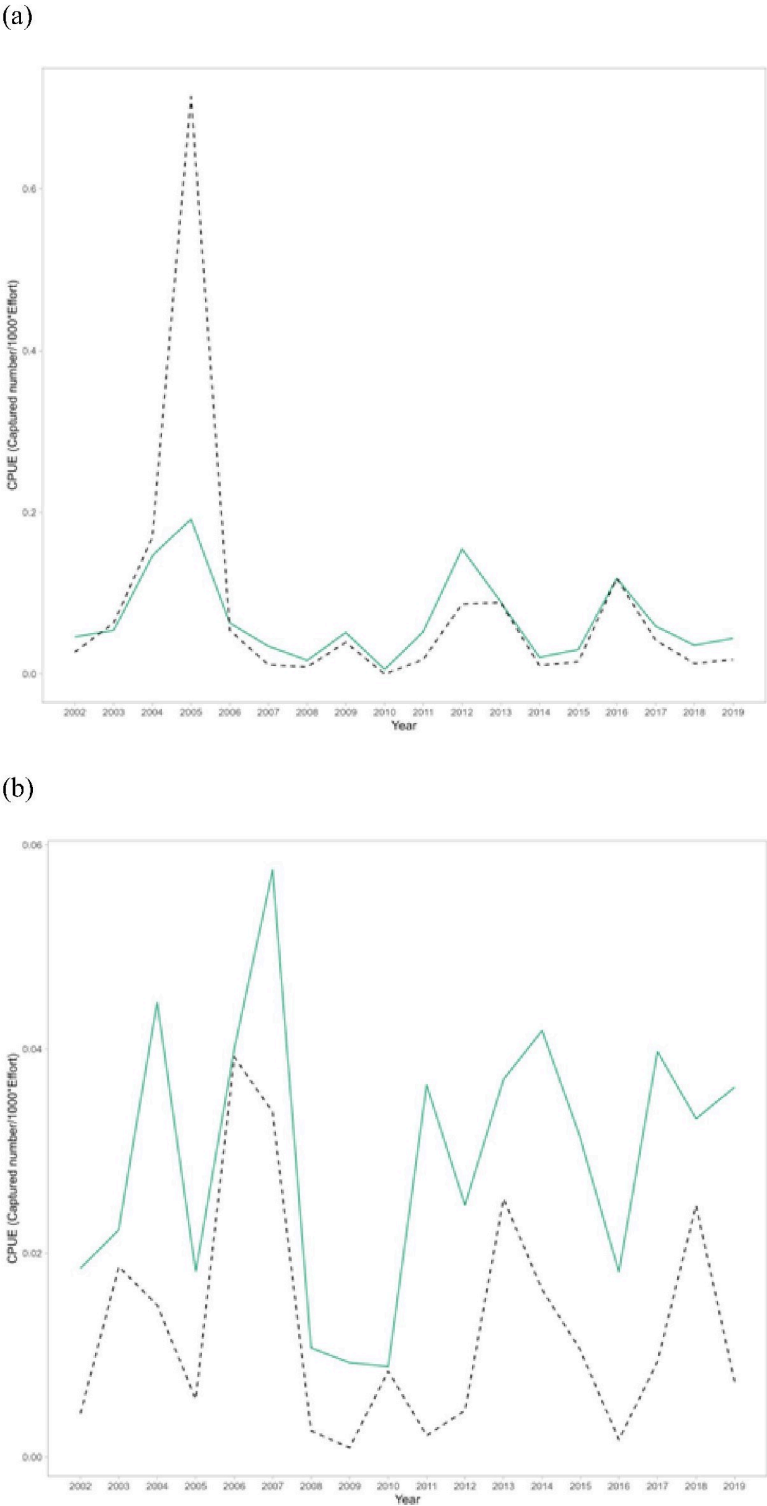
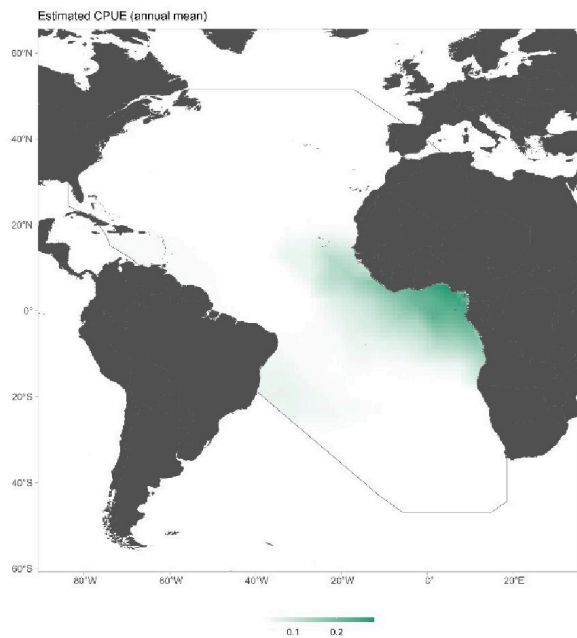


Figure 3

Figure 4. Over time changes in relative density in (a) Q1 and (b) Q4 at the observation sites. The solid green and dotted black lines in the figure indicate the estimated mean values and observed CPUE values, respectively.

(a)



(b)

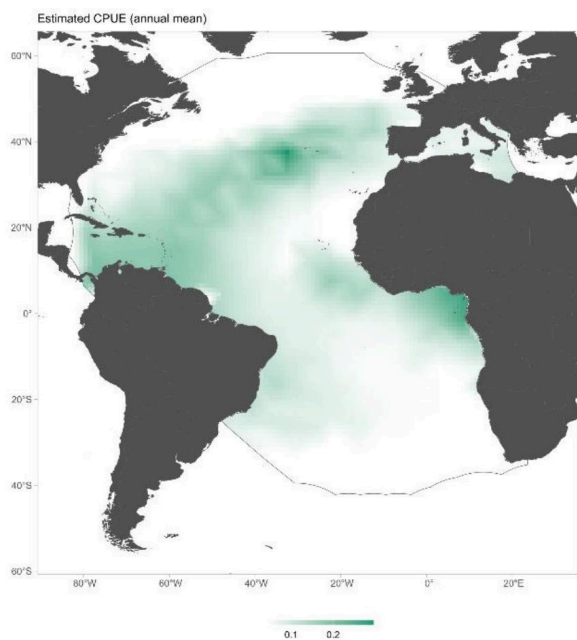
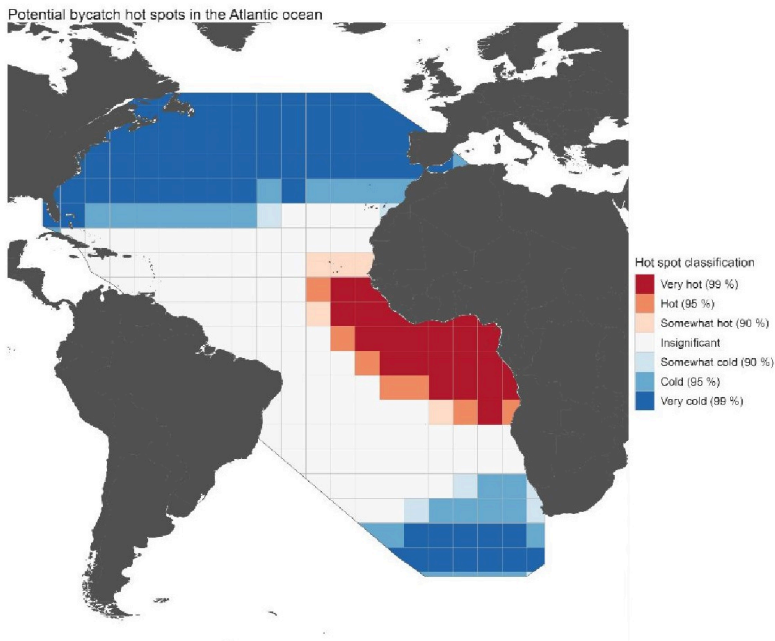


Figure 4

Figure 5. Spatial distribution of estimated relative abundance (annual mean values) in (a) Q1 and (b) Q4. The extent of the inner mesh including the observation points in figure 1 is shown in the figure to match the distribution limits of leatherback turtles.

(a)



(b)

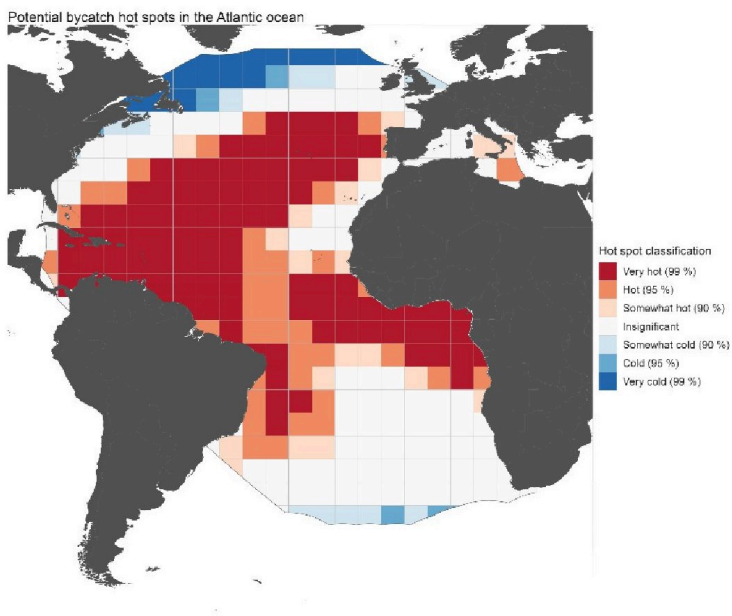


Figure 5

Figure 6. Spatial distribution of potential bycatch hot spots (annual mean values) in (a) Q1 and (b) Q4. Red areas indicate hotspots at risk of bycatch and blue areas indicate cold spots where the risk is lower than elsewhere.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [Supplementarymaterial.docx](#)