Original Article

Toward Climate-Informed Fisheries Assessment: Integrating Oceanographic Variables into Frigate Tuna Stock Assessment in the Southeast Atlantic Ocean

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Abstract

Frigate Tuna (*Auxis thazard*) is a top management priority for the International Commission for the Conservation of Atlantic Tunas (ICCAT). Yet, no stock assessment for the Southeast Atlantic has integrated catch data with ocean- and climate-standardized abundance indices to produce climate-informed stock status estimates. This study presents the first such assessment, using annual purse-seine catch and effort data from the ICCAT Task I and Task II databases (1991-2023) and five oceanographic variables from the National Oceanic and Atmospheric Administration (NOAA). Catch-per-unit effort (CPUE) was standardized using a Generalized Additive Model (GAM), and stock status was evaluated using the Stochastic Surplus Production Model in Continuous Time (SPiCT). The Task II-derived CPUE index (S1) outperformed the Task I-derived alternative (S2) in GAM's cross-validation (mean Root Mean Square Error = 0. 028, Mean Absolute Error = 0. 020), penalized likelihood fit (lower Restricted Maximum Likelihood - REML and scale estimates), and SPiCT's residual diagnostics (normality and homoscedasticity). Significant drivers of relative abundance included year, latitude, sea surface temperature, chlorophyll a concentration, and ocean surface wind, with abundance increasing northward under favorable conditions (peaking around 4°-6°S). SPiCT results indicate that biomass exceeds the target reference point [median biomass to biomass at maximum sustainable yield (B/BMSY) = 1.8] and that fishing mortality remains below the fishing mortality at maximum sustainable yield (F/FMSY = 0.2). High-stock resilience (median intrinsic growth rate (*r*) = 0. 65) was confirmed across four sensitivity scenarios. Retrospective analyses (Mohn's rho, ρ: 0.15 to 0.20), Ljung-Box and Shapiro-Wilk tests confirmed negligible bias and stable model performance. Although current exploitation is sustainable, the SPiCT assessment indicated that yield-maximising strategies may compromise long-term sustainability; thus, precautionary management is recommended. This assessment is also the first scientific evaluation of ICCAT Task II purse-seine data on small tunas in the Southeast Atlantic, providing a quantitative baseline for future regional assessments.

Categories: Aquatic animal health management, Biodiversity conservation, Fishery ecology

Keywords: climate, management, precautionary, purse seine, resilience, sensitivity

Introduction

The Frigate Tuna, *Auxis thazard* (Lacepède), a member of the Scombridae family, inhabits tropical and subtropical coastal and oceanic waters, with a preference for depths greater than 50 m [1,2]. In the Atlantic, its distribution ranges from 40°N to 35°S, making it a key mesopredator in these ecosystems. Frigate Tuna prey on small fishes (especially clupeids), cephalopods, planktonic crustaceans, and stomatopod larvae [3], thereby maintaining a critical trophic role. Economically and recreationally valuable, the species is exploited with a variety of surface and artisanal gear, including trolling lines, handlines, longlines, and various nets. Frigate Tuna commands a very high global market price [4,5] due to its exceptionally high-nutrient content [6].

International Commission for the Conservation of Atlantic Tunas (ICCAT) manages tunas and related species across the Atlantic, with a recent shift toward small tunas, including Frigate Tuna - now among its top three small-tuna assessment priorities [7-9]. ICCAT has defined four Atlantic regions for small-tuna data collection and management: Southwest (ATSW), Southeast (ATSE), Northwest (ATNW), and Northeast (ATNE) Atlantic (Appendix Figure *8*), as adopted in previous studies [10-12]. Small pelagic species, including Frigate Tuna, are highly sensitive to environmental variability, a vulnerability further amplified by climate change [13-15]. For Frigate Tuna, reproductive activity is closely linked to sea surface temperature, with mass spawning occurring at 21.6-30.5°C and peaking at 25-28°C [16,17]. African coastal regions, particularly vulnerable to climate change, face significant challenges in maintaining marine biodiversity [18,19].

In recent decades, tuna purse seine (hereafter PS) fisheries have become particularly significant in the eastern Atlantic, often capturing Frigate Tuna as bycatch alongside yellowfin and skipjack [2]. Frigate Tuna landings have surged in both the Northeast and Southeast Atlantic, with these regions accounting for 75% of Atlantic small tuna catches from 1991 to 2019. According to the ICCAT statistics database, PS fisheries in the Southeast Atlantic (hereafter, ATSE) region alone have landed over 258,674 t between 1950 and 2023. The growing prominence of these fisheries underscores the increasing exploitation of Frigate Tuna in the eastern Atlantic.

Despite their economic and ecological significance, most small tunas in the Atlantic - including frigate tuna - lack formal stock assessments due to limited and fragmented data [10,20]. Although semi-quantitative, length-based, and catch-based data-limited approaches have been applied [10,11,21], their reliability is fundamentally constrained by the lack of abundance indices - the most informative indicators of population trends and stock status [22-24]. This gap persists despite the availability of ICCAT-approved PS catch-and-effort series [25]. It is compounded by the fact that the influence of ocean-climate variability on Frigate Tuna abundance has never been systematically examined - despite growing evidence that climate-driven shifts are reshaping the distribution and productivity of small pelagic species [15,26]. Together, these gaps weaken the scientific foundation needed to develop evidence-based conservation and harvest strategies for a species of recognized importance within the ICCAT management framework.

This study addresses these gaps by providing the first climate-informed stock assessment of Frigate Tuna in the ATSE. It integrates PS catch and effort data from the ICCAT Task I (S2) and Task II (S1) databases (1991-2023) with five oceanographic variables from NOAA's OceanWatch platform - representing the first scientific evaluation of ICCAT Task II purse seine data for small tunas ahead of a formal ICCAT analytical request (ICCAT, 2022). The specific objectives were to: (1) evaluate and compare CPUE indices derived from the ICCAT Task I and Task II datasets; (2) quantify the effects of ocean-climate covariates on relative abundance using Generalized Additive Models (GAM); and (3) assess stock status and evaluate harvest strategies under uncertainty using the Stochastic Surplus Production Model in Continuous Time (SPiCT). The findings are intended to inform ecosystem-based fisheries management and environmentally responsive harvest strategies within the ICCAT framework.

Materials And Methods

Catch and effort data

Recognizing the challenges of data collection in fisheries science, this study synthesizes data from multiple sources to provide a comprehensive assessment of Frigate Tuna in the ATSE. Annual catch (kg) and fishing effort (hours) for purse seine fisheries were obtained from ICCAT's Task II (hereafter t2) database (t2Ce-ETRO-PS1991-21_bySchool), covering 1991-2023. This dataset was validated and approved by ICCAT for fisheries assessment [25] and has been adopted in previous studies [23,24]. t2 Fishing effort (hours) was standardized to fishing days (hours/24), and t2 catch data (kg) were converted to tons (kg/1,000). The t2 dataset's spatial structure enabled the extraction of time-series data within the ATSE, aligned with the ICCAT 1° × 1° grid, within latitude 0.5°S-20.5°S and longitude 13.5°E-29.5°W.

Additionally, annual nominal catch data (tons) from Task I (hereafter t1: 1991-2023), with a cumulative catch of 172,615 t, were paired with the corresponding t2 effort data (1991-2023) for the ATSE. Nominal CPUE was calculated for both t2 catch-t2 effort and t1 catch-t2 effort pairings:

$$\mathrm{NCPUE} = C_i / E_i \tag{1}$$

where C is catch (tons), E is effort (days), and *i* denotes year.

Total nominal catches (1950-2023) for all fleet types (258,674 t) were also retrieved from t1, providing the catch series for SPiCT stock status evaluation. To determine the most representative CPUE index for Frigate Tuna stock assessment in the ATSE region, this study evaluated the two alternative CPUE scenarios (S): one based on t2 subset catches paired with t1 effort (S1), and another combining t1 nominal catches with t2 effort (S2). That is,

S1: CPUE derived from t2 PS catches and t2 fishing effort (PS, by school).

S2: CPUE from t1 nominal catches (tons) and t2 fishing effort.

The scenario best matching the GAM model diagnostics was used for subsequent stock assessment and management advice.

Ocean-climate data

Tropical African coastal zones are highly vulnerable to climate change [18,19], and oceanographic variability plays a key role in shaping small pelagic fisheries [15,26,27]. The abundance dynamics of Frigate Tuna are likely driven by environmental factors, including sea surface temperature (SST), salinity (SSS), chlorophyll-a concentration (Chlor_a), surface currents (OSC), and winds (OSW) [2,5,28,29]. To investigate these relationships in the ATSE, environmental data were obtained from NOAA's OceanWatch ERDDAP Griddap server for 1993-2023 (https://oceanwatch.pifsc.noaa.gov/erddap), extracted within 0.5°S-21°S and 13.5°E-29.5°W, and exported as CSV files for analysis [23,24]; see Appendix Figure *9*. NOAA's ERDDAP graphical visualization tools enabled precise delineation of the study area and optimized data extraction (see Appendix Figure *9*). For comprehensive guidance on data retrieval from NOAA's ERDDAP platform, consult the NOAA website, and for illustrations, refer to Appendix Figure *9*.

Data analyses

Generalized Additive Model Analysis

Model fitting and covariates: Generalized Additive Model (GAM) was used to standardize PS CPUE for Frigate Tuna, assuming a delta-lognormal error distribution [30]. GAMs extend the Generalized Linear Model (GLM) framework by incorporating smooth functions of predictors, enabling flexible representation of ecological processes without restrictive parametric assumptions [31,32]. This flexibility is particularly valuable in fisheries science, where stock dynamics and catchability are often governed by nonlinear environmental relationships [33,34].

The model incorporated year, latitude, longitude, and environmental covariates as response variables. Year was modeled as a continuous, smooth term, *s*(Year), to capture nonlinear long-term abundance trends and regime shifts. Latitude and longitude captured spatial heterogeneity in the distribution of fishing activity. Environmental covariates - SST (°C), SSS (psu), Chlor_a (mg m^{-3}), OSC (m s^{-1}), and OSW (m s^{-1}) - represent key drivers of habitat suitability, productivity, and prey aggregation [15,26,27,35-37]. The GAM formulation was:

$$\log(\mathrm{CPUE}_i) = \alpha + \mathrm{s(Year)} + \mathrm{s(Lat)} + \mathrm{s(Long)} + \mathrm{s(SST)} + \mathrm{s(SSS)} + \mathrm{s(Chlor\_a)} + \mathrm{s(OSC)} + \mathrm{s(OSW)} + \varepsilon_i \quad (2)$$

where log(CPUE*i*) is the natural logarithm of CPUE for observation *i*, α is the intercept, s(·) denotes smooth functions of predictors estimated using thin-plate regression splines, and ε*i* is the error term, assumed to be Gaussian.

Smoothing parameters were estimated via restricted maximum likelihood (REML) to balance model fit and smoothness, thereby minimizing overfitting [38,39]. The GAM was implemented in R (v4.1.3) using the mgcv package [32].

GAMs have been widely used to standardize CPUE in PS and small-tuna fisheries [31,35-37,40,41], and are recognized by ICCAT for this purpose [30,42,43]. The resulting standardized CPUE (hereafter Std. CPUE) served as a proxy for the relative abundance of Frigate Tuna in the ATSE.

Model evaluation

Model adequacy and CPUE index reliability were therefore assessed using multiple complementary diagnostics: Five-fold cross-validation evaluated predictive performance across all covariates using Root Mean Square Error (RMSE), Mean Absolute Error (MAE), and R^2, where lower RMSE and MAE indicate greater predictive accuracy, and higher R^2 indicates greater deviance explained [40,44]. Residual diagnostics (i.e., Quantile-Quantile (QQ) plots; histograms) confirmed normality and adequacy of model assumptions, while overall goodness of fit was quantified using deviance explained and adjusted R^2 [30,42,45,46]. For smooth-term diagnostics, *F*-statistics measured each smooth's contribution relative to residual variance; *P*-values assessed statistical significance ($P \leq 0.05$ significant; $P \leq 0.001$ highly significant); edf-quantified smooth complexity, with higher values reflecting greater nonlinearity; the scale estimate measured residual variance; and the Restricted Maximum Likelihood (REML) score evaluated penalized likelihood fit, with lower values indicating better model parsimony [30,33,38,42,46]. Before modeling, a Pearson correlation heatmap was used to identify potential collinearity among predictors, as high collinearity can bias model inference [47]. Standard CPUE predictions were back-transformed and centered for interannual comparison, with uncertainty estimated via confidence intervals using the Bayesian covariance approximation from mgcv [48].

Stochastic surplus production model in continuous time

SPiCT is a state-space implementation of the Pella-Tomlinson surplus production model, in which fish biomass grows exponentially at low densities and asymptotically approaches the unfished biomass (K) [49]. Fishing mortality is modeled as a stochastic process that links observed catches and abundance indices to latent population states, with log-normal observation errors. Unlike traditional surplus production models, SPiCT incorporates stochasticity via random-process error terms, with the degree of stochasticity governed by the shape parameter (n) of the Pella-Tomlinson production function: $0 < n < 1$ yields predominantly deterministic dynamics, whereas $n > 1$ allows stochastic effects to influence reference-point estimation. Requiring only catch and CPUE data, SPiCT is well-suited to data-limited and data-moderate fisheries such as Frigate Tuna [50,51], unlike data-rich alternatives such as JABBA-Select [52] and Stock Synthesis [53].

The Schaefer model ($n = 2$) was adopted as a special case of SPiCT [49] for its precautionary properties: it sets BMSY at 50% of K, providing a conservative benchmark that reduces the risk of overestimating stock productivity [54]. The model is expressed as:

$$\frac{dB(t)}{dt} = rB(t)\left(1 - \frac{B(t)}{K}\right) - C(t) + \eta B(t) \tag{3}$$

where r is the intrinsic growth rate, K is the carrying capacity, C(t) is the catch, and ηB(t) is a zero-mean process term (Brownian motion on the log-scale). See Pedersen and Berg [49] for full methodological details.

The prior for K was set to eight times the maximum observed catch (12,131 t), with a standard deviation of K/2, consistent with ICCAT guidelines [25,55]. Because no stock-specific r prior was available, sensitivity analyses used alternative r priors, following previous applications [51]. Standardized CPUE served as the sole abundance index, with catch data spanning 1950-2023 and index data covering 1991-2023. All other priors were set to default values [49,50].

Model adequacy was evaluated using residual bias checks, the Ljung-Box test for serial autocorrelation, and the Shapiro-Wilk test for normality. Non-significant P-values ($P > 0.05$) across all diagnostics indicated that residuals were unbiased, serially independent, and approximately normally distributed [49,50]. Retrospective performance was assessed using Mohn's ρ ($n = 6$ years removed), with values between −0.15 and 0.20 indicating negligible bias [52,56].

SPiCT v3.1 was implemented in R using Template Model Builder (TMB) [49,50]. Its performance and accessibility have led several RFMOs, including ICCAT [30,57,58], to adopt it, and it has been used in recent assessments of small pelagic fisheries [51].

SPiCT prior sensitivity tests

Given the absence of a stock-specific resilience prior for Frigate Tuna, sensitivity analyses were conducted to assess how alternative r priors affect model outputs. This is critical because r directly influences estimates of K, sustainable yield, and key reference points, and uncertainty in r can bias assessments in data-limited fisheries [51,54,56,59].

Following resilience prior categories reflective of the likely productivity range for many fisheries [54,56], four scenarios were tested using the optimal S1 CPUE index, each with a user-defined K:

S1a: Default r

S1b: High r (mean = 1.05; range 0.6-1.5)

S1c: Medium r (mean = 0.5; range 0.2-0.8)

S1d: Low r (mean = 0.28; range 0.05-0.5)

The optimal r scenario is identified using conservation-focused criteria - the highest B/BMSY (biomass well above BMSY, providing a buffer against uncertainty) and the lowest F/FMSY (reducing the risk of overfishing). A lower MSY target is also selected as a precautionary measure in response to the inherent uncertainty in data-limited assessments. This scenario underpins subsequent stock status estimation and management advice.

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SPiCT harvest strategies

In this study, SPiCT projected stock status over a management period (e.g., 2024-2025) under a range of harvest scenarios, using the fitted stochastic dynamic model and the optimal resilience prior. The management scenarios included maintaining current catch and fishing mortality (F), fishing at FMSY, no fishing, implementing a ±25% change in F, applying the MSY hockey-stick rule, and adopting the advice rule of the International Council for the Exploration of the Sea (ICES). For each scenario, SPiCT generated projections of catch, terminal B/BMSY, and F/FMSY, explicitly accounting for uncertainty. These projections provide a basis for evaluating trade-offs between yield and recovery risk, thereby supporting informed management decisions [49]. The use of SPiCT to evaluate fish harvest strategies is well established in international fisheries management [43,60,61].

Stock Status Metrics

Under Schaefer dynamics, reference points are derived analytically as follows: BMSY = K/2, FMSY = r/2, and MSY = rK/4 [54]. SPiCT generates time series of relative stock-status metrics, such as B/BMSY and F/FMSY, that map directly to the quadrants of the Kobe plot: not overfished (B/BMSY > 1.0) versus overfished (B/BMSY < 1.0); overfishing (F/FMSY > 1.0) versus no overfishing (F/FMSY < 1.0). The model summarizes terminal-year medians and their associated confidence intervals to classify stock status and exploitation rates [49].

Results And Discussion

CPUE evaluations

Residual diagnostics revealed clear differences between the two GAM scenarios. In Scenario S1, residuals closely matched a theoretical normal distribution, as shown by strong alignment in the QQ plot and a symmetric, zero-centered histogram with low variance (Figure *1*). In contrast, Scenario S2 displayed pronounced deviations from normality in both tails of the QQ plot and a more dispersed residual distribution, indicating higher variance and violations of model assumptions (Appendix Figure *10*). These findings demonstrate that S1 provides a more reliable relative-abundance index than S2, while the residuals for S2 suggest greater variance and possible model misspecification [33,62].

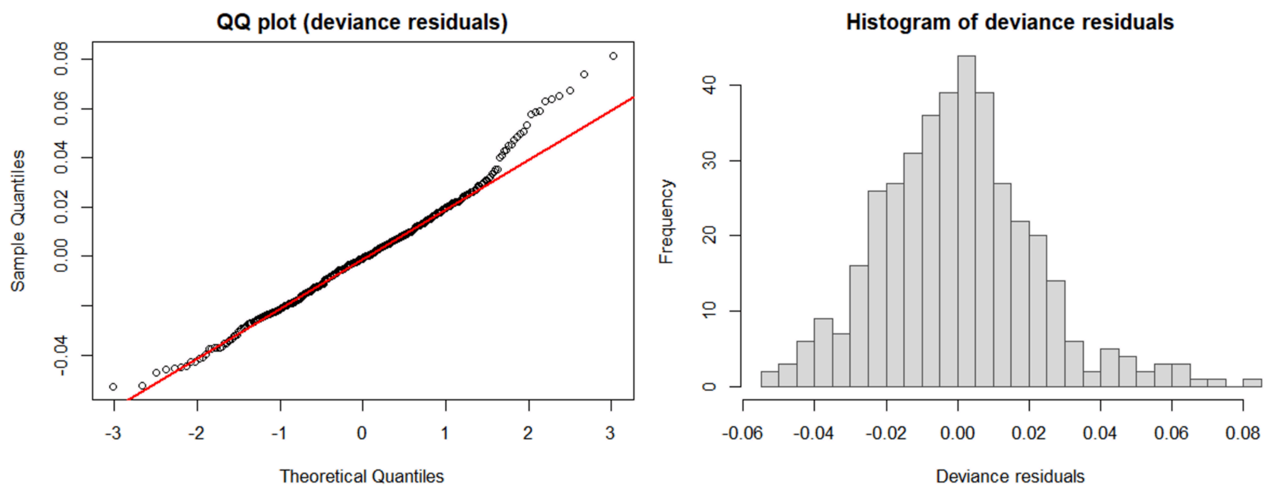

FIGURE 1: GAM residual diagnostic plots for Frigate tuna from PS fisheries in the Tropical Southeast Atlantic Ocean: QQ plot (left panel) and residual histogram (right panel).

PS, purse seine; GAM, Generalized Additive Model; QQ, Quantile-Quantile

While the GAM substantially improved raw CPUE for both S1 and S2, producing narrow confidence intervals (Appendix Figure *11*), the S1 Std. CPUE remained consistently low and stable throughout the time series, with only modest increases in recent years (Figure *2*). In contrast, S2 showed much higher values, with a sharp escalation after 2015 and pronounced peaks between 2018 and 2021, indicative of scale inflation and index instability [33].

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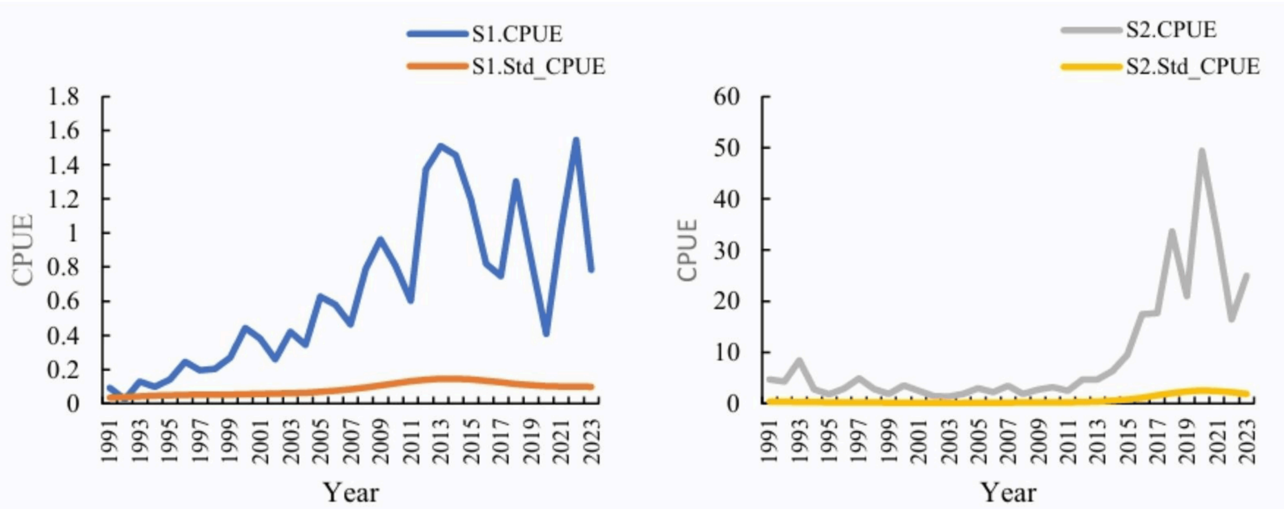

FIGURE 2: Nominal (as CPUE) and standardized CPUE (as Std. CPUE) plots for Frigate Tuna (based on S1 and 2 CPUES) from purse seine fisheries in the Tropical Southeast Atlantic Ocean.

CPUE, Catch-Per-Unit Effort

Cross-validation further supports S1's superior predictive performance (Table 1). S1 achieved consistently lower mean RMSE (0.028) and MAE (0.020) than S2 (RMSE = 0.509; MAE = 0.268), indicating substantially reduced prediction error. Although S2 had a higher mean R^2 (0.756) compared to S1 (0.665), this was accompanied by much greater error and instability across folds, suggesting overfitting rather than genuine explanatory power.

S1				**S2**			
Fold	RMSE	MAE	R^2	Fold	RMSE	MAE	R^2
1	0.021102	0.01557	0.785595	1	0.454946	0.230794	0.737057
2	0.042209	0.025383	0.471814	2	0.479976	0.268769	0.812278
3	0.025672	0.020282	0.742329	3	0.486047	0.269991	0.773214
4	0.024646	0.018837	0.666265	4	0.488032	0.272487	0.731828
5	0.027449	0.019553	0.658464	5	0.633798	0.297524	0.727683
Mean	0.028216	0.019925	0.664893	Mean	0.50856	0.267913	0.756412

TABLE 1: GAM's five-fold cross-validation for S1 and S2 CPUE of Frigate Tuna from purse seine fisheries in the Tropical Southeast Atlantic Ocean.

RMSE, Root Mean Square Error; GAM, Generalized Additive Model; CPUE, Catch-Per-Unit Effort; MAE, Mean Absolute Error

S2 also exhibited higher adjusted R^2 and deviance explained, but these metrics were largely driven by a dominant temporal (Year) effect, with most environmental covariates contributing weakly or nearly linearly (mean edf ≈ 2.82 for S2 environmental terms) (Table *2*). In contrast, S1 was more ecologically informative, with significant nonlinear contributions from multiple predictors -Year, Latitude, SST, Longitude, OSW, and Chlor_a. S1 also showed higher effective degrees of freedom (Table *2*) and substantially lower residual variance (scale estimate: 0.000515 vs. 0.024622), better capturing ecological heterogeneity [32,63]. The lower REML score for S1 (Appendix Table *5*) further supports a superior penalized likelihood fit and reduced overdispersion [32]. Overall, S1 provides a statistically superior fit and predictive accuracy, making it preferred for stock assessment and management advice.

S1					**S2**			
Smooth Term	edf	F-stat	*P*-value	Significance	edf	F-stat	*P*-value	Significance
s(Year)	6.750	45.537	$< 2^{e-16}$	***	7.582	158.082	$< 2^{e-16}$	***
s(Lat)	5.434	41.612	$< 2^{e-16}$	***	1.000	2.440	0.1191	ns
s(Long)	2.759	3.306	0.0164	*	1.000	0.014	0.9069	ns
s(SST)	3.954	6.394	1.99^{e-05}	***	5.006	3.859	0.0155	*
s(SSS)	1.813	0.564	0.7177	ns	1.000	0.191	0.6625	ns
s(Chlor_a)	1.249	3.918	0.0420	.	1.000	0.720	0.3966	ns
s(OSC)	1.001	1.417	0.2348	ns	1.739	1.480	0.2031	ns
s(OSW)	4.131	9.984	$< 2^{e-16}$	***	4.257	4.210	0.00101	**

TABLE 2: GAM's approximate significance of Smooth Terms in (based on S1 and S2 CPUES) for Frigate Tuna from purse seine fisheries in Tropical Southeast Atlantic Ocean (Family: gaussian)

Note: edf, effective degrees of freedom; F, F-statistic; *P*, significance probability.; Significance codes: 0 "***" 0.001; "**" 0.01; "*" 0.05; "." 0.1; " " 1.

GAM, Generalized Additive Model; OSC, Ocean Surface Current; OSW, Ocean Surface Wind; SST, Sea Surface Temperature; SSS, Sea Surface Salinity

Nonetheless, S2 remains a viable alternative when excess zeros compromise S1 data, consistent with its use for Little Tunny in previous studies, where a GLM outperformed a GAM for analogous data structures [23,24]. Further analysis incorporating alternative modeling frameworks - such as delta models or hurdle approaches - could refine abundance indices and improve understanding of the drivers of stock variability and fishery performance [64].

Variable effects on CPUE dynamics

The correlation heatmap is a crucial tool for evaluating potential multicollinearity among predictors, as high multicollinearity can bias model inference [47,65]. This study (Figure *3*) highlights that temporal factors and primary productivity (Chlor_a) are the primary drivers of frigate tuna abundance. Weaker OSW and OSC conditions are linked to higher abundance, while weak associations with SST, SSS, and latitude suggest a broad habitat distribution across environmental gradients [26,66].

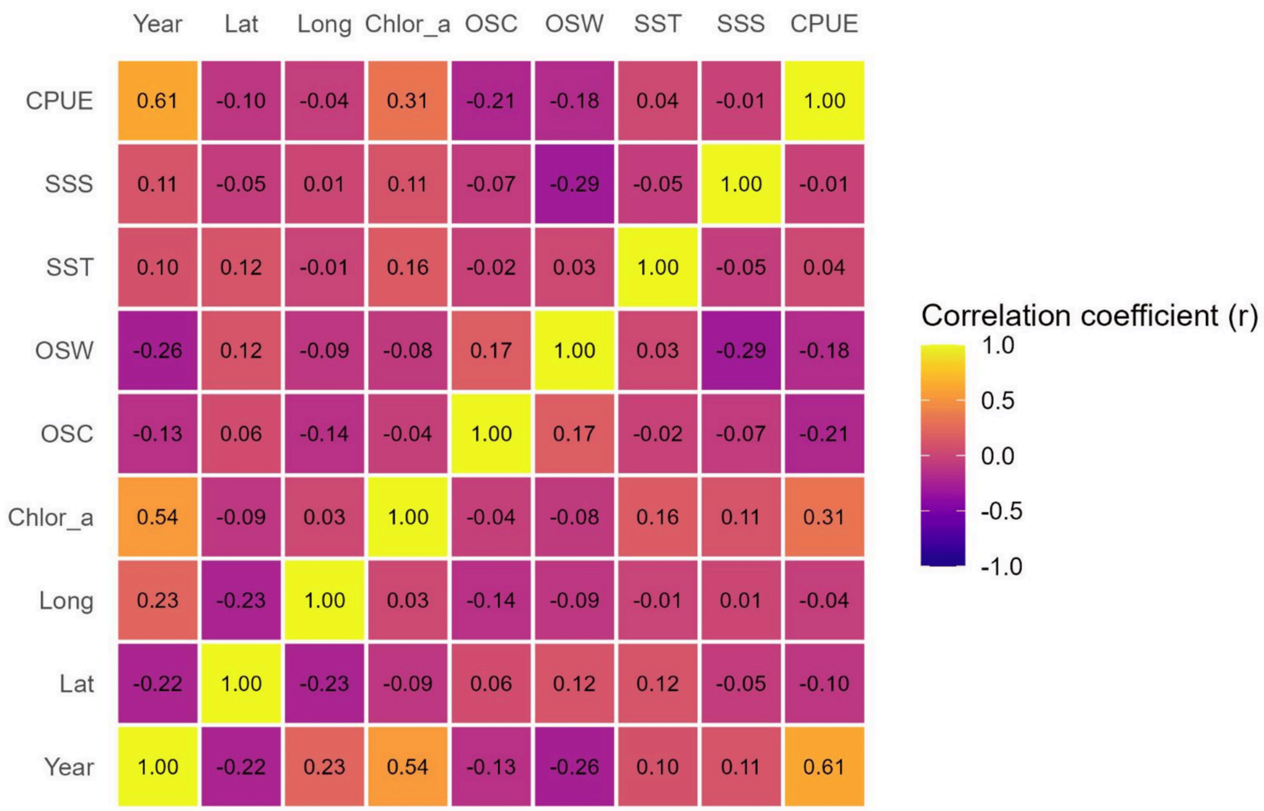

FIGURE 3: GAM correlation heatmap of temporal, spatial, and ocean-climate covariates for Frigate Tuna from purse seine (PS) fisheries in the Tropical Southeast Atlantic Ocean.

GAM, Generalized Additive Model; OSC, Ocean Surface Current; OSW, Ocean Surface Wind; SST, Sea Surface Temperature; SSS, Sea Surface Salinity; CPUE, Catch-Per-Unit Effort

Partial effect plots for S1 (Figure *4*) show that Std CPUE is influenced by temporal trends, spatial gradients, and ocean-climate variability. Standard CPUE increased from low levels in the 1990s, peaked around 2013-2015, then declined slightly but remained above early values, indicating a long-term increase rather than a simple regime shift. Latitude had a strong effect, with the lowest values in the south (~−20°) and the highest in the north (~−6° to −4°S), while longitude had little influence. Among environmental drivers, Chlor_a had the greatest impact, with higher concentrations associated with increased Std. CPUE. SST showed reduced CPUE at intermediate temperatures (22-25°C), but higher CPUE at both cooler (17-20°C) and warmer (26-28°C) extremes, whereas SSS had minimal effect. Standard CPUE also peaked at moderately negative OSW values, and OSC was weakly negatively associated.

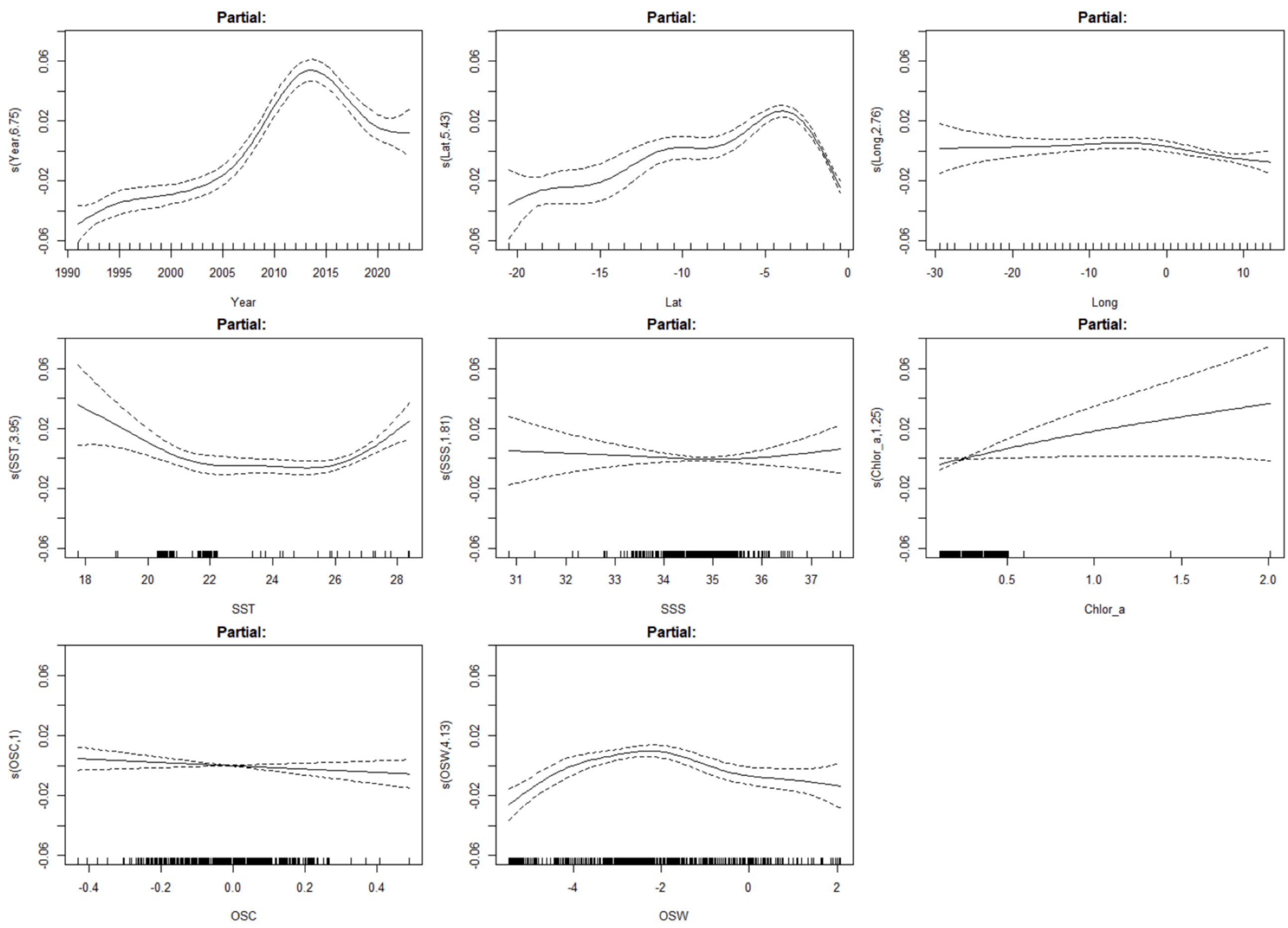

FIGURE 4: GAM partial effects of temporal, spatial, and ocean-climate covariates for Frigate Tuna from purse seine fisheries in the Tropical Southeast Atlantic Ocean.

GAM, Generalized Additive Model; OSC, Ocean Surface Current; OSW, Ocean Surface Wind; SST, Sea Surface Temperature; SSS, Sea Surface Salinity

Thus, spatially, relative abundance increased steadily northward from ~–20°S, peaking near –6° to –4°S-a region influenced by the Angola Current and associated thermal fronts, where warm equatorial waters interact with cooler upwelled waters to the south [67,68,69]. The Angola-Benguela Front (ABF; ~15°-17°S; [68] is a key transition zone further south, where the warm Angola Current meets the cold Benguela Current, generating high productivity [69]. Southeasterly trade winds (OSW) drive Ekman transport and coastal upwelling along the Benguela system (≈16°-34°S; [70]), bringing cool, nutrient-rich waters that enhance productivity (Chlor_a) and prey availability [69]. The observed northward shift in Frigate Tuna distribution is consistent with climate-driven range shifts in other species, where changing conditions lead to displacement from historical ranges or regional absence [71,72].

The SST-Std. CPUE relationship offers further ecological insight. Frigate Tuna generally inhabit warm epipelagic waters [2,5,16,73], but relative abundance is lowest at intermediate SSTs (22-25°C) characteristic of the ABF - a zone influenced by cooler Benguela upwelling [70,74,75] - and higher at both cooler (17-20°C) and warmer (26-28°C) extremes. This dual-peak pattern likely reflects different life-history stages: cooler SSTs align with adult foraging habitat within the species' documented thermal tolerance (13.8-27.1°C; [2,5]), while warmer SSTs coincide with spawning aggregations in the tropical Atlantic, where peak spawning occurs above 27°C [2,5,16]. In Atlantic coastal waters, Bahou et al. [76] reported peak spawning at 22.14-25.15°C and presence of gravid females at 27-28°C. Thus, the intermediate thermal regime (22-25°C) appears suboptimal for both core foraging and peak spawning. These findings align with previous studies that link thermal habitat to the distribution of small pelagic species [15,26,27,35,36,37,69,75,76]. Looking ahead, under intermediate-to-high emission scenarios, global surface temperatures are

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projected to rise by 1.4-4.4°C by 2,100 [77]. Species distributions are expected to shift faster than historical baselines [78,79,80], while eastern boundary upwelling systems face uncertain changes in upwelling intensity and timing [81,82], posing challenges for fisheries management [83,84].

SPICT assessments

Model Sensitivity and Diagnostics

As the *r*-prior decreases across S1a-S1d, K and B/BMSY increase while F/FMSY declines, consistent with the lower posterior *r* values (Table *3*). Despite these shifts, exploitation remains low across all scenarios (F/FMSY ≈ 0.20-0.22), and biomass remains well above target levels (B/BMSY ≈ 1.81-1.86). Scenario S1b (mean *r* = 1.05) is selected as the most precautionary basis for management advice on stock status because it yields lower biomass estimates, the lowest exploitation rate, and the lowest MSY - providing a conservative, risk-averse reference point.

Scenario	r	K	MSY	F/FMSY	B/BMSY
S1a	0.593	108,276	14,197	0.22	1.83
S1b	0.653	95,459	13,870	0.2	1.81
S1c	0.558	116,814	14,335	0.22	1.84
S1d	0.488	136,157	14,414	0.21	1.86

TABLE 3: SPiCT estimates of median posterior quantities across mean resilience (r) prior scenarios.

MSY, Maximum Sustainable Yield; F/FMSY, Relative Fishing Mortality at MSY; B/BMSY, Relative Biomass at MSY; *r,* Posterior Stock Resilience; K, Posterior Unfished Biomass and S, Scenarios (S1a-S1d); SPiCT, Stochastic Production in Continuous Times

The intrinsic population growth rate (*r*) is strongly correlated with life-history traits - particularly natural mortality (M), with *r* ≈ 1.73M for bony fish [85] - and can be approximated as 2 × FMSY, 3 × K (von Bertalanffy growth rate), 3/generation time, or 9/maximum age [5]. Sensitivity analyses confirmed that stock-status estimates were robust across *r* priors, with all scenarios indicating low exploitation and biomass above reference points [51]. Scenario S1b (mean *r* = 1.05) is recommended for management because it yields conservative biomass and MSY estimates, the lowest exploitation rate, and the strongest precautionary buffer. The median posterior *r* (*r* = 0.65; Table *3*) is consistent with high resilience and sustainability of the ATSE Frigate Tuna stock, slightly above the FishBase medium-resilience reference (*r* = 0.57), reflecting this study's use of stock-specific data. It also falls within the range of estimates reported elsewhere (*r* = 0.6-1.8; [73,86]).

Model diagnostics for S1b (Figure *5*) indicate an overall adequate fit, with some caveats. The Ljung-Box tests for Catch and Index show no significant autocorrelation, confirming that residuals are free of serial dependence. Bias tests are likewise non-significant, indicating no systematic estimation bias. However, the Shapiro-Wilk test indicates non-normality of the Catch residuals, suggesting a departure from the model assumptions, whereas the Index residuals satisfy the normality assumption. These diagnostics indicate a reasonable fit to the input data, with no significant autocorrelation or bias [49,50].

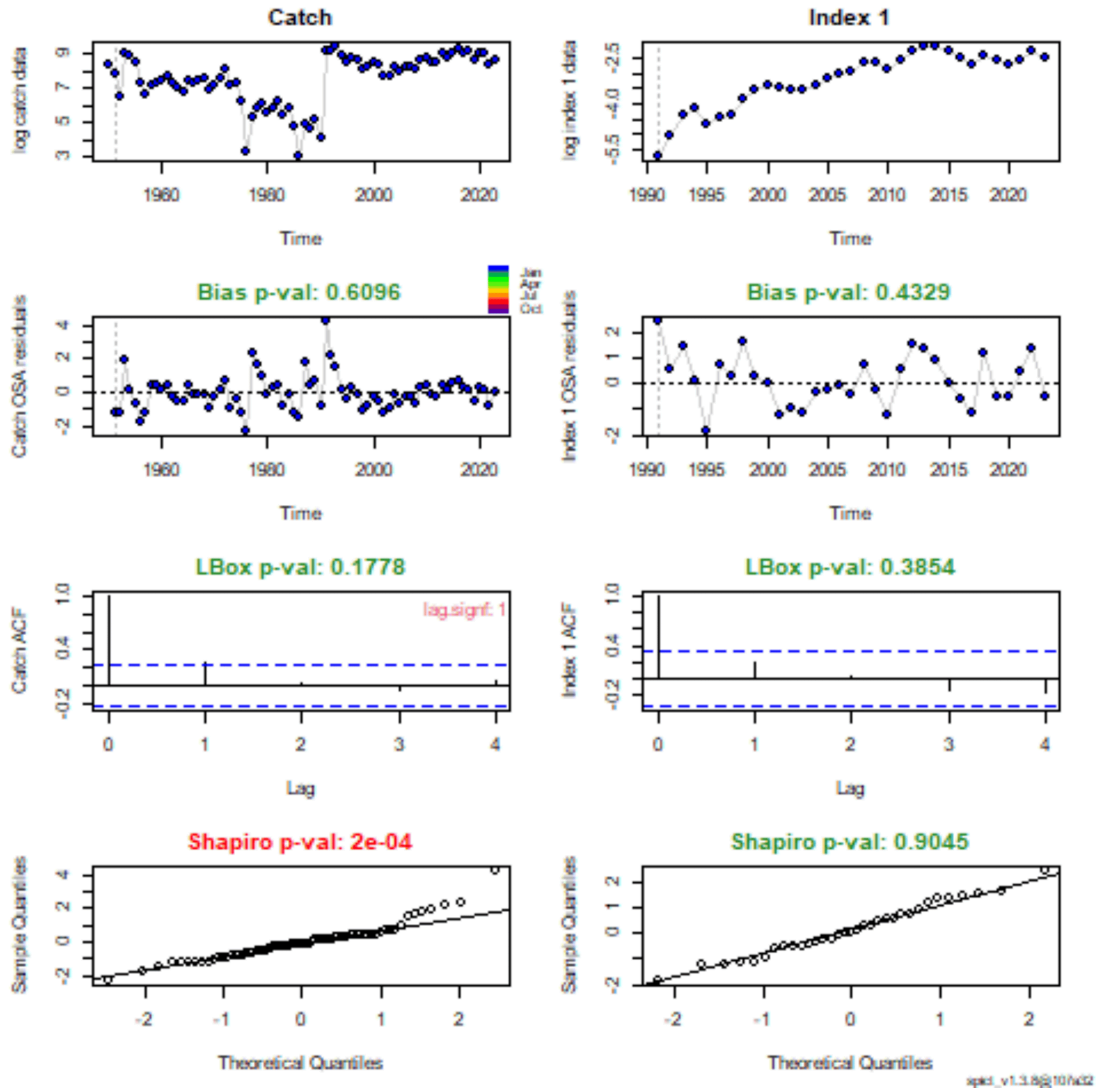

FIGURE 5: SPiCT residual diagnostics showing catch and index trajectories (1950-2023: Top panels), the Bias, Lbox, and Shapiro tests significance probabilities (P) of Frigate Tuna from purse seine fisheries in the Tropical Southeast Atlantic Ocean.

Retrospective analysis of absolute biomass (B_t), fishing mortality (F_t), and their reference ratios (B/BMSY; F/FMSY) showed strong consistency across peel runs (1-6 years; Fig. *6*). Minimal divergence from the full model and negligible Mohn's ρ values indicate no retrospective bias and stable model performance, supporting the overall reliability of the SPiCT assessment [52,54,56].

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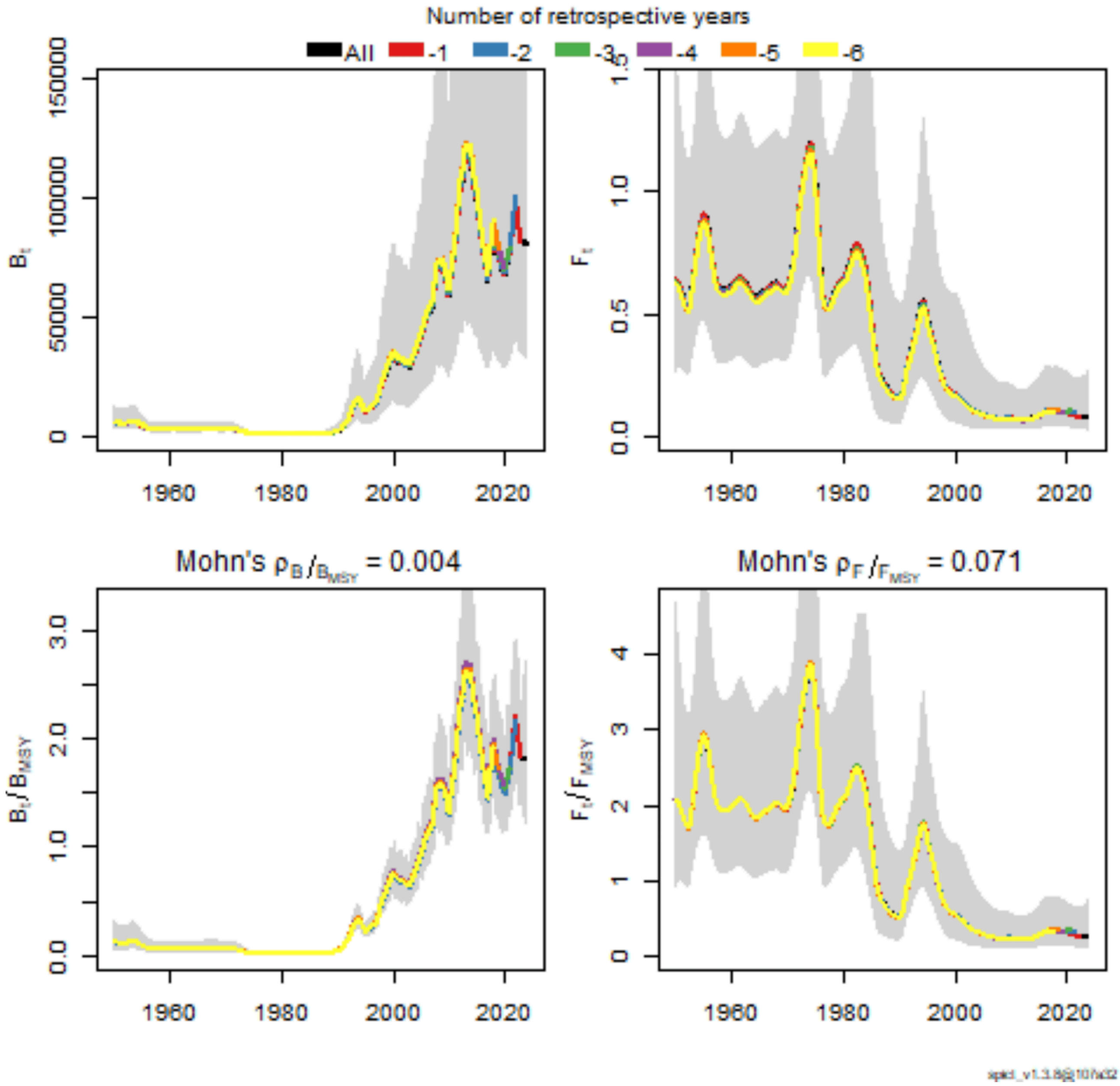

FIGURE 6: Retrospective analysis showing biomass and fishing mortality trajectories (1950-2023) of Frigate Tuna from purse seine fisheries in the Tropical Southeast Atlantic Ocean. Absolute biomass (B_t, top left) and fishing mortality (F_t, top right), along with their relative reference points (B/BMSY, bottom left; F/FMSY, bottom right) across six successive peel runs (n = 6 years).

Stock Status Evaluations

The SPiCT outputs in Figure 7 indicate that the stock is currently above target biomass levels and sustainably exploited. Biomass (top left) increased steadily after a prolonged period of depletion through the early 1990s, and recent levels have consistently exceeded BMSY (B/BMSY ≈ 1.5-2.5), despite interannual variability. Concurrently, fishing mortality (top right) declined from elevated historical rates to levels well below FMSY in recent years (F/FMSY < 1). The Kobe plot (bottom left) confirms a transition from overfished and overfishing conditions to the sustainable zone (B > BMSY; F < FMSY) in the terminal year. The surplus production curve indicates that the stock is operating near or slightly above BMSY, with moderate surplus production - consistent

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with the right-hand limb of the production curve, where high biomass is accompanied by declining marginal productivity. These results align with semi-quantitative risk assessments [21] and data-limited evaluations [2,10,11,20], and support adaptive, precautionary management under ICCAT.

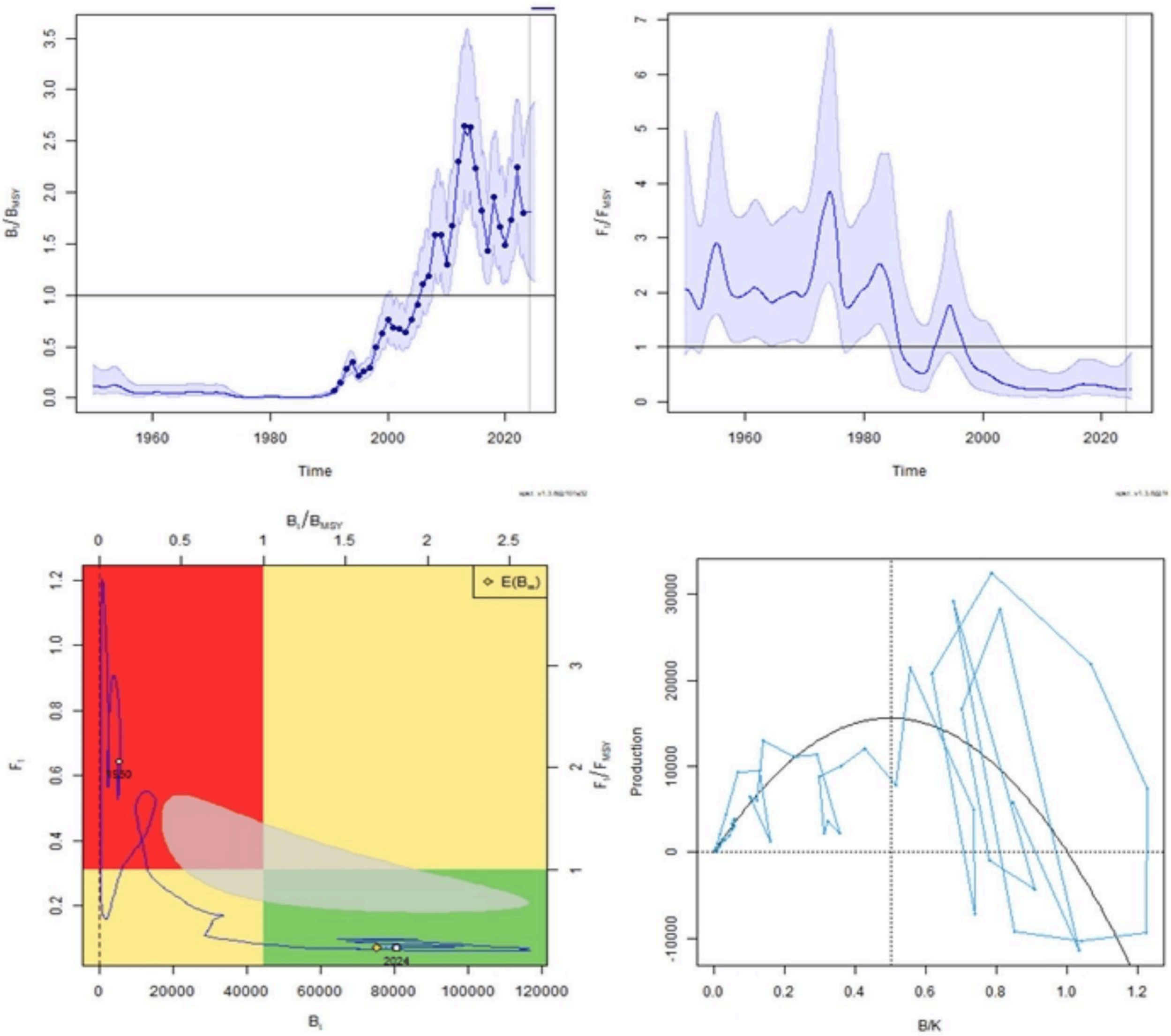

FIGURE 7: SPiCT-estimated stock status trajectory (1950–2023) of Frigate Tuna from purse seine fisheries in the Tropical Southeast Atlantic Ocean, showing relative biomass (B/BMSY), relative fishing mortality (F/FMSY), Kobe phase plot, and surplus production curve.

Harvest strategy projections indicate that biomass remains above BMSY across all evaluated scenarios (Table *4*). However, maintaining the status quo or reducing F by 25% offers the most prudent pathway, consolidating recovery gains before environmental or exploitation-related uncertainties erode the precautionary buffer [87,88]. This approach closely aligns with ICCAT recommendations [89]. Fishing at FMSY or applying the MSY hockey-stick rule, while technically sustainable, substantially narrows this buffer given uncertainties in future exploitation levels and climate-driven variability in stock productivity [49,54], making any increase in F inadvisable.

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Management Scenario	Catch (*t*)	B/BMSY	F/FMSY
Keep current catch	5888.7	1.52	0.55
Keep current F	5923.9	1.5.2	0.55
Fish at FMSY	9648.7	1.24	1.00
No fishing	6.8	1.95	0.00
Reduce F by 25%	4590.0	1.62	0.42
Increase F by 25%	7170.2	1.43	0.69
MSY hockey-stick rule	9648.7	1.24	1.00
ICES advice rule	8469.5	1.33	0.85

TABLE 4: SPiCT-based management scenarios for Frigate Tuna from purse seine fisheries in the Tropical Southeast Atlantic Ocean. Color bands denote stock status zones.

F/FMSY, Relative Fishing Mortality at MSY; B/BMSY, Relative Biomass at MSY; MSY, Maximum Sustainable Yield; International Council for the Exploration of the Sea

Limitations and future directions

This study advances the quantitative assessment of Frigate Tuna in the ATSE, yet key limitations remain. Annual data obscure seasonal dynamics, and traditional surplus production models assume equilibrium without explicitly accounting for age structure or size-selectivity [52]. Additionally, reliance on PS CPUE alone may introduce catchability bias. Future work should prioritize monthly datasets, biological sampling, and advanced population models to reduce uncertainty. Nonetheless, this study represents the first scientific evaluation of ICCAT t2 catch and effort data records (i.e., t2Ce-ETRO-PS, 1991-2023) for Frigate Tuna in the ATSE, preceding the customary ICCAT invitation for such analyses [25,30]. Given the critical role of small pelagic fisheries in the livelihoods and nutritional security of coastal African States in particular [90,91], these findings carry broader implications for food security and sustainable development, directly supporting progress toward United Nations Sustainable Development Goals 1, 2, and 14.

Conclusions

This study is the first to integrate catch and ocean-climate-standardized abundance data to produce climate-informed stock status estimates for Frigate Tuna (*A. thazard*) in the Southeast Atlantic, addressing a long-standing gap for a species of growing management concern to ICCAT. GAM analysis identified the ICCAT Task II PS CPUE index (S1) as the most reliable abundance proxy, outperforming the Task I catch-rate alternative (S2) in ecological interpretability and model diagnostics. Year, Latitude, Chlor_a, SST, and OSW were significant drivers of relative abundance, with abundance increasing northward under favorable conditions. SPiCT results indicate the stock is currently above BMSY (median ~80,900 t), with fishing mortality below FMSY (0.27 yr^{-1}) and a median posterior *r* of 0.65, consistent with high resilience. Nevertheless, yield-maximizing harvest strategies risk compromising long-term sustainability, and precautionary management is advised. Future work should prioritize monthly fishery and environmental data to support data-intensive assessment models.

Appendices

Toward Climate-Informed Fisheries Assessment: Integrating Oceanographic Variables into Frigate Tuna Stock Assessment in the Southeast Atlantic Ocean.

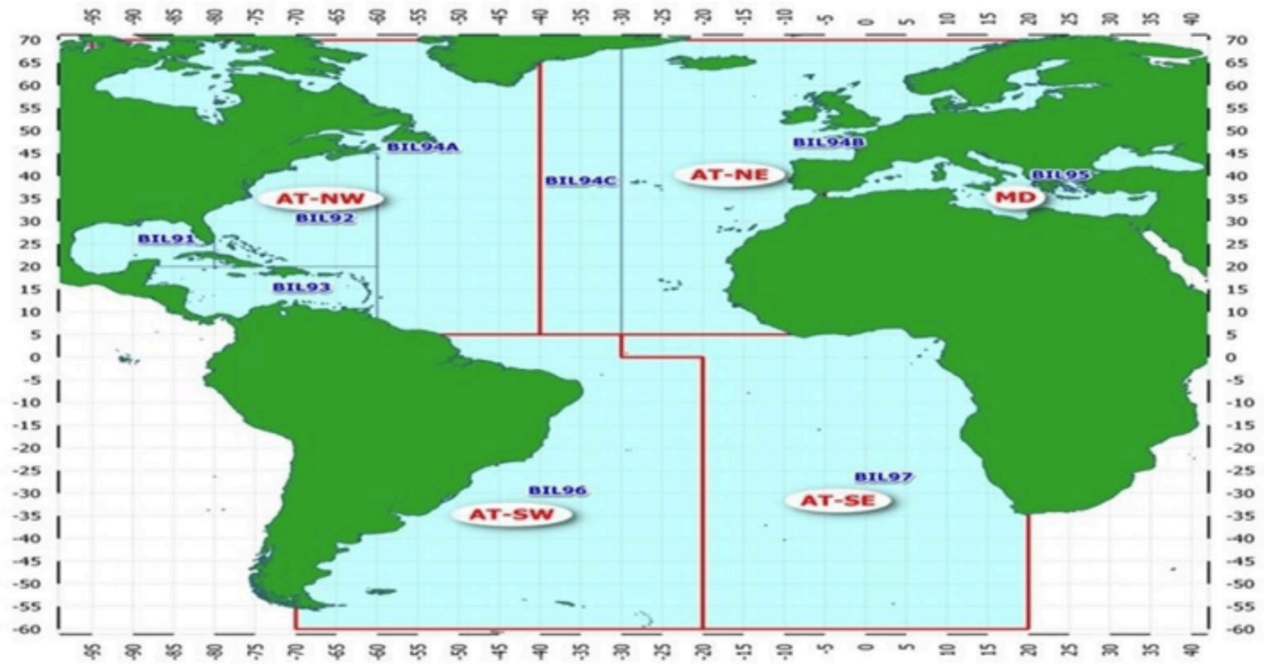

FIGURE 8: ICCAT-designated stock assessment regions for small tuna species.

ICCAT, International Commission for the Conservation of Atlantic Tunas

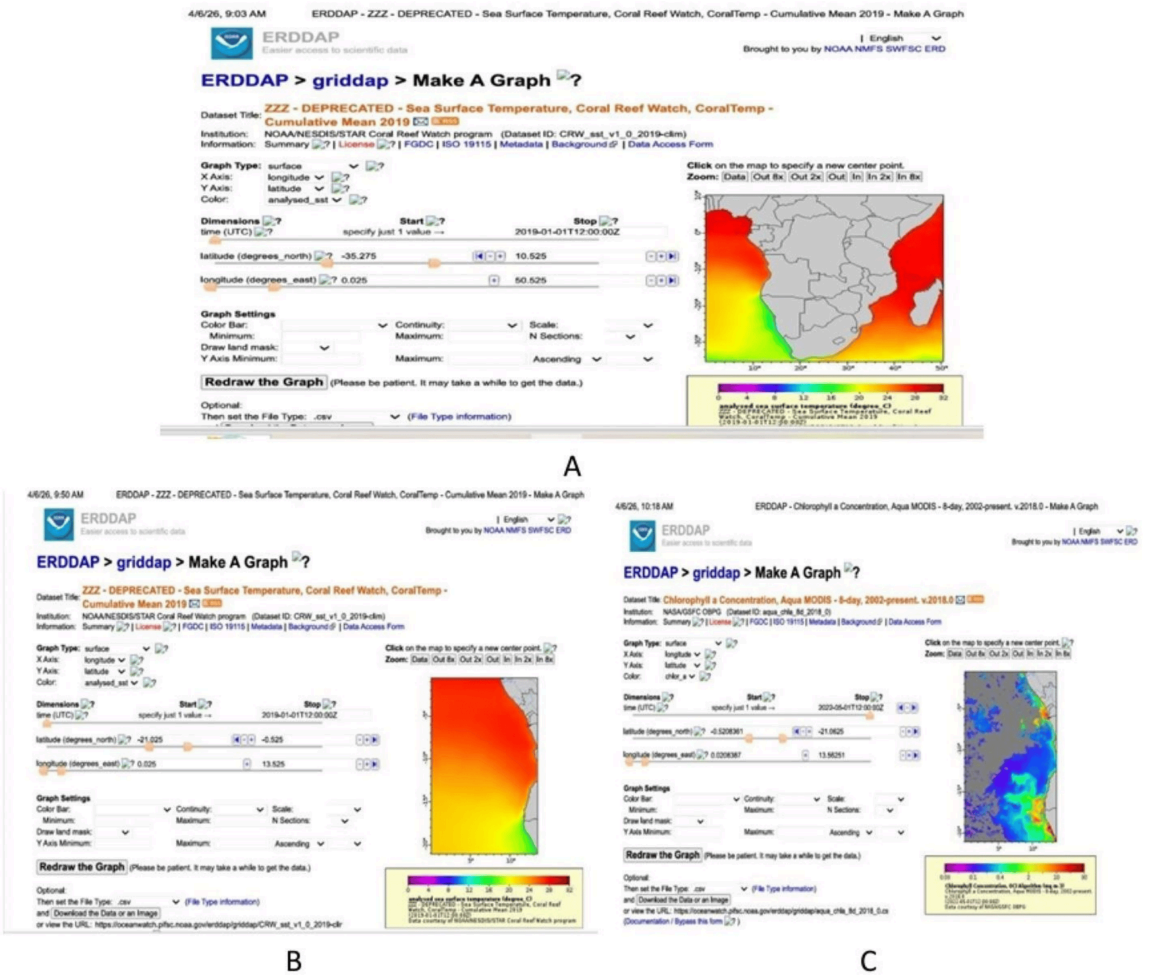

FIGURE 9: Illustrating the NOAA-ERDDAP data extraction graphical display. The top panel (A) illustrates the broad spatial search extent used to confirm accurate selection of the target African coastal region, while the bottom panels delineate the refined boundaries of the primary study area within the Atlantic Tropical Southeast (ATSE) for SST (B) and Chlor_a (C) extractions.

NOAA, National Oceanic and Atmospheric Administration; SST, Sea Surface Temperature

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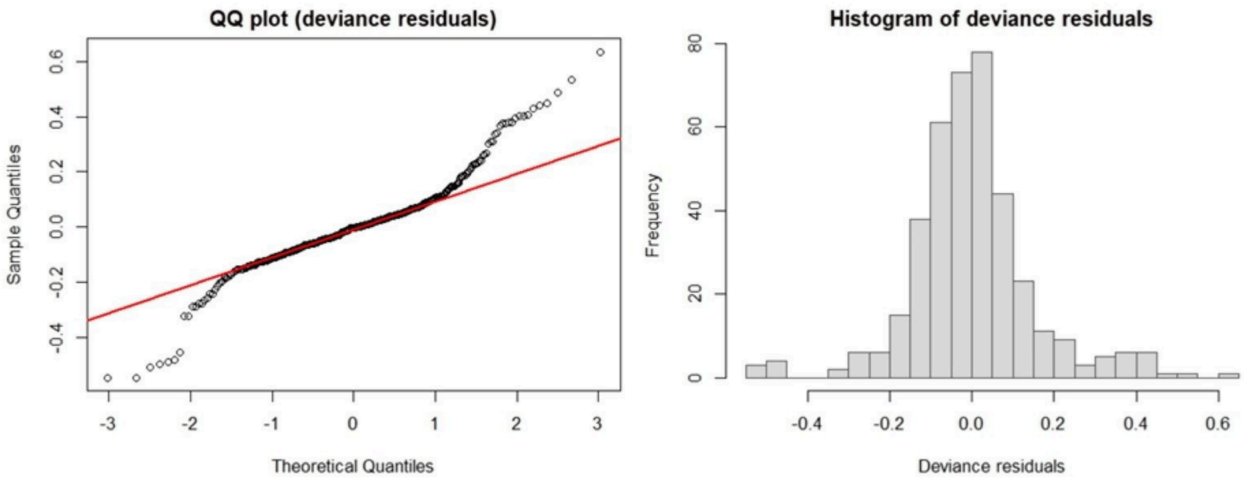

FIGURE 10: GAM model diagnostics (QQ Plot-left, and histogram of residuals-right) of Frigate Tuna in the Tropical Southeast Atlantic Ocean

GAM, Generalized Additive Model; QQ, Quantile-Quantile

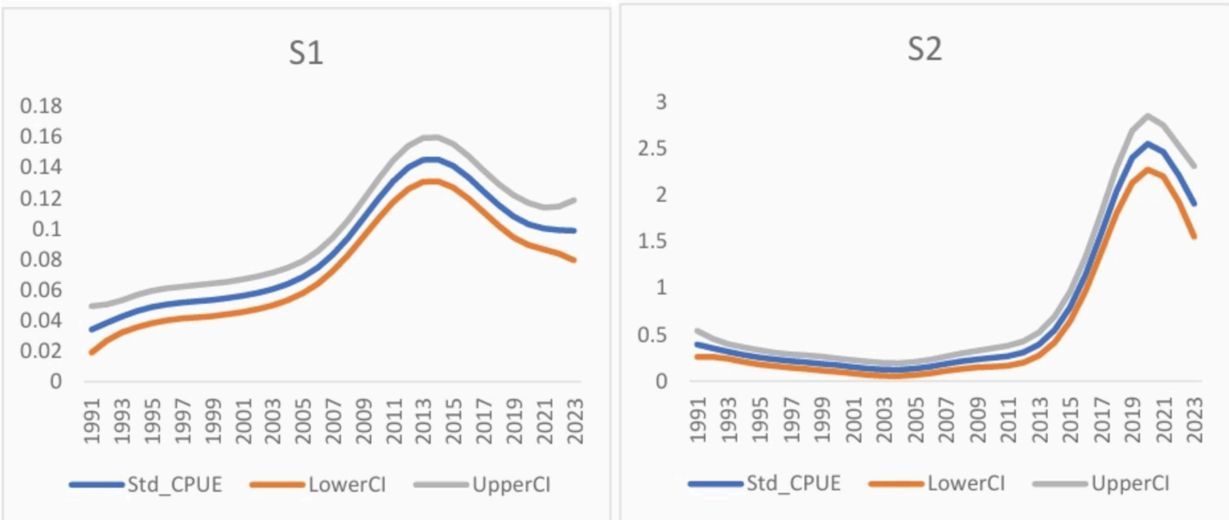

FIGURE 11: Standardized CPUE trends (midlines) for Scenarios S1 and S2, with the lower and upper bounds representing 95% confidence intervals.

CPUE, Catch-Per-Unit Effort

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Output	Statistic	S1	S2
Model specification	Family	Gaussian	Gaussian
	Formula	log(CPUE + 1) ~ *s*(Year, *k* = 9) + *s*(Lat, *k* = 7) + *s*(Long, *k* = 7) + *s*(SST, *k* = 7) + *s*(SSS, *k* = 7) + *s*(Chlor_a, *k* = 7) + *s*(OSC, *k* = 7) + *s*(OSW, *k* = 7)	
Parametric coefficients	Estimate	0.05087	0.462041
	Std. Error	0.00114	0.007885
	t value	44.61	58.60
	P value	$<2 \times 10^{-16}$ ***	$<2 \times 10^{-16}$ ***
Smooth terms	*s*(Year)	edf = 6.750; Ref.df = 7.496; F = 45.537; $P < 2 \times 10^{-16}$ ***	edf = 7.582; Ref.df = 7.925; F = 158.082; $P < 2 \times 10^{-16}$ ***
	s(Lat)	edf = 5.434; Ref.df = 5.852; F = 41.612; $P < 2 \times 10^{-16}$ ***	edf = 1.000; Ref.df = 1.000; F = 2.440; $P = 0.11909$
	s(Long)	edf = 2.759; Ref.df = 3.404; F = 3.306; $P = 0.0164$*	edf = 1.000; Ref.df = 1.000; F = 0.014; $P = 0.90686$
	s(SST)	edf = 3.954; Ref.df = 4.666; F = 6.394; $P = 1.99 \times 10^{-5}$ ***	edf = 5.006; Ref.df = 5.587; F = 3.859; $P = 0.01547$*
	s(SSS)	edf = 1.813; Ref.df = 2.328; F = 0.564; $P = 0.7177$	edf = 1.000; Ref.df = 1.000; F = 0.191; $P = 0.66248$
	s(Chlor_a)	edf = 1.249; Ref.df = 1.438; F = 3.918; $P = 0.0520$.	edf = 1.000; Ref.df = 1.000; F = 0.720; $P = 0.39660$
	s(OSC)	edf = 1.001; Ref.df = 1.002; F = 1.417; $P = 0.2348$	edf = 1.739; Ref.df = 2.222; F = 1.480; $P = 0.20309$
	s(OSW)	edf = 4.131; Ref.df = 4.863; F = 9.984; $P < 2 \times 10^{-16}$ ***	edf = 4.257; Ref.df = 4.998; F = 4.210; $P = 0.00101$**
Model performance	Adjusted R^2	0.740	0.861
	Deviance explained	75.8%	86.9%
	–REML	–861.16	–115.34
	Scale estimate	0.00051478	0.024622
	n	396	396

TABLE 5: GAM smooth term significance (fit diagnostics) for CPUE Scenarios S1 and S2 (Family: Gaussian).

CPUE, Catch-Per-Unit of Effort; GAM, Generalized Additive Model. Significance codes: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; . $P < 0.10$.

Additional Information

Author Contributions

All authors have reviewed the final version to be published and agreed to be accountable for all aspects of the work.

Concept and design: Komba Jossie Konoyima

Acquisition, analysis, or interpretation of data: Komba Jossie Konoyima

Drafting of the manuscript: Komba Jossie Konoyima

Critical review of the manuscript for important intellectual content: Komba Jossie Konoyima

Disclosures

Plant subjects: All authors have confirmed that this study did not involve any herbarium specimen. **Human subjects:** All authors have confirmed that this study did not involve human participants or tissue. **Animal subjects:** All authors have confirmed that this study did not involve animal subjects or tissue. **Conflicts of interest:** In compliance with the ICMJE uniform disclosure form, all authors declare the following: **Payment/services info:** All authors have declared that no financial support was received from any organization for the submitted work. **Financial relationships:** All authors have declared that they have no financial relationships at present or within the previous three years with any organizations that might have an interest in the submitted work. **Other relationships:** All authors have declared that there are no other relationships or activities that could appear to have influenced the submitted work.

Data Availability Statements

The datasets (and/or code) supporting this study are available from the corresponding author upon reasonable request.
https://www.iccat.int/Data/t2ce_PS1991-2024_bySchool.zip

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