



Modelling the oceanic habitats of two pelagic species using recreational fisheries data

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ABSTRACT

Defining the oceanic habitats of migratory marine species is important for both single species and ecosystem-based fisheries management, particularly when the distribution of these habitats vary temporally. This can be achieved using species distribution models that include physical environmental predictors. In the present study, species distribution models that describe the seasonal habitats of two pelagic fish (dolphinfish, *Coryphaena hippurus* and yellowtail kingfish, *Seriola lalandi*), are developed using 19 yr of presence-only data from a recreational angler-based catch-and-release fishing programme. A Poisson point process model within a generalized additive modelling framework was used to determine the species distributions off the east coast of Australia as a function of several oceanographic covariates. This modelling framework uses presence-only data to determine the intensity of fish (fish km⁻²), rather than a probability of fish presence. Sea surface temperature (SST), sea level anomaly, SST frontal index and eddy kinetic energy were significant environmental predictors for both dolphinfish and kingfish distributions. Models for both species

indicate a greater fish intensity off the east Australian coast during summer and autumn in response to the regional oceanography, namely shelf incursions by the East Australian Current. This study provides a framework for using presence-only recreational fisheries data to create species distribution models that can contribute to the future dynamic spatial management of pelagic fisheries.

Key words: fishery-dependent data, generalized additive mixed-effects model, point process model, recreational fisheries, species distribution model

INTRODUCTION

Species distribution models (SDMs) are tools for describing the environmental requirements of species, and for understanding how species may respond to a changing environment. For the last two decades, SDMs have been widely used in examining spatial patterns of terrestrial species (Ferrier *et al.*, 2004; Hernandez *et al.*, 2006), but there has been limited use of SDMs in the marine environment (i.e. Maxwell *et al.*, 2009; Robinson *et al.*, 2011; Mellin *et al.*, 2012). The application of SDMs to marine migratory species is challenging owing to spatiotemporal complexity in species occurrence (Elith and Leathwick, 2009), ontogenetic shifts in habitat (Einum *et al.*, 2006), and shifts in phenological events (Neeman *et al.*, 2015). This challenge is enhanced in the pelagic domain, where obtaining occurrence data for pelagic species is restricted by the logistical difficulties of sampling across large and remote spatial areas, as well as imperfect detections of species (MacKenzie *et al.*, 2002; Kaschner *et al.*, 2006).

Species occurrence data are frequently presented as time-space locations, where the presence location of a species is recorded, without comparable records of where the species is absent. Such data are termed 'presence-only' or a 'point event'. Fisheries catch records represent a useful species occurrence data source for populating SDMs, especially in environments that are generally poorly sampled, such as pelagic systems (Hobday, 2010; Robinson *et al.*, 2011). Catch records can be obtained from commercial fishing vessels, and,

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from recreational fishers in the form of cooperative tagging programmes. Fishery catch records are no different from typical presence-only data. However, recreational catch records differ from commercial catch records in that they commonly do not have measures of fishing effort. In the past, this has limited the use of such data in habitat suitability descriptions. Commercial catch records that have associated estimates of fishing effort have previously been used in producing SDMs for migratory marine species (Kaschner *et al.*, 2011; Jones *et al.*, 2012; Sequeira *et al.*, 2014). Few studies have used data from catch-and-release tagging programmes, which mostly rely on the voluntary efforts of recreational anglers to generate species point events. Nevertheless, these catch-and-release programmes can provide important sources of long-term presence-only data sampled from a broad geographical space for many pelagic fish and sharks (Casey and Kohler, 1992; Lucy and Davy, 2000; Domeier and Speare, 2012).

Presence-only data are widely used in SDMs and an extensive range of analytical approaches for presence-only analysis have been proposed (Elith *et al.*, 2006; Phillips *et al.*, 2009; Barbet-Massin *et al.*, 2012). The most common approach to analysing presence-only data is to estimate the probability of species presence by characterizing the environment through the random generation of pseudo-absences or 'background points'. The primary issue with this approach is that there is no robust way to assess the location, or number, of pseudo-absence points that should be generated, which can lead to issues in model specification, interpretation and implementation (Warton and Shepherd, 2010). Recently, point process models (PPMs) have been proposed as a technique for analysing presence-only data (Warton and Shepherd, 2010; Chakraborty *et al.*, 2011; Aarts *et al.*, 2012). For PPMs, the presence-only data are modelled as the intensity of species (individual per unit area) as a proxy for relative abundance, rather than a probability of presence (which is the case in logistic regression). This method solves the pseudo-absence selection problem by creating a framework in which to choose the location and number of pseudo-absences based on log-likelihood (Warton and Shepherd, 2010). The application of PPMs is relatively new to species distribution modelling but is effective in choosing pseudo-absence points and, in typical examples, is equivalent with MAXENT (Renner and Warton, 2013) and pseudo-absence logistic regression (Warton and Shepherd, 2010).

A second issue with presence-only data is that they are commonly subject to bias because the observers

that record the data are more likely to sample at some sites compared with others (i.e., fishing hot-spots). This sampling bias can also be related to accessibility, which, in the marine system, is related to the location of access points (boat ramps and marinas) and boat power. Such biases are a common problem in presence-only data, but can be accounted for by integrating the known biases as a covariate in SDMs (Warton *et al.*, 2013).

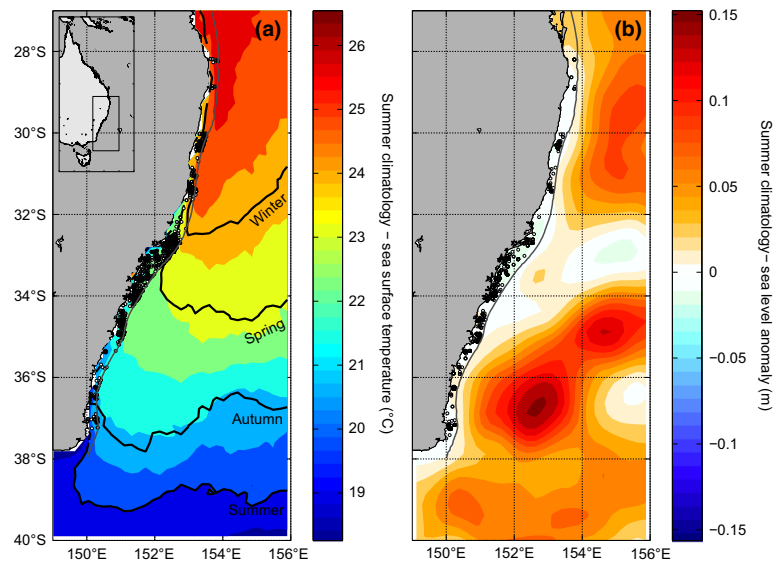
The goal of this study was to create a species distribution model for migratory marine species using data from a recreational fisheries tagging programme. Here the application of modern SDM methods was used to describe the oceanic habitats of two pelagic fish, dolphinfish (*Coryphaena hippurus*) and yellowtail kingfish (*Seriola lalandi*), off the east coast of Australia. The study region is oceanographically dynamic, dominated by an oligotrophic, poleward flowing western boundary current, the East Australia Current (EAC; Ridgway *et al.*, 2008; Suthers *et al.*, 2011). In this region, both dolphinfish and kingfish are major recreational species and commonly targeted in catch-and-release fishing, resulting in a large database of catch-and-release records (Gillanders *et al.*, 2001). These species act as comparative case studies for SDMs as they often occupy different pelagic habitats; dolphinfish being epipelagic (Oxenford and Hunte, 1999; Dempster, 2004; Young *et al.*, 2010) and kingfish reef-associated pelagic habitats where they have strong associations with near-shore topographic features (Dempster and Kingsford, 2003; Hobday and Campbell, 2009). The specific aims of this study were to: (i) create and evaluate SDMs for dolphinfish and yellowtail kingfish; and (ii) explore the seasonal oceanographic variation on the distribution of these species, as a prelude to understanding habitat use in eastern Australia.

METHODS

Recreational fisheries data

Presence-only data for both dolphinfish and kingfish were obtained from a cooperative recreational fisheries catch-and-release programme facilitated by the New South Wales Department of Primary Industries. These data consist of angler-recorded locations of fish captures. The data were spatially confined to New South Wales (NSW; 28°S–37.5°S; Fig. 1), Australia, and temporally limited from 1994 to 2012 to match the availability of a range of satellite-derived environmental predictors. There was no information on fishing effort in these data, so to reduce any bias and autocorrelation structure in the data we undertook two steps. First, only data representing the first fish captured on a

Figure 1. (a) Map of the east coast of Australia (inset) indicating the coastline of New South Wales (NSW). Black circles indicate the presence points of dolphinfish within the 200-m isobath for the period 1994 to 2012. Sea surface temperature (°C) climatology is shown, with colours showing the average summer temperatures, and the contours indicating the location of the 19°C isotherm for each season. (b) The NSW coastline with black circles indicating the presence points for yellowtail kingfish for the period 1994 to 2012. Sea level anomaly (m) summer climatology is shown. The grey line indicates the 200-m isobath.



unique day and location were included to satisfy the assumption of independence between presence points. Second, only catch records from continental shelf waters (< 200 m isobath) were included as this is where the majority of fishing occurs (Steffe *et al.*, 1996).

Environmental covariates

Physical environmental covariates were collated for both presence and pseudo-absence points, sourced using the Spatial Dynamics Ocean Data Explorer (Hartog and Hobday, 2011) and are: (i) sea surface temperature 3-day composite from AVHRR (SST; °C; 0.2° spatial resolution); (ii) sea level anomaly from Topex/Poseidon and ERS-1 (SLA; m; 0.4° spatial resolution); (iii) eddy kinetic energy derived from altimetry (EKE; $m^2 s^{-2}$; 0.2° spatial resolution); and (iv) the frontal index derived from daily SST image analysis as the number of temperature fronts in each pixel over an 8-day period (FI; Hobday and Hartog, 2014). To account for coastal shading in satellite-derived products, all pixels and presence points at < 40 m isobath were excluded from the analysis. Predictor covariates were examined for correlation using pair plots and Pearson's rank correlations. To avoid collinearity, one covariate from covariate pairs with a correlation > 0.5 and < -0.5 was removed from the model selection process. An 8-day chlorophyll-*a* composite from MODIS (L3 m) was removed owing to correlation with SST, and a bathymetry product was removed as a result of correlation with the 'distance to port' covariate (see Table 1). All other covariates

available for model selection had low cross-correlation scores.

The explanatory model

To predict the distributions of dolphinfish and kingfish as a function of environmental covariates, a point process model (PPM) was created for each species, with the binary response variable composed of presence and pseudo-absence points. A PPM was implemented using a down-weighted generalized additive mixed-effects model (GAMM) with a Poisson distribution and log link function using the 'gamm4' R package (Wood and Scheipl, 2013) in the R programming language (R Core Team, 2014), according to Renner *et al.* (2015). The down-weighted approach, known as a down-weighted Poisson regression (DWPR), forces predicted probabilities of fish presence to be very small. The combination of this small probability with a large number of point locations (> 50) allows the Poisson distribution to approximate the binomial distribution (presence versus pseudo-absence; Renner *et al.*, 2015). This approximation improves as the probability becomes smaller, and the numbers larger. This equivalence between Poisson PPM's and binary logistic regression allows the PPM intercept term to be estimated correctly within a generalized linear model framework. The down-weighting is achieved by setting the weights for the presence points equal to a small value (1×10^{-8}), and weights for the pseudo-absence points equal to the planimetric area of the study region (35712 km²) divided by the total number of pseudo-absence points. The fitted values of the PPM are in units of fish intensity per

Table 1. Summary of model covariates. The observed covariate range (presence and pseudo-absence) is provided for each species, where DOL refers to dolphinfish, and YTK to kingfish.

Covariate	Description	Units	Range
SST	Sea surface temperature; 3-day composite from AVHRR. Spatial resolution 0.2°.	°C	DOL: 10–30 YTK: 12–29
SLA	Sea level anomaly; from a gridded product of Maps of Sea Level Anomaly from Topex/Poseidon and ERS-1. Spatial resolution 0.4°.	m	DOL: –0.28–0.38 YTK: –0.25–0.37
EKE	Eddy kinetic energy; derived from altimetry. Spatial resolution 0.2°.	m ² s ⁻²	DOL: 0–1.5 YTK: 0–1.1
FI	Number of temperature fronts in each pixel over an 8-day period, derived from daily sea surface temperature image analysis. Spatial resolution 0.4°.		DOL: 0–14 YTK: 0–10
Port	Distance between presence point and nearest access port	km	DOL: 2–54 YTK: 1–40
Year	Calendar year		1994–2012

km², which is a measure of a species' relative abundance (Renner *et al.*, 2015).

The pseudo-absence points were randomly selected within the same spatial and temporal confines as the presence locations. The total number of pseudo-absence points included in the final model were chosen using the PPM approach by generating multiple models with varying numbers of pseudo-absence points (1000 to 40 000) and the number of points at which the log-likelihoods converged was the number of points used in the final models (Renner *et al.*, 2015). Based on this approach, 20 000 randomly generated pseudo-absence points were used in the dolphinfish and kingfish models.

The predictors available for model selection for both dolphinfish and kingfish models were four environmental covariates, a 'distance to port' covariate to account for the observer bias of fishing effort (see below), and calendar year (Year) as a random factor to account for inter-annual variability in fish abundance and fishing effort (Table 1). The body length of the captured fish was not included in the model because these data are biased as a result of sub-legal-sized fish being more commonly released, and thus recorded in catch-and-release fishing programmes, compared with larger 'trophy' fish. To account for observer bias of fishing effort in the fishery-dependent data, the great circle distance from each presence and pseudo-absence point to the closest port (i.e. access point) was calculated using the `SPDISTs` function in the 'sp' package (Bivand *et al.*, 2013). 'Distance to port' (Port; km) was included as a covariate in the model to allow presence locations to be modelled as a function of known observer bias in addition to the environmental covariates (Warton *et al.*, 2013).

The full model available for model selection was:

$$\text{Intensity} = s(\text{SST}) + s(\text{SLA}) + s(\text{EKE}) + s(\text{FI}) + s(\text{Port}) + \text{Year}_{\text{random}} \quad (1)$$

Where intensity (fish km⁻²) is the relative abundance of the species, *s* represents a penalized regression spline type smoother based on generalized cross-validation (GCV). To avoid over-fitting, model covariates were selected using an information theoretic approach by comparison of a nested set of *a priori* parameter combinations. If the estimated degrees of freedom (edf) of a parameter in the full model (Eqn 1) was close to one (indicating linearity) then the smoother was removed prior to model selection. The model in the set with the lowest Akaike information criterion (AIC) was chosen as the final model.

Model evaluation

Model evaluation for individual dolphinfish and kingfish models was done using cross-validation. This involved *k*-folds partitioning, where presence data were randomly partitioned into 10 equal subsamples (*k* = 10) and the model trained on 9 of the subsamples and tested against the 10th subsample. Each training subsample was run with 20 000 randomly chosen pseudo-absence points, and the testing subsample had a 1 : 1 ratio of presence and pseudo-absence points. The predictive power of each model was assessed by computing a confusion matrix for each training and testing combination using the `evaluate` function in the 'dismo' package (Hijmans *et al.*, 2013). The mean Area Under the receiver-operating Curve (AUC) and the mean True Skill Statistic (TSS) was calculated from each confusion matrix. The AUC

provides a single measure of overall model accuracy that is threshold independent, with an AUC value of 0.5 indicating the prediction is as good as random, whereas 1 indicates perfect prediction (Fielding and Bell, 1997). AUC has been extensively used in SDM modelling and measures the ability of the model to correctly predict where a species is present or absent (Elith *et al.*, 2006). An AUC value of >0.75 is considered to have a good predictive power and is acceptable for conservation planning (Pearce and Ferrier, 2000). TSS is an alternative measure of model accuracy that is threshold dependent and not affected by the size of the validation set (Allouche *et al.*, 2006). It is an appropriate evaluative tool in cases where model predictions are formulated as presence–absence maps (Allouche *et al.*, 2006). TSS is on a scale from -1 to $+1$, with 0 representing no predictive skill and is calculated from the confusion matrix outputs of sensitivity and specificity. Sensitivity is the rate of true positive model predictions, and specificity is the rate of true negative model predictions, with TSS equal to sensitivity plus specificity minus 1 (i.e. $TSS = sensitivity + specificity - 1$). Threshold dependent and independent statistics, such as AUC and TSS, are used in combination when evaluating the predictive power of a SDM (Pearson *et al.*, 2006).

Semi-variograms were created to examine any spatial and temporal autocorrelation in the dolphinfish and kingfish models. Semi-variograms relate the dissimilarity of points (or semi-variance) to the spatial or temporal distance that separates them. Data that are randomly distributed has no change in variance across distance and is considered uncorrelated. Semi-variograms were created using the `variogram` function in the 'gstat' package (Pebesma, 2004). Spatial coordinates were used in creating spatial semi-variograms, with a cutoff distance set at 5° . The date of fish catch was used in the temporal semi-variograms, with a cutoff distance set at 5 days. The spatial and temporal cut-off distances reflect the limit at which autocorrelation was expected.

Predictions of distributions

The derived dolphinfish and kingfish models of fish intensity were used to predict the seasonal distribution of both species. Two metrics were used to visualize and display the predicted seasonal distribution, the first is spatial maps of fish intensity across the study area, and the second, is a simplified line plot indicating the fish intensity across a latitudinal scale. To predict on a seasonal scale, the selected environmental covariates (SST; SLA; EKE; FI) were averaged across each of the four seasons from the period 1994–2012. Each

environmental covariate had been sampled at a different resolution (Table 1), so all were interpolated to a 0.2° spatial resolution. The study area available for dolphinfish predictions was extended east of the continental shelf to 156°E , consistent with the wide distribution of this species. While the model was trained on data for the shallower waters of the continental shelf, extending predictions is justified because of the epipelagic nature of dolphinfish (Young *et al.*, 2010). The study area available for kingfish predictions was only extended out to the 500-m isobath because kingfish are linked with near-shelf topographic features (Hobday and Campbell, 2009). The 'distance to port' (Port) covariate selected in both dolphinfish and kingfish models is fixed at a constant value prior to prediction, so that predictions correct for observer bias over the entire study region (Warton *et al.*, 2013). The allocation of a constant Port value will affect the predicted distributions depending on which value is selected. Thus, the chosen Port value for prediction was the distance that maximized fish intensity (13 km for dolphinfish, and 5 km for kingfish as determined from the models).

The distributions of fish intensity were then predicted against the seasonal averages of environmental covariates and the fixed Port value, using the `predict` function of the 'raster' package (Hijmans, 2014). The predicted distributions of fish intensity were plotted as spatial maps for each season and each species. The maps were then averaged zonally (across longitude) to provide a line plot that indicates the seasonal changes in fish intensity as a function of latitude, which is the dominant axis of variation owing to the influence of the East Australia Current. The prediction methods in this section were then repeated to determine a monthly prediction of the distribution of dolphinfish and kingfish intensity. Using the predicted line plots, the latitude at which fish intensity is at a maximum is extracted and used to create a climatology of the latitude where kingfish and dolphinfish intensity is at a maximum.

RESULTS

Data

A total of 2122 and 1235 presence points, collected over a 19-yr period, were included in the dolphinfish and kingfish models, respectively. Presence points for both species were concentrated in the central region of the NSW coast and shared similar patchiness on the northern and southern areas (Fig. 1). Kingfish presence points were < 40 km from any port, and this distance was consistent along the NSW coast.

Dolphinfish points were < 54 km from any port, but distances greater than 30 km occurred only between latitudes 32.5 °S and 34 °S. The summer SST and SLA climatology (Fig. 1) illustrates the typical summer oceanographic conditions off the east coast of Australia. The 19 °C isotherm for each season (Fig. 1a) illustrates the temporal variability in the regional oceanography.

The explanatory model

All oceanographic covariates were retained in both the dolphinfish and kingfish models (Table S1), which suggested complex relationships between oceanographic conditions and fish intensity. Smoothing factors were retained for all predictors in the dolphinfish model, but smoothing factors for SLA and 'distance to port' (Port) in the kingfish model were not retained in the final model, in favour of linear terms for these covariates (Table 2, Table S1). Spatial and temporal semi-variograms revealed no autocorrelation in the dolphinfish or kingfish models (Fig. S1). SST had a strong influence on fish intensity, with the intensity of dolphinfish peaking at ~24.5 °C (Fig. 2a) and kingfish at ~22.5 °C (Fig. 3a). The optimum SLA for dolphinfish intensity plateaued between -0.13 and 0.28 m SLA (Fig. 2b), and for kingfish a positive linear relationship with SLA was found (Table 2, Fig. 3d). A similar pattern between fish intensity and the frontal index (FI) occurred for both species, with intensity highest at FI between 0 and 4, and decreasing at a FI higher than 4 (Figs 2c and 3b). The fish intensity in

relation to eddy kinetic energy (EKE) differed between species, with dolphinfish showing two peaks in intensity at 0 and 0.8 m² s⁻² (Fig. 2d). Kingfish intensity peaked at EKE of 0.16 m² s⁻² and steadily decreased at EKE higher than this (Fig. 3c). The Port covariate was strongly correlated with fish intensity in both models, with an overall decrease in intensity with increasing distance from ports. The Port covariate in the kingfish model indicated a negative linear relationship (Table 1, Fig. 3e). The dolphinfish model highlighted two distinct peaks in fish intensity, the first at ~13 km from the nearest port and the next at ~38 km (Fig. 2e).

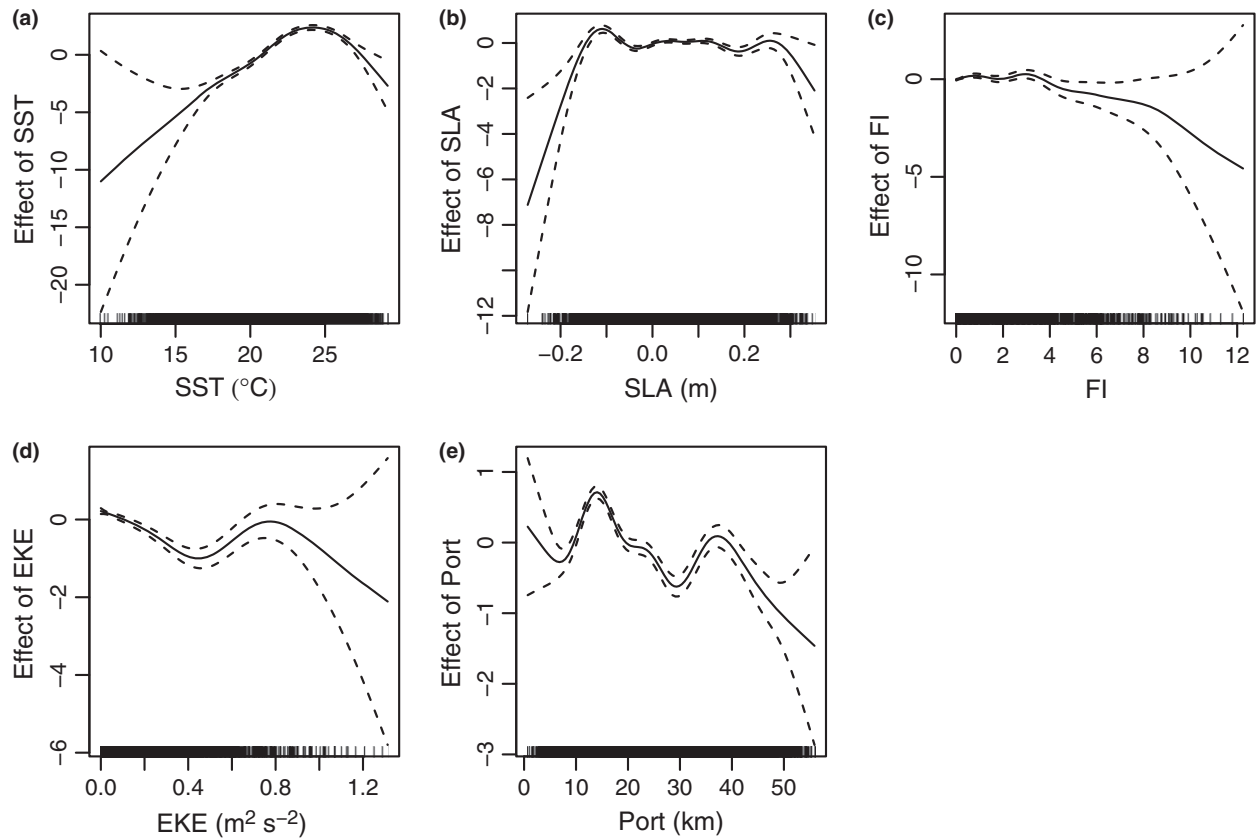
Predictions of distributions

The ability of both models to predict fish intensities was good, with AUC values of 0.80 ± 0.005 for dolphinfish, and 0.81 ± 0.003 for kingfish (Table 2). The TSS indicated a correlation between the predicted fish intensity and the observed intensity, with a TSS value of 0.50 ± 0.015 for dolphinfish, and 0.51 ± 0.01 for kingfish (Table 2). The predicted spatial patterns of fish intensity across each season demonstrated the complexity of fish responses to oceanographic conditions (Figs 4 and 5). Dolphinfish intensity along the entire NSW coast increased during summer and autumn. Kingfish intensity shifted south during summer and autumn, and to the north to subtropical waters during spring and winter. The kingfish distribution plots also indicate a pattern of offshore movement during the spring and winter months (Fig. 5). The

Table 2. Model results for dolphinfish and kingfish. A smoothing factor is indicated by 's'. The effective degrees of freedom (edf) for smoothers; the coefficient estimates; *P*-values; the mean (±SD) Area Under the receiver-operating Curve (AUC) statistic; and the mean (±SD) True Skill Statistic (TSS) are provided.

Species and covariate	edf	Estimate	<i>P</i>	AUC	TSS
Dolphinfish					
s(SST)	5.84	-0.5	<0.001		
s(SLA)	8.17	1.16	<0.001		
s(EKE)	5.30	-0.18	<0.001		
s(FI)	5.38	-0.4	<0.001		
s(Port)	8.44	-0.85	<0.001		
Year (intercept)		-4.22	<0.001		
Full Model				0.80 ± 0.005	0.50 ± 0.015
Yellowtail kingfish					
s(SST)	5.78	-0.26	<0.001		
SLA		1.21	<0.01		
s(EKE)	2.74	-0.4	0.001		
s(FI)	4.34	-1.33	<0.001		
Port		-0.15	<0.001		
Year (intercept)		-3.70	<0.001		
Full Model				0.81 ± 0.003	0.51 ± 0.01

Figure 2. Partial effect plots of each smoothed predictor in the dolphinfish model: (a) sea surface temperature (°C); (b) sea level anomaly (m); (c) frontal index; (d) eddy kinetic energy ($\text{m}^2 \text{s}^{-2}$); (e) 'distance to port' (km). The y-axis values are the contribution of the smoother to the model's fitted values. Dotted lines represent 95% confidence limits. Whiskers on the x-axis indicate the data (presence and pseudo-absence data) for each predictor.



latitude at which fish intensity is at a maximum shows a distinct annual cycle, where during summer months the maximum fish intensity for both species moved further south (Fig. 6).

DISCUSSION

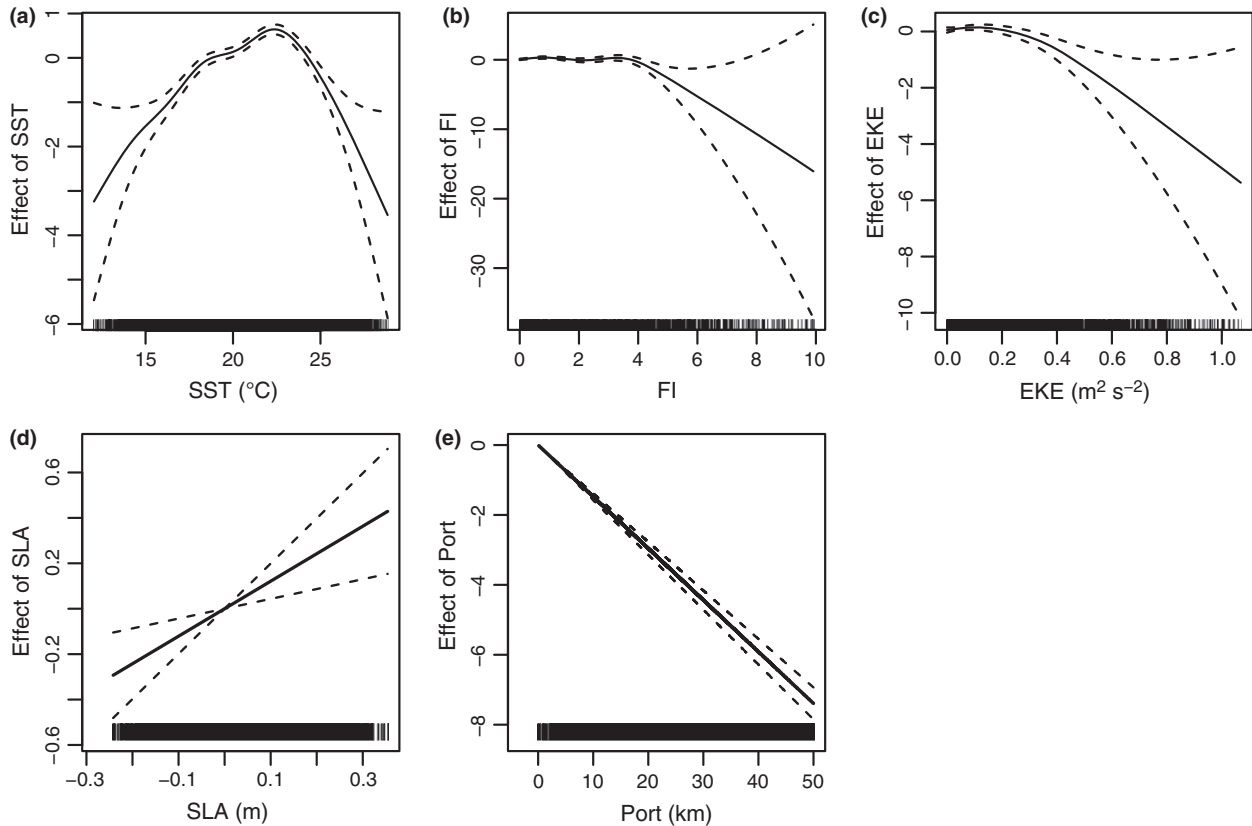
These results highlight the strong relationship between pelagic fish distributions and the ocean environment. Both dolphinfish and kingfish off the east Australian coast showed strong seasonal changes in their distribution in response to the regional oceanography. The complexities of the fish distributions are evident from the shapes of the partial effect GAMM plots, and the significance of all four environmental covariates in the best model. The application of the down-weighted Poisson regression approach was valuable in determining the number of pseudo-absences for analysis, but this approach makes model validation challenging. This study shows how presence-only fishery-dependent data can be used in creating species

distribution models to describe the habitats and ecology of pelagic species. The distribution models created in this study have potential application for single species and ecosystem-based management. For example, these distributions could be used to manage access to single species at certain times of the year, or to reduce unwanted bycatch of these species when seeking other target species (Hobday *et al.*, 2010; Baker and Hollowed, 2014). Managing recreational fisheries has been traditionally difficult, and these methods illustrate how data from such fishers can be informative.

Environmental drivers of dolphinfish and kingfish distributions

Identifying the environmental drivers of fish distributions gives insight into their physiological and ecological requirements within pelagic systems. The significance of the four environmental predictors (SST; SLA; FI; EKE) indicates the importance of physical oceanographic variables influencing the

Figure 3. Partial effect plots of each smoothed predictor in the kingfish model: (a) sea surface temperature ($^{\circ}\text{C}$); (b) frontal index; (c) eddy kinetic energy ($\text{m}^2 \text{s}^{-2}$); and each linear predictor: (d) sea level anomaly (m); (e) 'distance to port' (km). The y-axis values are the contribution of the smoother to the model's fitted values. Dotted lines represent 95% confidence limits. Whiskers on the x-axis indicate the data (presence and pseudo-absence data) for each predictor.

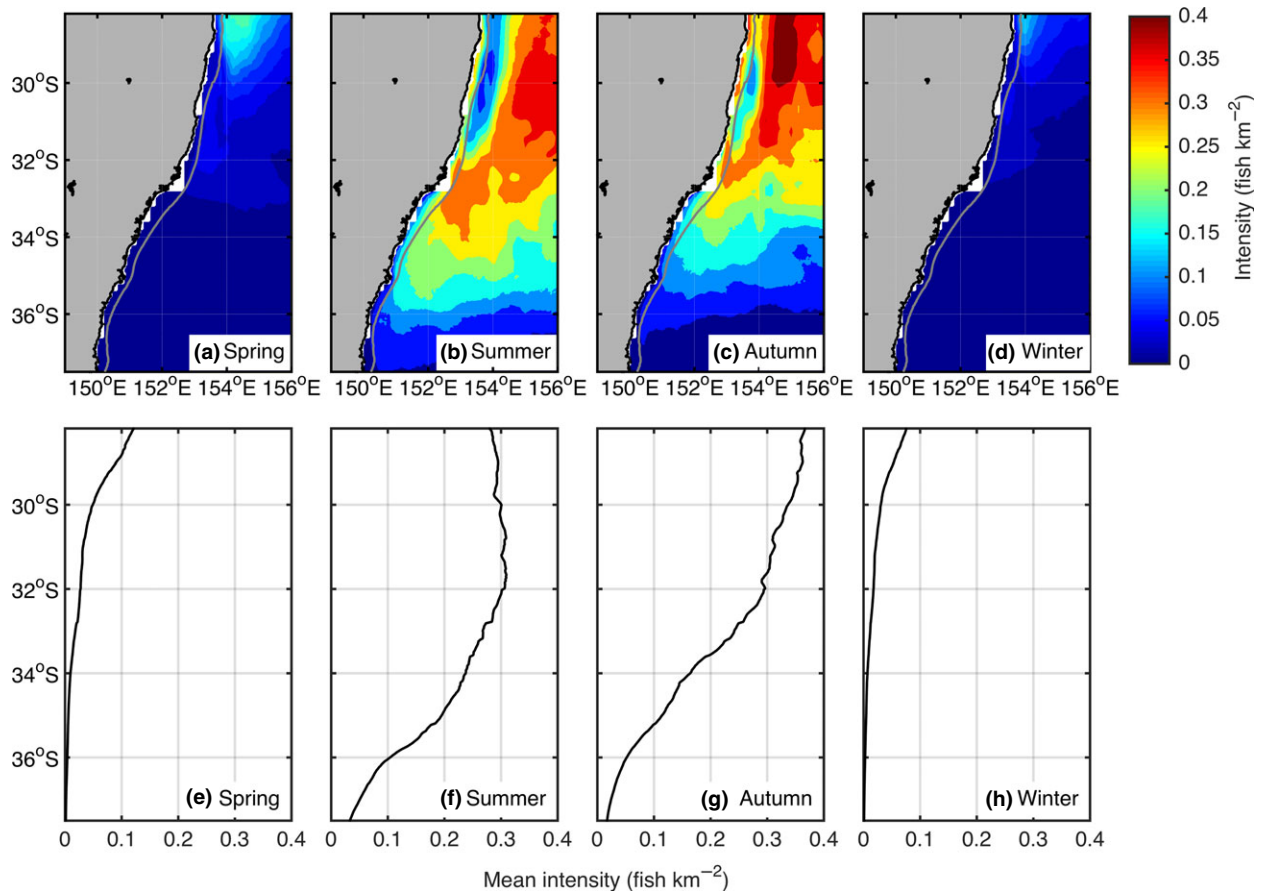


distribution of dolphinfish and kingfish. The relationships between fish intensity and SLA, FI and EKE covariates are indicative of a preference of both species for oceanographic fronts, compared with highly turbid areas characterized by high FI and high EKE. Pelagic species often aggregate in such oceanographic features, which can enhance feeding opportunities, as shown for tuna (Laurs *et al.*, 1984; Fiedler and Bernard, 1987) and swordfish (Podestá *et al.*, 1993), as a result of elevated production and retention that can concentrate prey (Scales *et al.*, 2014). The results of this study are consistent with those of Zainuddin *et al.* (2006) who found that albacore (*Thunnus alalunga*) were more abundant in frontal areas associated with anti-cyclonic eddies. In contrast to this study, dolphinfish presence along the U.S. East Coast was not related to SLA or EKE, but highly correlated with SST and chlorophyll-*a* (Farrell *et al.*, 2014). This could be as a result of differing oceanographic upwelling processes in the studies (Cresswell, 1994). In the current study, the EAC retroflects eastwards between 30°S and 34°S

(Godfrey *et al.*, 1980) leaving behind a poleward flowing eddy field (Ridgway and Godfrey, 1997; Everett *et al.*, 2012) that can produce productive fishing grounds (Young *et al.*, 2001, 2011) from elevated biomass and secondary consumers such as zooplankton (Everett *et al.*, 2011) and larval fish (Mullaney and Suthers, 2013). The signal of productive fishing grounds may be indicated by SLA, EKE and FI, and future work could focus on examining the relationships between chlorophyll-*a* and fish intensity.

The energetic requirements of feeding are an important driver of fish distributions (Golet *et al.*, 2013) but it is challenging to include such ecological factors into an SDM. SST is one variable that is closely linked with the physiological requirements of species and their prey, which may be why this covariate had the strongest relationship with fish intensity for both species. The physiological limits of species are an important driver in their pelagic distributions, and thermal preferences have been identified using SDMs for tunas (Arrizabalaga *et al.*, 2015), whale sharks

Figure 4. Spatial prediction of dolphinfish intensity across four seasons: (a) spring, (b) summer, (c) autumn and (d) winter. Colours represent the intensity of dolphinfish in number of fish km^{-2} , and the grey line represents the 200 m isobath. Line plots indicate average dolphinfish intensity against latitude (e) spring, (f) summer, (g) autumn and (h) winter.



(Sequeira *et al.*, 2014) and marlin (Su *et al.*, 2011; Lien *et al.*, 2014).

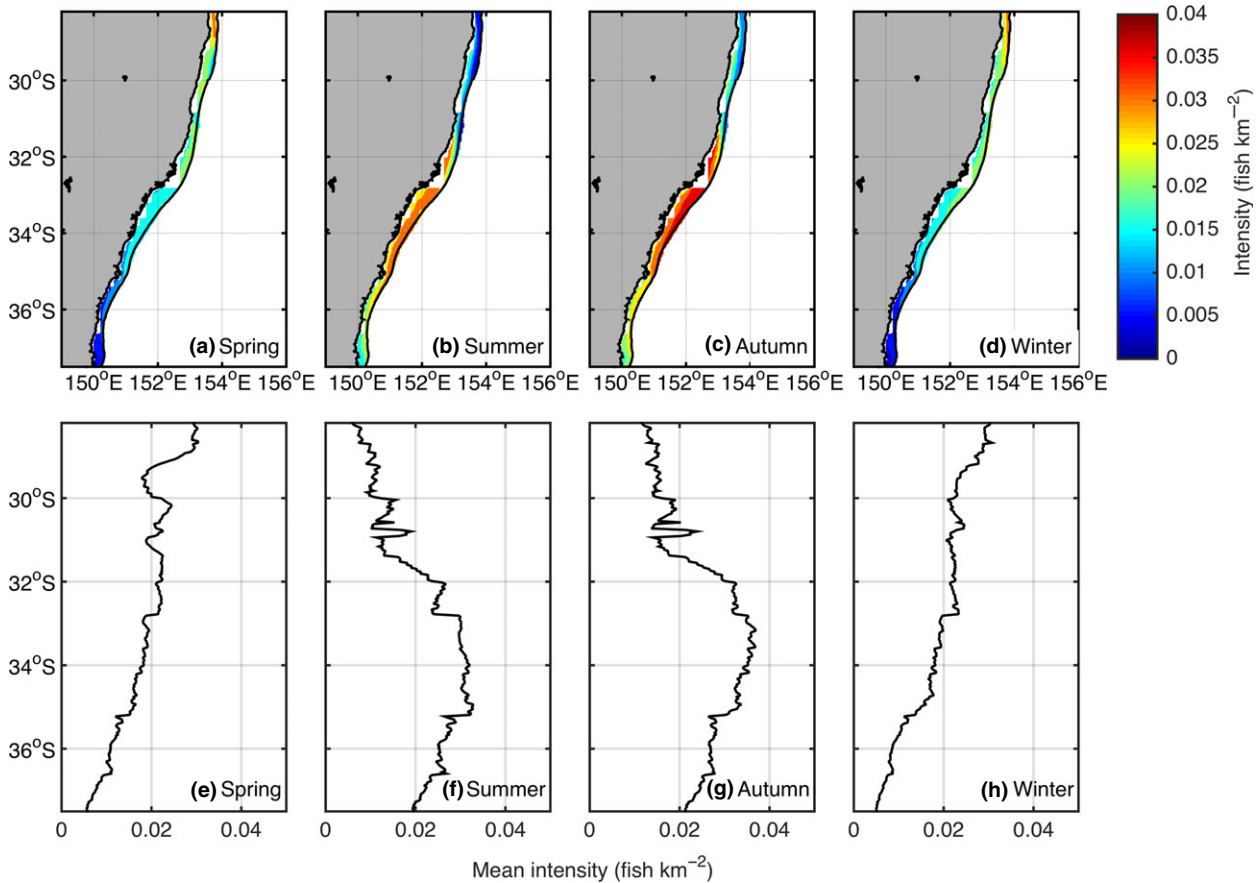
The explanatory models in this study revealed that SST is the factor driving most of the variation in habitats occupied by dolphinfish and kingfish. Dolphinfish intensity in this study peaked at 24.5 °C, which is consistent with the 24 °C temperature at which dolphinfish commercial catch peaks on the U.S. East Coast (Farrell *et al.*, 2014). There is limited research on kingfish ecology, but aquaculture-based research on kingfish has revealed that the optimum rearing temperature on the NSW coast is 22 °C (Fielder and Heasman, 2011) which is consistent with the 22.5 °C peak observed in this study. These differences in thermal preferences may indicate niche segregation between these two pelagic predators. The species distribution models presented in this study assumed physical environmental variables are the primary driver in fish distributions, an assumption justified by the high explanatory power of the models. To further improve

accuracy and predictive capacity, future research could include other ecological descriptors, including species (predator-prey) interactions, diets, energetics and ontogenetic changes.

Catch-and-release data

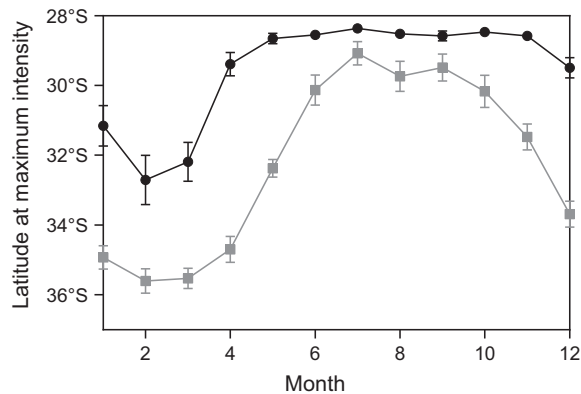
This study successfully used a novel approach of utilizing fishery-dependent recreational angler catch data for modelling the distributions of two pelagic fish species. Previous distribution modelling approaches have used commercial catch data with associated fishing effort for determining dynamic ocean habitats (Hobday *et al.*, 2011a), identifying tuna hot spots (Zainuddin *et al.*, 2006), forecasting tuna (Hobday *et al.*, 2011b) and shark habitats (Sequeira *et al.*, 2014), as well as spatial forecasts of catch per unit effort (Glaser, 2011). In this study, the interpretation of results must be approached cautiously and consider the scale at which the oceanographic covariates were sampled. To allow synoptic coverage over a long time period,

Figure 5. Spatial prediction of kingfish intensity across four seasons: (a) spring, (b) summer, (c) autumn and (d) winter. Colours represent the intensity of kingfish in number of fish km^{-2} , and the black line represents the 200-m isobath. Line plots indicate average dolphinfish intensity against latitude (e) spring, (f) summer, (g) autumn and (h) winter.



the oceanographic covariates were derived from satellite measurements that limit the coverage closer to the coast, where the majority of the fish presence-only

Figure 6. The average (\pm SE) latitude at which dolphinfish (black line) and kingfish (grey line) intensity was at a maximum, across calendar month, predicted from years 1994 to 2012 ($n = 19$ yr).



data were concentrated. This may result in reduced confidence for the kingfish model as kingfish are often associated with inshore coastal reef habitats on the continental shelf, and hence are more frequently caught in inshore areas. In contrast, dolphinfish occupies the epipelagic zone and are regularly associated with floating structures rather than reef habitats, thus, in this study predictions were extended off the continental shelf. The potential issue for the kingfish model was not reflected in the predictive power (AUC and TSS) of the model as the predictive power between dolphinfish and kingfish models was comparable. SDMs that use data from inshore coastal areas could be improved by ensuring that the environmental predictors have the best possible coverage of the areas of interest. For angler-based tagging data, this will most likely involve coastal regions where satellite derived products are less reliable. In order to create a realistic SDM for coastal areas, it is recommended coupling satellite-derived products with other data sources, such as those from long-term monitoring

stations, ship data, and, coastal models (Holt *et al.*, 2009).

The fishery-dependent catch data in this study had an unknown fishing effort and was spatially biased in the way the data were collected. Correcting for such biases in presence-only data can be attempted through modifications to the model (Warton *et al.*, 2013), rather than biasing the way pseudo-absence points are selected (Phillips *et al.*, 2009; Syfert *et al.*, 2013). In this study, creating the *Port* covariate accounted for sampling bias in the model estimates, with the results indicating a general decrease in fish intensity with increasing distance to the port. There were two distinct peaks in fish intensity in the dolphinfish model; the first peak at 13 km from the nearest port and the second at 38 km. The first peak is within the range of moored Fish Aggregation Devices (FADs) that attract fish for the purpose of increasing catch rates. These FADs are placed between 9 and 28 km from the closest port (mean of 16 km) and concentrate fishing effort around these devices (Dempster, 2004). The spatial dependence that FAD locations may have introduced to the presence-only data was reduced by removing duplicate fish catches for the same day and location. Alternative approaches to dealing with spatial dependence could be to use: spatial autocorrelation terms; Gibbs processes that relaxes the independence assumption by assuming interactions between sets of points (Baddeley *et al.*, 2013; Renner *et al.*, 2015); block resampling methods that divide data into blocks to force approximate independence between blocks (Slavich *et al.*, 2014); and Cox processes that provide a way of dealing with clustering and the effects of unmeasured covariates (Møller *et al.*, 1998; Renner *et al.*, 2015). The location of the second peak in fish intensity revealed a localized pattern in the data where, between 32.5 °S and 34 °S, fishing catches extended out to ~54 km. This extension in distance is as a result of increased population density in this area that results in wider fishing grounds being used, as well as a decreased density of available ports between 32 °S to 34 °S.

Analysing presence-only data using Poisson point process models (PPM) is a recent approach to SDMs and provides an effective and simple method of choosing the number of pseudo-absences needed for species distribution modelling (Warton and Shepherd, 2010; Aarts *et al.*, 2012; Renner *et al.*, 2015). The primary limitation of this PPM approach is the reduced ability to undertake model validation. This is because the down-weighted Poisson regression (DWPR) approach allows the GAMM to fit a PPM even although the response variable is not a count. *K*-functions can be

used to check for clustering and spatial homogeneity (Renner *et al.*, 2015) but this adds a substantial level of complexity to model validation. In comparison to the widely used logistic regression approaches (Maxwell *et al.*, 2009; Reglero *et al.*, 2014; Sequeira *et al.*, 2014), PPMs change the response variable to a metric of abundance rather than probability, and can thus improve the biological interpretation of results. The concepts of the PPM and the straightforward application of the DWPR used in this study can be applied to other pelagic species that are targeted by cooperative tagging programmes, such as tunas, billfish, mackerels and sharks. Other fishery-dependent and independent data can also be used within the DWPR framework, with model parameters modified to reflect the study species. For example, including the surface area of topographic features in the analysis may help to determine habitat preferences of demersal species that are not related to oceanic conditions. Like any model that generates spatial density estimates, application of the DWPR across large spatial scales will need to ensure that variation in grid size is taken into account. This can be achieved by ensuring that the units of intensity match whatever spatial units have been determined after the projection of the coordinate system.

Implications for species management

SDMs in the marine environment are primarily used for spatial conservation planning and management (Crowder and Norse, 2008; Robinson *et al.*, 2011), including, marine park implementation (Leathwick *et al.*, 2008), single species fishery regulatory measures (Murawski *et al.*, 2000), as well as ecosystem-based fisheries management (Maxwell *et al.*, 2009). The annual cycles of fish intensity modelled in this study have implications for dolphinfish and kingfish fishery management, where dynamic management strategies, such as pelagic protected areas (Game *et al.*, 2009) may be effective. For example, both dolphinfish and kingfish in New South Wales are targeted through a recreational fisheries enhancement programme that deploys artificial reefs (permanent deployments) and Fish Aggregation Devices (FADs; seasonal deployments) to increase fishing opportunities in coastal waters. By understanding the ecological drivers of dolphinfish and kingfish distributions, the deployment of enhancement structures could be improved by implementing a dynamic deployment approach. For example, this could involve deploying fewer FADs in areas where fish intensity is high, and more FADs in areas where fish intensity is low (Sempo *et al.*, 2013).

Knowledge of the ecological drivers of pelagic fish distributions can enhance marine management

strategies so they reflect the spatial and temporal complexities of the pelagic environment and ensure that conservation planning and management is based on important marine features, rather than coincidental protection (Game *et al.*, 2009). Seasonal maps and climatologies of fish habitats, as presented in this study, only represent a static illustration of past fish events. While this is a useful tool, the next step in marine conservation planning is dynamic spatial management of pelagic species (Hobday *et al.*, 2014). This can involve creating forecasts of fish distributions on short timescales (weeks to months) that allow user groups and management to adapt to spatial and temporal variability in fish distributions (Hobday *et al.*, 2011b). Fish forecasts can also be created on long timescales (years to decades) that can predict species invasions (Lee *et al.*, 2008), as well as fish distributions under climate change scenarios (Hartog *et al.*, 2011; Lenoir *et al.*, 2011; Hobday *et al.*, 2015). The framework presented here for analysing presence-only fishery-dependent data can potentially contribute to the future development of SDMs both here and elsewhere, as effective tools for the management of pelagic species.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. Semi-variograms of the residuals of the dolphinfish and kingfish models. Spatial semi-variograms for dolphinfish (A) and kingfish (B) models used spatial coordinates. Temporal semi-variograms for dolphinfish (C) and kingfish (D) models used the fish catch date. *x*-axis distance units are in degrees for spatial plots (A & C) and days for temporal plots (B & D).

Table S1. Model selection results for dolphinfish and kingfish. A smoothing factor is indicated by 's'. The difference in Akaike Information Criteria (AIC) values and the corresponding weights for each model is provided, with the best model indicated in bold.