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Fishery Bulletin
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Spatiotemporal dynamics of dolphinfish (*Coryphaena hippurus*) in the western Atlantic Ocean

Matthew D. Damiano (contact author)[1]
Mandy Karnauskas[2]
Wessley Merten[3]
Jie Cao[4]

Email address for contact author: matt.damiano@noaa.gov

[1] Cooperative Center for Marine and Atmospheric Studies
University of Miami
4600 Rickenbacker Causeway
Miami, Florida 33149
Present address: Southeast Fisheries Science Center
National Marine Fisheries Service, NOAA
75 Virginia Beach Drive
Miami, Florida 33149

[2] Southeast Fisheries Science Center
National Marine Fisheries Service, NOAA
75 Virginia Beach Drive
Miami, Florida 33149

[3] Beyond Our Shores Foundation
P.O. Box 3506
Newport, Rhode Island 02871

[4] Center for Marine Sciences and Technology
Department of Applied Ecology
North Carolina State University
303 College Circle
Morehead City, North Carolina 28557

Abstract—Dolphinfish (*Coryphaena hippurus*) are caught throughout the western Atlantic Ocean over varying spatial and temporal scales. Prior attempts to quantify the population dynamics of dolphinfish in this region have been inhibited by an inability to model the spatiotemporal dynamics of this stock. We fit a seasonal vector autoregressive spatiotemporal (VAST) model to quantify the spatiotemporal dynamics of western Atlantic dolphinfish, to estimate standardized relative indices of abundance during 1986–2022 at regional scales, and to estimate changes in spatial distribution. The magnitude of abundance was greatest during spring and summer in northern spatial strata and was comparable over seasons in southern spatial strata. Abundance of dolphinfish appeared to be stable during 1986–2018 and then declined during 2019–2022. This trend occurred in all regions, except for in Atlantic waters from Cape Hatteras, North Carolina, to the southern border of Georgia, where abundance remained stable during 2019–2022. No shift in the distribution of the population was detected, but regional patterns of abundance provide insight into changes in the timing of availability. This study resulted in the first standardized index of relative abundance to capture the spatiotemporal dynamics of western Atlantic dolphinfish. These results have increased our understanding of the population dynamics of this species in this region and should prove useful in future attempts to manage the population at different spatial and temporal scales.

Manuscript submitted 21 August 2023.
Manuscript accepted 18 March 2024.
Fish. Bull. 122:26–43 (2024).
Online publication date: 3 April 2024
doi: 10.7755/FB.122.1-2.3

The dolphinfish (*Coryphaena hippurus*) is a mid-level trophic predator and migratory, cosmopolitan species of pelagic fish that is found throughout tropical and subtropical regions (Palko et al., 1982; Luckhurst, 2017; Moltó et al., 2020). The stock structure of dolphinfish caught in the western Atlantic Ocean, specifically in the southern extent of Food and Agriculture Organization of the United Nations (FAO) major fishing area 21 (the northwestern Atlantic Ocean) and FAO major fishing area 31 (the western Central Atlantic Ocean), is not precisely known (Damiano, 2023). Using analyses of size composition in catches over space, life history traits, and allelic frequencies, Oxenford and Hunte (1986) found evidence of a northern and southern stock in the western Central Atlantic Ocean and hypothesized that there are 2 unique seasonal migration patterns. The northern stock migration has been defined by seasonal movements into waters of Puerto Rico during late fall and early winter, movement along the Greater Antilles and Bahamas and into Florida waters during the spring, then into waters of the eastern United States during late spring and summer, and finally outward toward Bermuda during late summer (Oxenford and Hunte, 1986; Oxenford, 1999).

Tagging experiments conducted by Merten et al. (2014a, 2014b, 2016) revealed further complexity in the stock connectivity between dolphinfish caught along the eastern United States, in the Caribbean Islands, and in the Caribbean Sea, expanding the northeastern circuit to include coastal waters along the northeastern United States, and dolphinfish caught along an additional pathway to waters in Florida from the Caribbean Sea and through the Straits of Florida (Damiano, 2023). The connectivity between populations of dolphinfish in the western Atlantic Ocean and the Gulf of Mexico remains unclear (Damiano, 2023). Results from the DNA sequencing conducted by Merten et al. (2015) indicate shallow genetic differences among dolphinfish caught along the eastern United States and parts of the Caribbean Sea, and although the DNA sequencing results do not present conclusive evidence of a single stock, multiple subpopulations have been identified at smaller geographic scales in other ocean basins (Duarte-Neto et al., 2008; Ochoa-Zavala et al., 2022). Strong genetic separation of populations is likely driven by oceanographic barriers (Maggio et al., 2019), of which there are none known for the regions composing the western Atlantic Ocean (Damiano, 2023). However, despite this uncertainty, sufficient evidence exists of stock mixing and movement linkages in dolphinfish caught in the eastern United States and parts of the Caribbean Sea (Merten et al., 2014a, 2015, 2016), and that evidence indicates the need to model the spatiotemporal dynamics of a western Atlantic stock (Damiano, 2023).

According to a recent review of the condition of international dolphinfish fisheries in the western Central Atlantic Ocean that builds on the work of Mahon (1999), dolphinfish continue to support numerous high-value commercial, recreational, and artisanal fisheries at different seasonal and spatial scales (Merten et al., 2022a). Management of dolphinfish in the western Atlantic Ocean falls under the purview of the International Commission for the Conservation of Atlantic Tunas, but landings of this species are labeled as those of *other fishes* along with commercial bycatch taxa and therefore are not actively managed (Merten et al., 2022a).

In the eastern United States, the dolphinfish is managed under the Dolphin and Wahoo Fishery Management Plan by the South Atlantic Fishery Management Council (SAFMC, 2003). The annual catch limit for this species in the eastern United States is determined by using an average of past catches; this approach is a data-limited management procedure employed when biological reference points cannot be reliably estimated from an assessment model (Prager[1]). At the state level, effort-reducing and size-based management measures, such as bag limits and minimum size limits, are implemented for recreational and for-hire fisheries, but not all states implement both types of measures (SAFMC, 2003; Damiano, 2023).

The Caribbean Fishery Management Council, also a U.S. management body, and the Western Central Atlantic Fishery Commission, established by the FAO, do not have fishery management plans for dolphinfish, but they provide some monitoring and guidance for sustainable management of dolphinfish (Damiano, 2023). Practical management in Caribbean island waters and the Caribbean Sea falls to individual island nations and countries and territories of the Americas (Mahon, 1999; Merten et al., 2022a).

Such a lack of spatially consistent management measures is uncommon for transboundary stocks for which management and governance normally must adhere to an international policy (Levesque, 2008). Despite advances in spatiotemporal models and enhanced knowledge of the stock structure and movement connectivity of dolphinfish in the western Atlantic Ocean, no indices of relative abundance and no stock assessments are based on explicit modeling of the spatiotemporal dynamics of the population or subpopulations that make up this stock (Damiano, 2023). There are several other concerns regarding the western Atlantic stock. Lynch et al. (2018) reported a negative trend in estimated abundance of dolphinfish throughout the western Central Atlantic Ocean on the basis of catch per unit of effort (CPUE) data from the U.S. pelagic longline (U.S. PLL) logbook for the period 1987–2013. In addition, 23 nations still do not report landings of dolphinfish to the FAO (Merten et al., 2022a), and increases in sea-surface temperatures (SSTs) due to climate change may affect stock productivity and distribution (Barange et al., 2018; Damiano, 2023).

As is the case for highly migratory species, such as the swordfish (*Xiphias gladius*) and tuna species, catch and effort information come primarily from fishery-dependent sources (Forrestal et al., 2019), and apart from tagging programs, there are no fishery-independent data collection or monitoring programs for dolphinfish. Sources of fishery-dependent data, such as landings and CPUE data, also have mostly been disparate over both space and time for this species (Rose and Hassler, 1968; Mahon, 1999; Arocha et al., 2021; Merten et al., 2022a; Damiano, 2023). Consequently, past efforts to model the population dynamics of dolphinfish in the western Atlantic Ocean have generally been accomplished by using a surplus production model that has been fit to an index of relative abundance derived from fishery-dependent CPUE information for a discrete subsection of the stock's distribution (Damiano, 2023). Each of these cases has involved fitting standardization models to CPUE data (Prager[1]; Parker et al.[2]; Kleisner, 2008) in order to develop model-based indices that address the commonly violated assumption of constant catchability (Maunder and Punt, 2004), then fitting a surplus production model.

In each of these efforts, CPUE data were not sufficiently informative because of short time series, "one-way trip" patterns, or other common features of fishery-dependent data (Maunder et al., 2006; Magnusson and Hilborn, 2007), and their use resulted in highly uncertain estimates of biological reference points that could not be

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[1] Prager, M. 2000. Exploratory assessment of dolphinfish, *Coryphaena hippurus*, based on U.S. landings from the Atlantic Ocean and Gulf of Mexico, 18 p. Southeast Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Beaufort, NC. [Available from website.]

[2] Parker, C., K. M. Kleisner, and J. S. Nowlis. 2006. Preliminary assessment of the western Central Atlantic dolphinfish (*Coryphaena hippurus*) stock: a Caribbean regional fisheries mechanism project, 13 p. Sustainable Fisheries Division Contribution SFD-2005-041. [Available from Sustain. Fish. Div., Southeast Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, 75 Virginia Beach Dr., Miami, FL 33149.]

used to inform fisheries management. Kleisner (2008) accurately concluded that for assessment of dolphinfish to be successful, estimating robust indices of relative abundance must be employed with new techniques that account for spatiotemporal structure in observed catch data (Damiano, 2023).

The spatiotemporal dynamics of dolphinfish in the western Atlantic Ocean are also likely linked to SST (Kleisner, 2008), given that dolphinfish reproduce year-round within their optimal thermal habitat (Schwenke and Buckel, 2008; Merten et al., 2015; Schlenker et al., 2021) and that high catch rates are associated with warm fronts with SSTs near 24–25C° (Farrell et al., 2014) and with mats of *Sargassum* macroalgae (Farrell et al., 2014; Rudershausen et al., 2019). Lynch et al. (2012) developed a 2-stage delta-generalized linear mixed model (GLMM) capable of modeling temperature regimes and habitat use of pelagic fish. They applied this method by fitting a delta-GLMM to CPUE data for highly migratory species, including dolphinfish, from the U.S. PLL logbook for the period 1987–2013 and by treating *year* as a random effect (Lynch et al., 2018). The indices derived by Lynch et al. (2018) are currently the most robust indices of relative abundance for dolphinfish in the western Atlantic Ocean. Although the majority of dolphinfish landings that are reported within the western Atlantic Ocean come from recreational fisheries (Merten et al., 2022a), the U.S. PLL logbook remains the most robust data set because of the long time series of observations of dolphinfish made at the fishing set level, which is a fine temporal resolution, throughout the western Atlantic Ocean.

Spatiotemporal autocorrelation is often present in commercial data because sampling (fishing) by fishing fleets is preferential and not random (Maunder and Punt, 2004). Spatiotemporal autocorrelation can lead to positively biased estimates of abundance (Xu et al., 2018), particularly for undersampled regions (Pennino et al., 2019). Lynch et al. (2018) noted that future work should consider other treatments of spatiotemporal data when estimating indices of relative abundance from fishery-dependent data and made specific reference to geostatistical delta-GLMMs (Thorson et al., 2015). Geostatistical delta-GLMMs include the use of vector autoregressive spatiotemporal (VAST) models that are built on a 2-stage modeling philosophy similar to that of a delta-GLMM. In a VAST model, covariates can be assigned specifically to effects related to environmental conditions or habitat and to catchability, spatial and spatiotemporal variation can be estimated explicitly as random effects, and spatiotemporal autocorrelation can be estimated (Thorson et al., 2015; Thorson, 2019) instead of implicitly assuming that sampling over space is independent (Conn et al., 2017). In the model in the R package VAST, the space over which spatial and spatiotemporal processes are measured can also be treated as being evenly distributed to address the unbalanced and preferential nature of sampling in fishery-dependent data (Thorson, 2019).

Findings from several studies indicate that spatiotemporal models can be used to reliably estimate indices of relative abundance from fishery-dependent data (Maunder et al., 2020; Ducharme-Barth et al., 2022; Hansell et al., 2022). The use of VAST models fit to data has generally resulted in improved estimation of abundance (Thorson et al., 2020; O'Leary et al., 2022) and of spatial population dynamics (Cao et al., 2017), with success demonstrated when models have been fit to fishery-dependent longline data for other highly migratory pelagic fish species, such as tunas (Maunder et al., 2020; Hansell et al., 2022). Our goals were to quantify the spatiotemporal dynamics of dolphinfish in the western Atlantic Ocean and to develop a model-based index of relative abundance that is unaffected by variation over space and time. Additionally, we sought to answer the following questions with our study:

1. Can the VAST model be used to estimate the seasonal patterns in the spatiotemporal dynamics of the density of the dolphinfish population in the western Atlantic Ocean?
2. How do the spatiotemporal dynamics of dolphinfish differ at regional scales?
3. Has a range shift occurred at the population level for dolphinfish in the western Atlantic Ocean?
4. Do estimates from use of the VAST package reveal spatiotemporal signals similar to those found in other data sources?

Materials and methods

Fishery data

For our analysis, we used U.S. PLL logbook data from the National Marine Fisheries Service (NMFS). Although the fishing effort of the U.S. PLL fleet is not uniform over space and time (Lynch et al., 2018), the logbook data contain 37 years of detailed catch and effort information on dolphinfish to the longline set level and compose the only data set with long-term observations collected over nearly the full extent of the geographic range of western Atlantic dolphinfish. Additionally, the dolphinfish, although targeted by the fleet, is not the primary target species of the U.S. PLL fleet, which primarily targets the swordfish and tunas (Luckhurst, 2017). Therefore, dolphinfish sampling (i.e., CPUE) is less likely to be biased by preferential sampling that results from the targeting behavior of the fleet. Vessels in the U.S. PLL fleet report the date and location of catch to the set level, SST, the type of gear and bait used, the number of hooks per set, whether dolphinfish were targeted or not, the number of dolphinfish caught, and the numbers of dolphinfish discarded dead and discarded alive. We used all logbook data from reports of catch in the western Atlantic Ocean for which latitude, longitude, SST, and CPUE information were available. The data we used contain approximately 255,000 observations, of which approximately 160,000 were observations in which zero encounters with dolphinfish were recorded.

Nominal catch calculation

We treated the number of hooks used in a longline set as the unit of effort (Lynch et al., 2012). We calculated the nominal CPUE as the number of dolphinfish caught per 1000 hooks, including any dolphinfish caught and retained or caught and discarded, whether dead or alive. We explored the number of set hours as an additional measure of effort; however, the results of analysis of catch versus hourly effort indicate a gear saturation effect in which CPUE declines exponentially after 5 h of soak time. This decrease in CPUE violates the assumption that the probability of catch is the same over every hour (Peterson et al., 2017; Hansell et al., 2022).

Spatial domain

The spatial domain included what we have defined as the western Atlantic Ocean, which extends approximately from 0°N to 55°N and from 25°W to 86°W. We stratified the spatial domain by using the discrete management areas for the U.S. PLL fishery described in the U.S. PLL logbook data set. These areas are defined, east to west and north to south, as follows: the region closest to the coast from Cape Cod, Massachusetts, to Cape Hatteras, North Carolina, which in the logbook data set is referred to as the *Mid-Atlantic Bight* (MAB); northeast coastal waters (NEC), farther to the north and east from the MAB; northeast distant waters on the Grand Banks (NED); the region closest to the coast from Cape Hatteras to the southern border of Georgia, described in the logbook data set as the *South Atlantic Bight* (SAB); waters off the Florida east coast and around the Florida Keys (FEC); the eastern part of the Sargasso Sea (SAR); the region in the north-central Atlantic Ocean that forms the western part of the Sargasso Sea (NCA); the Caribbean Sea (CAR); and offshore waters (OFS) (Fig. 1) (Damiano, 2023). To map data, we used a custom extrapolation grid to encompass all strata (Damiano, 2023).

Seasonality

The VAST model was configured to estimate indices for 4 seasons to capture the pattern of seasonal availability throughout the range of dolphinfish in the Western Atlantic Ocean. We assigned seasonal IDs to U.S. PLL logbook data at the monthly level: *winter* included December of a given year and January and February of the following year; *spring* included March, April, and May of the same year; *summer* included June, July, and August of the same year; and *fall* included September, October, and November of the same year (Damiano, 2023). The VAST model was configured with a total of 148 time steps over 4 seasons and 37 years. We also explored a monthly time step.

Spatiotemporal model description

The models implemented in the VAST package (vers. 3.5.0; Thorson and Barnett, 2017) in statistical software R (vers. 4.0.3; R Core Team, 2020) were fit to nominal CPUE values to derive standardized indices of relative abundance. The model in the VAST package functions like a delta-GLMM, also called a *hurdle* or *delta* model, that separately models the probability of non-zero catches (i.e., positive encounters) and positive catch rates from each encounter (i.e., positive catch rates) (Thorson et al., 2015; Lynch et al., 2018). We used the binomial GLMM with a logit link for the first linear predictor and explored lognormal, gamma, and Tweedie distributions for the second linear predictor. We chose the delta-lognormal configuration so that we could compare the results with those of Lynch et al. (2018) and could report the optimal model configuration, which was identified on the basis of model diagnostics, by using the following equations:

$$P_{1,\mathrm{i}} = \beta_1\left(t_\mathrm{i}\right) + \omega_1\left(s_\mathrm{i}\right) + \varepsilon_1\left(s_\mathrm{i}, t_\mathrm{i}\right) + \sum\nolimits_{p=1}^{n_\mathrm{p}} \gamma_1\left(p\right) X\left(p, s_\mathrm{i}, t_\mathrm{i}\right), \text{ and} \tag{1}$$

$$P_{2,\mathrm{i}} = \beta_2\left(t_\mathrm{i}\right) + \omega_2\left(s_\mathrm{i}\right) + \varepsilon_2\left(s_\mathrm{i}, t_\mathrm{i}\right) + \sum\nolimits_{p=1}^{n_\mathrm{p}} \gamma_2\left(p\right) X\left(p, s_\mathrm{i}, t_\mathrm{i}\right), \tag{2}$$

where $P_{1,\mathrm{i}}$ = the probability of positive dolphinfish encounter for observation i;
$P_{2,\mathrm{i}}$ = the positive dolphinfish catch rates (i.e., number of dolphinfish caught per 1000 hooks) given that they were encountered, for observation i;
$\beta(t_\mathrm{i})$ = the intercept for each time step t for observation i;
$\omega(s_\mathrm{i})$ = the spatial variation that is constant over time for knot s for observation i;
$\varepsilon(s_\mathrm{i}, t_\mathrm{i})$ = the time-varying spatiotemporal autocorrelation variation for knot s and time step t for observation i;
$\gamma(p)$ = the habitat effect p on the univariate response variable;
n_p = the number of habitat covariates; and
$X(p, s_\mathrm{i}, t_\mathrm{i})$ = the value of covariate p in knot s in time step t for observation i.

Note that $\beta(t_\mathrm{i})$ was treated as an independent and identically distributed random effect. Because of the seasonality in availability of dolphinfish to the U.S. PLL fishery over space, we included *season* as a spatially varying random effect of habitat; this treatment is also the standard for seasonal implementations of a VAST model. The spatial processes, $\omega_1(s_\mathrm{i})$ and $\omega_2(s_\mathrm{i})$, and spatiotemporal processes, $\varepsilon_1(s_\mathrm{i}, t_\mathrm{i})$ and $\varepsilon_2(s_\mathrm{i}, t_\mathrm{i})$, were modeled as Gaussian Markov random fields (random effects) (Lindgren et al., 2011) with an isotropic Matérn covariance function (i.e., correlation over a 2-dimensional spatial grid). We conducted correlation analyses by using the COR (vers. 0.0.1; Guo, 2020) and corrplot (vers. 0.92; Wei and Simko, 2021) packages in R with spatially stratified nominal CPUE for each season to determine the appropriate spatiotemporal structure for the second linear predictor. Although

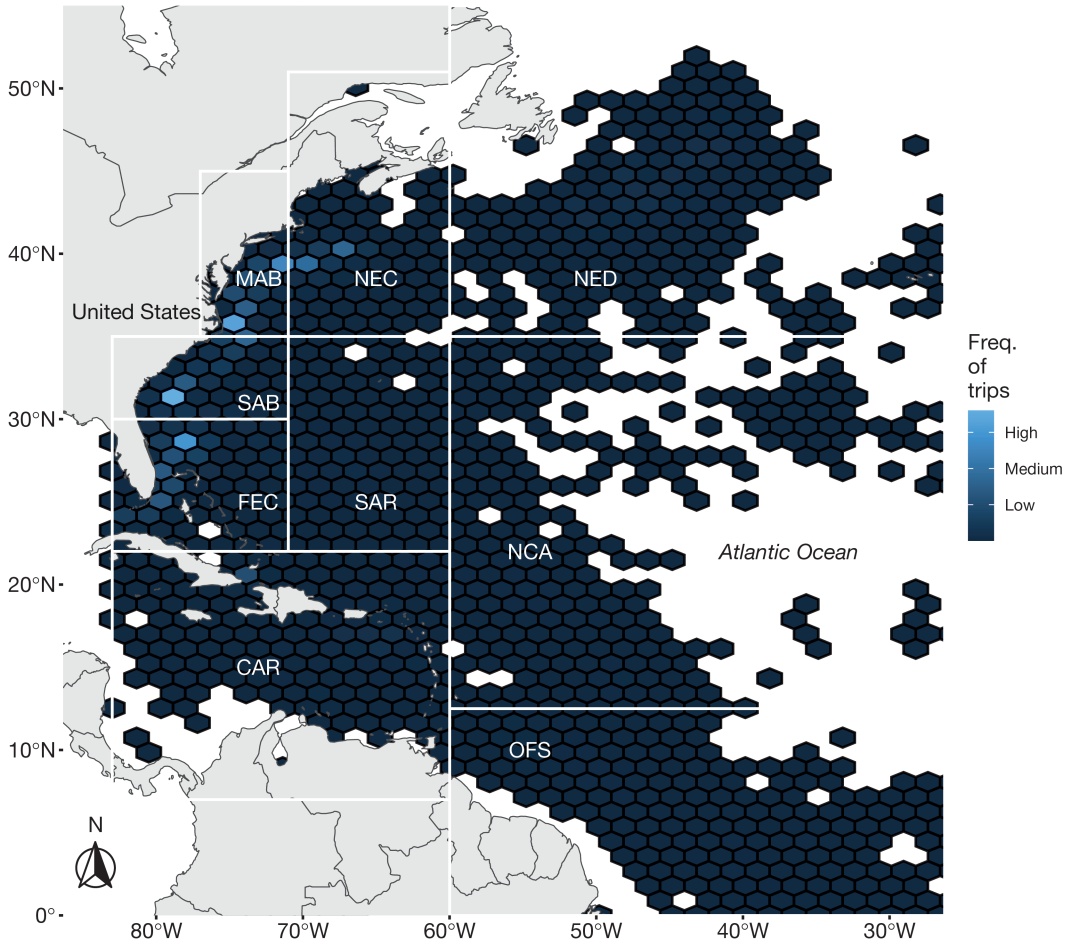

Figure 1

Map of the relative frequency of commercial trips in which dolphinfish (*Coryphaena hippurus*) were caught during 1986–2022, based on data from the U.S. pelagic longline logbook for the following management areas: the region closest to the coast from Cape Cod, Massachusetts, to Cape Hatteras, North Carolina, which in the logbook data set is referred to as the *Mid Atlantic Bight* (MAB); northeast coastal waters (NEC) farther to the north and east from the MAB; northeast distant waters on the Grand Banks (NED); the region closest to the coast from Cape Hatteras to the southern border of Georgia, referred to in the logbook data set as the *South Atlantic Bight* (SAB); waters off the Florida east coast and around the Florida Keys (FEC); the eastern part of the Sargasso Sea (SAR); the region in the north-central Atlantic Ocean that forms the western part of the Sargasso Sea (NCA); the Caribbean Sea (CAR); and offshore waters (OFS). Colors indicate relative frequency of trips made to the geographic coordinates within each hexagon.

correlation was high among some strata during specific seasons, there was no consistent pattern (Suppl. Fig. 1); therefore, we assumed that spatiotemporal random effects were independent and identically distributed. We fit the VAST model by using a mesh approach with 500 knots, the unit of measure over which to measure the spatial and spatiotemporal processes.

Parameters were determined through maximum likelihood estimation, in which fixed and random effects were integrated, by using the R package Template Model Builder (vers. 1.9.6; Kristensen et al., 2016). We used estimated log-scale densities to calculate indices as the predicted local density d for knots s and time step t multiplied by area a, summed over the total number of knots (n_s). In the VAST model, standardized indices of relative abundance are labeled as biomass in kilograms by default when the response is continuous CPUE (Thorson, 2019). However, we rescaled the index (I) estimates by using a constant so that the values would be unitless:

$$I\left(t\right) = \sum\nolimits_{s=1}^{n_s} \left(a\left(s\right) \times d\left(s,t\right)\right). \tag{3}$$

We rescaled the index for each time step t as a product of local density and area a over knots s summed over the total number of knots. We calculated the change in spatial distribution using the center of gravity, which is the estimated centroid of the population's distribution:

$$Z(t) = \sum_{s=1}^{n_s} \frac{\left(z(s) \times a(s) \times d(s,t)\right)}{I(t)}, \tag{4}$$

where $Z(t)$ = the center of gravity over time t that sums the center of gravity statistic z multiplied by area and density over the index I over the number of knots s.

The changes in population distribution were measured in kilometers in eastings and northings (Thorson et al., 2015). Following Li et al. (2014), we also calculated the center of gravity for the nominal effort data (Z_e), using the effort contained in the U.S. PLL logbook data set, as the sum of the product of seasonal effort (E_t) and space (i.e., latitude and longitude) (L_t) over the sum of total effort to explore spatial changes in the distribution of U.S. PLL effort:

$$Z_e = \frac{\sum (E_t L_t)}{\sum E_t}. \tag{5}$$

Model selection, sensitivities, and diagnostics

We identified the optimal configuration of the model described in the previous section on the basis of the percentage of deviance explained and Akaike information criterion (AIC) (Akaike, 1973). In the "Results" section, we report these values in relation to the null model, which was constant intercept-only and required for calculating the percentage of deviance explained. We also provide results for a time-varying intercept-only model. Model fit was evaluated by using the R package for residual diagnostics, DHARMa (vers. 0.4.6; Hartig, 2022); diagnostics for all models were acceptable, and the optimal model diagnostics are provided in Supplementary Figure 2.

Correlation analysis

The final research question was whether the VAST estimates could pick up spatiotemporal signals in other sources of data on dolphinfish. In order to address this question, we used the COR and corrplot packages to analyze correlations between indices of estimated abundance by spatial strata and season with independent catch time series. These data include recreational catch and effort information for the period 2002–2019 from the Large Pelagics Survey of private and for-hire recreational vessels conducted by the Marine Recreational Information Program (NMFS, website), commercial landings for fishing operations that were not longline in spring and summer in North Carolina and Florida during 1991–2021 (M. Karnauskas, personal commun.), and recreational dolphinfish tournament data for the period 2000–2019 from the Marine Recreational Fishing Program of the Puerto Rico Department of Natural and Environmental Resources (Rodríguez-Ferrer[3]). Analysis of correlations with other fisheries data sets, especially those from recreational sources, will help to determine if an index fit to commercial data is consistent with noncommercial fishery trends (Damiano, 2023). A description of the indices and catch time series that were analyzed is provided in Table 1.

Results

Optimal model selection

We experimented with several model configurations to explore the effects of covariates and alternate distributions. Excluding intercept-only models, only 3 models

Table 1

The time series and seasons used to estimate the indices of abundance, of dolphinfish (*Coryphaena hippurus*) in the western Atlantic Ocean by spatial strata, for which correlation analyses were conducted. The spatial strata include the following regions: the region closest to the coast from Cape Cod, Massachusetts, to Cape Hatteras, North Carolina (NC), which in the U.S. pelagic longline (U.S. PLL) logbook data set is referred to as the *Mid-Atlantic Bight* (MAB); the region closest to the coast from Cape Hatteras to the southern border of Georgia, referred to in the U.S. PLL logbook data as the *South Atlantic Bight*; waters off the Florida east coast and around the Florida Keys (FEC); and the Caribbean Sea (CAR). The time series include data from the Large Pelagics Survey (LPS) of the Marine Recreational Information Program, commercial landings in NC and Florida (FL) from the NOAA Southeast Fisheries Science Center, and data from the Marine Recreational Fishing Program (MRFP) of the Puerto Rico Department of Natural and Environmental Resources.

Region	Catch time series	Period	Seasons
MAB	LPS recreational catch and effort	2002–2019	Summer and fall
SAB, FEC	Hook-and-line catch in FL and NC	1991–2021	Spring and summer
CAR	MRFP recreational tournament	2000–2019	Winter, spring, and fall

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[3] Rodríguez-Ferrer, Y. 2022. Personal commun. Mar. Recreat. Fish. Progr., Puerto Rico Dep. Nat. Environ. Resour., 1375 Ave. Ponce de León, San Juan, Puerto Rico 00926.

converged to a solution. We attempted to fit set-level observations of SST using a 3-parameter basis spline function because of the association of dolphinfish with a relatively narrow, dome-shaped band of warm SSTs that varies over space and likely leads to positive catch rates (Farrell et al., 2014; Moltó et al., 2020; Schlenker et al., 2021). We also experimented with treating SST as a spatially varying random habitat effect. Given that the U.S. PLL targeted dolphinfish in only approximately 8% of observations during the period examined, we also tested one catchability covariate to account for variation in fleet behavior: a 3-level factor describing targeting behavior; in the U.S. PLL logbook data, most observations are assigned a *Yes* or *No* for targeting dolphinfish. For each observation with no targeting assignment, we added the letter *U*, for *Unknown*, in the blank cell. In this configuration, *targeting behavior* was treated as a spatially varying linear random effect. We considered *bait* as a potential catchability covariate, but bait type was nearly uniform throughout the data set. Therefore, it was not included.

We also attempted to model an individual *vessel* effect to account for spatiotemporal changes in fishing power (O'Leary et al., 2022). However, it either became computationally infeasible when used as a random effect, resulting in hundreds of thousands of new parameters, or resulted in computer memory allocation issues when treated as a fixed effect, likely because of approximately 700 individual vessels being treated as individual levels of a factor. We conducted a sensitivity analysis in which a geometric anisotropy spatial smoother was used in the optimal model; however, a solution could not be found with this model. We also experimented with gamma and Tweedie distributions for the observation model in the second linear predictor, but a solution could not be obtained with either model.

The optimal model (i.e., the basic seasonal spatiotemporal model) explained 30.8% of deviance and had an AIC of 880,221. The time-varying intercept model, which was used to explore the effect of temporal variation, explained 9.9% of deviance and had an AIC of 962,118. Adding SST as a spatially varying linear random effect resulted in a model with 31.6% of deviance explained and an AIC of 876,181. Although the percentage of deviance explained is greater and the AIC is lower for this model, the relationship between catch rates for dolphinfish and SST is not linear (Farrell et al., 2014). Furthermore, the relationship between catch rates and SST is likely confounded with seasonality, and the additional 0.8% of deviance explained may account for the variation in set-level SST observations.

The model that included both SST and *targeting behavior* as spatially varying random linear covariates related to habitat and catchability, respectively, explained 32.4% of deviance and had an AIC of 871,608. Although this model technically achieved the best performance metrics, using it did not result in different patterns in estimates of abundance or center of gravity. Still, use of this model did result in substantially larger standards for those estimated quantities, indicating that the addition of spatially varying random linear covariates, which added tens of thousands of additional random effects for estimation, did not alter the pattern and overall magnitude of trends obtained from the basic seasonal spatiotemporal model. This result further indicates that variation in estimates due to environmental effects or targeting behavior of fleets was confounded or "absorbed" by seasonal, spatial, and spatiotemporal process error. Therefore, we chose the basic spatiotemporal VAST model, which was the most parsimonious model, as the optimal configuration.

Spatiotemporal patterns in abundance

The total estimated seasonal index of relative abundance for the western Atlantic Ocean (Fig. 2) was defined by several peaks and troughs with no trend until 2018, after which the magnitude of subsequent peaks and troughs declined. Overall, the greatest levels of total abundance of dolphinfish occurred during 1986, 1995, and 2015, and abundance was generally highest in spring. The lowest abundance occurred in 2020. The trend of the total index among seasons was similar but stratified by magnitude; total relative abundance was greatest in spring, followed by summer and fall in some years, and then winter. Stratified by region, indices had considerable variability in trend and seasonality.

Estimates from northern coastal strata, such as the NEC, MAB, and SAB, had the highest variability among seasons, with higher abundances during spring and summer and lower abundances during fall and winter (Fig. 2); trends in abundance in spring and summer were similar through 2012 but began to deviate afterward. This pattern was most pronounced in the SAB, where abundance in summer declined to fall and winter levels after 2014 and abundance in spring remained relatively high and relatively stable during 2020–2022. Additionally, it is worth noting that the magnitude of abundance in fall increased relative to other seasons toward the north and the east (e.g., the magnitude of abundance in fall rose from the SAB to the MAB, from the MAB to the NEC, and from the NEC to the NED) (Fig. 2).

Estimates from the more southern strata and offshore strata (i.e., FEC, SAR, NCA, CAR, and OFS) indicate weaker or low variability in seasonality and mirror the index of estimated total abundance that has no trend until the decline during 2019–2022 (Fig. 2). Estimates were most certain (had the lowest standard errors) for abundance in the MAB and SAB, followed by those for abundance in the FEC and CAR, and were most uncertain (had the highest standard errors) for abundance in the offshore strata NED, SAR, and NCA (Fig. 2). These patterns in uncertainty were most likely due to higher and lower rates of sampling (i.e., fishing within those strata) respectively (Fig. 1). Furthermore, the highest estimates of abundance relative to the total index were found for the NCA, likely influencing the shape of the overall estimated trend in seasonal abundance.

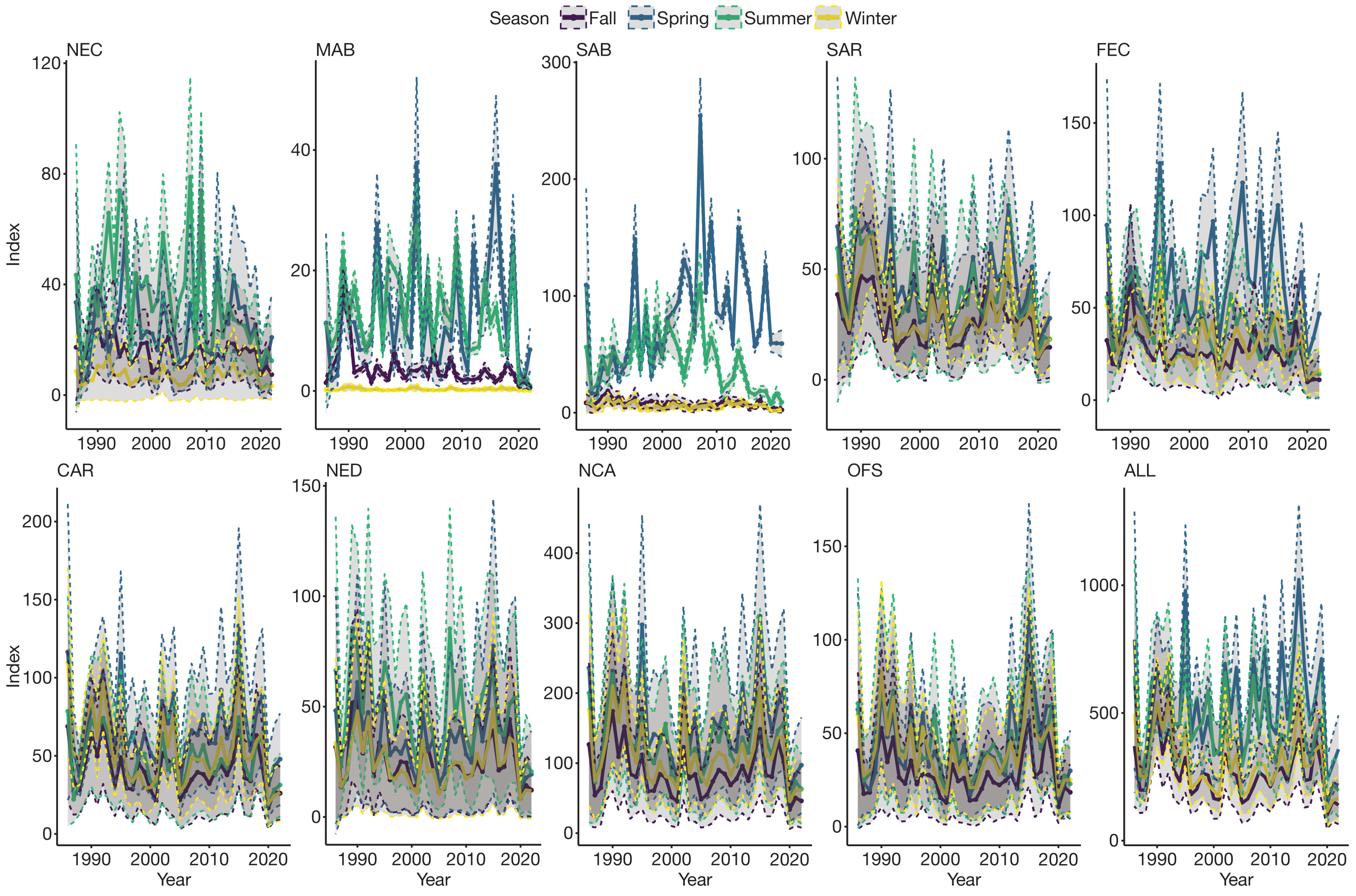

Figure 2

Standardized seasonal spatiotemporal indices of relative abundance for dolphinfish (*Coryphaena hippurus*) in the western Atlantic Ocean derived with data from the U.S. pelagic longline logbook. Indices were estimated for the period 1986–2022, by season, for all regions combined (ALL) and for each of the following management areas: northeast coastal waters (NEC), the region along the Atlantic coast referred to in the logbook data set as the *Mid-Atlantic Bight* (MAB), the region along the coast of the southeastern United States referred to in the logbook data set as the *South Atlantic Bight* (SAB), the eastern part of the Sargasso Sea (SAR), the east coast of Florida and the Florida Keys (FEC), the Caribbean Sea (CAR), northeast distant waters (NED), the western part of the Sargasso Sea in the north-central Atlantic Ocean (NCA), and offshore waters (OFS). For each season, a gray area outlined with colored dashed lines indicates the 95% confidence interval.

Shift in center of gravity

For the indices of estimated abundance, the eastings that approximate the spatial distribution from west to east from the bottom of the *y*-axis have no obvious trend (Fig. 3A). The northings that approximate the spatial distribution from south to north from the bottom of the *y*-axis also have no trend (Fig. 3B). For the nominal CPUE, the center of gravity in eastings indicates a strong westward shift (~120 km) during 1986–1994, then a gradual eastward shift during 1995–2022 (~90 km) that was consistent among seasons (Fig. 3C). The center of gravity in northings for nominal CPUE indicates an overall southern shift during 1993–2022 (~40 km), with some seasonal stratification: trends were similar between summer and winter and between spring and fall (Fig. 3D). We used box plots to visualize the average seasonal pattern in centers of gravity for the index of estimated abundance and for nominal CPUE (Fig. 4, A–D). The average seasonal pattern in the center of gravity for the estimated abundance index was defined by abundance shifting north and west as winter transitions to spring, slightly south and east during the transition to summer, and then south and east during fall (Fig. 4, A and B). For the nominal CPUE, the average seasonal pattern in the box plots more closely mirrored the time series shown in Figure 3, C and D, with a net southeastern movement throughout the year (Fig. 4, C and D).

Correlation analysis

Correlations among the VAST-estimated index and indices based on data sources independent of the U.S. PLL logbook, by spatial strata, were consistent with the timing of large migrations of dolphinfish and the overall seasonal pattern in the center of gravity (Fig. 4, A and B). The strong positive correlations between the Marine Recreational Fishing Program tournament catches in fall and the abundance estimates for winter and spring in the CAR (Fig. 5) are consistent with the timing of the movement of dolphinfish through the Antilles Current, which flows along the archipelago that separates the Caribbean Sea from the Atlantic Ocean, and with lower seasonal variation in abundance in this region compared with the variation in other regions (Fig. 3). Similarly, hook-and-line catches in North Carolina and Florida had the strongest correlations with estimates of abundance in the FEC and SAB during spring and summer months, and the CPUE data from the Large Pelagics Survey was most correlated with the estimate of abundance for the MAB in the fall (Fig. 5). Weak or negative correlations generally occurred between the estimated abundance index and the indices

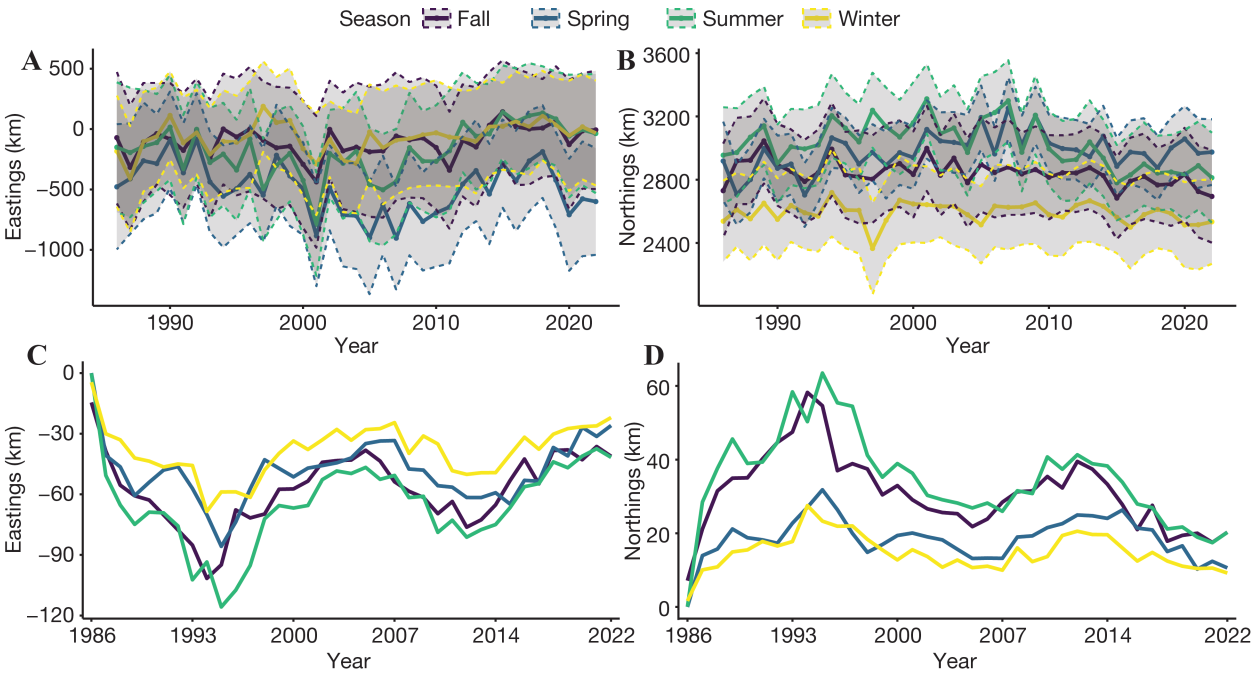

Figure 3

Seasonal estimates of the centroid or center of gravity of the distribution of dolphinfish (*Coryphaena hippurus*), by (**A**) eastings and (**B**) northings, in the western Atlantic Ocean during 1986–2022, based on abundance indices created with a vector autoregressive spatiotemporal model. Also shown are the seasonal centers of gravity calculated for nominal catch per unit of effort from the U.S. pelagic longline logbook for the same period, by (**C**) eastings and (**D**) northings. In the top panels, a gray area for each season outlined with colored dashed lines indicates the 95% confidence interval for that season.

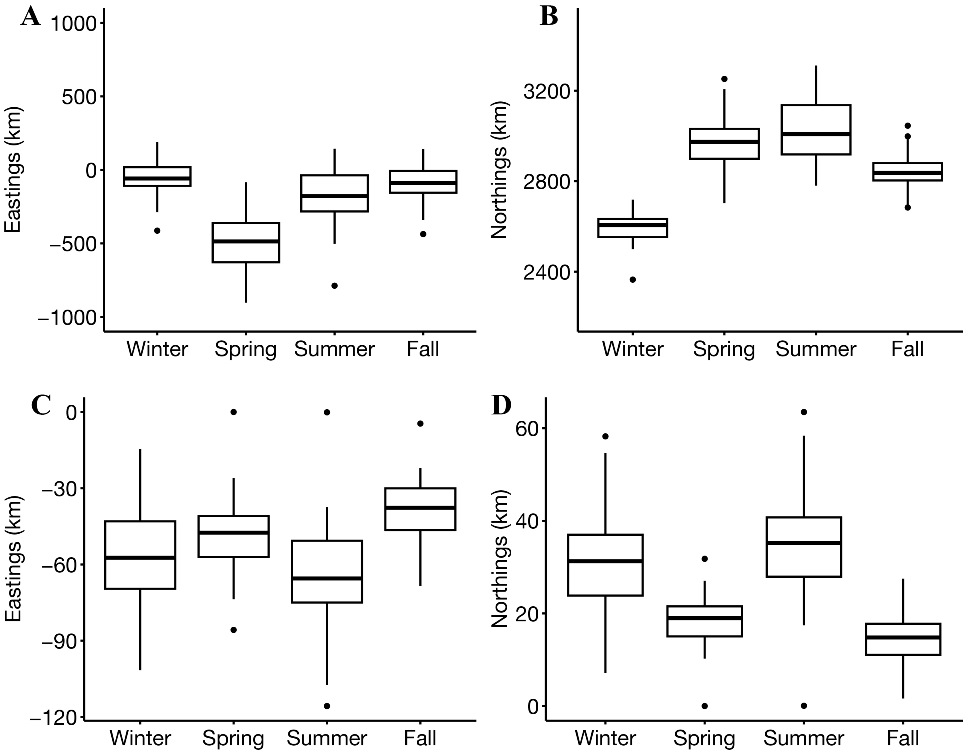

Figure 4

Box plots of seasonal estimates of the centroid or center of gravity of the distribution of dolphinfish (*Coryphaena hippurus*), by (**A**) eastings and (**B**) northings, in the western Atlantic Ocean during 1986–2022, based on abundance indices created with a vector autoregressive spatiotemporal model. Also shown are the seasonal centers of gravity calculated for the nominal catch per unit of effort from the U.S. pelagic longline logbook for the same time period, by (**C**) eastings and (**D**) northings. The thick line within the box indicates the median, the upper and lower parts of the box represent the first and third quartiles (the 25th and 75th percentiles), the whiskers extending above and below the box correspond to 1.5 times the interquartile range, and points represent values outside this range.

based on other data sources when season or region did not overlap (Fig. 5). Additionally, results of the correlation analysis provide some validation for estimated spatiotemporal patterns in abundance and indicate that using a VAST model to estimate spatial and spatiotemporal random effects can reveal broader spatiotemporal signals in the population dynamics of dolphinfish.

Discussion

Our model results reveal several important features of the population dynamics for western Atlantic dolphinfish. The overall abundance of dolphinfish in the western Atlantic Ocean was relatively stable during 1986–2018, followed by a decline during 2019–2022; seasonal patterns in abundance vary at different spatial scales. The stable trend in estimated abundance for 1986–2018 was somewhat surprising given the more pronounced negative trends found by Kleisner (2008) and Lynch et al. (2018). However, as of 2023, the U.S. PLL logbook has become a much larger data set than the one that was available during either of these previous studies, and in light of the results of our study (Fig. 2), the negative trends identified previously may have been driven by natural downward fluctuations in abundance that happened to occur during the terminal year of each analysis. Apart from the overall negative trend, our results are consistent with the general pattern in estimated abundance of dolphinfish that has been reported for the periods 1987–2005 (Kleisner, 2008) and 1987–2013 (Lynch et al., 2018). Furthermore, because we modeled spatial and spatiotemporal process errors, our results likely explain variation in numerous albeit aggregated latent processes (e.g., variation due to the behavior of the Gulf Stream or changes in fleet composition and behavior) that could not be explicitly modeled in previous research efforts.

Movement of dolphinfish generates seasonally and spatially explicit availability of abundance to many fisheries (Oxenford and Hunte, 1986; Mahon, 1999). Our results (Fig. 4, A and B) matched expectations for both the

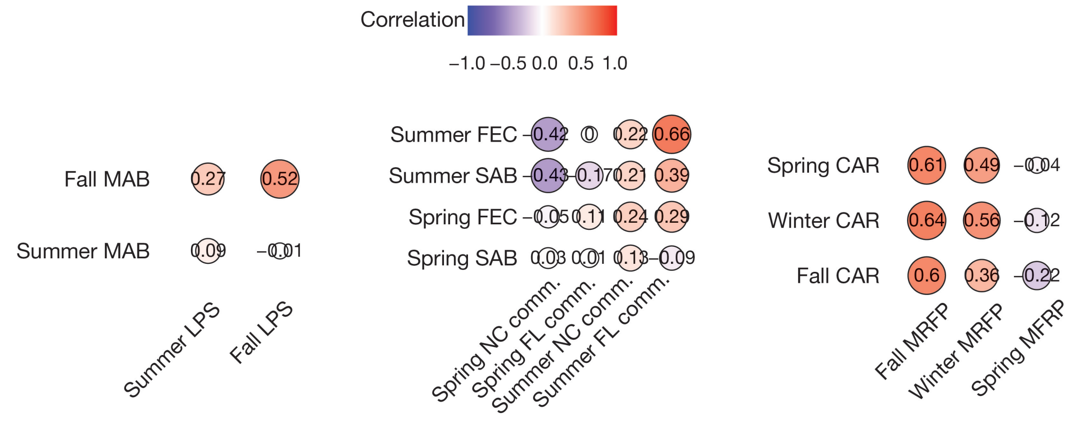

Figure 5

Correlations between indices of estimated abundance of dolphinfish (*Coryphaena hippurus*) in the western Atlantic Ocean and independent catch time series, by spatial strata and season. The correlations on the left side are between the indices of estimated abundance in summer and fall in the region closest to the coast from Cape Cod, Massachusetts, to Cape Hatteras, North Carolina, which in the U.S. pelagic longline logbook data set is referred to as the *Mid-Atlantic Bight* (MAB), and catch and effort data for the period 2002–2019 from the Marine Recreational Information Program's Large Pelagics Survey (LPS). The correlations in the middle are between estimated abundance indices for spring and summer in the region closest to the coast from Cape Hatteras to the southern border of Georgia, referred to in the logbook data set as the *South Atlantic Bight* (SAB), and in waters on the east coast of Florida and around the Florida Keys (FEC) and commercial catches (comm.) in spring and summer in North Carolina (NC) and Florida (FL) during 1991–2021. The correlations on the right side are between indices of estimated abundance in the fall, winter, and spring in the Caribbean Sea (CAR) and recreational tournament catch data for the same seasons during 2000–2019 from the Marine Recreational Fishing Program (MRFP) of the Puerto Rico Department of Natural and Environmental Resources.

seasonal distribution of abundance of dolphinfish and the spatiotemporal pattern of movement outlined by Oxenford and Hunte (1986) for the northern stock and expanded on by Merten et al. (2014a, 2014b, 2016). The estimates of abundance during spring and summer within strata along the East Coast of the United States were consistent with documented patterns of seasonal abundance (Merten et al., 2014a, 2015, 2016). Additionally, movement rates of dolphinfish slow in the SAB because of the Charleston Gyre (Merten et al., 2014a), an eddy off the coast of Charleston, South Carolina, that may be responsible for increased availability for extended pulses of fishing effort in spring and summer (Damiano, 2023). In the northern regions, the magnitude of abundance in spring and summer is substantially greater than in fall and winter, but this seasonal difference in magnitude (i.e., inter-seasonal variability) is lower in the southern regions.

The timing of the movement of the northern stock through the Caribbean Sea generates broad seasonal availability of dolphinfish to fisheries (Oxenford and Hunte, 1986), as reflected in estimates of abundance for southern spatial strata (Damiano, 2023). For example, although estimates of abundance in spring in the CAR were still the greatest among seasons, the magnitude of abundance in fall and winter were comparable with that of abundance in spring. These peaks in abundance in fall and winter may coincide with the movement of dolphinfish traveling to and from the Strait of Florida (Merten et al., 2014b, 2015) and the appearance of large dolphinfish (>90 cm in total length) in the waters of Caribbean islands (such large dolphinfish are caught in recreational tournaments; W. Merten, personal commun.), but these peaks may be more indicative of patterns in abundance of dolphinfish in certain U.S. territories in the Caribbean region than patterns in the broader CAR stratum (Damiano, 2023).

The increases in abundance in spring in the MAB and SAB during 2010–2018 and the associated decrease in abundance in summer in the SAB are also consistent with perceptions of commercial, recreational, and for-hire fishermen regarding local availability of dolphinfish in waters of North Carolina, including those north of the Outer Banks; they have observed either an increase in or stable catches of dolphinfish during the period approximately from 2015 through 2018 or 2019 (McPherson et al., 2022). The linear negative trend in abundance in the FEC region during 2015–2022 is similarly consistent with observations by stakeholders from eastern Florida and the Florida Keys of lower catches of dolphinfish in recent years leading up to a workshop held in 2021 (McPherson et al., 2022). Some local perceptions of abundance in Puerto Rico also have matched the recent decrease in estimated abundance in the CAR (Merten et al., 2022a; W. Merten, personal commun.).

These stakeholder observations provide some validation for the regional estimates of spatiotemporal indices of relative abundance (Damiano, 2023). Additionally, it is worth noting that the estimated trends in total abundance, and in abundance in the MAB, SAB, and FEC, strongly resemble those of the catch time series for dolphinfish from the Marine Recreational Information Program (NMFS, website). Further, the results of our correlation analysis indicate that the modeled spatial and spatiotemporal processes are identifying signals observed in data for other fisheries and in the Large Pelagics Survey that are independent of the U.S. PLL fleet. However, additional information, specifically from other Caribbean island nations and countries bordering the Caribbean Sea, would be required to determine if the index for the CAR is sufficiently representative of spatiotemporal dynamics of dolphinfish in the western extent of the Caribbean Sea where the U.S. PLL fleet fishes less than it does in U.S. territories (Fig. 1) (Damiano, 2023).

We suggest that there are 2 potential explanations (which are not mutually exclusive) for the recent decrease in abundance of dolphinfish during 2019–2022. The recent decline may be a lagged effect of a protracted period of high fishing pressure by commercial, recreational, and artisanal sectors throughout the western Atlantic Ocean (Damiano, 2023). Private recreational fishing in the coastal United States has been the dominant source of reported removals of dolphinfish in the western Atlantic Ocean (Merten et al., 2022a), and recreational effort linearly increased during 1986–2010 and then plateaued (NMFS, website). In the northeastern states located within the NEC and MAB, recreational catches have remained high (NMFS, website) despite the estimated decreases in abundance (Fig. 2). Consequently, these increases in recreational exploitation rates in specific areas may explain the recent reductions in abundance (Fig. 2, Suppl. Fig. 3).

With respect to commercial effort, although the number of trips of the U.S. PLL fleet has decreased since 1994 and effort has linearly declined (senior author, personal observ.), commercial fishing throughout the northwest Atlantic and western Central Atlantic Oceans in numerous countries in aggregate has linearly increased (FAO FishStat, website); this trend does not include those countries where fishing occurs but landings of dolphinfish are not reported (Merten et al., 2022a). In Barbados, landings of dolphinfish have slowly decreased while CPUE has remained relatively stable during 1994–2018 (Oxenford et al.[4]), with higher sustained effort coupled with reduced landings (i.e., availability of fish), indicating the possibility of an effect on stock productivity.

Concerning the effect of artisanal fisheries, artisanal fishing in Venezuela also is reportedly a large source of removals of dolphinfish in the Caribbean Sea (Arocha et al., 2021), and other Caribbean island countries are reportedly developing artisanal fleets that target pelagic fish, including dolphinfish, for which data are not available (W. Merten, personal commun.). Cumulatively, a scenario in which overexploitation is occurring throughout the western Atlantic Ocean is plausible, although this notion is subject to a high degree of uncertainty because of the lack of reporting.

Alternatively, or in concert with fishing activity, environmental effects may explain the overall trend and recent decline in estimated abundance. Mean SST is rising throughout the world (Garcia-Soto, 2021) and in the large marine ecosystems that compose the western Atlantic Ocean (Kessler et al., 2022). Within the western Atlantic Ocean, the most pronounced rates of increased warming are occurring in the North and northwest Atlantic Oceans (Saba et al., 2016; Kessler et al., 2022) due to a combination of natural climate variability and anthropogenic climate change (Chen et al., 2020). Consequently, northward shifts in the distribution of abundance have been observed for many species along the continental shelf of the Atlantic coast of the United States (Kleisner et al., 2017; Morley et al., 2018). Additionally, the heat transported northward by the Gulf Stream that had normally been quite variable has steadily declined since 2008 (Bryden et al., 2020), with a pronounced decrease occurring in 2020 that has since been followed by a period of uncharacteristically low heat transport (NOAA Atlantic Oceanographic and Meteorological Laboratory, website).

Dolphinfish appear to prefer warm water within a relatively narrow band (Moltó et al., 2020), and like individuals of other marine fishes, they will seek to remain within their optimal thermal habitat (Schlenker et al., 2021). However, temperature preferences of populations of dolphinfish are not geographically uniform; for example, dolphinfish prefer waters with temperatures of 22–24°C off the coast of Peru (Torrejón-Magallanes et al., 2019), but dolphinfish have been caught in waters as warm as 36–37°C in the Gulf of Oman, an arm of the Arabian Sea (W. Merten, personal commun.). A recent lab experiment conducted by Heuer et al. (2021) off eastern Florida confirmed that a dolphinfish's ability to physically move was optimal within the well-documented preference of western Atlantic dolphinfish for waters with temperatures of 24–29°C (Farrell et al., 2014; Merten et al., 2014b; Schlenker et al., 2021). However, exposure to temperatures beyond 31°C has resulted in reduced mobility or death for this species (Heuer et al., 2021). These results may explain the reduction in abundance of dolphinfish in spring in the FEC during 2015–2022 and subsequent divergence in abundance in spring and summer in the SAB (Fig. 2); the timing of fish migrating north from the Antilles may be occurring earlier during the year so that dolphinfish can avoid inhospitable temperatures. Salvadeo et al. (2020) estimated a northward shift in the population of dolphinfish in the eastern Pacific Ocean at similar latitudes. These distribution changes across different ocean basins are consistent with the broadscale effects of climate change on marine species globally (Poloczanska et al., 2013; Damiano, 2023).

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[4] Oxenford, H. A., D. Johnson, S.-A. Cox, and J. Franks. 2019. Report on the relationships between *Sargassum* events, oceanic variables, and dolphinfish and flyingfish fisheries, 25 p. Cent. Resour. Manage. Environ. Stud., Univ. West Indies, Cave Hill Campus. Bridgetown, Barbados. [Available from website.]

A shift in population distribution is also consistent with stakeholder observations in the FEC region: fishermen from the Florida Keys could not find dolphinfish in waters warmer that than the temperatures preferred by dolphinfish (>29°C), and fishermen from more northern regions (e.g., NEC, MAB, and SAB) have perceived more stable abundance and availability and done so earlier in the year (McPherson et al., 2022). Although it is highly plausible that dolphinfish exposed to near-lethal temperatures (>31°C) would move, the overall pattern in estimated abundance closely mirrors that of an SST "fingerprint" that indicates the recent weakening of the Atlantic Meridional Overturning Circulation and consists of cooling in the subpolar Atlantic Ocean and warming in the Gulf Stream region (Caesar et al., 2018; Ditlevsen and Ditlevsen, 2023). The behavior of these oceanographic features may indicate a more complex relationship between the Gulf Stream and spatiotemporal dynamics of dolphinfish.

Changes in fishing pressure and in the environment are likely contributing to the observed patterns in abundance, and data gaps make it challenging to discern the drivers of shifts with more accuracy. Additionally, some of the changes in fishing pressure and in the environment are aligned spatially and temporally, making it more challenging to disentangle the forces. For example, increases in landings from the Eastern Caribbean in 2014 coincided with significant changes in temperature, upwelling, and productivity in the region from Cape Hatteras through the Florida Keys (Craig et al., 2021). Sudden warming of the Florida Straits (Volkov et al., 2019), which connects the Gulf of Mexico and Atlantic Ocean and is a major migration pathway for dolphinfish, may also have contributed to changes in presence of dolphinfish. Most of the variation in these overlapping processes is likely absorbed by the estimation of spatial and spatiotemporal process errors with small contributions to deviance (i.e., variation) explained by modeling explicit habitat and catchability covariates. Differentiating between the drivers related to habitat and catchability will require more intensive analysis of patterns in ocean conditions and fishing exploitation in relation to patterns in the abundance discussed herein.

We recommend further investigation into the relationship between SST anomalies and the behavior of the Atlantic Meridional Overturning Circulation and Gulf Stream and the abundance of western Atlantic dolphinfish by using fine-scale fishery-independent oceanographic and movement data. Such an analysis would allow further differentiation between changes in fishing pressure and changes in the environment as drivers of distribution patterns and would provide some insight into whether these patterns will continue in the future given the shifts in temperature and current systems that are predicted to occur with climate change (Alexander et al., 2020; Damiano, 2023). Spatiotemporal models may not be appropriate for these analyses because of the tendency to aggregate estimated spatial and spatiotemporal process errors. Furthermore, although the seasonal patterns in the estimated center of gravity (Fig. 4, A and B) indicate that a generalized movement circuit was captured with the VAST model, we acknowledge that movement of dolphinfish is likely much more complex than the patterns described herein, potentially with patterns markedly different from those reported in the literature (Peterson[5]) and may include connectivity with regions not included in this analysis (e.g., the Gulf of Mexico and West Africa).

The configuration of the VAST model used in this study and described herein does not include any age or size structure in the population. Therefore, any spatiotemporal differences in ontogeny (e.g., documented differences in feeding habits) (Pincay-Espinoza and Varela, 2022), in spawning and larval distribution (Park et al., 2017), in changes in growth rate with size and age, or in vertical habitat use (i.e., association with fish aggregating devices or *Sargassum*) (Ortega-Garcia et al., 2022) were also likely to have been absorbed by the estimation of spatial and spatiotemporal random effects. No relationship was detected between influxes of *Sargassum* and CPUE for dolphinfish in the Eastern Caribbean (Oxenford et al.[5]), but large quantities of *Sargassum* may make fishing more difficult (i.e., fishing methods are negatively affected and fish are harder to detect and, therefore, less likely to be encountered). This notion warrants some investigation into the precise nature of the effects of *Sargassum* on catchability. We recommend that future research prioritize collection of age- or length-structure information sufficient for estimating age or size bins by using VAST or other spatiotemporal modeling techniques (Cao et al., 2020; Hansell et al., 2022).

The U.S. PLL logbook data have substantial spatial limitations and, therefore, uncertainty in eastern areas outside of the U.S. exclusive economic zone and the western extent of the Caribbean Sea (Fig. 1). This uncertainty is evidenced by stronger extrapolation to the CAR and OFS regions and by larger standard errors and confidence intervals for regionally stratified indices from those regions (Fig. 3). Furthermore, although the average pattern of the seasonal center of gravity (Fig. 4, A and B) appears to have captured the movement circuit of the northern stock, the dynamics of a purported southern stock found in the CAR and OFS strata are likely confounded (Oxenford and Hunte, 1986). Despite this caveat, fitting a VAST model to these data may help inform the estimation of abundance in neighboring cells in the model's extrapolation grid if both stocks occur. Future efforts to quantify the spatiotemporal dynamics of western Atlantic dolphinfish may benefit from calibrating the CPUE data from the U.S. PLL logbook with foreign longline fleet data sets from areas with low U.S. PLL fleet activity (O'Leary et al., 2022). Such an exercise will also help to determine the accuracy of this study's model extrapolations to undersampled regions and consistency with signals appearing in other data sets. Lastly, we acknowledge that the optimal VAST model was sensitive to different configurations, smoothers, and assumptions concerning the second linear predictor's error

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[5] Peterson, C. 2023. Personal commun. Southeast Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, 101 Pivers Island Rd., Beaufort, NC 28516-9722.

structure. Future efforts dedicated to teasing apart fishery and environmental drivers of the population dynamics of western Atlantic dolphinfish by using models that are not spatiotemporal may help elucidate reasons for these sensitivities.

The development of an index of relative abundance for western Atlantic dolphinfish through modeling with spatiotemporal variation is a vital step toward understanding the population dynamics of western Atlantic dolphinfish and improving the robustness of management measures (Damiano, 2023). Ideally, a spatially explicit stock assessment would be the next step toward determining stock status. However, despite advances in modeling software and in technology available for data collection and despite a growing citizen science data collection program (Merten et al., 2022b), the quality and temporal resolution of most data sources for western Atlantic dolphinfish have not changed radically since previous assessments were conducted in 2000 and 2006. Therefore, assessments would likely continue to be confined to surplus production models. Kleisner (2008) found that fitting surplus production models to geostatistical indices did not improve the ability to obtain reference points. Although McDonald et al. (2021) demonstrated that a spatially explicit biomass dynamics model can capture time-varying spatial patterns in both population processes and fishing effort, most removal data are available only at an annual time step, precluding modeling of the seasonal dynamics reported in this study.

If improved data collection or monitoring are not possible or stock status cannot be determined from an assessment, an alternative and perhaps more realistic use of the spatiotemporal index of relative abundance could be to guide an index-based management approach to setting catch advice (Apostolaki and Hillary, 2009; Little et al., 2011; Fischer et al., 2020; Sánchez-Maroño et al., 2021; Damiano, 2023). Indeed, empirical index-based management procedures that have been simulation-tested through a management strategy evaluation have been shown to have promise for data-limited stocks (Geromont and Butterworth[6]; Sagarese et al., 2019). For western Atlantic dolphinfish, correlations at various time lags should be analyzed to identify appropriate lead times, and rigorous evaluation through simulations or a management strategy evaluation should be pursued to test the robustness of such management procedures to alternative spatial and temporal scopes (Bosley et al., 2019; Cadrin et al., 2020) and to the substantial uncertainty found in this study and described herein. Additionally, a management strategy evaluation would be useful in determining if an empirical management procedure will be more or less responsive than, or as responsive as, the current catch-averaging strategy for quantifying the spatiotemporal dynamics of western Atlantic dolphinfish (Walter et al., 2023).

Conclusions

The dolphinfish possesses a unique life history characterized by fast growth and early maturation (Oxenford, 1999; Perrichon et al., 2019) that hypothetically makes individuals of this species capable of withstanding high levels of fishing pressure (Schwenke and Buckel, 2008; Damiano, 2023). The population abundance and distribution of dolphinfish in the western Atlantic Ocean appear to have been relatively stable during 1986–2018, but that period was followed by one of declining abundance during 2019–2022. High fishing pressure in concert with changing ocean conditions may be responsible for the recent decline in and changes to abundance at finer spatial scales (Damiano, 2023). Having used VAST models in our study, we provide the first spatiotemporal index of relative abundance for dolphinfish caught in the western Atlantic Ocean at seasonally and spatially explicit scales. The general consistency of our results with those of past studies and with stakeholder observations and the relatively strong spatiotemporal correlations with recreational catch time series indicate that our index is robust and reliably captures the spatiotemporal dynamics of western Atlantic dolphinfish (Damiano, 2023). This research addressed the need for a reliable index of relative abundance and improved upon the work of Kleisner (2008) and Lynch et al. (2018) by accounting for spatial and spatiotemporal variation in abundance of dolphinfish. Spatiotemporal modeling techniques, although complex and data-intensive, provide more information than nonspatial configurations (Berger et al., 2017) and are especially useful for standardizing fishery-dependent data (Maunder et al., 2020; Izquierdo et al., 2022) when improved monitoring programs are too costly (Damiano, 2023).

Resumen

El dorado (*Coryphaena hippurus*) se captura en todo el océano Atlántico occidental a distintas escalas espaciales y temporales. Los intentos previos de cuantificar la dinámica poblacional del dorado en la región se han visto inhibidos por la incapacidad de modelar la dinámica espaciotemporal de esta población. Ajustamos un modelo vectorial espaciotemporal, estacional y autorregresivo (VAST) para cuantificar la dinámica espaciotemporal del dorado del Atlántico occidental, para estimar los índices abundancia relativos estandarizados de durante 1986–2022 a escalas regionales y estimar los cambios en la distribución espacial. La magnitud de la abundancia fue mayor durante la primavera y el verano en los estratos espaciales del norte y fue comparable a lo largo de las estaciones en los estratos espaciales del sur. La abundancia del dorado pareció estabilizarse durante 1986–2018y luego disminuyó durante 2019–2022. Esta tendencia ocurrió

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[6] Geromont, H., and D. Butterworth. 2015. A review of assessment methods and the development of management procedures for data-poor fisheries, 198 p. University of Cape Town, Cape Town, South Africa. [Report produced for the FAO.] [Available from website.]

en todas las regiones, excepto en las aguas del Atlántico desde el cabo Hatteras, Carolina del Norte, hasta la frontera sur de Georgia, donde la abundancia se mantuvo estable durante 2019–2022. No se detectó ningún cambio en la distribución de la población, pero los patrones regionales de abundancia proporcionan información sobre los cambios en el momento de la disponibilidad. En el presente estudio se reporta el primer índice de abundancia relativa estandarizado que capta la dinámica espaciotemporal del dorado del Atlántico occidental. Estos resultados incrementaron nuestra comprensión sobre la dinámica poblacional de esta especie en la región y deberían resultar útiles en futuros intentos de manejar la población a diferentes escalas espaciales y temporales.

Acknowledgments

We would like to thank the NMFS and North Carolina Sea Grant for funding this research through the NMFS-Sea Grant Fellowship in Population and Ecosystem Dynamics (award no. NA20OAR4170468), J. Buckel and M. Karp for their insights during the development of this manuscript, and the peer reviewers for their helpful feedback.

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