



Dolphinfish (*Coryphaena hippurus*) distribution in relation to biophysical ocean conditions in the northwest Atlantic[☆]



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ABSTRACT

We analyzed temporal and spatial catch per unit effort (CPUE) of dolphinfish (*Coryphaena hippurus*) along the U.S. east coast using pelagic longline logbook data (1999–2007). A zero-inflated negative binomial model was fit using a variety of oceanographic variables to better understand distribution and abundance. The two most important dynamic oceanographic variables were sea surface temperature and chlorophyll-*a* concentration. We also used catch and release locations of dolphinfish caught by recreational fishermen (2002–2007) to compare conditions between datasets and for model evaluation. Dolphinfish CPUE was highest at 22–25 °C with a peak at 24 °C for the longline dataset, while recreational dolphinfish were caught in waters >19 °C with peak catches occurring at 27 °C. Dolphinfish CPUE was highest when chlorophyll-*a* concentration was <0.2 mg m⁻³, and the majority of recreational dolphinfish were captured in waters <0.1 mg m⁻³ with a peak at 0.02 mg m⁻³. We also found that a majority (73.26%) of recreational dolphinfish were caught in association with *Sargassum* spp., and larger dolphinfish (>82.3 cm FL) are caught more frequently outside of the floating mats.

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1. Introduction

Dolphinfish (*Coryphaena hippurus*) inhabit the tropical and subtropical waters of the world, where they are sought in commercial and recreational fisheries. Their distribution is generally limited by the 20° isotherm (Palko et al., 1982) and their local catch rate and abundance are influenced by inter-annual and seasonal temperature changes (Kleisner, 2009; Kraul, 1999; Norton, 1999; Zúñiga Flores et al., 2008). Along the east coast of the United States, archival tags revealed dolphinfish can tolerate temperatures as low as 16 °C, and they prefer surface waters (0–10 m) between 27.2 °C and 28.9 °C (Hammond, 2008). Recently, Kleisner (2009) found that

the seasonal abundance of dolphinfish along the east coast of the United States and Gulf of Mexico is heavily influenced by sea surface temperature and distance to temperature fronts.

While the seasonal ingress of dolphinfish off the U.S. east coast is correlated to temperature, it is also influenced by a voracious appetite to sustain their rapid growth rate (Palko et al., 1982; Schwenke, 2005). Prey items include a wide variety of perciformes, tetradontiformes, cephalopods, crustaceans, and juvenile conspecifics (Gibbs et al., 1959; Shcherbachev, 1973). Additionally, the western north Atlantic provides a unique habitat for dolphinfish due to an abundance of *Sargassum* spp. (hereafter 'Sargassum') production within and adjacent to the Sargasso Sea (Carpenter and Cox, 1974; McGillicuddy et al., 1998). The presence of dolphinfish around *Sargassum* has been well documented (Casazza and Ross, 2008; Moser et al., 1998; Oxenford, 1999; Rooker et al., 2006; Ross, 2004), and the relationship is generally characterized by the floating mats providing habitat for prey items and physical shelter from predators.

High growth rate, early maturity, and high fecundity have enabled sustained high exploitation rates of dolphinfish during recent decades. The fisheries for dolphinfish along the U.S. east coast include recreational and commercial fishing, but is traditionally dominated by the recreational sector (SAFMC, 2003). The estimated recreational landings data show that along the U.S. Atlantic coast approximately 3600 m (~1.3 million individuals) of

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dolphinfish were caught each year between 1981 and 2010 (NOAA, 2012a). In the recreational fishery for dolphinfish some fishermen utilize aggregations of *Sargassum*, while others are caught intentionally or incidentally in the troll fishery for tuna and marlin. In comparison, commercial fisheries take an additional 260 m each year (NOAA, 2012b). There are a handful of longline vessels that specifically target dolphinfish off the coast of North and South Carolina (SAFMC, 2003), but the majority of longline vessels are targeting tunas and swordfish (Beerkircher et al., 2004). Despite the increase and subsequent leveling off of annual harvest since the 1960's, there has been no evidence of changes in length-at-age or size-at-maturity for dolphinfish along the U.S. Atlantic Coast (Schwenke and Buckel, 2008).

Accurate understanding and prediction of species distribution and abundance is central to applications in ecology and fisheries management (Jennings et al., 2001). This is particularly challenging in the marine environment when considering a migratory species that primarily inhabits offshore waters. Consequently, current understanding of dolphinfish distribution and abundance must be done using catch reports, which are potentially biased due to the non-random nature of fishing fleet distribution. Some of the bias in catch data comes from gear selection and effort, while other sources are a result of the biophysical environment (i.e. habitat suitability). Fortunately, we can account for much of the bias and uncover environmental and habitat preferences that are associated with catch by using a combination of remote sensing technology and geostatistical modeling techniques (MacNeil et al., 2009; Minami et al., 2007; Nishida and Chen, 2004; Punt et al., 2000). Incorporating environmental information into catch estimates not only provides better understanding of catch rates, but can enable abundance estimates and ecological inference.

Linking oceanography to species distribution using spatial statistical models fall within the broad scope of species distribution models (SDM), which describe empirical correlations between where species are found (or not) and the associated biological and physical conditions at those locations (Franklin and Miller, 2009). Typically, species occurrence is modeled using a statistical model that links the environmental covariates to an explicit geographic location. Thus, SDMs are useful in fisheries ecology, biogeography, and conservation biology (Guisan and Thuiller, 2005). SDMs are the latest in a compilation of ecological methods such as climatic envelope modeling, ecological niche modeling, and habitat suitability modeling (Araújo and Peterson, 2012; Guisan and Thuiller, 2005; Guisan and Zimmermann, 2000). SDMs are strongly based on the niche concepts of Hutchinson (1957) and Grinnell (1917) and simply describe the environment–occurrence relationship in geographic space rather than in multidimensional niche space, and should always be evaluated for ecological realism (Franklin and Miller, 2009). SDMs encompass aspects of all of these concepts but do not actually model a species niche. Instead, SDMs are abstract geographic projections that are related to niches (Soberón, 2007).

Here, we apply the concepts of SDM to a fisheries dataset, in which occurrence is measured by fishermen catching dolphinfish. Using remotely sensed oceanographic data to understand the relationship between pelagic fish and their environment has recently become an effective method. The distribution of a variety of epipelagic species has been shown to be correlated with remotely sensed sea surface temperature (Block et al., 2001; Laurs et al., 1984; Teo et al., 2007; Weng et al., 2009), especially when the species is inhabiting the latitudinal extent of its range (Block et al., 1997). The use of satellite altimetry to estimate mesoscale oceanographic features has elucidated species' preferences for particular water masses such as cyclonic eddies and currents (Teo and Block, 2010; Teo et al., 2007; Zainuddin et al., 2006), as well as basin-wide influences on sea surface height (Howell and Kobayashi, 2006). Chlorophyll-*a* concentration is also an accurate predictor of

catch “hot spots” for albacore tuna (*Thunnus alalunga*) in the Pacific (Polovina et al., 2001; Zainuddin et al., 2006).

In this study, our goal is to understand catch patterns of dolphinfish in the U.S. Atlantic pelagic longline (PLL) fleet and recreational fisheries in relation to physical and biological oceanographic features. PLL gear is designed to target multiple species (e.g. shark, tuna, swordfish), and is also very effective at catching dolphinfish. The numbers of dolphinfish caught on each longline set were fit to a zero-inflated negative binomial model (ZINB), with local oceanographic conditions and gear specifics (i.e. hook depth and number of light sticks) as explanatory variables. The ZINB model is spatially and temporally explicit since geographic location and month are included as explanatory variables. Since recreational fishing accounts for the majority of dolphinfish taken off the U.S. Atlantic coast, we wanted to determine if dolphinfish were being taken in the same times/areas and under similar oceanic conditions. We evaluated the ZINB model predictions using an independent recreational dataset from the Dolphinfish Research Program (DRP, <http://dolphintagging.homestead.com/>) in order to determine if the model is transferable to the recreational fishery and how well it predicts dolphinfish presence using independent data. Evaluating our statistical model using a separate independent dataset is an appropriate method for gauging accuracy of the original model (Guisan and Zimmermann, 2000), as well as determining the efficacy of using a spatially explicit PLL model to predict recreational catch. Running the ZINB model using DRP catch data evaluation of the recreational dataset enabled comparative analysis as well as gauging the usefulness of direct comparison between commercial and recreational fishery data.

In addition to geographic location, the DRP recreational dataset included information on dolphinfish size and *Sargassum* presence or absence. We used these data to investigate the importance of *Sargassum* to the recreational catch of dolphinfish. We analyzed the size of fish caught within and away from *Sargassum* patches. The expectation is that *Sargassum* presence is a dominant feature of the DRP observations based on consistent scientific observation (Beardsley, 1967; Casazza and Ross, 2008; Coston-Clements et al., 1991; Moser et al., 1998; Rooker et al., 2006; Rose and Hassler, 1974) and anecdotal evidence. Rose and Hassler (1974) found that larger male dolphinfish were typically caught outside of *Sargassum* weed lines, while smaller females were found within the lines. We hypothesize that dolphinfish caught within the *Sargassum* patches will be smaller in size than dolphinfish caught outside of the patches.

The results from the current study will help to improve our understanding of the biophysical habitat of dolphinfish along the U.S. east coast and how their abundance changes seasonally and in relation to specific oceanographic conditions. Dolphinfish are an underpinning to the offshore recreational and pelagic longline commercial fisheries and knowledge of temporospatial abundance is crucial for dolphinfish management and conservation. Considering both commercial and recreational fisheries datasets that have temporospatial overlap will provide a complete picture of species distribution. Thus, the goal of the analysis is to improve ecological understanding of dolphinfish and to gain insight on factors that affect their distribution within the context of a diverse multi-user fishery.

2. Methods

2.1. Study area

The study area covers the coastal and offshore waters of the U.S. Atlantic coast. We adapted the four contiguous statistical areas used by U.S. National Oceanic and Atmospheric Administration (NOAA) Southeast Fisheries Science Center (SEFSC) (Beerkircher et al., 2004;

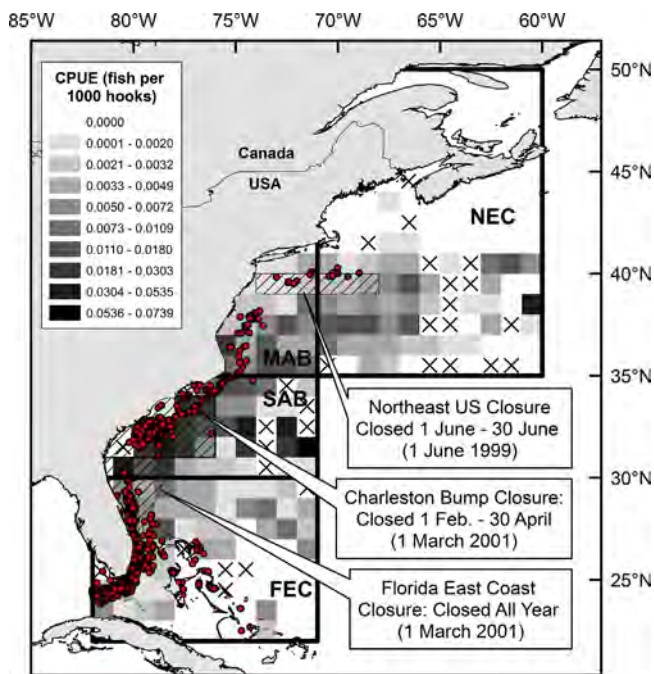


Fig. 1. Map of study area with statistical areas and pelagic longline closed areas overlaid. See text for descriptions of statistical areas. Each square represents a $1^\circ \times 1^\circ$ area where one or more longline sets ($n = 36,325$) were made during the study period (individual set locations are not shown due to privacy concerns). An \times indicates cells where one or more sets were made and no dolphinfish were captured. Individual DRP release locations are represented as red dots ($n = 8111$). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

Cramer, 2002; Kot et al., 2010). These regions comprise the Florida East Coast (FEC), South Atlantic Bight (SAB), Mid-Atlantic Bight (MAB) and North East Coastal (NEC) fishing regions.

2.2. Fishery data

Pelagic longlines are the dominant fishing gear of the open ocean. One way of monitoring catch levels and fishing effort is the fisheries logbook system that is managed by the NOAA SEFSC. Since 1986, fishermen have been required to record multiple pertinent fishery variables (e.g. time, location, gear specifications, species counts) in order to ensure oversight for management and conservation. We chose this dataset in order to obtain large sample size and encompass a wide geographic area (SEFSC, 2012). Although these data are self-reported and may contain errors in temporal and/or spatial variables, effort, and catch numbers (Johnson et al., 1999), it is unparalleled in terms of temporospatial range and number of observations (>300,000 sets from 1986 to 2008).

We downloaded the datasets from 1986 through 2008 and initially excluded sets where: location was not recorded or was outside of the Atlantic Ocean, location intersected a land mass, any date field was not recorded, or there was any indication that longline gear was not being used. We only selected sets that fell within (or on the border) one of the four statistical zones (Fig. 1). Then, we retained only logbook data from 1999 through 2007 after determining that the required satellite derived oceanographic data only had temporal overlap during this time period (i.e. temporal overlap between all fisheries datasets used in this study).

We extracted the gear set date (YEAR, MONTH), location (LAT, LONG), number of fish caught (dolphinfish, bigeye tuna, bluefin tuna, yellowfin tuna, albacore tuna, blackfin tuna, other tuna, swordfish, wahoo, king mackerel, escolar, greater amberjack, bonito, and skipjack), gangion length, floatline length, and number of lightsticks per set (LTSTK) from the archive. We estimated hook

depth (HKDPH) by adding gangion length to floatline length due to the high level of spatial and temporal variability of set location and diversity of fishing techniques within the PLL fleet, whereas catenary geometry may not provide any increase in accuracy (Rice et al., 2007). Sets having gangion or floatline length of zero, or suspiciously large hook depth were eliminated from the analysis. Finally, we calculated catch per unit effort (CPUE) for all species as # fish caught/# hooks for each set. Any set having a catch per unit effort above 1 was then eliminated, leaving 36,913 sets.

The Dolphinfish Research Program (DRP) has administered a conventional tagging project on dolphinfish in the Atlantic since 2002. The program provides 0.15 m plastic tipped dart tags (Hallprint Pty Ltd., 27 Commerce Crescent, Hindmarsh Valley, South Australia 5211) that are inserted into the dorsal musculature using a needle tool. Following release, an information card (provided by DRP) is filled out and mailed to DRP with the following information; release location, date, *Sargassum* presence/absence, surface water temperature, fork length, and sex. Caveats to this data set are similar to the commercial longline dataset concerning errors in location and date. Furthermore, qualitative errors in *Sargassum* presence/absence and sex may be present as most individual taggers are not given any training. We obtained data from 2002 to 2007 from the DRP that fell within one of the four statistical zones for a total of 8241 locations. The locations were then sampled for oceanographic variables for analysis and comparison to the PLL dataset.

2.3. Environmental data

Knowledge of the environmental conditions where dolphinfish were captured provides information about their habitat preferences in relation to abundance, and identifies particular areas that are preferentially exploited. Even though the pelagic longline logbook data and the recreational data report information about sea surface temperature and depth measured by the fishermen, these data are incomplete and we wish to know about the biophysical conditions at each location. Thus, we chose to use nine temporospatially overlapping environmental variables that were likely to be useful predictors of dolphinfish catch in this study; sea surface temperature (SST), chlorophyll concentration (CHL), sea surface height (SSH), sea surface height anomaly (SSHA), geostrophic velocity (GVEL), geostrophic velocity anomaly (GVELA), eddy kinetic energy (EKE), bathymetry (BATHY), and bathymetric slope (BATHYSLP). We chose SST because many large pelagic fish species are influenced by temperature (Block et al., 2011; Schick et al., 2004; Yen et al., 2012), including dolphinfish (Kleisner, 2009). CHL is an indicator of primary productivity and has also been shown to correlate with the abundance of pelagic fish (Block et al., 2011; Polovina et al., 2001; Tseng et al., 2010). We chose SSH, SSHA, GVEL, GVELA, and EKE to investigate if CPUE was higher as a result of sea surface height, current speed, or an eddy feature due to some unique oceanographic conditions (e.g. Gulf Stream). The associated environmental variables were sampled for each longline set and recreational locations using the Marine Geospatial Ecology Toolbox (Roberts et al., 2010) in ArcGIS 10 (Environmental Systems Research Institute, Redlands, CA).

Archived SST values were extracted from the gridded Pathfinder AVHRR SST daytime dataset (v5, <http://www.podaac.jpl.nasa.gov>). The sampled data consisted of 8-day and monthly averaged temperatures on a 4 km equal angle grid. We preferentially used 8-day values (they are more accurate than monthly) and only used the monthly values when 8-day values were unavailable. If no temperature value was available from Pathfinder (e.g. due to cloud cover or poor quality), then the location was excluded from further analysis.

Surface chlorophyll concentration was extracted from the sea-viewing wide field-of-view sensor (SeaWiFS) (<http://www.oceans>

gsfc.nasa.gov). The sampled gridded data consisted of 8-day and monthly averaged chlorophyll concentration values on a 9 km equal angle grid. Similar to the SST filtering process, 8-day measurement was given priority over monthly values. If no chlorophyll value was available from the archive, then the location was excluded from further analysis.

Gridded 7-day altimetry data (SSH, SSHA, GVEL, GVELA) were derived from the delayed merged products of four satellite altimeters (Jason-1, ENVISAT/ERS, Geosat Follow-On, and Topex/Poseidon) (Centre National d'Etudes Spatiales AVISO database, <http://www.aviso.oceanobs.com>) on a 1/3° Mercator projection. Sea surface height and anomaly data can be used to identify large scale current patterns such as Gulf Stream System, as well warm and cold ring mesoscale eddies (Cheney and Marsh, 1981; Fu et al., 1987; Kelly et al., 1999; Siegel et al., 1999). Warm core eddies associated with the Gulf Stream System are anti-cyclonic with positive SSHA, while cold core eddies are cyclonic and have negative SSHA. Geostrophic velocity can be used to further identify areas like the Gulf Stream System with high velocity flow (Fofonoff, 1981; Kelly, 1991; Manning and Watts, 1989). Eddy kinetic energy is used to measure the turbulent flow of surface currents and can identify regions where eddies and current meanders are common (Ducet et al., 2000; Pascual et al., 2007, 2006; Stammer, 1998). The EKE (per unit mass) is derived from GVELA components and was calculated by

$$\text{EKE} = 0.5(u^2 + v^2) \quad (1)$$

where u and v were the zonal and meridional geostrophic velocity anomalies, respectively.

Bathymetry for each release and set location was derived from the composite topographic dataset (Marks and Smith, 2006), which is a 1-min × 1-min grid. Bathymetric gradients were expressed as a percentage, which was calculated using a 3 × 3 pixel window using

$$\text{BATHYSLP} = \left| \frac{\text{Depth}_1 - \text{Depth}_2}{(\text{Depth}_1 + \text{Depth}_2)/2} \right| \times 100 \quad (2)$$

where Depth_1 and Depth_2 are the cells with minimum and maximum topography, respectively.

A total of 32,290 longline sets and 8111 recreational release locations remained after locations that did not have values for all environmental layers. The fishery and environmental predictor variables were then normalized and standardized in order to make them comparable during analysis. We log-transformed CHL, GVEL, GVELA, EKE, BATHY, and BATHYSLP. Then, we normalized all of the non-categorical variables (YEAR, LAT, LONG, HKDPTH, LTSTK, SST, CHL, SSH, SSHA, GVEL, GVELA, BATHY, and BATHYSLP) by subtracting the mean. Month of each location was not normalized, rather it was treated as a categorical factor using dummy variables with January as the reference month (Table 1).

2.4. Zero-inflated negative binomial model

Dolphinfish CPUE (fish per 1000 hooks, rounded to the nearest integer) represents the standardized count of fish per effort during each set, and was used as the response variable in order to simplify the models (rather than having an additional offset variable for effort). Common count regression models include Poisson and negative binomial, where a set of continuous and/or categorical predictors are used to estimate probability of counts. Poisson regression is the simplest way to model count data but often becomes ill-suited when considering real counts because most data do not have equality between the mean and variance (i.e. overdispersion, when variance > mean). Conversely, negative binomial regression allows for overdispersion as well an increased ability to handle excessive zeros (Hilbe, 2011), and has been applied

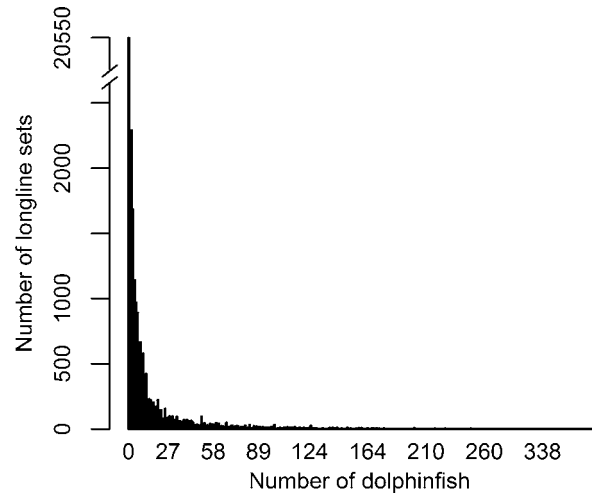


Fig. 2. Numbers of dolphinfish per longline set. Bars indicate the number of sets containing each unique count of dolphinfish. Slash marks indicate a break in the vertical axis.

to fishery data (Pradhan and Leung, 2006; Punt et al., 2000; Teo and Block, 2010). Zero inflation is added to the negative binomial model in order to fully account for the zero counts, effectively functioning as a mixture model (Minami et al., 2007; Zuur et al., 2009). After examining the data, it was apparent that our data were zero-inflated (Fig. 2) and were not equidispersed, so we decided to use a ZINB model to estimate counts of dolphinfish using the generalized linear model (GLM) framework.

To construct and evaluate our predictive model, we used a partitioning approach where we randomly selected 70% of the sets for use as a “training” dataset and 30% of the sets as a “validation” dataset (22,603 and 9687 sets, respectively). Random splitting of the observations is useful for evaluating model accuracy (Guisan and Zimmermann, 2000) and guards against the possibility of overfitting. The training model is then used to predict the CPUE of the validation dataset to calculate percent error using root mean square error of prediction (Rawlings et al., 1998).

The zero-inflated distribution model for count data is a mixture of a binomial and a negative binomial model. The binomial model is used to predict the probability of a zero count, π , and the probability of a non zero count, $1 - \pi$. The count process for the model is used to estimate expected counts of dolphinfish and is modeled using the negative binomial probability function which is given by,

$$f_{\text{NB}} = f(Y_i | \mu_i, \theta) = \frac{\Gamma(Y_i + \theta)}{\Gamma(\theta) \Gamma(Y_i + 1)} \left(\frac{\theta}{\mu_i + \theta} \right)^\theta \left(1 - \frac{\theta}{\mu_i + \theta} \right)^{Y_i} \quad (3)$$

where Y_i is the estimated count (0, 1, 2, 3, ...) and μ and θ are the mean and dispersion parameters, respectively. The mean of the ZINB is equal to the expected count, $E(Y)$, and is given by

$$E(Y_i) = \mu_i (1 - \pi_i), \quad (4)$$

and the variance, $\text{Var}(Y)$, is given by

$$\text{Var}(Y_i) = (1 - \pi_i) \left(\mu_i + \frac{\mu_i^2}{\theta} \right) + \mu_i^2 (\pi_i^2 + \pi). \quad (5)$$

As θ^{-1} approaches zero the negative binomial is reduced to a Poisson distribution, and therefore the zero-inflated Poisson (ZIP) and the ZINB models are nested.

The purpose of our model is to estimate the expected CPUE, $E(\text{CPUE})$, for a given longline set, i , where catch is standardized by effort and environmental variables. When we set $E(\text{CPUE})$ equal

Table 1

Characteristics of fishery and environmental variables. The MONTH variable was treated as categorical and was modeled using dummy variables for each month other than January.

Predictor	Description	Mean	SD	Min	Max
YEAR	Year of longline set	2002	2.69	1999	2007
MONTH	Month of longline set. categorical				
LAT	Latitude of longline set (decimal degrees)	33.94	4.76	22.43	44.66
LONG	Longitude of longline set (decimal degrees)	-75.34	3.88	-81.98	-60.17
HKDPH	Estimated depth of hook (m)	18	5.9	2	50
LTSTK	Number of light sticks per set	273	222.6	0	1600
SST	Sea surface temperature at longline set (°C)	24.48	3.61	5.56	32.78
CHL	Surface chlorophyll- <i>a</i> concentration at longline set (mg m ⁻³)	0.269	0.294	0.0139	16.993
SSH	Sea surface height at longline set (cm)	24.35	31.78	-33.36	138.85
SSHA	Sea surface height anomaly at longline set (cm)	2.39	8.6	-78.21	96.15
GVEL	Geostrophic velocity at longline set (cm s ⁻¹)	3.21	36.88	0.2	182.12
GVELA	Geostrophic velocity anomaly at longline set (cm s ⁻¹)	2.64	16.87	13.07	146.09
EKE	Eddy kinetic energy at longline set (cm ² s ⁻²)	227.81	418.38	0.002	10,671.77
BATHY	Bathymetry at longline set (m)	901	809.1	11	5563
BATHYSLP	Bathymetric slope at longline set (percent change in 3 × 3 kernel)	27.72	31.9	0	198.5

to $E(Y_i)$ (Eq. (4)) the regression model can be expressed by the probability function

$$f(\text{CPUE}_i | B_i, G_i, \beta, \gamma, \theta) = \begin{cases} \pi_i + (1 - \pi_i) f_{\text{NB}}(0 | \mu_i, \theta) & \text{for CPUE}_i = 0 \\ (1 - \pi_i) f_{\text{NB}}(\text{CPUE}_i | \mu_i, \theta) & \text{for CPUE}_i = 1, 2, \dots \end{cases} \quad (6)$$

where f_{NB} is given by (3). The explanatory variables are related to the mean of the count model which is given by the function

$$\ln(\mu_i) = B_{i0} + B_{i1}\beta_1 + \dots + B_{ik}\beta_k = B_i\beta. \quad (7)$$

The variables are also used to calculate the probability of observing a zero count which given by

$$\text{logit}(\pi_i) = \ln\left(\frac{\pi_i}{1 - \pi_i}\right) = G_{i0} + G_{i1}\gamma_1 + \dots + G_{ik}\gamma_k = G_i\gamma, \quad (8)$$

where B_i and G_i are vectors of explanatory variables (Table 1) for the i th set. The variables β , and θ are vectors of the coefficients to be estimated by maximizing the log-likelihood function (Hilbe, 2011). The vectors B_i and G_i are assigned differently in this case because the variables used in the count process (Eq. (7)) may be different than the variables used to model the zero-inflated process (Eq. (8)), although they are initially the same. Since the negative binomial distribution is used to model counts in the model we will operationally refer to this portion of model as the “count” portion. Likewise, the portion of the model that calculates the probability of zeros will be operationally referred to as the “binomial” or “zero process”, interchangeably.

The ZINB model was fit using a backward stepwise procedure using Akaike's information criterion (AIC) in conjunction with successive likelihood-ratio tests as criterion for removing variables from the model (Zuur et al., 2009). We investigated inclusion of catch rates of other species as possible covariates, but no correlations were found so they were not included. After we determined the list of explanatory variables, we fit a fully saturated ZINB model with all available variables, then calculated the AIC. We removed each variable independently for the count and binomial portions, then calculated the AIC and performed a likelihood-ratio test between the model with and without the variable removed. If the AIC was relatively un-changed and the likelihood-ratio test was not significant, the variable with the highest X^2 statistic was dropped from the model. We subsequently removed variables until their exclusion significantly reduced model fit, which resulted in the best fit final model. Model estimation and evaluation was done using R (v2.12) using the “pscl” and “MASS” packages.

One of the best ways to test robustness of a predictive model is to introduce an independent dataset to evaluate accuracy (Guisan and Zimmermann, 2000). Here, we use the DRP dataset to evaluate our final model and to bridge the proverbial gap between commercial and recreational fisheries. We used the recreational release

locations along with their environmental covariates as input into the final model in order to model predicted counts. Since the DRP data are “presence-only”, we know with certainty that dolphin-fish occur at each particular location. Obviously, the catch per unit effort is fundamentally different between longline and recreational fisheries due to different catchability coefficients and effort. However, applying the commercial model to recreational data enables us to compare the predicted results of the ZINB at locations where least one dolphin-fish was present, as well as directly compare the oceanographic conditions between the two datasets to evaluate if commercial and recreational fishermen are targeting the same areas and/or conditions.

2.5. Recreational *Sargassum* presence/absence and dolphin-fish size

Recreational anglers participating in the DRP reported the presence or absence of *Sargassum* within the vicinity of the catch/release location. The fishermen are not trained observers with the ability to discern species types, so we operationally refer to *Sargassum* spp. as simply *Sargassum*. Measured fork lengths were also reported for many of the dolphin-fish catches. We investigated if there was any difference between the size of dolphin-fish caught in association with *Sargassum* and outside of the *Sargassum*. First, we performed a Mann-Whitney test to determine if the two groups came from the same distribution. We then investigated the probability of being caught in association with *Sargassum* based on length using a binomial generalized linear model (GLM) with a logit link, which is given by

$$P(s) = \frac{e^u}{1 + e^u} \quad (9)$$

Equation (9) is a logistic regression which calculates the probability of a dolphin-fish being caught in association with *Sargassum*, $P(s)$, where u is a linear model on the predictor variable LENGTH, which is in the form

$$u = b_0 + b_1 \times \text{LENGTH}. \quad (10)$$

We used the p -value of the z -scores for the intercept and the LENGTH variable to evaluate the significance of the linear predictor. To estimate the significance of the model, we used deviance (i.e. twice the log-likelihood ratio) which is distributed as X^2 .

3. Results

3.1. Temporospatial catch patterns

Dolphin-fish were caught year round in the study area with a strong seasonal pulse, over a wide geographic area. Overall, mean

Table 2
Dolphinfish catch summary for Atlantic pelagic longline from 1999 to 2007 by month in each statistical zone. The total number (i.e. sum) of sets (# Sets) and fish (# Fish) are shown for each month during each zone, and the mean catch rate (CPUE) during the same time/area is per 1000 hooks.

Month	NEC			MAB			SAB			FEC		
	# Sets	# Fish	CPUE	# Sets	# Fish	CPUE	# Sets	# Fish	CPUE	# Sets	# Fish	CPUE
January	5	1	0.16	390	4	0.02	662	313	0.73	729	593	1.83
February	9	1	0.09	307	0	0.00	353	63	0.25	989	1194	2.39
March	6	3	0.39	374	23	0.11	505	389	1.03	1442	3513	4.34
April	17	94	6.06	467	399	1.51	678	3703	7.21	1368	5328	7.32
May	97	376	4.86	744	6864	15.73	2357	119,706	72.11	687	2933	10.72
June	726	6877	11.34	1057	16,206	23.61	1580	49,882	48.51	563	937	4.56
July	1442	5628	4.65	1283	5489	6.51	759	1230	3.38	656	376	1.59
August	1361	2349	2.11	1677	2132	1.86	543	236	1.05	593	263	1.22
September	1047	1450	1.71	1864	3084	2.29	318	155	1.24	573	347	1.73
October	556	975	2.08	2242	2507	1.53	373	252	1.69	496	310	1.78
November	167	83	0.55	1779	322	0.24	424	418	2.07	384	344	2.72
December	66	20	0.37	827	80	0.13	387	302	1.33	396	324	2.42
Total	5499	17,857	3.91	13,011	37,110	4.14	8939	176,649	31.80	8876	16,462	4.19

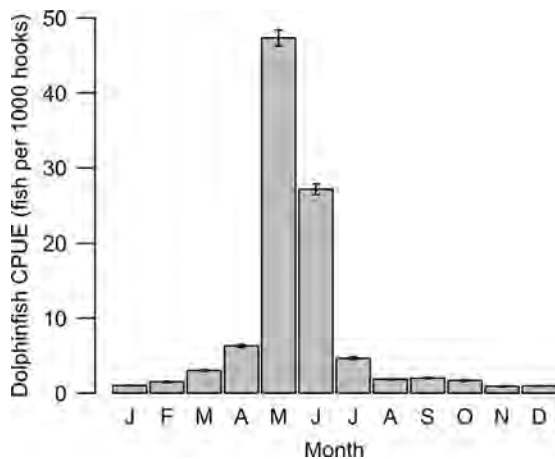


Fig. 3. Monthly mean (\pm SE) dolphinfish CPUE (1999–2007) in study area.

dolphinfish CPUE for all sets was 10.0 ± 31.52 SD. Catch rates were consistently high during the months of May (47.6 ± 1.1 SE) and June (mean 27.5 ± 0.73 SE) during the study period (Fig. 3). Rates were lowest during the winter months with a minimum during November (0.90 ± 0.06 SE). The catch numbers reflect the high intra-annual variance within and between zones (Table 2). The FEC zone has peak catch during April but the highest catch rate is during May. Catches in the SAB are highest during May and June with the highest CPUE of any zone (Table 2; 72.11 and 48.51, respectively). The same pattern of peak catch in May and June is seen in the MAB, and catch numbers remain in the thousands through October. The NEC has the latest peak catch in June, and catch numbers remain in the thousands through September. The SAB is the dominant catch zone with 8939 sets and 176,649 dolphinfish caught during the study period. The SAB not only has the highest peak rates, but the highest overall catch rate of 31.80 dolphinfish per 1000 hooks (Table 2).

The geographic distribution of pelagic longline catch shows that dolphinfish catch varies temporally and spatially (Fig. 1). Virtually no dolphinfish are caught in the NEC and MAB areas during January, February, and March. Instead, the catch during the early spring predominantly occurs in the SAB and FEC areas. With the onset of April, catch rates increase in the FEC and SAB and increasing numbers of dolphinfish are caught in the two northern zones. The peak month of May has high catch rates across all zones with the highest rates close to the coast in the SAB (Fig. 4). During June, the center of highest catch rates moves northward. June brings high catch rates across the entire SAB, most of the MAB, and the largest geographic

extent of dolphinfish catch in the NEC. While there are still numbers of dolphinfish being caught across large areas of each zone, the catch rate drops substantially across the study area in July. During early summer there is a precipitous drop in catch rate, but dolphinfish are still landed across all zones. After August, catch rates decline slowly through December although dolphinfish are still caught in each zone during these months.

3.2. Modeling PLL catch rate using zero-inflated negative binomial (ZINB) regression

The result of the model selection process was a well fit ZINB model. After splitting the dataset into a training and validation datasets, we started the selection procedure on the training dataset by comparing a zero-inflated Poisson (ZIP) model to a ZINB model with all 15 predictor variables (Table 1). A likelihood-ratio test comparing the variance structure of the two models showed that the ZINB model had a better fit to the data ($\chi^2 = 153,226$, $df = 1$, $p < 0.0001$) as well as reducing the AIC substantially from 253,045.97 to 99,782.12. From there, the backward stepwise process resulted in dropping SSHA and GVLE from the count portion of the model and YEAR and SSH from the binomial portion of the model (Table 3). Determination of variable importance and ultimate inclusion in the model was done by calculating the increase in AIC for each variable after dropping it from the model (Table 3). Evaluation of the final model on the validation dataset resulted in a mean squared error of prediction of 2.26%, which indicates good model fit to the data with no overfitting (i.e. accurate predictions can be made outside of the training dataset).

The final model included many of the original variables which includes static and dynamic oceanographic variables, temporal, spatial, and explicit fishery variables. The binomial and count portions of the model complement one other (Eq. (6)) in prediction of CPUE and are thus non-independent, but can be considered separately to understand the dynamics of the model. The two static oceanographic variables (BATHY and BATHYSLP) were retained in both portions of the model which is an indicator of overall importance of these variables. Furthermore, BATHY and BATHYSLP had the largest Δ AICs (excluding MONTH) in the count portion of the model (Table 3). The negative coefficients for both BATHY and BATHYSLP in the count portion (Table 3) suggest high catch rates in shallower water with low topographic slope, which is most likely above the continental shelf.

The dynamic oceanographic variables SST and CHL have strong effects across both portions of the model. The Δ AIC after dropping SST in the binomial portion was 400.28, which was the largest Δ AIC in the binomial portion besides MONTH. However, dropping

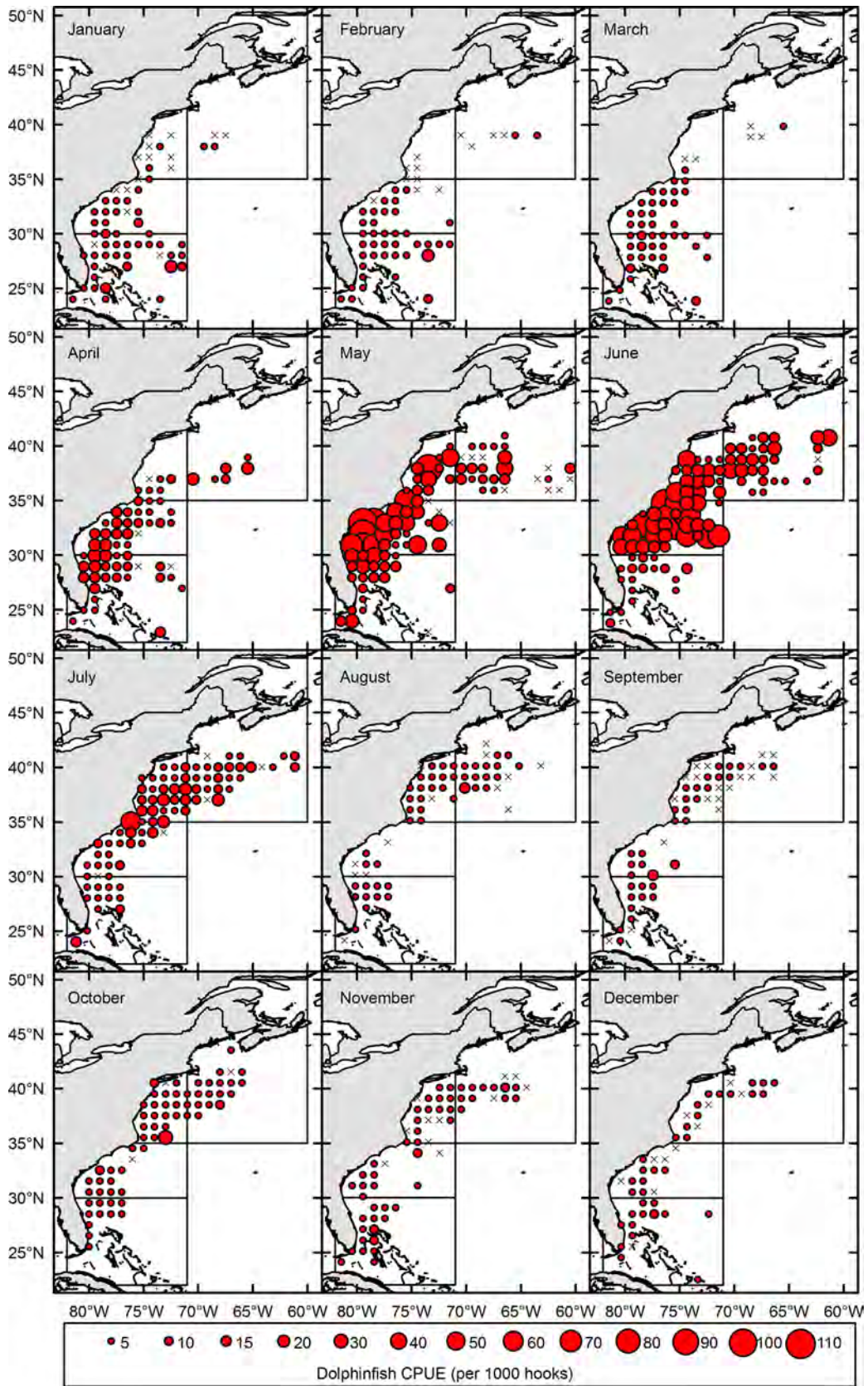


Fig. 4. Temporospatial variability of dolphinfish CPUE in 1° x 1° cells. Black x indicates areas where more than 1000 hooks were set but no dolphinfish were caught.

Table 3
Summary table of the retained variables in the final ZINB model for the count portion (top) and the binomial portion (bottom). MONTH is treated as a categorical dummy variable that is referenced to January (month 1). Δ AIC is the difference (increase) in AIC value by when each variable is excluded from the model.

Count model	Estimated coefficient	Standard error	Z score	p-value	Δ AIC
(Intercept)	1.496525	0.082779	18.079	2.0×10^{-16}	
YEAR	0.036896	0.00443	8.329	<0.000001	67.33
LAT	0.052394	0.009233	5.675	<0.000001	29.6
LONG	-0.03121	0.009062	-3.444	0.000573	9.71
HKDPTH	-0.03325	0.002355	-14.121	<0.000001	193.0
LTSTK	-0.00058	5.39×10^{-5}	-10.75	<0.000001	106.33
SST	0.02036	0.007108	2.864	0.00418	6.12
CHL	-0.26592	0.028227	-9.421	<0.000001	84.08
SSH	-0.00446	0.000705	-6.325	<0.000001	37.84
GVELA	-0.38386	0.149418	-2.569	0.010198	4.11
EKE	0.191872	0.066006	2.907	0.00365	5.70
BATHY	-0.26546	0.018142	-14.632	<0.000001	220.19
BATHYSLP	-0.19202	0.013721	-13.994	<0.000001	191.28
MONTH 2 – February	0.576962	0.105619	5.463	<0.000001	4052.33*
MONTH 3 – March	0.53319	0.088645	6.015	<0.000001	
MONTH 4 – April	0.841199	0.08601	9.78	<0.000001	
MONTH 5 – May	2.156235	0.088209	24.445	<0.000001	
MONTH 6 – June	1.701514	0.090023	18.901	<0.000001	
MONTH 7 – July	0.219235	0.096003	2.284	0.022394	
MONTH 8 – August	-0.34967	0.100917	-3.465	0.00053	
MONTH 9 – September	-0.26197	0.098327	-2.664	0.007715	
MONTH 10 – October	-0.01503	0.096468	-0.156	0.876228	
MONTH 11 – November	0.061126	0.103767	0.589	0.555813	
MONTH 12 – December	0.098686	0.122004	0.809	0.418589	
Log(theta)	-0.12469	0.021135	-5.84	<0.000001	
Binomial model	Estimated coefficient	Standard error	Z score	p-value	
(Intercept)	-0.26399	0.099973	-2.641	0.008275	
LAT	-0.22046	0.013885	-15.878	<0.000001	239.86
LONG	0.079966	0.014708	5.437	<0.000001	26.54
HKDPTH	0.029355	0.004334	6.772	<0.000001	43.61
LTSTK	-0.00083	0.000107	-7.777	<0.000001	63.41
SST	-0.21139	0.010922	-19.356	<0.000001	400.28
CHL	0.618794	0.04569	13.543	<0.000001	179.77
SSHA	-0.00818	0.002687	-3.044	0.002335	7.25
GVEL	0.251654	0.025351	9.927	<0.000001	101.25
GVELA	-1.0528	0.325854	-3.231	0.001234	10.02
EKE	0.448047	0.143459	3.123	0.001789	9.31
BATHY	-0.09415	0.028272	-3.33	0.000868	9.15
BATHYSLP	0.088929	0.022131	4.018	0.0000586	14.13
MONTH 2 – February	-0.12672	0.123467	-1.026	0.304734	1725.37*
MONTH 3 – March	-1.09273	0.117673	-9.286	<0.000001	
MONTH 4 – April	-1.49254	0.122188	-12.215	<0.000001	
MONTH 5 – May	-2.11674	0.125297	-16.894	<0.000001	
MONTH 6 – June	-1.11396	0.119825	-9.297	<0.000001	
MONTH 7 – July	0.380041	0.124606	3.05	0.002289	
MONTH 8 – August	1.329785	0.131139	10.14	<0.000001	
MONTH 9 – September	1.086958	0.128453	8.462	<0.000001	
MONTH 10 – October	0.83242	0.119945	6.94	<0.000001	
MONTH 11 – November	0.736626	0.122153	6.03	<0.000001	
MONTH 12 – December	0.544462	0.138135	3.942	0.000081	

* Δ AIC for MONTH represents exclusion of all months.

SST from the count portion has a diminished effect but is nonetheless significant. The coefficients for SST in the final model (Table 3) indicate that higher SST values increase the probability of catching dolphinfish (Fig. 5a). The moderate Δ AIC in the count portion and high Δ AIC (Table 3) in the binomial portion of CHL suggests a strong effect of primary productivity on the catch rate of dolphinfish. The coefficients for CHL indicate that areas with low concentration of chlorophyll-*a* are more likely have high dolphinfish catch rates (Table 3 and Fig. 5b). The other dynamic oceanographic variables (SSH, GVELA, EKE, SSHA, GVEL) contributed to the predictive ability of the model, but to a lesser extent. The most important of these dynamic variables were GVEL and SSH which had Δ AICs of 101.25 and 37.84, respectively, but each was only included in one portion of the model (Table 3). The positive coefficient for GVEL (Table 3, Binomial Model) indicates that the probability of catching zero dolphinfish is positively correlated with surface current velocity. The negative coefficient for SSH in the count portion of

the model (Table 3) indicates higher CPUE values when sea surface height is lower.

The temporal and spatial predictor variables played a large role in the accuracy of the final model. MONTH, in particular, had the largest Δ AIC on both portions of the model (Table 3). This is undoubtedly due to the strong seasonal abundance of dolphinfish off the U.S. east coast. The MONTH variable does not exert a physical or biological force on dolphinfish, but is designed to capture the non-explicit seasonal effects that were not included in the model (e.g. prey/predator abundance, wind, oxygen concentration, salinity, etc.). The YEAR variable was not expected to have a great influence on the model, but it was retained in the count portion (Table 3). The positive coefficient for YEAR indicates higher catch rates later in the study period. The LAT and LONG variables were retained in both portions of the final model, indicating a high spatial sensitivity of the model. The count and binomial coefficients agree that catch rates are higher at higher latitude and lower longitude

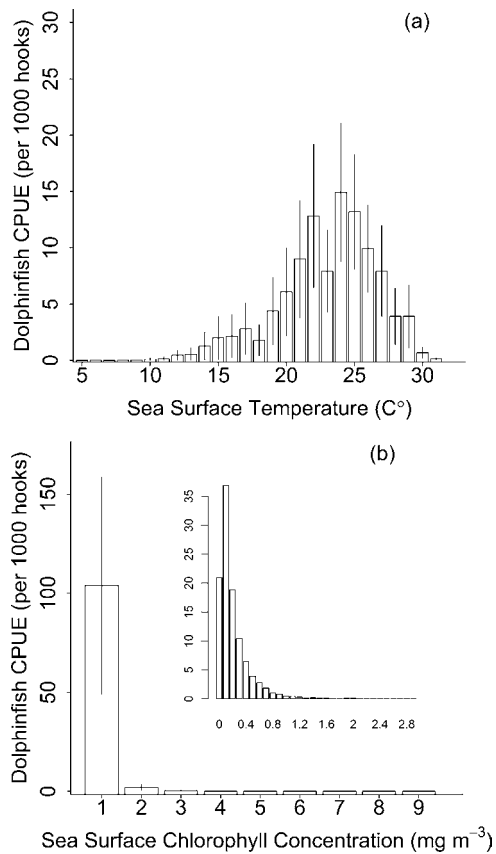


Fig. 5. Dolphinfish CPUE in relation to the mean \pm SD (error bars) of (a) sea surface temperature, (b) surface chlorophyll concentration.

within the temporospatial context of the study area. Higher catch rates at lower longitude indicate higher rates in the western portions of the study area, which is consistent with lower bathymetric values that are characteristic of the continental shelf, or continental rise.

Both of the fishery variables, HKDPTH and LTSTK, were retained in both portions of the final model. Shallower longline hook depth was consistent with higher catch rates of dolphinfish as indicated by positive and negative coefficients for the count and binomial portions, respectively (Table 3), which is consistent with previous observations of dolphinfish occurring in the upper portion of the water column (Hammond, 2008; Kleisner et al., 2010; Oxenford, 1999). A low number of light sticks per set was correlated with increased catch rates in the count portion of the model, and is important for detecting presence or absence of dolphinfish to a lesser extent (Table 3).

3.3. Recreationally caught dolphinfish

The Dolphinfish Research Program (DRP) provided dolphinfish catch/release locations during each month, with the highest catches during May–July (Fig. 6a). With the exception of 2006, the number of fish tagged by recreational fishermen grew in subsequent years (Fig. 6b). The average number of dolphinfish released each year was 1351.8 ± 579.1 SD with a peak of 2199 during 2007.

The oceanographic conditions of the recreationally caught dolphinfish were generally similar to the longline caught fish. We sampled each location using the archived oceanographic layers for the retained variables of the final ZINB model. The mean depth where dolphinfish were caught was 324.63 ± 253.49 m SD, and the mean BATHYSLP was $41.40 \pm 43.42\%$ SD. The mean SST in waters

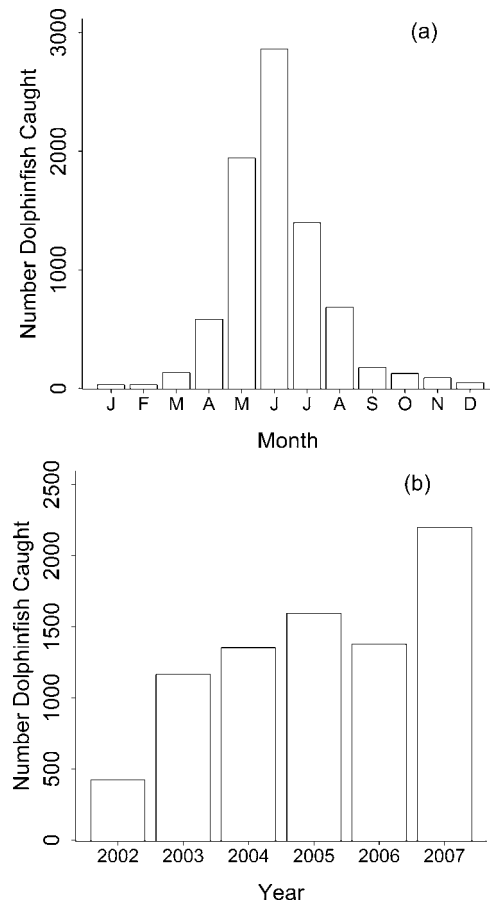


Fig. 6. Histogram of total dolphinfish caught during each month from the DRP dataset (a). Frequency of dolphinfish caught during each year of the DRP dataset (b).

where dolphinfish were caught was 27.62 ± 1.91 °C SD (Fig. 7a), and the mean CHL value was 0.203 ± 0.23 mg m⁻³ SD (Fig. 7b).

Applying the final commercial ZINB model to the recreational locations obtained by the Dolphinfish Research Program (DRP) resulted in high predicted catch rates (Fig. 8). The mean predicted CPUE at the recreational locations was 21.2 ± 20.3 SD dolphinfish per 1000 hooks, which is well above the mean of the longline dataset. Only 2.5% of the recreational locations were predicted to have a zero catch rate (Fig. 8). The high probability of catching more than one dolphinfish at the DRP locations (97.5%) suggests that the recreational fishermen are targeting areas with very favorable static and dynamic oceanographic conditions as well as favorable months of the year (Fig. 6a).

A high percentage of dolphinfish were caught in association with floating mats of pelagic *Sargassum*. Of the 8241 dolphinfish records, recreational anglers reported the presence or absence of *Sargassum* during 3373 releases. Of these, 2471 (73.26%) dolphinfish were caught in the presence of *Sargassum* and 902 (26.74%) were caught away from *Sargassum*.

Measured fork length of dolphinfish was reported for 1835 of the 3373 *Sargassum* records, resulting in 1468 and 357 length measurements in the presence and absence of *Sargassum*, respectively. The median length for dolphinfish caught in the presence of *Sargassum* was 45.72 cm, while the median length in the absence of *Sargassum* was 50.8 cm (Fig. 9). A Mann–Whitney test of dolphinfish lengths when *Sargassum* was present versus absent showed that dolphinfish caught outside of the patches were larger ($W=192,497.5$, $p < 0.001$). The binomial GLM indicated that LENGTH can be used as a predictor for determining *Sargassum* presence or absence

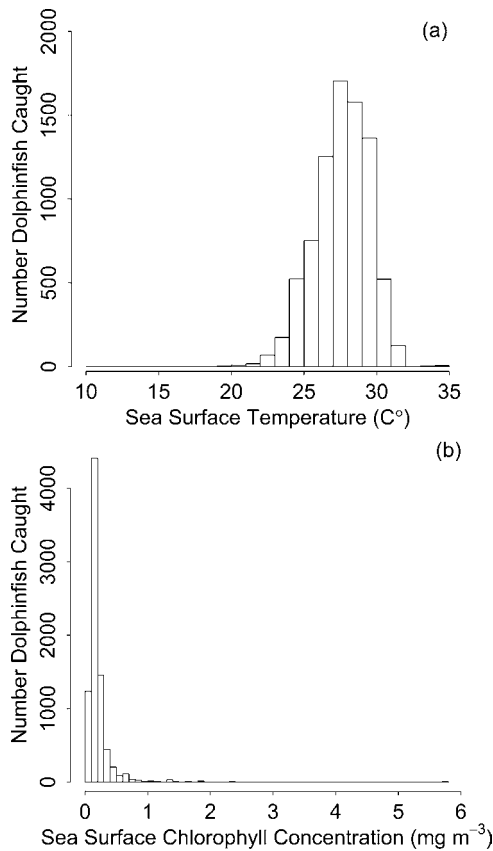


Fig. 7. Recreational dolphinfish catch in relation to sampled (a) sea surface temperature, (b) surface chlorophyll concentration.

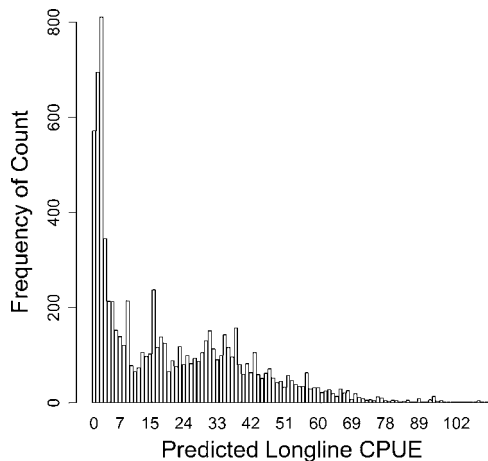


Fig. 8. Predicted CPUE (per 1000 hooks) using the final ZINB model under the temporospatial and oceanographic conditions of the DRP recreational catch records.

($\chi^2 = 114.08$, $p < 0.001$; $Z_{\text{LENGTH}} = -10.43$, $p < 0.001$). Specifically, small sized dolphinfish are more likely to be associated with *Sargassum*, and larger dolphinfish are more likely to be caught away from *Sargassum*. The maximum length at which there is more than a 50% probability of being classified as being associated with *Sargassum* is 82.3 cm. Likewise, if the dolphinfish is above 82.3 cm then there is a greater than 50% chance that it will be found away from *Sargassum* patches. The designation of 0.5 probability as a cutoff value gives a classification accuracy 80.87% (Table 4). Classification is hardly the goal here because we do not expect large or small dolphinfish to exist in exclusive habitats with respect to *Sargassum*. We do, however, expect different size dolphinfish to spend more time in one habitat or the other.

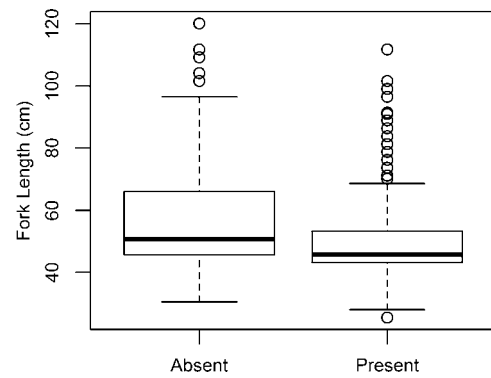


Fig. 9. Boxplot of fork length measurements on dolphinfish that were caught outside of *Sargassum* patches, "Absent", and within patches, "Present". The lower and upper sides of the boxes are the first and third quartiles, and the middle dark line is the median. The whiskers extending from the boxes are no longer than $1.5 \times$ the interquartile range. Values outside of the whiskers are hollow circles.

Table 4

Confusion matrix of predicted versus observed dolphinfish caught in association with *Sargassum*. Bold values are marginal totals, and the value in lower right diagonal is the grand total. Accuracy is calculated as (True Absence + True Presence)/Grand Total which resulted in 80.87%.

Predicted	Observed		
	Absence	Present	
Absent	39	23	62
Present	328	1445	1773
	367	1468	1835

4. Discussion

Our results confirm that dolphinfish caught in the pelagic longline fishery off the U.S. east coast are seasonally abundant and have spatial patterns in catch rate. Temporospatial analysis of the PLL data showed strong and predictable seasonal abundance, with highest CPUEs in the months of April through July, coinciding with the peak spawning season (Beardsley, 1967; Rose and Hassler, 1974; Schwenke and Buckel, 2008). Peak CPUE occurred during May in the FEC and SAB zones and in June and in the two northern zones (MAB and NEC), with the highest monthly CPUE in the SAB during May (Table 2). Peak catch rates vary spatially within the study area, with higher CPUE in the southern portion of the study area earlier in the year and peak CPUE in the northern areas later in the year. This sequential CPUE pulse starting in the south and moving north each spring may be the result of a northward movement of dolphinfish in the late spring and early summer months. This provides support for the seasonal south to north migration hypothesis (Oxenford and Hunte, 1986), but shows little evidence of a reverse southward movement. However, the PLL effort in the the MAB and NEC during January–April is minimal (Fig. 4), resulting in a higher degree of uncertainty concerning dolphinfish catch. Conversely, the PLL effort in the MAB and NEC from May to December is much higher and the "zero" observations on these sets are stronger evidence for dolphinfish absence. The effect of YEAR on the count portion of the final ZINB model is most likely tracking recruitment between years. Overall, the temporospatial range of dolphinfish in the study area is large, which reflects the presumably large population size in the western North Atlantic (Prager, 2000; SAFMC, 2003). The large geographic area where dolphinfish are caught coupled with high catch rates reinforces the fact that this species is important to the pelagic longline fishery.

Dolphinfish are clearly sensitive to environmental and physical conditions, as evidenced by the retention of numerous variables in

the final ZINB model. One of the most important dynamic oceanographic variables was sea surface temperature, which is positively correlated with high catch rates. CPUE is greatest when sea surface temperature was above 19 °C and peaked at 24 °C (Fig. 5a). As expected, higher catch rates of dolphinfish were associated with elevated sea surface temperatures, but catch rates decreased as the temperature reaches >27 °C. This could be a physiological preference, but is more likely a result of northward migration following the seasonal increases in SST, rather than intolerance to high temperatures. The SST values at the DRP locations have a similar distribution with a peak between 27 °C and 29 °C (Fig. 7a). The higher modal temperature for the DRP locations is most likely a result of a bias by recreational fishers towards fishing later in the spring/summer season (Fig. 6a) when weather conditions are better and SSTs are warmer in comparison to the longline fleet whose peak catch typically occurs in May (Table 2).

Commercial and recreational dolphinfish catch was higher in areas with low sea surface chlorophyll-*a* concentration (Figs. Fig. 55b and Fig. 77b). CPUEs were highest for dolphinfish caught in waters with chlorophyll-*a* concentrations <1.2 mg m⁻³, while DRP dolphinfish were typically caught in concentrations <0.9 mg m⁻³. A preference for low levels of surface chlorophyll-*a* concentration may be associated with warm water masses in the western Atlantic (i.e. Gulf Stream system) which are known to be nutrient poor, while the adjacent shelf waters have much higher primary productivity (O'Reilly and Zetlin, 1998; Schollaert et al., 2004). The highly vagile nature of dolphinfish makes them particularly suited for life in low nutrient waters as they can cover great distances in search of widely dispersed prey items. This is similar to other highly migratory pelagic fish such as blue marlin (*Makaira nigricans*) who typically inhabit Pacific waters with chlorophyll-*a* concentrations below 0.2 mg m⁻³ (Suet al., 2008), spawning bluefin tuna (0.10–0.16 mg m⁻³) and swordfish (<0.2 mg m⁻³) (Teo et al., 2007; Young et al., 2003), and yellowfin tuna (0.090–0.099 mg m⁻³) (Song et al., 2008).

Dolphinfish were found in high numbers in the shallow waters of the continental shelf and adjacent slope waters (Fig. 4). The strong effect of BATHY and BATHYSLP on the model is likely due to the U.S. Atlantic longline fleet targeting areas adjacent to the continental shelf break (i.e. 200 m isobath) in order to exploit the abundance of apex predators due to upwelling features and abundant food resources (Jennings et al., 2001). The recreational fleet typically fished waters that were shallower than the commercial fleet (324.63 ± 253.49 m SD and 901 ± 809.1 m SD, respectively), which is not surprising given the limitations in range (e.g. boat size, fuel capacity, etc.) between the two fleets. The recreational fleet routinely fished over areas with more topographic relief than the commercial fleet (41.40 ± 43.42% SD and 27.72 ± 31.9% SD, respectively), which is most likely due to recreational fishermen targeting specific areas with high relief (e.g. submarine canyons).

Modeling CPUE using the recreationally caught dolphinfish locations resulted in catch rates that were much higher than the PLL data. The mean predicted catch rate for the DRP dolphinfish was 21.2 ± 20.3 SD, which is higher than what was observed for the commercially caught dolphinfish (10.0 ± 31.52 SD). This is not entirely surprising because the majority of recreational fishermen participating in the DRP are fishing in the SAB and FEC zones (Fig. 1) primarily from April through August (Fig. 6a). However, we found that the SST values of the recreational locations appear slightly higher and consequently result in a higher predicted CPUE (Figs. Fig. 55a and Fig. 77a). Also, the range in observed SST values for the longline caught dolphinfish was much wider (10–32 °C; Fig. 5a), while the DRP dolphinfish were caught in a much narrower range of temperatures (22–32 °C; Fig. 7a). Surface chlorophyll-*a* concentrations were very similar between the commercial and recreational

dolphinfish (Figs. Fig. 55b and Fig. 77b), with both falling in a narrow band generally below 0.1 mg m⁻³.

Applying the final ZINB model using the DRP dataset resulted in 97.5% of the locations where recreational fishermen caught dolphinfish having a prediction of 1 or more dolphinfish per 1000 hooks. In other words, almost all of the DRP locations were predicted to occur in highly productive waters based on physical and biological oceanography and temporal variables. This is a useful exercise because it further validates the final ZINB model through independent evaluation, albeit based on a non-identical fishery. Furthermore, this approach provides insight into the data poor recreational fishery whose annual catch statistics are much higher than the commercial sector, but information on spatial catch and habitat are scarce. Applying the final model to the DRP shows that recreational fishermen are specifically targeting productive areas of the ocean which may overlap the commercial fishery, regardless of how many individuals are participating in the recreational fishery.

The presence of *Sargassum* is an important habitat feature for dolphinfish of the U.S. Atlantic coast. Of the DRP catch and release locations where *Sargassum* presence was recorded, the majority of dolphinfish were caught in the presence of the floating brown algae. *Sargassum* is virtually the only natural surface feature of temperate and tropical offshore waters, and is essentially comprised of two species (*S. natans* and *S. fluitans*). Pelagic *Sargassum* supports a diverse community of fishes, invertebrates, turtles, and other species (Casazza and Ross, 2008; Coston-Clements et al., 1991). Dolphinfish feed heavily on the abundance of species that use *Sargassum* as habitat (Dooley, 1972; Gibbs et al., 1959; Manooch et al., 1984).

We investigated the relationship between *Sargassum* presence and size to test the hypothesis that larger (possibly males) dolphinfish are found outside of the mats, while smaller (possibly female) dolphinfish are found in association with *Sargassum*. We found that size is an accurate predictor of *Sargassum* presence or absence (>80% accuracy) using a logistic regression. Specifically, dolphinfish that are found outside of the brown algae mats are typically 5 cm larger than dolphinfish caught near or within the mats. The regression showed that dolphinfish with a fork length of larger than 82.3 cm had a greater than 50% probability of being caught away from *Sargassum*, while dolphinfish shorter than 82.3 cm had a greater than 50% probability of being caught in association with *Sargassum*. Unfortunately, there was a paucity of accurate records of sex for the dolphinfish in the DRP dataset and examining sexual differences in this pattern was not possible, but should be in the future. It has been established that male dolphinfish have higher growth rates (Schwenke and Buckel, 2008; Uchiyama et al., 1986) as well as higher weights at length (Uchiyama and Boggs, 2006), and it is quite possible that the observed size difference in the presence or absence of *Sargassum* is a result of habitat partitioning between male and female dolphinfish. Rose and Hassler (1974) observed highly skewed sex ratios across dolphinfish size classes with large males making up the majority of the dolphinfish >80 cm and a predomination of females in the <60 cm size class. These uneven ratios were a result of fishermen incidentally catching large male dolphinfish while targeting blue marlin off North Carolina, and catching small females near *Sargassum* lines later in the season. The *Sargassum* complex in the open ocean is not only important habitat for adult dolphinfish, but plays an important ontogenetic role for a variety of species in early life stages (Rooker et al., 2006; Wells and Rooker, 2004). Regardless of the sex distribution of the DRP dataset, it appears that there is an ontogenetic habitat shift for dolphinfish. Since there is currently an interest in harvesting *Sargassum* (SAFMC, 2002), any commercial taking would certainly effect habitat for many larval and juvenile organisms as well as adult species that are important to fisheries (SAFMC, 2003).

Although *Sargassum* is a predominant physical structure on the surface of the open ocean in the lower latitudes, structure can also be found in the form of fronts (Olson, 2002), which are any sharp change in the physical properties of the ocean over a short spatial scale (Le Fevre, 1986). Kleisner (2009) found a correlation of dolphin presence with temperature fronts in the western Atlantic. In this study, dolphins are likely aggregating along temperature fronts due to the abundance of prey items commonly found at frontal features (Acha et al., 2004; Olson, 2001). Oceanographic fronts are attractive for dolphins because the convergence of different water masses concentrates phytoplankton and zooplankton (Olson, 2002), as well as floating debris and organisms (e.g. *Sargassum*, driftwood, detritus, and other flotsam) (Owen, 1981; Witherington, 2002) which creates a habitat complex. The negative SSH coefficient could be indicative of dolphins aggregating at convergence zones where water masses are downwelling at a frontal boundary. Although we did not include fronts in our analysis, the association of dolphins with fronts (low SSH in particular) could be further investigated by including explicit frontal variables for SST, CHL, or salinity, and including interaction terms with SSH or other appropriate variables.

The exploratory stock assessment by Prager (2000), which is the only formal evaluation of dolphin stocks in U.S. Atlantic and Gulf of Mexico, suggests that the levels of exploitation during the study period are sustainable but a more comprehensive assessment is needed. In the current analysis, we have shown that each year the bulk of dolphin catch (in individuals) and high catch rates are centralized in the south Atlantic bight during May and June. A more in depth analysis of temporospatial exploitation rates may reveal particular areas, or “hot spots”, beyond what we have shown, which would be useful for a more fine scale understanding catch rate. Also, dividing the statistical zones based on species assemblages and oceanography (i.e. large marine ecosystems; (Sherman, 1991)) may be appropriate and could be integrated into ecosystem based management efforts (Latour et al., 2003; Link, 2002; Link et al., 2002; Pikitch et al., 2004).

This study provides new evidence that dolphins are sensitive to a variety of static and dynamic oceanographic conditions. The comparison and linkage between commercial pelagic longline logbook records and recreational catch and release records showed that dolphins in both fisheries are caught under similar conditions. Furthermore, recreational fishermen are targeting dolphins and other pelagic fish in areas with highly favorable oceanic conditions as predicted by the final ZINB model. This is an important finding because the dolphin fishery is dominated by the recreational sector. Currently, assessment based on recreational location and effort are virtually unfeasible due to lack of data. The model can be used for prediction and for further understanding of oceanographic effects on abundance. These results would be useful for dolphin management planning to ensure conservation of the fishery by enabling temporospatially explicit management actions for both the recreational and commercial sectors. Furthermore, this analysis also supports the quantification and importance of pelagic *Sargassum* habitat, as well as providing insight into the size distribution of dolphins that are caught near and outside of *Sargassum*. As pressure increases on pelagic fisheries and catch rates remain high, we present an additional tool for managers to ensure a sustainable offshore fishery along the U.S. Atlantic coast.

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