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# Title: Dynamic habitat suitability modelling reveals rapid poleward distribution shift in a mobile apex predator

**Running head: Rapid distribution shift in pelagic predator**

*Nicholas J. Hill[1]*, Andrew J. Tobin[1], April E. Reside[2], Julian G. Pepperell[3], Tom C.L. Bridge[4,5]*

[1] *Centre for Sustainable Tropical Fisheries and Aquaculture, College of Marine and Environmental Sciences, James Cook University, Townsville, Queensland 4811, Australia*

[2] *Centre for Tropical Environmental & Sustainability Sciences, College of Marine and Environmental Sciences, James Cook University, Townsville, Queensland 4811, Australia*

[3] *Pepperell Research and Consulting Pty Ltd., P.O. Box 1475, Noosaville DC, Queensland 4566, Australia*

[4]*ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Queensland 4811, Australia*

[5]*Australian Institute of Marine Science, PMB #3, Townsville MC, Queensland 4810, Australia*

*Corresponding author email: nicholas.hill@my.jcu.edu.au

Phone: +614 11 212 230

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**Primary research article**

## Abstract

Many taxa are undergoing distribution shifts in response to anthropogenic climate change. However, detecting a climate signal in mobile species is difficult due to their wide-ranging, patchy distributions, often driven by natural climate variability. For example, difficulties associated with assessing pelagic fish distributions has rendered fisheries management ill-equipped to adapt to the challenges posed by climate change, leaving pelagic species and ecosystems vulnerable. Here we demonstrate the value of citizen science data for modelling the dynamic habitat suitability of a mobile pelagic predator (black marlin, *Istiopmax indica*) within the south-west Pacific Ocean. The extensive spatial and temporal coverage of our occurrence data set (n=18717), collected at high resolution (~1.85km$^2$), enabled identification of suitable habitat at monthly time-steps over a 16-year period (1998-2013). We identified considerable monthly, seasonal and inter-annual variability in the extent and distribution of suitable habitat, predominately driven by chlorophyll-a and sea surface height. Inter-annual variability correlated with El Nino Southern Oscillation (ENSO) events, with suitable habitat extending up to ~300 km further south during La Nina events. Despite the strong influence of ENSO, our model revealed a rapid poleward shift in the geometric mean of black marlin habitat, occurring at 88.2 km decade$^{-1}$. By incorporating multiple environmental factors at monthly time-steps, we were able to demonstrate a rapid distribution shift in a mobile pelagic species. Our findings suggest that the rapid velocity of climate change in the south-west

Pacific Ocean is likely affecting mobile pelagic species, indicating that they may be more vulnerable to climate change than previously thought.

## Introduction

Rapid and extensive distribution shifts in response to global climate change have been detected in numerous marine and terrestrial taxa (Parmesan & Yohe, 2003; Chen *et al.*, 2011; Pinsky *et al.*, 2013). These shifts are predicted to continue in coming decades, resulting in a reassembly of current ecological communities (Loarie *et al.*, 2009; Hazen *et al.*, 2012; Burrows *et al.*, 2014). Although numerous shifts have been predicted, empirical evidence via retrospective detection has proven elusive for the majority of species due to inadequate spatial and/or temporal coverage of baseline occurence data (Booth *et al.,* 2011; Hobday & Evans, 2013). This has inhibited the development and implememntation of appropriate management strategies to assess species vulnerability to climate change (Conroy *et al.*, 2011).

Where species occurrence data is patchy, modelling changes in habitat suitability has proven useful for identifying distribution shifts (Elith *et al.*, 2006, 2010). However, habitat suitability metrics are often focused on temperature (Loarie *et al.*, 2009; Burrows *et al.*, 2014) which can result in underestimation of the rate and magnitude of distribution shifts expected to occur (VanDerWal *et al.*, 2012). Species distributions are driven by multiple, interacting factors and therefore, their response to climate change is likely to be more complex and region specific than simple models based solely on temperature suggest (Ackerly *et al.*, 2010; Bell *et al.*, 2013a). Data paucity is particularly prevalent in pelagic ecosystems, which are difficult to survey at fine spatial and temporal scales (Hobday & Evans, 2013). Increasing atmospheric $CO_2$ concentrations have caused fundamental changes to the world's oceans, including increased sea surface temperatures and shifts in oceanic circulation and primary productivity patterns (Boyce *et al.*, 2010; IPCC, 2014). However, our understanding of the impacts these physical changes will have on pelagic species, and the resulting consequences, is poorly understood.

Apex predators exert important top-down control of food webs, and are critical for maintaining ecosystem function (Myers *et al.*, 2007; Estes *et al.*, 2011). Many large-bodied pelagic predators are highly-mobile, and regularly undertake migrations of hundreds to thousands of kilometres at annual and inter-annual timescales (Block *et al.*, 2011). Despite their widespread distributions, mobile pelagic predators have declined in abundance due to overfishing (Baum & Worm, 2009), causing changes to open ocean food webs (Myers *et al.*, 2007; Worm & Tittensor, 2011). Climate-induced distribution shifts are likely to alter the functioning of pelagic ecosystems already under pressure from anthropogenic stressors (Beaugrand *et al.,* 2008; Hazen *et al.*, 2012; Robinson *et al.*, 2014). Furthermore, mobile pelagic predators represent 20% of total economic value in global marine capture fisheries (FAO, 2012). Distribution shifts in commercially important species will have serious implications for food security and human welfare globally (Brander, 2010; Cheung *et al.*, 2010; Madin *et al.*, 2012). Early detection and characterisation of species responses to climate change is therefore vital for bolstering the resilience and adaptive capacity of fisheries, allowing appropriate management contingencies to be implemented (Hobday & Evans, 2013; Holbrook & Johnson, 2014; Maxwell *et al.,* 2015).

Detecting distribution shifts in mobile marine species has proven difficult due to naturally low densities, high mobility and the remoteness of preferred habitats. Acoustic and archival tagging technologies have improved understanding of species movements across space and time (Schaefer *et al*., 2014; Maxwell *et al.,* 2015), but are costly and can be logistically difficult to undertake. In the absence of sophisticated tagging data, species distribution modelling has proven useful for illustrating the dynamic habitat suitability of mobile species, and presents itself as a potential tool for dynamic ocean management (Elith *et al.,* 2006; Lehodey e*t al.,* 2006; Maxwell *et al.,* 2015). Habitat suitability of mobile species is determined by a range of environmental (eg: temperature; Boyce *et al.,* 2008) and ecological parameters (eg: prey abundance; Griffiths *et al.,* 2010) which vary across both space (metres – 1000's km) and time (minutes – multi-decadal). Therefore, modelling distribution shifts using environmental data averaged over broad climatic scales (eg: Perry *et al.,* 2005; Montero-Serra *et al.,* 2015), may inaccurately represent habitat suitability for mobile species (Reside *et al.,* 2010). Low spatial resolution data and use of inappropriate modelling techniques has hindered the detection of underlying long-term shifts in some mobile species (Hobday & Evans, 2013).

Utilizing citizen science to assist with the spatial and temporal coverage of data sampling can help overcome problems associated with data paucity. For example, citizen science has proven critical in establishing the projected impacts of climate change on the distribution and volume of remaining viable habitat for mobile bird species (VanDerWal *et al.,* 2012; Abolafya *et al.,* 2013). In Australia, a large-scale tagging program utilising recreational fishermen to collect data on targeted pelagic species has been operating since 1974 in collaboration with fisheries management (NSW DPI, 2014). Participants apply a conventional streamer tag to captured fish before release and record the capture date, release location and approximate length and weight of each fish. Under the program, recreational anglers have tagged over 419 000 individual fish across 25 different species, providing a spatially and temporally extensive dataset of the distribution of pelagic fishes (NSW DPI, 2014).

Black marlin (*Istiopmax indica*) are a common target of recreational anglers in many locations throughout the south-west Pacific Ocean, and are regularly recorded in the NSW

DPI Gamefish Tagging Program (NSW DPI, 2014). The distribution of black marlin extends throughout tropical and sub-tropical regions of the Pacific and Indian Oceans predominately found in epipelagic waters (Pepperell, 1990; Domeier & Speare, 2012). Although geographically widespread and capable of crossing ocean basins (Pepperell, 1990), black marlin show a seasonal affinity for continental margins and sea-mounts (Campbell *et al.*, 2003; Gunn *et al.,* 2003), increasing their accessibility to recreational anglers. Recently Williams *et al.* (2015) identified three distinct genetic populations in the south-west Pacific, eastern Indian Ocean and the south China Sea. In the south-west Pacific population examined in this study, spawning occurs from September-November adjacent to the continental shelf of north-east Australia (Leis *et al.,* 1987; Domeier & Speare, 2012). From September-April, juveniles 1–4 years old undertake a southerly migration along Australia's eastern continental margin (17-34$^{o}$S) (Pepperell, 1990). Although the south-west Pacific population is targeted by a substantial recreational fishery, little is known about population status (Collette *et al.,* 2011) or where else the species might occur.

Here, we demonstrate the value of citizen science collected data for investigating distribution shifts in the south-west Pacific population of black marlin. We model the dynamic habitat suitability of black marlin using high resolution spatial and temporal data to investigate 1) environmental factors that characterise suitable habitat of black marlin; 2) the variation in location of suitable habitat across seasonal and inter-annual timescales in relation to natural climate oscillations; and 3) whether a long-term distribution shift has occurred and is consistent with the effects of climate change observed in the south-west Pacific Ocean.

## Materials and methods

### *Study region*

The study was conducted in the south-west Pacific Ocean (3-39$^{o}$S/142-180$^{o}$E; Fig. 1a). The study area encompasses the ‘core’ range of the south-west Pacific black marlin population identified using genetic analysis, archival tagging and historical commercial catch data (Williams *et al.,* 1994; Domeier & Speare, 2012; Williams *et al.,* 2015). The dominant oceanographic feature of this region is the East Australian Current (EAC), a poleward-flowing western boundary current that transports warm, oligotrophic waters along Australia’s east coast (Ridgway, 2007). The EAC originates from the westward-flowing South Equatorial Current (SEC), which bifurcates at the Australian continental margin at 17-19$^{o}$S (Brinkman *et al.*, 2001). A seasonal strengthening in the EAC occurs from September-April (Luick *et al.*, 2007). The EAC departs from the east coast at 32-34$^{o}$S, flowing east towards New Caledonia and New Zealand, forming the Tasman Front (Baird *et al.*, 2008; Suthers *et al.*, 2011). The Tasman Front is a transition zone, representing the collision of cold (Tasman Sea) and warm water (Coral Sea) bodies, often exhibiting strong thermal gradients of >2$^{o}$C (Baird *et al.*, 2008). Over winter (April-August), subantarctic cold waters push north, forcing the EAC and Tasman Front to retreat towards the equator.

These major oceanographic features vary across numerous temporal scales, attributed to the influence of climate oscillations. El Nino Southern Oscillation is the dominant force, which drives strong inter-annual variability in the oceanography of the south-west Pacific Ocean (Holbrook *et al.,* 2009). El Nino events are characterised by anomalously high sea surface temperatures adjacent to Australia’s south-east coast and anomalously cool temperatures in the north as the West Pacific Warm Pool disperses east. In contrast, during La Nina events trade winds strengthen, forcing West Pacific Warm Pool water to remain in the south-west

Pacific (Holbrook & Bindoff, 1997; Holbrook *et al.,* 2009). Decadal variability is also present, characterised by extended warm, El Nino like conditions or conversely cold, La Nina like conditions. Combination of these various climatic influences create highly variable oceanographic conditions within the south-west Pacific Ocean. Globally, western boundary currents such as the EAC are warming 2-3 times faster than the global mean (Wu *et al.*, 2012; Hobday & Pecl, 2013; Hu *et al.,* 2015). Despite this substantial natural variability in oceanographic features, a long term incessant poleward shift in these features has been recorded (Cai *et al.,* 2006; Ridgway, 2007) and is predicted to continue (Cai *et al.,* 2005; Ridgway & Hill, 2012), with subsequent shifts in numerous marine taxa documented (Frusher *et al.,* 2014; Verges *et al.*, 2014).

### *Occurrence data*

Occurrence records were obtained from black marlin tagged by recreational anglers in the New South Wales Department of Primary Industries Tagging Program (NSWDPI, 2014). The database covers the period from 1974-present. However, in this study we only used a subset from the period 1998-2013. This period was chosen due to the availability of high-resolution environmental data, and also to account for the increased fishing effort present in the database in the 1970s and 1980s. Occurrence data was binned into monthly time-steps, leaving a total of 24344 occurrence records available at a spatial resolution of one minute of latitude/longitude (~1.85km$^2$) (Fig. 1b). Although the distribution of tag records is predominately restricted to within close proximity of coastlines, the use of this data enabled analysis at a much finer spatial scale than would be possible using commercial catch per-unit effort data, which is often collected at a resolution of 5x5$^o$ (~556.63km$^2$) (eg: Su *et al.*, 2011).

### ***Environmental data***

Environmental factors (Table S1) were chosen as potential explanatory variables based on their availability and demonstrated influence on pelagic species distributions (Su *et al.*, 2011). Spatial layers for environmental factors were acquired using the Marine Geospatial Ecology Tool (MGET) (Roberts *et al.*, 2010) in ArcGIS. Daily measurements for each factor were averaged at monthly time-steps (n=192) from 1998-2013 to reduce the influence local minima/maxima and no-data cells (e.g. due to cloud cover). No-data cells were interpolated using the del2a method within MGET which uses laplacian interpolation (D'errico, 2005). All environmental layers were resampled to a common spatial resolution (4 km$^2$) to satisfy requirements of MaxEnt. Mixed layer depth and bathymetry were also investigated, but were not included in the final model as they led to over-fitting of the data.

### *Species distribution model*

We used the species distribution modelling algorithm MaxEnt, which estimates the probability distribution of a species occurrence based on constraints from biologically relevant environmental factors (Phillips *et al.*, 2006). MaxEnt is a robust technique that performs well against similar methods when modelling non-systematically collected occurrence data even if sample sizes are small (Elith *et al.*, 2006). This technique accurately models species distributions, despite data limitations and biases (Elith *et al.,* 2006; Pearson *et al.,* 2007). MaxEnt generates a continuous layer of habitat suitability (ranging from 0-1) across a specified domain by distinguishing the distribution of a species occurrence from the available surrounding environment (Phillips *et al.*, 2006; Elith *et al.*, 2011).

We generated a background data set to representatively sample the environment surrounding each occurrence record. MaxEnt assumes the occurrence data was randomly sampled, with all locations within the study area equally likely to be sampled. To account for our occurrence data being biased towards areas more accessible to recreational anglers, we selected background data with equivalent spatial and temporal bias to ensure the model reflected the distribution of black marlin rather than sampling effort (Phillips *et al.*, 2009). Background points were randomly placed within a specified buffer distance surrounding each occurrence record and assigned to the same monthly time-step. Four different buffer sizes were investigated (50, 100, 200, 300n. mi.) to assess model performance (VanDerWal *et al.*, 2009). The final models used the 200n. mi. buffer, which most effectively balanced habitat sensitivity and specificity, offering the most biologically informative and logical results (VanDerWal *et al.,* 2009).

Occurrence and background points within close proximity to the coastline that did not contain data coverage from all environmental factors were omitted. A total of 18717 occurrences and 23242 background points were used in the final models. The value for each environmental factor was recorded at each point and derived from the relevant monthly time-step. For the final model, environmental factors investigated included sea surface temperature, chlorophyll-a concentration, sea surface height anomaly, current direction and current magnitude. All models were run using MaxEnt in R 3.0.2. Model performance was evaluated with a ten-fold cross-validation (500 iterations each) using Species Distribution Modelling (SDM) Tools (VanDerWal *et al.,* 2015). To test model performance, occurrence data was randomly partitioned into subsets, with 70% of occurrence records used to train the model and the remaining 30% for testing. Each ‘fold’ of cross-validation was compared using area under the receiver-operating characteristic curve (AUC) to provide estimates of model performance. Values approaching 1 suggest the model accurately predicts species occurrence, whereas a value of 0.5 suggests the model is no better than a random selection. The importance of each environmental factor in the training model was determined using a jack-knife test. The final model was run using all occurrence data and projected onto a series of monthly spatial surfaces from 1998-2013 to hindcast the distribution of suitable black marlin habitat within the study area (Reside *et al.*, 2010).

MaxEnt provides a series of threshold values which can be used to generate discrete binomial suitable/non-suitable outputs. These threshold values represent natural breaks in the scale of habitat suitability (0-1) defined by MaxEnt. After visual inspection of binomial outputs produced using all thresholds, the MaxEnt-derived 'equate entropy of thresholded and original distributions logistic threshold' value of 0.282 was used to define non-suitable habitat from suitable habitat. This value was chosen as alternative thresholds provided by MaxEnt were considered too high and therefore too restrictive for a highly-mobile generalist species, omitting suitable habitat (Anderson *et al.*, 2012).

The geometric mean of suitable habitat was calculated for each month (n=192) by taking the average of all cells within the study area based on their suitability value and location (latitude/longitude). This provided a single point that estimated the core or centre of suitable habitat for each time-step. Comparison of the latitudinal/longitudinal location of geometric means was used to investigate annual and inter-annual variability in the geographic location of suitable habitat. Points were assigned to three different El Nino Southern Oscillation (ENSO) states (El Nino, La Nina and Neutral) and compared using boxplots. To investigate long-term trends in the geometric mean of suitable habitat from 1998-2013, we used a linear model that included season (Jan-Apr, May-Aug, Sep-Dec) and ENSO state (El Nino, La Nina, neutral) as fixed effects to remove variability they impart on the observed latitudinal trend throughout the study period. Residual plots were used to confirm that the model satisfied assumptions of normality and heterogeneity of variance.

## Results

The distribution of modelled suitable habitat represented the spread of occurrence records well, giving confidence that this model is ecologically informative (Fig. S1). Cross-validated AUC value (0.634) indicated that the model was acceptable for a highly-mobile generalist species with a broad environmental niche (Reside *et al.*, 2011). Environmental factors that contributed most to the model were chlorophyll-a (chl-a) (47%) and sea surface height anomaly (ssha) (30%), while current magnitude (14%), SST (4%) and current direction (5%) were less important (Fig. S2).

### *Seasonal variability*

The model supported a seasonal latitudinal shift in the distribution of suitable black marlin habitat in the south-west Pacific Ocean (Fig. 2). In the late austral winter (August-September), suitable habitat occurs within a $10^{o}$ latitudinal band extending across the south-west Pacific Ocean adjacent to north-eastern Australia centred on ~$17^{o}$S (Fig. 2a). From September-April, suitable habitat shifts south and is more proximal to Australia's east coast, in conjunction with the strengthening EAC (Fig. 2b). Suitable habitat extends to the central (~$25^{o}$S) and south-east (~$33^{o}$S) coast of Australia throughout the austral summer, reaching its most southern extent at the conclusion of summer (Fig. 2c). At its most southerly extent (~32-34°S), suitable habitat is bounded by unsuitable waters of the Tasman front, forcing suitable habitat eastwards towards New Caledonia before shifting northwards again over the austral winter (June-August) (Fig. 2d). The distribution of geometric means within each year supported the occurrence of a seasonal latitudinal shift in the distribution of suitable habitat (Fig. S3).

### *Inter-annual variability*

Considerable variability was observed in the latitudinal range of suitable habitat across the study area (142-180$^o$E) among years (Fig. S4). Latitudinal variability in suitable habitat among years was lowest during May-August, when marlin occurred at lower latitudes. In contrast, the latitudinal position of suitable habitat was far more variable among years in January-April, when suitable habitat shifted to higher latitudes. Variability in the southerly extent of suitable habitat among years was correlated with ENSO, with suitable habitat extending up to 300km further southwards during La Nina state in comparison to Neutral or El Nino state (Fig. 3).

### *Poleward shift in suitable habitat*

Despite substantial variation in the latitudinal extent of suitable habitat due to natural climate oscillations, our model indicated an overall poleward shift in suitable habitat for all seasons over the period 1998-2013. After accounting for season and ENSO as factors, the model indicated that the geometric mean of suitable black marlin habitat has shifted polewards at a velocity of 88.2 km decade$^{-1}$ (Fig. 4). When each season was considered individually, significant trends were observed in both May-August ($R^2$=0.59, p<0.001) and September-December ($R^2$= 0.52, p<0.01). In both seasons, the velocity of poleward distribution shifts was 77 km decade$^{-1}$. The velocity of poleward shifts was greater during January-April (111 km decade$^{-1}$). However, this trend was only marginally significant (p=0.06) due to greater inter-annual variability during the summer months ($R^2$=0.16).

## Discussion

Our model indicated a rapid poleward shift in the latitudinal distribution of suitable black marlin habitat. Suitable habitat is shifting south at a mean rate of 88.2 km decade$^{-1}$, independent of considerable variation observed due to season and ENSO. The velocity of the poleward distribution shift reported here for the period 1998-2013, based on empirical observations and multiple environmental factors, is considerably faster than predictions made for similar mobile pelagic predators using modelled climate scenarios ranging from 2030-2100 (Hobday, 2010; Robinson *et al.*, 2014). Our results indicate that climate change may be rapidly changing the geographic location of suitable habitat for black marlin. Given that many mobile pelagic predators respond to a similar suite of environmental factors and oceanographic features, climate change may already be exerting a strong influence on pelagic ecosystems and fisheries (Pereira *et al.*, 2010; Barnosky *et al.*, 2012; Burrows *et al.*, 2014).

Detecting distribution shifts on the decadal timescales for which data are commonly available has proven difficult for most mobile pelagic predators (Hobday & Evans, 2013). Furthermore, many predictions of distribution shifts consider too few explanatory factors (e.g. temperature) (Hobday, 2010; Montero-Serra *et al.*, 2015), despite evidence that species distributions are determined by numerous, interacting factors (Brill & Lutcavage, 2001; Ackerly *et al.*, 2010; Grenouillet & Comte, 2014). Our results suggest that multiple factors interact to determine suitable habitat for black marlin, and support the hypothesis that models based on a single factor may underestimate the fingerprint of climate change (VanDerWal *et al.*, 2012). Given that species distributions are likely influenced by multiple interacting factors (Ackerly *et al.*, 2010; Grenouillet & Comte, 2014), fine-scale examination of species distributions is important in accurately assessing species vulnerability and likely responses to shifting habitat suitability driven by climate change.

The velocity of poleward shift in suitable habitat reported here (88.2 km decade$^{-1}$) is rapid considering our study used geometric means. Studies of range expansion tend to focus on the margins of species distributions (Lenoir & Svenning, 2015), which are likely to be more dynamic than geometric means. Although rapid leading-edge range expansions have been reported for marine fishes (277 km decade$^{-1}$), shifts in the location of geometric means are generally slower (30 km decade$^{-1}$) (Poloczanska *et al.*, 2013). Given the highly-mobile nature of black marlin, geometric means compared amongst equivalent seasons provide greater insight into climate-induced distribution shifts than overall range-edge dynamics (Pinsky *et al.*, 2013; Bates *et al.*, 2015). After accounting for annual migration by considering seasons separately, our model indicates that the 'leading edge' (in this case, the geometric mean of suitable habitat during January-April, when black marlin occur at their more southerly limit) is shifting poleward at a faster rate (111 km decade$^{-1}$) than the 'trailing edge' (77 km decade$^{-1}$). The greater velocity of the leading edge for black marlin is likely driven by changes in the strength and southward penetration of the EAC (Ridgway, 2007; Ridgway & Hill, 2012), and provides further evidence of the influence of strengthening boundary currents on marine ecosystems (Wu *et al.*, 2012; Hobday & Pecl, 2013). Higher latitudes are warming more rapidly overall than lower latitudes, although they also experience greater annual variability. Our findings of more rapid poleward extension at the leading edge supports empirical observations that leading edges are shifting more rapidly than trailing edges (Poloczanska *et al.*, 2013), despite theoretical evidence that leading and trailing edges are equally responsive to warming for marine ectotherms (Sunday *et al.*, 2012).

Traditionally, mobile species such as black marlin have been considered less vulnerable to climate change due to their ability to track suitable habitat (Pearson & Dawson, 2003; Robinson *et al.,* 2009). However, this hypothesis fails to consider that many mobile pelagic species are site attached to features for critical life history processes such as spawning (Block *et al.*, 2011; Anderson *et al.*, 2013). Climate change may render these key features less suitable (Hobday & Pecl, 2013), decreasing the resilience of some species (Robinson *et al.*, 2009; Anderson *et al.*, 2013). For example, climate change will likely decrease the suitability of many spawning locations, driving declines in recruitment and overall abundance (Satoh, 2010; Bromhead *et al.*, 2014). Tropicalisation of temperate environments may progressively disconnect foraging and spawning grounds, increasing the distance required of species to travel (Robinson *et al.*, 2009; Anderson *et al.*, 2013). Furthermore, the distribution of productive upwelling zones are likely to shift, decreasing the abundance and availability of prey in some regions (Hazen *et al.*, 2012; Boyce *et al.*, 2014). Our results suggest that shifts in the timing and suitability of key oceanographic features may limit the adaptability of mobile pelagic predators, making them more vulnerable to climate change than initially thought.

Our results indicate substantial seasonal and inter-annual variability in the distribution of suitable habitat. Seasonal shifts suggest that black marlin move in conjunction with a warm-water pulse in the East Australian Current (EAC) from September-April. Our modelled results are concordant with tag-recaptures of juvenile black marlin (Pepperell, 1990) and other similar species known to undertake seasonal migrations in association with western boundary currents, such as Atlantic bluefin tuna (*Thunnus thynnus*) within the Gulf Stream (Block *et al.,* 2005) and striped marlin (*Kajikia audax*) within the Kuroshio Current (Lien *et al.,* 2013). Our model also identified the Tasman Front as a region of suitable habitat which has not been previously reported for black marlin. Transition zones have been identified as important migratory corridors and foraging habitat for numerous mobile marine species (Polovina *et al.,* 2001; Block *et al.,* 2005; Block *et al.,* 2011), supporting model results regarding the potential importance of the Tasman Front. Our model also indicated inter-annual variability in the distribution of suitable habitat, at least partially driven by ENSO. Although the southward migration of juveniles has been inferred from tag-recaptures (Pepperell 1990), the effects of ENSO on the southerly penetration of black marlin was previously undocumented. There is not a strong ENSO signature in the behaviour of the EAC (Holbrook *et al.,* 2009). Despite this, the southerly shift in distribution of suitable habitat during La Nina events is likely due to an overall increase in the presence of tropical mode water across the south-west Pacific Ocean.

Pacific Decadal Oscillation (PDO) influences environmental parameters throughout the south-west Pacific Ocean (Linsley *et al.,* 2000; Ridgway, 2007) and is known to influence species distributions and abundance (Polovina, 1996; Lehodey, 2006). Recent shifts in regional climate indicators suggest that PDO has shifted to a cool, La Nina like phase in recent years (Cai & Rensch, 2012). Due to the relatively short time period examined here (16 years), we cannot exclude the possibility that climatic factors operating on decadal scales (e.g. PDO) may help explain the poleward shifts observed here. However, long-term records show that poleward shifts are occurring in the climate (Cai *et al.,* 2006) and oceanography (Ridgway, 2007) of the south-west Pacific irrespective of PDO phase (Ridgway & Hill, 2012; Hu *et al.,* 2015) which is warming at 2-3 times the global average rate (Wu *et al.,* 2012; Hobday & Pecl, 2013). Subsequently, poleward distribution shifts have been reported for numerous marine species (Poloczanska *et al.,* 2013; Frusher *et al.,* 2014). Furthermore, this poleward trend in climatic and oceanographic features is predicted to continue (Cai *et al.,* 2005; Ridgway & Hill, 2012; Hu *et al.,* 2015), suggesting the shift in suitable habitat reported here is likely to continue.

Mobile pelagic predators play a key functional role in pelagic ecosystems, and their decline has resulted in trophic cascades in some regions (Myers *et al.*, 2007; Baum & Worm, 2009). Poleward distribution shifts in mobile pelagic predators could therefore have severe consequences for food webs in pelagic ecosystems, particularly in the tropics (Block *et al.*, 2011; Bell *et al.*, 2013a). Tropical nations are predicted to experience significant changes in fisheries production during the 21st century, with severe consequences for regional economic development and food security (Allison *et al.*, 2009; Cheung *et al.*, 2010; Bell *et al.*, 2013b). Our results indicate that rapid changes are already occurring in pelagic ecosystems. With emphasis of management shifting to a dynamic framework (Lewison *et al.,* 2015; Maxwell *et al.,* 2015), application of this model in conjunction with more sophisticated tagging technology presents itself as a potential method to manage key, mobile pelagic resources in real-time as access to and quality of high-resolution remote sensing data improves.

Investigating the population status and distribution of mobile pelagic predators is difficult due to the remote nature of their habitat and naturally low population densities. These factors lead to a lack of data at suitable spatial or temporal resolution to identify trends in populations, inhibiting studies of distribution shifts or population trajectories (Hobday & Evans, 2013). While some tagging technologies (satellite archival and passive acoustic tagging) can yield valuable information for fisheries managers and climate modelling (Block *et al.*, 2011; Hazen *et al.*, 2012), they are prohibitively expensive for many applications. Here, we show that citizen science can provide a valuable and cost-effective method of obtaining long-term, spatially-explicit occurrence records for a mobile pelagic predator (Booth *et al.,* 2011). This model could be applied to facilitate broad-scale implementation of a dynamic ocean management framework for a number of pelagic species where use of more sophisticated tagging technology is not viable. Combining occurrence records with remotely-sensed environmental data, we have shown a rapid, poleward shift in suitable habitat for black marlin. Given the success of our technique over such a short timescale (16 years), we advocate wider application of this method for studying mobile marine species. Increased utilization of such citizen science data may provide a valuable source of historical species occurrence records across a wide range of marine and terrestrial taxa, facilitating improved understanding of the impacts climate change will have on species distributions.

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## Supporting Information captions

Figure S1: Animation of model outputs, showing the distribution of suitable black marlin habitat at monthly time steps (n=192) from 1998-2013.

Figure S2: Variable contributions to final MaxEnt model output and model strength in the absence of each environmental factor determined using a jack-knife test.

Figure S3: Distribution of geometric mean points from 1998-2013 grouped into months showing seasonal latitudinal variability in the distribution of suitable black marlin habitat.

Figure S4: Inter-annual variability in the distribution of suitable black marlin habitat within the south-west Pacific Ocean. These four outputs represent suitable habitat during February from 2009-2012. Unsuitable habitat <0.282. a) 2009: There is a clear distribution of suitable habitat along Australia's east coast which has extended eastwards. b) 2010: Suitable habitat is much more refined to Australia's east coast and is fragmented with unsuitable habitat. c) 2011: A clear band of suitable habitat stretches east towards New Caledonia as cold water currents shift north. d) 2012: Unsuitable habitat is present at both the northern and southern extent of the south-west Pacific Ocean with suitable habitat extending as a narrow band along Australia's south-east coast and eastwards towards New Caledonia.

## Figure captions

Figure 1: The study area of the south-west Pacific Ocean (3-39°S/142-180°E), its major oceanographic features and the distribution of occurrence data within. a) A depiction of regional oceanographic features, including: 1. The South Equatorial Current 2. The East

Australian Current 3. The Tasman Front. b) All tag release locations recorded from the tagging program within the study area.

Figure 2: Seasonal variability in the distribution of suitable black marlin habitat within the south-west Pacific Ocean and its association with major oceanographic features. Unsuitable habitat <0.282. a) August-October: A broad $10^o$ latitudinal band of suitable habitat extends across the south-west Pacific Ocean adjacent to north-east Australia as the South Equatorial Current strengthens and collides with the continental shelf. b) November-February: The East Australian Current extends south supplying suitable habitat to the mid and south-east coast of Australia. c) March-April: Suitable habitat has reached its most southern extent and is now extending east in conjunction with the Tasman Front. d) May-July: Cold water currents shift towards the equator, forcing suitable habitat north.

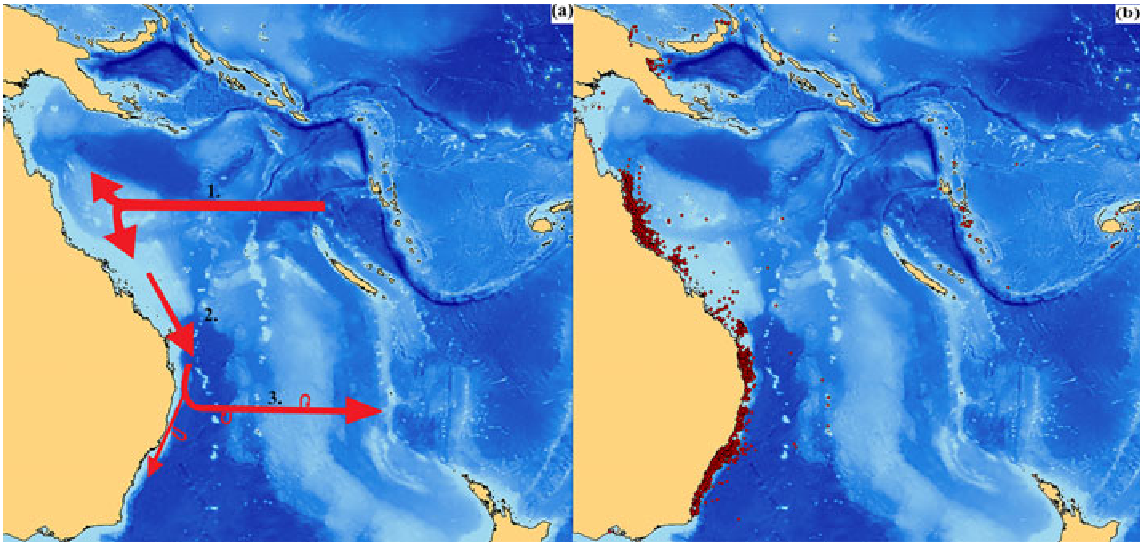
Figure 3: El Nino Southern Oscillation signature in the distribution of suitable black marlin habitat within the south-west Pacific Ocean with a clear southerly extension occurring during La Nina events.

Figure 4: A poleward shift in the distribution of suitable black marlin habitat across all seasons from 1998-2013 independent of ENSO. May-August ($R^2$=0.59, p<0.001) and September-December ($R^2$= 0.52, p<0.01) are both significantly shifting poleward at 77km decade$^{-1}$. January-April is shifting faster at 111 km decade$^{-1}$ but was only marginally significant ($R^2$=0.16, P=0.06) due to greater inter-annual variability.

**Candidate cover image**

Suggested caption: “Can pelagic apex predators keep up with the pace of climate change?”

Photo credit: Nicholas J. Hill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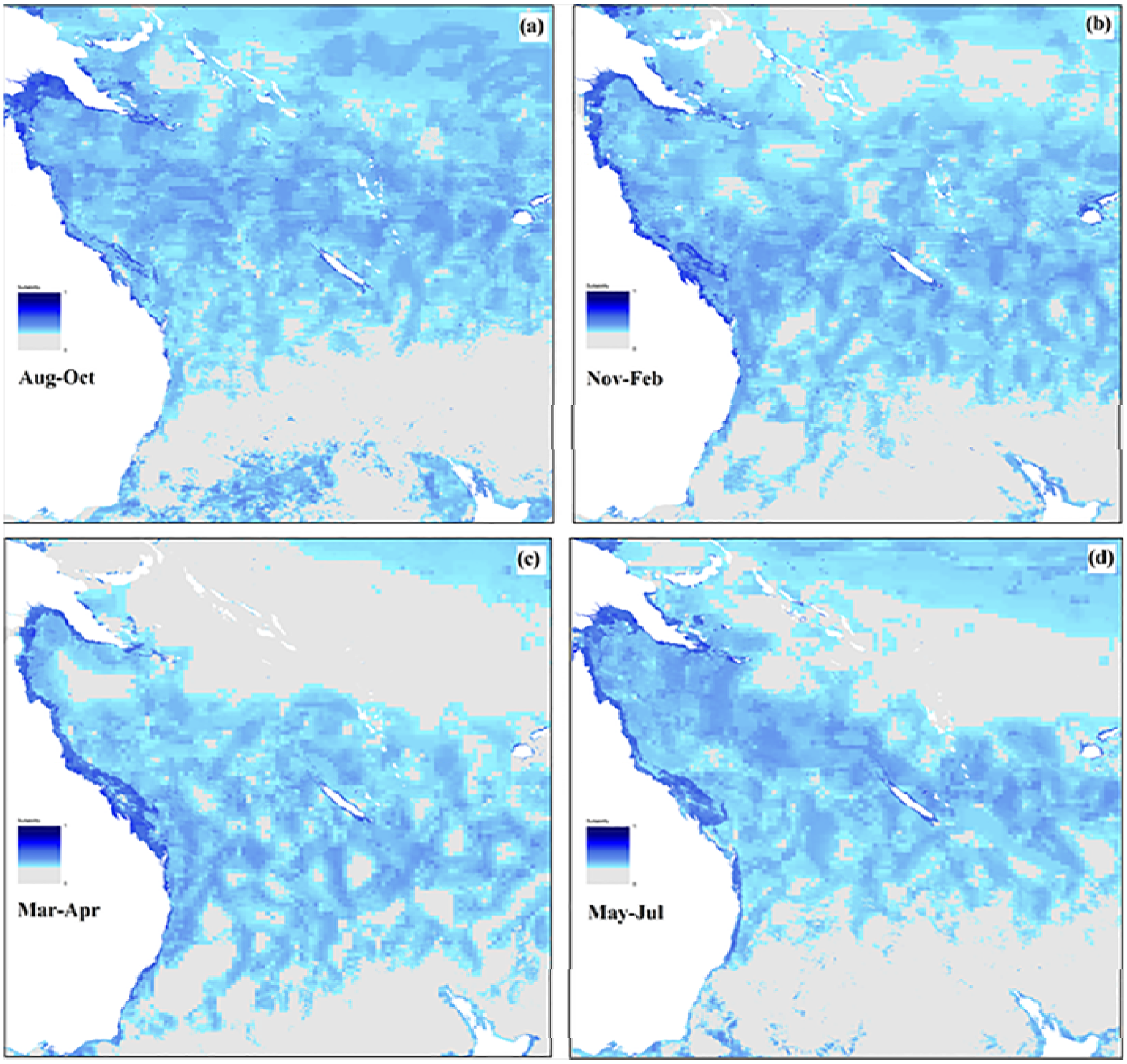
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Nov-Feb
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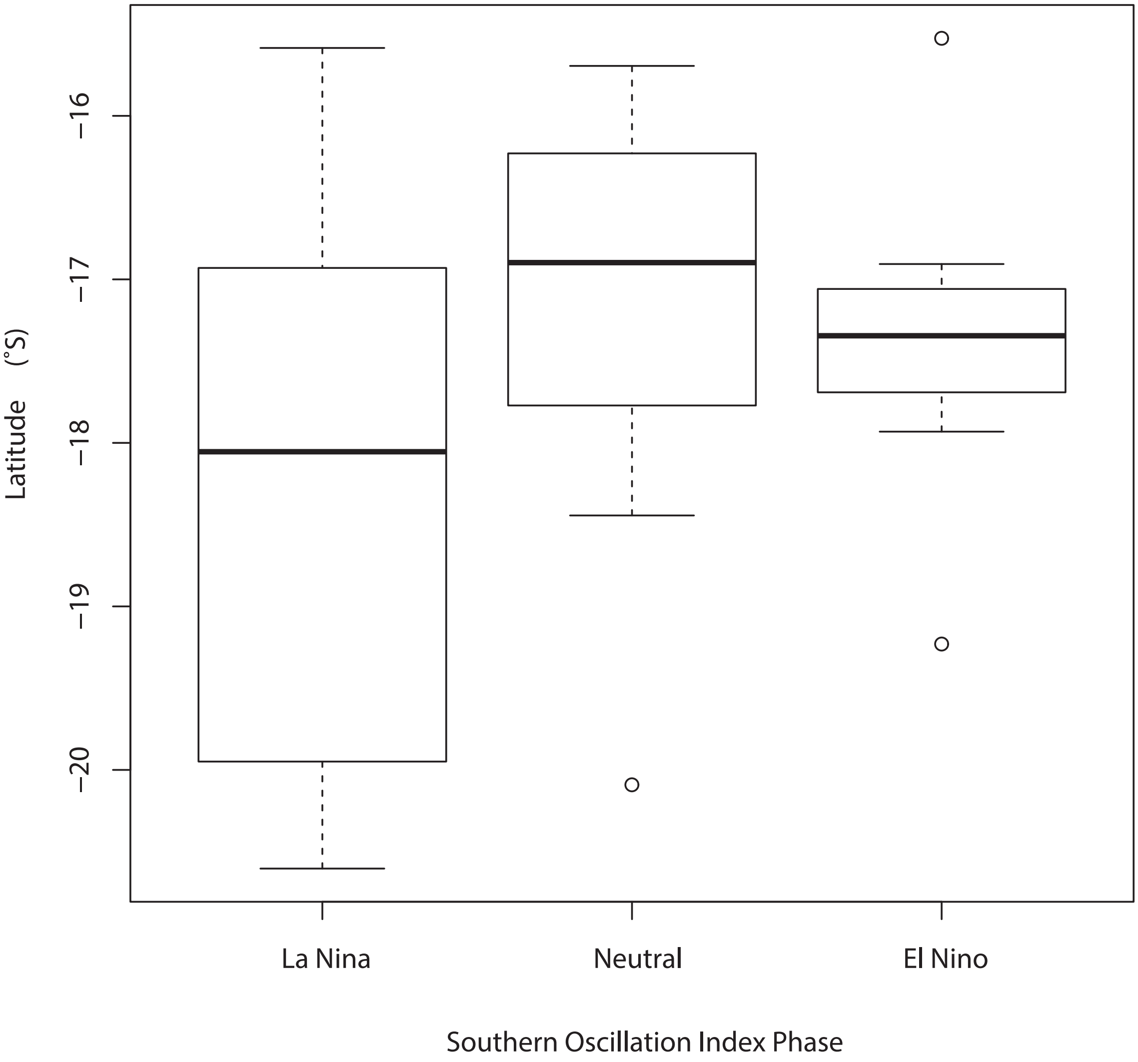
Mar-Apr
(d)
May-Jul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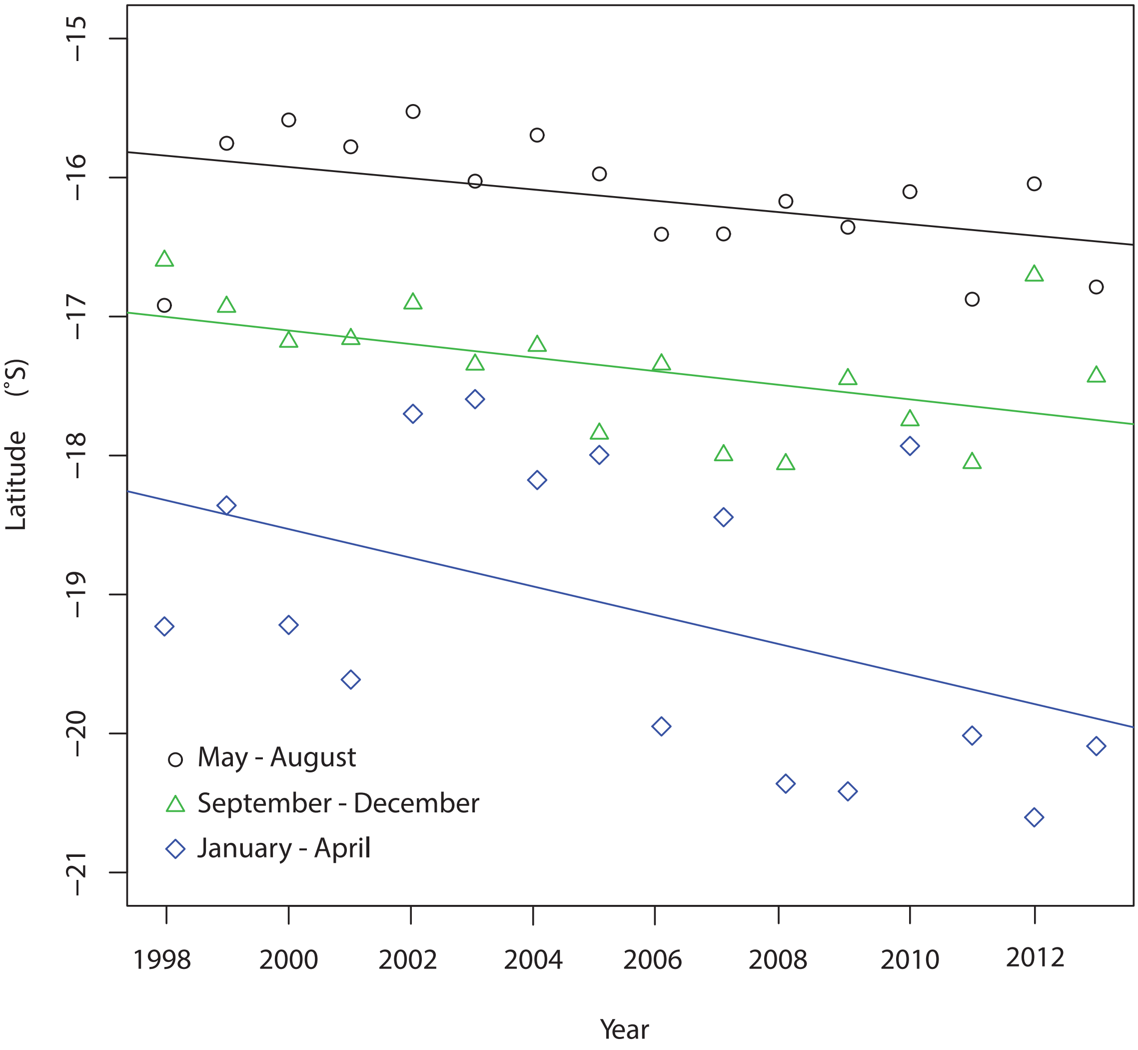
La Nina
Neutral
El Nino
Southern Oscillation Index Phase


−15
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Latitude (°S)
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○ May - August
△ September - December
◇ January - April