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Rapid shifts in distribution and high-latitude persistence of oceanographic habitat revealed using citizen science data from a climate change hotspot

Running head: Climate-driven spatiotemporal habitat change

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Abstract

The environmental effects of climate change are predicted to cause distribution shifts in many marine taxa, yet data are often difficult to collect. Quantifying and monitoring species' suitable environmental habitats is a pragmatic approach for assessing changes in species distributions but is underdeveloped for quantifying climate change induced range shifts in marine systems. Specifically, habitat predictions present opportunities for quantifying spatiotemporal distribution changes while accounting for sources of natural climate variation. Here we demonstrate the utility of a marine-based habitat model parameterised using citizen science data and remotely-sensed environmental covariates for quantifying shifts in oceanographic habitat suitability over 22-years for a coastal-pelagic fish species in a climate change hotspot. Our analyses account for the effects of natural intra- and inter-annual climate variability to reveal rapid poleward shifts in core ($94.4 \text{ km decade}^{-1}$) and poleward edge ($108.8 \text{ km decade}^{-1}$) oceanographic habitats. Temporal persistence of suitable oceanographic habitat at high-latitudes also increased by approximately three months over the study period. Our approach demonstrates how marine citizen science data can be used to quantify range shifts, but necessitates shifting focus from species distributions directly, to the distribution of species' environmental habitat preferences.

Introduction

Climate-driven species redistributions are occurring at approximately an order of magnitude faster in the marine environment than in terrestrial systems (Chen *et al.*, 2011, Poloczanska *et al.*, 2013, Sorte *et al.*, 2010). These range shifts are altering the structure of ecosystems and affecting human societies that depend on them (Pecl *et al.*, 2017, Vergés *et al.*, 2014). The rapid and pervasive nature of climate-driven ecological change within marine systems highlights the need to identify changes to the distributions of key species to enhance our

capacity for developing adaptive management strategies (Hobday *et al.*, 2016a, Pecl *et al.*, 2014b). However, poor spatiotemporal resolution of species occurrence records and a paucity of longitudinal surveys of species presence and abundance, which can describe range-shifts directly, commonly prevents the identification of a climate change signal from natural variability in species distributions (Hobday & Evans, 2013).

Predicting the preferred environmental habitat for species of interest is an alternative, pragmatic approach for assessing the ecological effects of climate change across species lacking sufficient direct observations (Araújo *et al.* 2005). Species distribution models (SDMs) commonly facilitate this approach by relating available species occurrence records (presence-only or presence-absence data) with environmental variables to define habitat preferences and estimate species' distributions (Barbet-Massin *et al.*, 2012, Elith *et al.*, 2006). Marine-based applications of SDMs are increasing but remain under-developed (Brodie *et al.*, 2018), particularly for understanding and predicting climate-driven species redistributions (Elith *et al.*, 2010, Robinson *et al.*, 2011). For example, pelagic fishes are predicted to undergo large spatial redistributions under climate change partly due to high adult mobility allowing these species to better track their thermal preferences (Sunday *et al.*, 2015). However, SDMs have identified high seasonal variation in the distribution of environmental habitats for pelagic fishes (Brodie *et al.*, 2015), suggesting a need to account for sources of natural climate variability when using SDMs to assess the effects of anthropogenic climate change on species distributions.

The physiological responses of species are predicted to vary in relation to environmental habitat suitability (Del Raye & Weng, 2015). Concurrent reductions in reproduction, growth and feeding occur across a declining gradient of habitat suitability (Helaouët & Beaugrand,

2009), ultimately affecting species' survival in areas of low quality habitat (Schmidt-Nielsen, 1990). Spatial predictions from SDMs provide a useful summary of variation in environmental suitability that may be used to identify areas where species' physiological requirements are likely met, and where species' performance or survival may be compromised (Helaouët & Beaugrand, 2009). Subsequently, spatial predictions of habitat suitability may be used to identify locations where species are progressing through stages of climate-mediated range shifts (Bates *et al.*, 2014). For example, small, non-viable or vagrant adult populations of marine fishes representing early stages of the range extension pathway are likely to be found in regions predicted to correspond with low environmental habitat suitability (Bates *et al.*, 2014, Booth *et al.*, 2011).

Mapped indices of habitat suitability have previously been used to identify species core habitats (Hill *et al.*, 2015), but are rarely used to identify shifts in the range boundaries of marine species (but see Robinson *et al.* 2015a). Combining spatial predictions of species' probability of occurrence from SDMs with sampling effort information has recently proved useful for identifying range boundaries for terrestrial species based on minimum relative abundance values (Ashcroft *et al.*, 2017). When sampling effort is unknown, independent species occurrence data may be compared with spatial predictions from SDMs to define range boundaries or habitat edges in terms of a threshold probability of occurrence or a minimum habitat suitability value (Champion *et al.*, 2018). Approaches that utilise data-driven criteria for defining range boundaries or edges of species suitable environmental habitats are necessary to improve measures of climate-driven range shifts derived from SDMs. For example, robust summary statistics derived from SDM spatial predictions can form response variables for additional quantitative analyses (Hill *et al.*, 2015, Hobday, 2010), such as correlative mixed models, that are well-suited for quantifying rates of climate-driven

species redistributions. Analyses that allow for random effects can facilitate the incorporation of temporal data dependency structures (Zuur *et al.*, 2013) and subsequently account for the often strong influence of natural climate variability (Hobday & Evans, 2013) to reveal an underlying climate change signal in spatiotemporal species distribution patterns. Because species' responses to multiple environmental covariates are commonly used to make spatial predictions (Brodie *et al.*, 2015), this approach can also incorporate the effects of simultaneous climate-driven changes in multiple environmental variables that influence species' distributions.

Strong regional climate velocity, or relatively high rates of shifting isotherms (Burrows *et al.*, 2011), is an important environmental indicator of locations where species' distributions are rapidly changing (Sunday *et al.*, 2015). The marine environment adjacent to south-eastern Australia is a prominent climate change hotspot (Hobday & Pecl, 2014), where climate-driven oceanographic changes have resulted in a 350 km poleward extension of isotherms between 1944 – 2002 (Ridgway, 2007). By acting as natural laboratories and early learning locations, ocean warming hotspots such as south-eastern Australia provide opportunities to demonstrate approaches for better understanding climate-driven ecological change (Pecl *et al.*, 2014b). Given time and resource limitations, it is important for research undertaken in climate change hotspots to prioritise species of key ecological and economic importance (Booth *et al.*, 2011) in order to maximise our capacity to develop effective adaptation options and management strategies (Hobday *et al.*, 2016a, Miller *et al.*, 2017).

The yellowtail kingfish *Seriola lalandi* (hereafter 'kingfish') is a coastal-pelagic species extending along the southern coast of mainland Australia (Dempster & Kingsford, 2003, Hobday & Campbell, 2009). Kingfish are a high-value target species in eastern Australian

fisheries, where the estimated annual recreational catch exceeds the average annual commercial catch (Henry & Lyle 2003; Lowry *et al.*, 2016). Recently, observations of kingfish by recreational anglers in south-eastern Australia have been made approximately 200 km poleward of the previous southernmost occurrence record for this species (Stuart-Smith *et al.*, 2016). These observations provide strong evidence for the detection of kingfish outside of its usual range, but low confidence in the historical range boundary for kingfish has resulted in overall low confidence of this species undergoing a range extension (Robinson *et al.*, 2015a). Nevertheless, observations of fishes outside their usual distributions can be early indicators of climate-driven range shifts (Fogarty *et al.*, 2017) and warrant further analysis.

The aim of this study was to use citizen science data of kingfish occurrences recorded by recreational anglers to create, and demonstrate the utility of, a marine-based SDM for quantifying climate-driven species redistributions while accounting for short- and long-term natural climate variability. In addition, we also (1) quantify climate-driven shifts in the core and poleward edge of suitable kingfish oceanographic habitat from south-eastern Australia from January 1996 to July 2017, and (2) quantify trends in the temporal persistence of suitable oceanographic habitat for kingfish at the poleward edge of its distribution.

Materials and methods

Study extent

The spatial extent of this study encompassed the marine environment adjacent to eastern Australia (20-46°S, 144-160°E; Fig. 1), where a single population of kingfish is known to occur across coastal and pelagic environments (Miller *et al.*, 2011). The oceanography of this region is dominated by the poleward flowing East Australian Current (EAC), which is

strengthening due to increased wind stress over a broad region of the South Pacific associated with climate change (Cai *et al.*, 2005, Sloyan & O'Kane, 2015). Subsequently, sea surface temperatures off south-eastern Australia have increased at a rate approximately four times the global average (Ridgway, 2007), leading to the redistribution of diverse marine taxa (Malcolm & Scott, 2017, Nimbs *et al.*, 2016, Ramos *et al.*, 2015, Robinson *et al.*, 2015a, Sunday *et al.*, 2015) and altered ecosystem structure (Ling, 2008, Vergés *et al.*, 2014) and function (Marzloff *et al.*, 2016).

Kingfish occurrence records

Kingfish location data (GPS coordinates) from eastern Australia were obtained from fish tagged by recreational anglers as part of a catch-and-release tagging program administered by the New South Wales Department of Primary Industries. Kingfish occurrence records had a temporal range from 1974 – present, but were restricted to 1996 – 2015 to match the availability of satellite-derived environmental covariates. Spatial and temporal independence among kingfish occurrence records was satisfied following the methods of Brodie *et al.* (2015); which involved retaining only occurrences from a unique day and location, and retaining only those that were greater than 0.1 degree (~ 20 km) apart. Following these procedures, a total of 1,203 kingfish occurrence records were available for model fitting and cross-validation.

In order to characterise unsuitable oceanographic habitat for kingfish and provide a binomial response variable for statistical modelling, pseudo-absence points were generated inshore of the continental shelf break within the study region and randomly matched with a date from the set of occurrence records. A large number (i.e. > 10,000) of randomly selected pseudo-absences is recommended for regression-type analyses for species distributions

(Barbet-Massin *et al.*, 2012). Given the broad spatial scale of this study, a total of 20,000 randomly generated pseudo-absence points were selected in order to adequately describe the spatiotemporal variation in oceanographic covariates throughout the study extent (Brodie *et al.*, 2015). We note that although data used to parameterise habitat models fall inshore of the continental shelf break, habitat predictions are extended to the entire study area as kingfish are also known to occur in offshore pelagic environments (Gillanders *et al.*, 2001).

Oceanographic predictors

Explanatory oceanographic variables were initially selected based on their likely importance to coastal-pelagic fishes (Hobday & Hartog, 2014) and matched to occurrence and pseudo-absence points using the Spatial Dynamics Ocean Data Explorer (Hartog & Hobday, 2011).

The oceanographic variables considered for model selection were: (i) sea surface temperature (SST), (ii) sea level anomaly (SLA), (iii) dissolved oxygen (DO) and (iv) eddy kinetic energy (EKE; Table 1). In this region, satellite-based chlorophyll estimates are significantly correlated with SST and have incomplete spatial and temporal coverage so were not included in model selection.

Collinearity among predictor variables was assessed using pair plots and Spearman rank correlation coefficients. Correlated (> 0.5 and < -0.5) environmental pairs were identified and the explanatory variable with the clearest ecological interpretation from covarying pairs was retained for model selection (Zuur *et al.*, 2013). A strong correlation between sea surface temperature and dissolved oxygen ($r = -0.77$) resulted in the removal of dissolved oxygen from the set of oceanographic predictors prior to model selection. Because correlation coefficients only describe pairwise correlations, variance inflation factors (VIFs) were used to assess the extent of any collinearity among the remaining explanatory variables. VIFs were

low (i.e. < 1.5) for all remaining explanatory variables, indicating that collinearity would not affect model performance (Zuur *et al.*, 2007).

Oceanographic habitat modelling

Oceanographic habitat suitability for kingfish from eastern Australia was described by applying a generalised additive mixed model (GAMM). This model used the logistic link function to relate the binomially distributed response variable (i.e. occurrence or pseudo-absence) to oceanographic predictor variables (Zuur *et al.* 2009). Calendar year was included as a proxy for fishing effort because effort information was not available in the catch-and-release database. To optimise smoothing functions and avoid over-fitting to the data, penalized regression spline type smoothers of moderate rank were applied using generalised cross validation. However, these were removed from individual predictors if their estimated degrees of freedom was approximately equal to 1, which indicates linearity with the log-of-odds transformed response variable (Zuur *et al.* 2009). The optimal GAMM has the form (in script notation):

$$Response = s(SST) + SLA + s(EKE) + (1/Year) \quad (1)$$

where *Response* is the relative probability of kingfish presence modelled as a function of sea surface temperature (*SST*), sea level anomaly (*SLA*) and eddy kinetic energy (*EKE*), with *Year* included as a random factor. Smoothers are denoted by *s*. Furthermore, the model's *Response* was converted to an index of kingfish 'oceanographic habitat suitability' because:

1. relative probability of presence values are dependent on the ratio of occurrence to pseudo-absence data used to fit the model (Pearce & Boyce, 2006), and
2. the *Response* is a function of oceanographic covariates that reflect habitat suitability and not the distribution of kingfish

directly. Oceanographic habitat suitability was scaled between 0 (unsuitable) and 1 (highly suitable) by dividing all relative probability of occurrence predictions by the maximum relative probability predicted throughout the spatial and temporal extent of the study.

Forward model selection was applied using an information theoretic approach to identify single term additions from the available environmental predictors that most improved model quality (Warren & Seifert, 2011). The resulting set of exploratory models contained nested covariate combinations of increasing complexity (Table S1), and the model in this set with the lowest Akaike information criterion (AIC) value was considered the most parsimonious model. All available occurrence data across the spatial and temporal extent of this study were used in modelling fitting.

Spatial and temporal autocorrelation was a concern in the present study because occurrence data were recorded by recreational anglers whose fishing effort may be spatiotemporally biased (e.g. favour fishing locations or fish more on weekends/holidays etc.). Autocorrelation was evaluated using spatial and temporal variograms to relate the semi-variance of points to the spatial (degrees) and temporal (days) distance separating them (Zuur *et al.*, 2009, 2013). Cut-off distances were chosen to reflect the spatial and temporal limits that autocorrelation is likely to arise from angler bias, and these distances defined the limits of our assessment for autocorrelation. Dates of fish captures were converted to Julian days in order to create a temporal semi-variogram with a cut-off distance of five days. Coordinates of fish captures were used to create a spatial semi-variogram with a cut-off distance of one degree (~111 km). In exploratory analyses, both spatial and temporal correlation was judged to be consistent across distances (Fig. S1), except at fine spatial scales (0.1 – 0.3 degrees) where there was lower correlation (higher semi-variance) than at other distances (e.g. as seen in Smith *et al.*

2017). This is likely to reflect the spatial influence of pseudo-absences existing close to occurrence observations (i.e. between 0.1 – 0.2 degrees), resulting in increased residual variation at fine spatial scales where a binary response characterises relatively similar environmental habitats. Regardless, there was no evidence to suggest positive spatial or temporal autocorrelation in the present study, indicating that the methods for establishing independence among angler-recorded species occurrences from Brodie *et al.* (2015) were also effective in this study.

The accuracy and predictive skill of the optimal model was evaluated using k -fold cross-validation. This was done by randomly partitioning the full dataset into five subsets ($k = 5$) containing an equal number of occurrence data and a random selection of 10,000 pseudo-absences (Barbet-Massin *et al.*, 2012). To compute a set of confusion matrices for calculating measures of model accuracy (Swets, 1988), the optimal model was trained on each of the four subsets and each model tested against the 5th subset. Five-fold cross-validation was selected due to concern that too few occurrence data would be used to create the evaluation models if data were partitioned into a greater number of folds (Smith *et al.*, 2017). The area under the receiver operating characteristic curve (AUC) and true skill statistic (TSS) are appropriate measures of model accuracy for predictions of species presence and absence in geographic space (Allouche *et al.*, 2006), and are commonly used in combination when evaluating overall model skill (Brodie *et al.*, 2015). Rates of true positive (sensitivity) and false positive (1-specificity) predictions were used to calculate the mean AUC value from k -fold cross-validations. The AUC avoids the need to assume an arbitrary cut-off probability to differentiate between predictions of suitable and unsuitable oceanographic habitat, and is thus a valuable measure of the accuracy of species distribution models (Elith *et al.*, 2006). AUC values range from 0 – 1, where an AUC of 0.5 indicates the prediction is no better than

random and an AUC greater than 0.8 indicates good model accuracy (Araújo *et al.*, 2005, Swets, 1988). Additionally, the mean TSS was calculated as an alternative, threshold dependent, measure of model accuracy obtained from average measures of model sensitivity and specificity (i.e. $TSS = sensitivity + specificity - 1$). TSS values ranges from -1 to 1, where 0 or less reflects models with no predictive skill.

The optimal model was used to create monthly spatial predictions of oceanographic habitat suitability for kingfish in eastern Australia from January 1996 – July 2017. This temporal range (i.e. > 20 years) is sufficient to capture long-term climate change responses (Brown *et al.*, 2016) in addition to short-term seasonal and multi-year variation, and is commonly used as a minimum temporal criteria for syntheses of climate change impacts (Poloczanska *et al.*, 2013, Rosenzweig *et al.*, 2008). Spatial surfaces for each environmental predictor in the optimal model were interpolated to the largest common resolution (Table 1), and as a result all predictions of kingfish oceanographic habitat were resolved to 0.2°.

Range shift models

Monthly spatial predictions were used to assess evidence for a latitudinal shift in the ‘core’ and ‘poleward edge’ of oceanographic habitat for kingfish from eastern Australia. Core oceanographic habitat was specified as the location of maximum oceanographic suitability in each monthly spatial prediction (Robinson *et al.*, 2015b). The poleward edge of suitable oceanographic habitat was determined by comparing the locations of an independent set of kingfish occurrence records, not used in model fitting, with spatial predictions of modelled habitat. To do so, we compared kingfish occurrences ($n = 31$) recorded by the Range Extension Database and Mapping Project (Redmap; www.redmap.org.au) between March 2002 and April 2017 with day-specific predictions of oceanographic habitat suitability at

corresponding locations (Fig. S2). Redmap data are particularly well-suited for identifying a minimum habitat suitability value that is likely to reflect species' range edge habitats because these observations represent species outside their usual distributions and are useful indicators of the early stages of climate-driven range shifts (Fogarty *et al.*, 2017). A total of 31 day-specific predictions of the poleward edge of suitable oceanographic habitat were created with 0.2° spatial resolution, and oceanographic suitability values for grid cells containing Redmap occurrence records were extracted from each of these predictions (Fig. S2). The minimum habitat suitability value (min = 0.064) from the resulting dataset was considered to represent the edge of suitable oceanographic habitat for kingfish in this study. This is likely to be a conservative estimate for the edge of suitable oceanographic habitat for kingfish given the minimum value has been determined using only 31 observational data points. Regardless, our objective was to quantify relative change in the distribution and temporal persistence of kingfish habitat, which is possible if the criteria used to define the core and poleward edge of suitable habitats are held constant throughout the study period.

Climate-driven shifts in the core and poleward edge of oceanographic habitat were assessed using linear mixed effects models to test for latitudinal trends in suitable oceanographic habitat through time, while accounting for natural climate variability. Initially, simple linear models testing for latitudinal trends in kingfish habitat through time were applied and residuals plotted against sources of natural intra- and inter-annual climate variability to assess for dependence between observations from the same month (intra-annual variability) and El Niño Southern Oscillation (ENSO; inter-annual variability) state (Southern Oscillation Index). There was evidence that the spatial distribution of kingfish oceanographic habitat was dependent on 'month' and 'ENSO state' (Fig. S3). Subsequently, dependency structures among spatial predictions of core and poleward edge habitats from the same 'month' and

‘ENSO state’ were incorporated in linear mixed models (Zuur *et al.* 2013). This was done so that spatiotemporal shifts in oceanographic habitat would be estimated through time while accounting for sources of natural climate variability. The resulting linear mixed effects model has the form (in script notation):

$$Response = Year + (1/Month) + (1/ENSO\ state) \quad (2)$$

where *Response* is the latitudinal value corresponding to the location of core and range edge oceanographic habitats for kingfish (separate models for core and range edge habitats) modelled as a function of time (*Year*), with *Month* and *ENSO state* included as random terms. Rates of spatial shifts (km decade⁻¹) were derived from models fitted to monthly latitudinal predictions of core and poleward range edge habitats from January 1996 to July 2017 because continuous time series more accurately quantify rates of change than infrequent measures (Brown *et al.*, 2016).

Finally, the temporal persistence of suitable oceanographic habitat in novel, high-latitude areas was calculated as the number of months per year that the poleward edge of suitable oceanographic habitat (as defined herein) occurred south of 41°S (i.e. within Tasmanian waters; Stuart-Smith *et al.* 2016). Simple linear models were used to test for trends in temporal persistence (months per year) from 1996 – 2016. Residual plots were assessed visually to confirm both simple linear and linear mixed effects models satisfied assumptions of normality and homogeneity of variance.

Statistical analyses were undertaken using the R programming language (R Core Team 2017): GAMMs were fitted using the 'gamm4' package (Wood & Scheipl 2016), spatial and temporal semi-variograms were constructed using the 'gstat' package (Gräler *et al.* 2016), *k*-fold cross validation was undertaken using the 'dismo' package (Hijmans *et al.* 2013) and linear mixed effects models were fitted using the 'lme4' package (Bates *et al.* 2014).

Results

Oceanographic habitat model

Spatial predictions of oceanographic habitat from January 1996 – July 2017 show seasonal variation in the distribution of suitable kingfish habitat in eastern Australia, which undergoes an annual poleward extension during the Austral summer and autumn and retreats to lower latitudes during winter and spring (Fig. 1).

The optimal model for kingfish oceanographic habitat contained the predictors sea surface temperature, sea level anomaly and eddy kinetic energy (Table S1), demonstrating that the distribution of kingfish from eastern Australia is driven by simultaneous responses to multiple oceanographic factors. SST and EKE were highly significant, nonlinear, predictors of kingfish habitat suitability (Table 2; Fig. 2a & 1c). SST had a clear, unimodal influence on habitat suitability, with the maximum positive effect on model parameters occurring at approximately 22°C (Fig. 2a). The effect of EKE on habitat suitability was more complex, but generally had a positive effect on model parameters then declined at values greater than approximately 0.11 m² s⁻² (Fig. 2c). The smoothing function was dropped from SLA in the optimal model in favour of a positive linear term (Fig. 2b), which was a marginally significant predictor of habitat suitability (Table 2).

Five-fold cross validation revealed that the optimal model had good predictive accuracy (mean AUC = 0.887 ± 0.002 SD) according to the AUC interpretation criteria of Swets (1988), and that predictive skill (mean TSS = 0.645 ± 0.013 SD) exceeded the acceptable standard for conservation planning applications (Pearce & Ferrier, 2000). Mean values of the TSS and AUC statistics indicate that the optimal model contained an appropriate number and combination of environmental predictors to effectively describe suitable oceanographic habitat for kingfish from eastern Australia and provided reliable spatial predictions for subsequent range shift analyses.

Range shift analyses

Linear mixed effects models revealed significant poleward shifts in the core and poleward edge of oceanographic habitat for kingfish from eastern Australia (Fig. 3). Core oceanographic habitat was found to have shifted towards higher latitudes at a rate of $94.4 \text{ km decade}^{-1}$ from 1996 – 2017 ($50.5 - 137.9 \text{ km decade}^{-1}$ 95 % CI; Fig 3a; parameters for fixed component of the model: int = 136.91, slope = -0.09, $t = 4.20$, $P < 0.0001$; intra-class correlation coefficients for random terms: month = 0.72, ENSO state = 0.02). The random ‘ENSO state’ term was dropped from the model predicting latitudinal values for core oceanographic habitat due to having a negligibly low intra-class correlation coefficient. This indicates that the spatial distribution of core oceanographic habitat for kingfish from eastern Australia was not dependent on ENSO state over the temporal extent of this study. The poleward edge of suitable oceanographic habitat for kingfish was also found to have shifted towards higher latitudes from 1996 – 2017 at a rate of $108.8 \text{ km decade}^{-1}$ ($87.1 - 128.2 \text{ km decade}^{-1}$ 95 % CI; Fig. 3b; parameters for fixed component of the model: int = 153.72, slope = -0.09, $t = 9.55$, $P < 0.0001$; intra-class correlation coefficients for random terms: month = 0.86, ENSO state = 0.14).

The temporal persistence of the poleward edge of suitable oceanographic habitat for kingfish poleward of 41°S was found to have significantly increased from 1996 to 2017 (Fig. 4).

Specifically, the number of months per year that oceanographic habitat suitable for kingfish occurred poleward of 41°S increased from ~ 2 months in 1996 to ~ 5 months in 2016 (Fig 4; $\text{int} = -318.41$, $\text{slope} = 0.19$, $F_{1, 19} = 36.92$, $P < 0.001$).

Discussion

Given that spatial shifts in large numbers of marine species are expected with climate warming (Poloczanska *et al.*, 2013, Sunday *et al.*, 2012), pragmatic approaches that utilise increasingly available marine-based citizen science data sources (Bonney *et al.*, 2014, Dickinson *et al.*, 2012, Pecl *et al.*, 2014a) to quantify species redistributions are required (Hill *et al.*, 2015). Here, we demonstrate the utility of a marine habitat suitability model fitted using citizen science data for quantifying climate-driven spatiotemporal shifts in oceanographic habitat, while accounting for the effects of natural intra- and inter-annual climate variability.

Our approach revealed that core oceanographic habitat for kingfish from south-eastern Australia has shifted poleward at a rate of 94.4 km decade⁻¹ in response to climate-driven changes in regional oceanography, while the leading edge of suitable habitat was found to be extending poleward at a rate of 108.8 km decade⁻¹. The velocity of this poleward distribution shift is notably faster than historical rates of range change identified for a suite of nearshore fishes using observational data (38 km decade⁻¹; Sunday *et al.*, 2015) and for a mobile apex predator using habitat suitability predictions (88.2 km decade⁻¹; Hill *et al.*, 2015) from eastern Australia. Our results also markedly exceed future rates of poleward range shifts predicated for 16 commercially important offshore pelagic species from Australia by 2100 (average rate of range change = 40 km decade⁻¹; Hobday, 2010), suggesting the contemporary effects of

climate change may be driving the redistribution of coastal-pelagic marine fishes faster than nearshore or truly pelagic species. Importantly, our results are based on predictions of oceanographic habitat suitability determined from kingfish occurrences, which are known to produced faster range shift estimates than abundance-based measures that better reflect whole populations (Brown *et al.*, 2016).

The velocity of spatial shifts in kingfish oceanographic habitat was found to be greater for the poleward range edge than for the core habitat. Spatial variation in the velocity of shifts across the distribution of suitable environmental habitat for marine species is likely to be closely linked with the effects of climate change on regional oceanography. Increased wind stress over a broad region of the South Pacific associated with climate change has resulted in a poleward advance of the south-flowing east Australian current (Cai *et al.*, 2005, Sloyan & O'Kane, 2015). Subsequently, sea surface temperature off Tasmania (i.e. the region corresponding to the poleward edge of oceanographic habitat herein) has risen at a rate of $2.28^{\circ}\text{C century}^{-1}$ (Ridgway, 2007). Because the effect of temperature on species occurrence is commonly non-linear (Elith & Leathwick, 2009), usually displaying a unimodal peak representative of species' thermal optima (Arrizabalaga *et al.*, 2015, Brodie *et al.*, 2017, Lien *et al.*, 2014), the effects of ocean warming on species habitat suitability are similarly non-linear. For this reason, marked increases in habitat suitability for temperate marine ectotherms are likely in high-latitude environments due to ocean warming, whereas similar levels of warming in environments that already represent species' thermal preferences, such as core habitats, will have a relatively smaller effect on habitat suitability. For example, a greater positive effect of SST on kingfish habitat suitability (i.e. increase in y-axis value in Fig. 2a) will result from a 1°C increase in cooler environments (e.g. 16°C) as opposed to the same level of ocean warming in thermally optimum habitats (e.g. 22°C). These findings,

viewed in light of recent increases in sea surface temperature off south-eastern Australia, explain the strong velocity of the poleward shift in kingfish range edge habitat from this region and also account for variation between rates of range change identified for core and range edge oceanographic habitats.

Intra-annual variation in the distribution of suitable environmental habitats for coastal-pelagic species (Brodie *et al.*, 2015) is likely to underpin climate-driven range shifts over decadal time-scales. Oceanographic habitat for kingfish off eastern Australia was found to extend poleward during the Austral summer/autumn and retreat to lower latitudes during winter/spring. However, the effects of climate change on intra-annual spatiotemporal trends such as these are often overlooked when quantifying species redistributions, particularly for marine species that associate with dynamic oceanographic features (Mannocci *et al.*, 2017).

In coastal and pelagic systems, temporal persistence of suitable environmental habitat is an important factor that can both facilitate and restrict species movements (Briscoe *et al.*, 2016).

Similarly, the duration of suitable habitat within novel environments is a critical factor for predicting the ecological effects of range-shifting species (Champion *et al.*, 2018). For example, ocean warming has increased the proportion of winter months that exceed the thermal threshold for larval development of the poleward extending long-spine urchin *Centrostephanus rodgersii* at their range edge in Tasmania (Ling *et al.*, 2009), contributing to increased grazing pressure on macroalgal beds (Ling & Johnson, 2009).

Creating monthly spatial predictions of oceanographic habitat over a 22-year period allowed for intra-annual temporal trends in the distribution of suitable habitat to be investigated. It was previously believed the southern range boundary for kingfish from Australia was located at approximately 41.5°S (Atlas of Living Australia, 2016), but recent photo-verified

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observations of kingfish from approximately 43.5°S have been reported (Stuart-Smith *et al.*, 2016). Subsequently, our analysis focused on the number of months per year that the poleward edge of suitable oceanographic habitat persisted poleward of 41°S, and revealed that a significant increase have occurred from 1996 to 2016. These findings add considerable detail to species redistribution analyses that can be used to infer a level of confidence in range shifts. Bates *et al.* (2014) propose that range extensions occur as a sequence of arrival, population increase, and persistence, and that confidence in species range changes also increases as colonisation progresses across this spectrum. Increased persistence of suitable environmental habitat at species range edges, as for kingfish, indicates greater opportunity for individuals to progress through critical life history stages, allowing for population increases and ultimately persistence in novel environments (Ling *et al.*, 2009).

Intra-annual shifts in the persistence of suitable oceanographic habitat are also relevant to range-shifting species targeted in commercial and recreational fisheries. For example, greater fishing opportunity for kingfish off Tasmania is likely to result from the increasing number of months per year that suitable oceanographic conditions for this species is persisting at higher-latitudes. Assessing the effects of climate change on the temporal persistence of suitable habitat in the spatial domains of different commercial and recreational fisheries is an appropriate avenue for the development of spatially explicit adaption strategies (Champion *et al.*, 2018, Eveson *et al.*, 2015), and one that requires further work.

Like other studies of distribution shifts in pelagic fishes (Dell *et al.*, 2011, Hill *et al.*, 2015, Hobday, 2010, Robinson *et al.*, 2015b), our results are derived from spatial predictions of oceanographic suitability and thus do not directly represent spatiotemporal changes in kingfish distribution. Instead, our results reflect climate-driven shifts in the combination of

environmental variables that define suitable oceanographic habitat for this species. Inferring changes in species distributions from spatial shifts in their environmental habitat preferences reflects the limitations of marine citizen science data sources for quantifying species distributions. For example, the utility of presence-only citizen science data for quantifying species distributions is affected by sample size (Stockwell & Peterson, 2002) and spatiotemporal sampling biases (Phillips *et al.*, 2009, Stolar & Nielsen, 2015), which are particularly relevant to marine applications due to the relative difficulty of accessing and observing marine habitats (Dickinson *et al.*, 2010, Hobday & Evans, 2013). While our study had the luxury of a large marine citizen science dataset (i.e. > 1000 occurrence records), this is unlikely to be the case for all citizen science programs where low sample size combined with sampling biases may compromise robust SDM application. Nevertheless, marine citizen science programs are becoming increasingly valuable for characterising species habitat preferences as more data are reported (Pech *et al.*, 2014a) and biases are addressed by recording observational effort (Edgar & Stuart-Smith, 2014) or data removal procedures (Brodie *et al.*, 2015). Range shift analyses for marine species based on predictions of environmental suitability, like those herein, capitalise on citizen science data for understanding species redistributions, but also limit the interpretation of results to species' preferred environmental habitats and not their distributions directly.

Quantifying shifts in species range boundaries is an important priority for species redistribution science (Bonebrake *et al.*, 2017), yet difficulty identifying range edges from observational data make distinguishing shifts problematic (Ashcroft *et al.*, 2017). For example, range boundaries determined directly from occurrence data are sensitive to sampling intensity (Brown *et al.*, 2016), and variation in sampling effort through time can lead to incorrectly inferring range edge shifts (Bates *et al.*, 2015, Hassall & Thompson,

2010). Instead, studies have focused on the mean or centroid location of species occurrence records (Maclean *et al.*, 2008, Shoo *et al.*, 2006), which allow for changes in species core habitat to be assessed, but neglect range edges. Spatial predictions from SDMs with proven predictive skill provide an opportunity to define clear criteria for the extended range boundary, for example, in terms of a minimum relative abundance threshold derived from SDM predictions and sampling effort information (Ashcroft *et al.*, 2017). Methods to select habitat edge thresholds will likely vary for species with differing traits. For example, marine species with high adult mobility, such as kingfish, generally occupy broad latitudinal ranges (Sunday *et al.*, 2015), and periodically encounter areas of low environmental habitat suitability at their range edges due to dynamic oceanographic processes (Briscoe *et al.*, 2016). Therefore, it is pragmatic and conservative to match independent observational data from species putative range edges with spatial predictions from SDMs to determine threshold values that maximise the agreement between observed and predicted distributions and the interpretability of results (Liu *et al.*, 2005). This approach for determining habitat suitability thresholds is dependent on the response of single individuals and our ability to detect them (Brown *et al.*, 2016), and spatial shifts in threshold habitats are likely to represent a relatively small number individuals from a population expanding into new environments (Booth *et al.*, 2011).

Sources of natural climate variability occurring at intra- and inter-annual time-scales strongly influences species distributions and abundance (Lehodey *et al.*, 2006, Polovina, 1996, Zanardo *et al.*, 2017), and efforts to account for these are necessary to reveal the effects of contemporary climate change. Our results indicate that oceanographic habitat for kingfish from eastern Australia is subject to substantial monthly variability (Fig. S3a) in response to the intra-annual extension and contraction of the EAC (Young *et al.*, 2011). While seasonal

variability in pelagic fish distributions from eastern Australia have been documented (Brodie *et al.*, 2015, Brodie *et al.*, 2017), spatial predictions of kingfish habitat at a monthly temporal resolution have not previously been made. Doing so improved our ability to account for intra-annual variation in kingfish oceanographic habitat when assessing spatial shifts over the 22-year study period. Specifically, this approach allowed for a dependency structure between observations from the same ‘month’, rather than ‘season,’ to be incorporated into our range shift models, which reduced standard error estimates and improved confidence in the rates of change reported for kingfish oceanographic habitat from eastern Australia.

This study also considered the influence of natural climate variability on environmental habitat for kingfish at inter-annual time-scales, and is among few examples from the marine realm that have attempted to account for these effects in order to delineate a climate change signal from natural variation (Hill *et al.*, 2015). The influence of ENSO state on the distribution of kingfish habitat in the study region was relatively minor, and only detectable at the poleward boundary of suitable oceanographic habitat. La Nina phases were associated with a slight poleward advance of range edge habitat, which concurs with effects of ENSO on the distribution of black marlin (*Istiompax indica*) from eastern Australia (Hill *et al.*, 2015). Subsequently, only range shift models that assessed for distribution shifts in the poleward range boundary included ‘ENSO state’ as a random effect, and doing so led to a minor reduction in standard error. Accounting for the short- and long-term influences of natural climate variability should be a key consideration when seeking to attribute spatiotemporal shifts in species distributions to anthropogenic climate change, and we demonstrate that correlative mixed-effects models provide a suitable quantitative framework for doing so.

While SDMs are broadly used to infer spatial responses of species to changing environmental conditions (Bonebrake *et al.*, 2017), particularly in terrestrial systems (Elith *et al.*, 2010), few attempts have been made to utilise their spatial output to quantitatively assess marine range-shifts while accounting for sources of natural climatic variation (Hill *et al.*, 2015). Given the utility of citizen science observations for fitting marine-based SDMs, and trends of increasing access to these data sources (Kullenberg & Kasperowski, 2016), we suggest this approach as a pragmatic method for assessing the effects of climate change on the distributions of species that have been poorly observed. However, we note that this approach necessitate that subsequent range shift analyses focus on spatiotemporal shifts in species' suitable environmental habitats and not their distributions directly, limiting the interpretability of results. This approach is likely to prove more informative for coastal and pelagic species that strongly associate with oceanographic variables (Hobday & Hartog, 2014) and less informative for highly reef-associated species where habitat suitability is related to non-environmental predictors, such as distance to reef structure (Smith *et al.*, 2017). Biotic factors (e.g. prey availability) are also likely to have an important effect on the realised distribution and temporal persistence of kingfish (Mellin *et al.*, 2016). To extend the interpretation of our results from the oceanographic habitat for kingfish to the distribution of kingfish directly would also require consideration of climate-driven effects on, for example, the spatiotemporal distribution of important prey species (Potts *et al.*, 2016).

Given that poleward shifts in the distributions of marine species are expected to continue in response to climate-induced changes in regional oceanography (Poloczanska *et al.*, 2012), predictions of suitable environmental habitat for key species under future climate change scenarios are now required to underpin adaptation strategies (Hobday *et al.*, 2011, Hobday *et al.*, 2016b). It is important that future predictions of dynamic marine habitats are made over

time-scales that are relevant to natural resource managers and user groups (e.g. recreational and commercial fishers). These time-scales may range from seasonal predications to assist quota-limited commercial fisheries (Eveson *et al.*, 2015, Hobday *et al.*, 2016b), to yearly predictions (i.e. political time-scales) that aid natural resource managers in the development of climate change adaptation strategies. For example, analyses that quantify the temporal persistence of suitable habitat for species of interest over yearly periods, like those presented herein, may be used to trigger management responses (Champion *et al.*, 2018).

Recent advances in the ability to forecast more oceanographic variables under climate change scenarios (Payne *et al.*, 2017) hold great potential to improve future estimates of species distributions, which have traditionally been restricted to forecasts of sea surface temperature alone (Brodie *et al.*, 2017, Eveson *et al.*, 2015). The inclusion of multiple environmental predictors in habitat forecasts will facilitate an improved understanding of the effects of climate change on species distributions and increase our capacity to anticipate and respond to these changes.

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Table 1. Descriptions of explanatory covariates and their range of values for kingfish presence (*P*) and pseudo-absence (*pA*) points. Oceanographic predictors were interpolated to the largest common resolution (0.2°) when making spatial predictions. *Explored but not included in model fitting.

Predictor	Description	Range	Units
SST	Sea surface temperature from Advanced Very High Resolution Radiometer (AVHRR) with 0.04° spatial resolution	<i>P</i> : 13 - 27 <i>pA</i> : 9 - 29	°C
SLA	Sea level anomaly from synthetic temperature and salinity (synTS; Ridgway & Dunn, 2010) with 0.2° spatial resolution	<i>P</i> : -0.2 - 0.25 <i>pA</i> : -0.3 - 0.4	m
DO*	Dissolved oxygen from CSIRO Atlas of Regional Seas (Condie & Dunn, 2006) climatology with 0.2° spatial resolution	<i>P</i> : 4.5 - 6 <i>pA</i> : 3.8 - 7.5	ppm
EKE	Eddy kinetic energy derived from altimetry with 0.2° spatial resolution	<i>P</i> : 0 - 0.4 <i>pA</i> : 0 - 1.2	m ² s ⁻²
Year	Calendar year (incorporated as a random term in mixed models)	1996 - 2015	

Table 2. Summary of results for the optimal kingfish habitat suitability model. Smoothing factors are denoted by *s*.

Variable	Effective degrees of freedom	Coefficient estimate	<i>P</i> -value
<i>s</i> (SST)	5.01	- 0.25	< 0.001
SLA	-	1.21	0.04
<i>s</i> (EKE)	7.78	2.28	< 0.001
Year _(intercept)	-	- 5.55	< 0.001

Fig. 1. Spatial predictions of kingfish oceanographic habitat suitability for eastern Australia from January 1996 – July 2017. Monthly spatial predictions have been time-binned (5 years) and seasonally aggregated (Summer = December-February, Autumn = March-May, Winter = June-August, Spring = September-November). Note the most recent period covers 2016 and 2017 only.

Fig. 2. Partial effects of (a) sea surface temperature (SST), (b) sea level anomaly (SLA) and (c) eddy kinetic energy (EKE) on the fitted values of the optimal kingfish habitat model, bound by 95 % confidence intervals (dashed lines). Rugs on the x -axes indicate presence and pseudo-absence data for each predictor.

Fig. 3. Seasonally explicit latitudinal trends in monthly predictions of the (a) core and (b) poleward edge of suitable oceanographic habitat for kingfish. Dashed lines represent monthly trends fitted as a random effect within linear mixed effects models. The Australian coastline has been underlaid to aid spatial interpretation of the trends presented.

Fig. 4. Temporal persistence of the poleward edge of suitable kingfish oceanographic habitat south of 41°S (i.e. the northern edge of the Tasmanian coastline; $r^2 = 0.68$). Dashed lines denote the 95 % confidence interval.





