Title: Using historical fisheries data to predict tuna distribution within the British Indian Ocean Territory marine protected area, and implications for its management

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ABSTRACT

1. Recently, several large marine protected areas (MPAs) have been established globally and it is hoped that they will aid the recovery of populations of highly-mobile, large pelagic species. Understanding the distribution of these species within MPAs is key to delivering effective management but monitoring can be challenging over such vast areas of open ocean.
2. Historical fisheries data, collected prior to reserve establishment, can provide an insight into the past distributions of target species. We investigated the spatial and temporal distribution of yellowfin (*Thunnus albacares*) and skipjack (*Katsuwonus pelamis*) tuna catch using logbook data from the purse seine fishery in British Indian Ocean Territory (BIOT) from 1996 to 2010, before it was established as an MPA in April 2010.
3. Generalized additive models (GAMs) were used to predict tuna presence and relative abundance from fishing records in relation to temporal and environmental variables. Significant variables included sea salinity, temperature and water velocity.
4. Predictions from the models identified a distinct hotspot for large yellowfin tuna within the MPA, and areas of high predicted relative abundance of skipjack tuna. We recommend that these areas are used as focal points from which populations can be monitored and investigations into tuna residency time can occur, so that the effectiveness of the MPA in conserving highly-mobile pelagic fish can be determined.

Keywords: Marine Reserve, fish, ocean, habitat mapping

1. INTRODUCTION

Since the Convention on Biological Diversity set Aichi Biodiversity Target 11, which included the aim to protect 10% of coastal and marine areas by 2020, the number of marine protected areas (MPAs) has increased worldwide. In the last decade, this trend has continued with the establishment of several large-scale MPAs, >240,000km^2 (Toonen et al., 2013), to protect marine ecosystems (Leenhardt, Cazalet, Salvat, Claudet, & Feral, 2013; Lubchenco & Grorud-Colvert, 2015). These large-scale MPAs offer protection to marine biodiversity by encompassing a range of habitats (Wilhelm et al., 2014) and potentially safeguarding fauna throughout multiple life stages (Sale et al., 2005).

If designed appropriately, MPAs can provide substantial benefits to biodiversity (Edgar et al., 2014) and no-take marine reserves are considered most effective for protecting marine ecosystems (Lester & Halpern, 2008). The benefits of MPAs have been shown in recent studies (Boerder, Bryndum-Buchholz, & Worm, 2017; White et al., 2017). However, the efficacy of MPAs to protect highly-mobile, large pelagic species is still subject to debate, particularly as they often cover only a portion of the entire range of these species (Breen, Posen, & Righton, 2015; Game et al., 2009). Despite this, a recent study considering the evolution of movement rates showed in simulations that MPAs can be highly effective for the conservation of pelagic fish if decreased movement rates evolve as a result of protection within the protected area boundaries (Mee, Otto, & Pauly, 2017).

One of the major threats to MPAs is illegal fishing within the boundaries of the protected area (Lubchenco & Grorud-Colvert, 2015). This can become a serious issue in large-scale MPAs where there is insufficient enforcement capacity to cover the vast expanse of ocean, resulting in some areas being left exposed for long periods of time. We must understand the ecology and distribution of vulnerable species within MPAs so that the area can be effectively managed and regulations suitably enforced. Whilst monitoring techniques, including satellite and acoustic tagging (Gunn & Block, 2001; Hammerschlag, Gallagher, & Lazarre, 2011), and Baited Remote Underwater Video systems (BRUVs) (Bouchet & Meeuwig, 2015; Santana-Garcon et al., 2014), are improving, knowledge of the ecology and status of many large pelagic species within MPAs is limited. Where areas previously used for commercial fishing have been established as no-take marine reserves, the past fisheries data can theoretically provide information on the distribution and potentially the ecology of target species.

One such area with this potential is the British Indian Ocean Territory (BIOT), surrounding the Chagos Archipelago in the centre of the Indian Ocean (Figure 1). The waters within the 200 nautical mile (Nmi) Exclusive Economic Zone (EEZ) of BIOT were established as an MPA in 2010 and given full protection as a no-take marine reserve to conserve its biodiversity (Sheppard et al., 2012). Prior to reserve establishment, the British government granted licences for both longline and purse seine fishing of tuna within the EEZ of BIOT, but not within 12Nmi of the central atolls (Dunne, Polunin, Sand, & Johnson, 2014). At 640,000km^2, the BIOT MPA is one of the largest in the world and whilst it was not established specifically for the protection of tuna and other pelagic species, its size and remote location makes it ideal for assessing the role of large marine reserves for highly-mobile pelagic species.

Purse seine fishing is surface-level and schools caught are either free-swimming or associated with floating objects (Castro, Santiago, & Santana-Ortega, 2002; Dagorn & Fréon, 1999; Fréon & Dagorn, 2000), which can either be natural flotsam or man-made fish aggregating devices (FADs). The Indian Ocean accounts for 19% of the total tuna catches worldwide (ISSF, 2017) and has three principal target tuna species, yellowfin (*Thunnus albacares*), skipjack (*Katsuwonus pelamis*) and bigeye (*Thunnus obesus*). Whilst yellowfin stocks are considered *overfished and subject to overfishing* in the Indian Ocean, skipjack and bigeye stocks remain within biologically sustainable levels (FAO, 2016; IOTC, 2017). The purse seining of free-schools in the Indian Ocean targets large, mature yellowfin, whereas fishing on FADs allows fishers to target skipjack and often results in in incidental catch of juvenile yellowfin and bigeye tuna (Fonteneau, Chassot, & Bodin, 2013; Fonteneau, Pallarés, & Pianet, 2000; Maufroy et al., 2016). It has been suggested that unanchored, drifting FADs could represent ecological traps for tuna as a result of fish remaining associated with them as they drift out of productive habitats (Hallier & Gaertner, 2008; Marsac, Fonteneau, & Ménard, 2000).

Whilst the BIOT fishery was open, the purse seine fishing season ran between November and February, with most catches taken between December and January (Mees, Clarke, & Wilson, 2009). Overall, purse seine fishing in BIOT contributed just 2.73% of the total purse seine catch of tuna in the Indian Ocean between 1993 and

2008 (Dunne et al., 2014). During the creation of the BIOT MPA, it was suggested that the area was potentially large enough to support the recovery of populations of large, highly-mobile pelagic species, including tunas and sharks (Koldewey, Curnick, Harding, Harrison, & Gollock, 2010; Sheppard et al., 2012). However, some studies suggested that, due to its status as neither a significant tuna fishery nor a potential spawning ground, the BIOT MPA would be ineffective at reducing the impacts of the Indian Ocean tropical tuna fisheries (Kaplan et al., 2014) and models suggested that the closure would have a minor impact on the skipjack tuna population within the Indian Ocean because of the migratory nature of these fish (Dueri & Maury, 2013).

Previous studies have demonstrated that the distribution of yellowfin tuna can be influenced by a wide range of environmental variables, including sea surface temperature, chlorophyll-*a* concentration, sea surface height anomalies and oxygen concentration (e.g. Arrizabalaga et al., 2015; Brill & Lutcavage, 2001; Lopez et al., 2017; Maury, Gascuel, Marsac, Fonteneau, & Rosa, 2001; Potier, Bach, Ménard, & Marsac, 2014; Romena, 2001; Song, Zhang, Xu, Jiang, & Wang, 2008; Zagaglia, Lorenzzetti, & Stech, 2004). The distribution of skipjack tuna can also be impacted by sea surface temperature, chlorophyll-*a* concentration and surface height anomalies (e.g. Arrizabalaga et al., 2015; Lopez et al., 2017; Mugo, Saitoh, Nihira, & Kuroyama, 2010; Potier et al., 2014). However, current knowledge of the catch, distribution and movement of yellowfin tuna within BIOT is limited to a few studies (Carlisle et al., 2019; Davies, Mees, & Milner-Gulland, 2014; Mees et al., 2009) and there is very little known about skipjack tuna in the territory. In this study, we begin to address this knowledge gap by using logbook data from the purse seine fishing fleet in BIOT between 1996-2010, combined with remotely-sensed environmental variables, to investigate the past distributions of yellowfin and skipjack tuna in the area.

2. MATERIAL AND METHODS

2.1 Study area

Within the waters of BIOT, the Chagos Archipelago consists of five islanded atolls and several more submerged atolls, including the Great Chagos Bank (Sheppard et al., 2012). Bounds of 64-78°E and 1-12°S were set for the study area to encompass BIOT and its surrounding waters as some fishing sets were recorded just outside of the 200Nmi EEZ.

2.2 Logbook data

Fisheries data from purse seine logbooks from BIOT waters were provided by the Marine Resources Assessment Group (MRAG) from 1996 to 2010. As BIOT does not contain a commercial port no port sampling occurred, and the data represents raw logbook submitted by the vessels. For each fishing set, there was information on the date and location, the catch of each species to the nearest tonne, and the fishing vessel that took the catch. Yellowfin were reported as either large (>10kg) or small (<10kg) individuals. In addition, there was information on whether the school caught was associated with a FAD, if it was a free-school, or if it was associated with birds and mammals.

Records outside of the main fishing season (n = 43) and records with zero overall catch (n = 627), which were assumed to have either been unsuccessful skunk sets or a recording error, were also removed from the dataset prior to analysis (Maunder

& Punt, 2004). Although most catches were reported to the nearest tonne, there were 11 cases of non-integer values, these were rounded to their nearest integer value for compatibility. Months were numerically reclassified to better represent the fishing season with November as month one and January as month four of the season. This allowed month to be used as continuous variable in the generalized additive models. The fishing seasons were also numbered from 1 (1996/97) to 14 (2009/10) and used as a continuous variable in the models. All analyses were performed in R-studio (R Development Core Team, 2016) and a significance level (α) of 0.05 was set for the modelling.

2.3 Environmental data

Depth data, in metres (m), for the area encompassing BIOT were obtained from 30 arc-second bathymetry estimates provided by Satellite Geodesy (Becker et al., 2009) and the slope of change in bathymetry in each cell (Slope, %) was calculated using raster analysis in QGIS (QGIS, 2015).

For each month with recorded fishing sets (n = 42), average sea surface salinity (SOS, PSU) was obtained from the Global SOS/SSD-L4 Reprocessed dataset from the Copernicus Marine Environment Monitoring System (CMEMS) website (http://marine.copernicus.eu/; Nardelli 2012, Nardelli et al. 2016, Droghei et al. 2016). As the purse seine fishery is surface-level, monthly average sea temperature at depths of 0m (SST, °C) and 50m (TO.50, °C), salinity at 50m (SO.50, PSU), geopotential sea height (ZO, m), northward water velocity (VGO, ms^{-1}) and eastward water velocity (UGO, ms^{-1}) were downloaded from the Global ARMOR3D L4 Reprocessed dataset on the CMEMS database (Guinehut, Dhomps, Larnicol, & Le

Traon, 2012; Guinehut, Le Traon, Larnicol, & Philipps, 2004; Mulet, Rio, Mignot, Guinehut, & Morrow, 2012). Data were downloaded at 0.25° spatial resolution. The corresponding environmental variables for each fishing set were then retrieved based on date and location, one event with unrealistic bathymetry (-26m) was removed from the data. The final dataset contained 2082 fishing records.

A Spearman's correlation matrix was created between the environmental variables. When one variable correlated >0.70 or <-0.7 with another, one of the covariates was removed from the dataset to avoid correlation within the models (Dormann et al., 2013). Based on this sea height was removed from the analysis due to its correlation with temperature at 50m which was regarded as a more informative variable for tuna habitat preference.

2.4 Modelling

Generalized additive models (GAMs), in the R-package '*mgcv*' (Wood, 2006), which allow for non-parametric and non-linear relationships to be modelled, were used to model the presence/absence and then catch abundance of skipjack, large yellowfin tuna and small yellowfin tuna. Delta GAMs were run, whereby data were first analysed for the presence or absence of each group, using a binomial error distribution with a logistic link function, followed by investigation into the abundance in tonnes of each group per successful fishing set, for which the positive-catch data were log-transformed and modelled using a Gaussian error distribution with the identity link function. The linear predictor comprised of thin plate regression smooths of the fishing season, reclassified month and each environmental variable. To limit the maximum degrees of freedom used and avoid overfitting, the basis dimension, k, was fixed at four for each thin plate smoother following Lopez et al. (2017). To account for spatial autocorrelation in the data, a tensor product-based smoothed function of the interaction between longitude and latitude was included in the models, the basis dimension for this smooth was set at 10 to allow the impact of longitude and latitude to be appropriately captured. The use of the penalized thin plate regression spline allows terms in the model to be reduced to zero (Wood 2006), therefore, any terms that were not impacting the model were shrunk to zero in the model itself and for this reason no subsequent model selection was performed.

2.5 Spatial predictions

For each month in which a fishing event took place, the raster files for each environmental variable were resampled using bilinear interpolation to match the spatial resolution of the bathymetry layer. Data points shallower than 250m were removed from the prediction dataset as these represent areas around the atolls within which fishing was not allowed. Predictions from the GAMs were then made for each tuna group for each month using each environmental variable value in each cell. The monthly predictions were averaged to produce the predicted probability of presence and abundance of each group over the whole time series. Following Grüss, Drexler, & Ainsworth, maps of the overall delta-GAMs, showing the relative abundance for each group, were produced by multiplying the probability of presence by the abundance value in each raster cell (Grüss, Drexler, & Ainsworth, 2014).

3. RESULTS

3.1 Logbook data

Between 1996 and 2010, the number of fishing events was highly variable, with almost twice the number of events reported in the 1996/97 season (n = 747) than any other (Figure S1). Fishing effort was most concentrated to the north-east and north-west of the atolls (Figure 2 & S2) and most sets were taken in December (n = 1080), followed by January (n = 720). Many fewer fishing events occurred in February (n = 147) and November (n = 135) (Figure S3). Large yellowfin tuna were caught in 60.4% (n = 1257) of sets, skipjack tuna were caught in 44.6% (n = 928), and small yellowfin tuna were caught in 19.4% (n = 403) of sets.

When only considering the catch of each group, there were no clear trends in catch per season (Figure S4). The average catches of large yellowfin, skipjack and small yellowfin tuna per set were 23 tonnes (t), 20.6t and 9.5t respectively.

3.2 Generalized additive models

The binomial model for the presence and absence of skipjack tuna in purse seine sets was significantly impacted by seven variables (Table 1). The model explains 24.6% of the deviance with an adjusted-r^2 of 0.28. The interaction between longitude and latitude has a significant impact on the model, with highest presence in sets taken to the south of the atolls (Figure S5). Presence of the species in sets was least likely during the 2004/05 and 2005/06 seasons and skipjack were most likely to be present in sets taken in November. Presence was highest when associated with faster water velocity in a westward direction and decreased with increasing eastward water velocity (Figure 3).

The lognormal model for the abundance of skipjack tuna in successful sets explains 7.22% of the deviance and has an adjusted-r^2 of 0.060, seven variables were significant in the model (Table 2). Abundance was highest in the 2000/01 season and increased with each month of the fishing season. Abundance decreased with shallower depths and as the slope of change in bathymetry increased. Abundance was lowest at surface salinity levels below 34.8 PSU and decreased as water velocity increased in the northward and eastward directions (Figure 4).

The binomial model for the presence/absence of large yellowfin tuna in fishing sets was significantly associated with five variables (Table 1), the model explains 20.9% of the deviance, with an adjusted-r^2 of 0.235. Longitude and latitude had the greatest impact on the model to the northeast of the atolls (Figure S5), large yellowfin tuna presence was highest between the 2003/04 season until 2005/06, and presence was lowest in November. Salinity below 34.8 PSU, both at the surface and at 50m, was associated with lower presence, whilst presence increased with increasing water velocity in the eastward direction and water temperature at 50m (Figure 3).

The lognormal model explains 12.7% of the deviance for the abundance of large yellowfin tuna in successful sets, with an adjusted-R^2 of 0.104 and six significant environmental variables (Table 2). Abundance was lowest in the 2000/01 season and highest in 2007/08, abundance was also highest in sets taken in January. Water velocity impacts the model with lowest abundance associated with faster water velocity to the south, and west. Abundance also decreased with increasing water temperature at 50m (Figure 4).

The binomial model to explain the presence/absence of small yellowfin tuna explains 11.9% of the deviance and has an adjusted-r^2 of 0.108, with six significant variables (Table 1). The presence of small yellowfin tuna was lowest in sets taken in the southeast of the area. The presence of small yellowfin in fishing sets increased each season, but decreased over the course of each season. Presence decreased as water velocity increased in the eastward direction, was highest at salinity levels at 50m below 35 PSU and peaked around temperatures at 50m of 23°C (Figure 3).

Small yellowfin abundance in successful sets is associated with four significant variables, the lognormal model explains 11.7% of the deviance with an adjusted-R^2 of 0.089 (Table 2). Abundance peaked in the 2005/06 season and around 34.8 PSU of surface salinity. Abundance decreased with faster water velocity to the north and with salinity at 50m below 35 PSU (Figure 4).

3.3 Spatial predictions

Skipjack tuna have areas of high predicted probability of presence in the south, northeast and northwest of the MPA, the lowest probability of presence is predicted around the northern atolls (Figure 5a). There is an area of very high predicted probability of presence for large yellowfin tuna to the east of the northern atolls, predicted probability of presence is also relatively high to the west of the central atolls, and in the southeast and northwest of the MPA (Figure 5b). The predicted probability of presence for small yellowfin tuna is generally low within the MPA, but is highest for the group to the south of the atolls and in the east of the MPA (Figure 5c). Due to their mathematical relationship, the overall abundance estimates from the combined delta-GAM predictions are closely related to the probability of presence predictions and show that predicted relative abundance of skipjack tuna is lowest around the atolls and highest in the south of the MPA (Figure 6a). There are hotspots of high predicted relative abundance for large yellowfin tuna to the northeast of the atolls and on the southeast boundary of the MPA (Figure 6b), and predicted relative abundance of small yellowfin tuna is low, with highest values among the southern atolls and on the central-eastern boundary of the MPA (Figure 6c).

4. DISCUSSION

This study investigated the spatial and temporal trends of yellowfin and skipjack tuna in the British Indian Ocean Territory, using data from the purse seine fishery between 1996 and 2010. Although fisheries data are inherently biased by only providing data from areas that were visited by the fishing fleet (Walters, 2003), it is often the only source of information for the monitoring of pelagic systems (Maunder & Punt, 2004). Fishing effort is not, however, a random sample of the environment, and is often a strong indicator of abundance and species composition (Kaplan et al., 2014). The monitoring of species within protected areas is a key part of conservation (Nichols & Williams, 2006) and is particularly challenging in marine habitats (Lammers, Brainard, Au, Mooney, & Wong, 2008; Wilhelm et al., 2014). Results from this study, which improve our understanding the distributions of highly-mobile tuna species in BIOT, may help to guide more effective and efficient management in the MPA. It is important to consider that data used in this study is only representative of the purse seine fishing season between November and February and that the spatial and temporal distributions of skipjack and yellowfin tuna will also be influenced by large scale climatic variation that spans longer than the relatively short time series analysed in this study. However, the significant environmental variables identified here may guide studies that aim to determine the impact of climate change on tuna in the MPA and areas of high predicted relative abundance can be used for research into the residency of tuna within the MPA.

During the creation of the BIOT MPA, it was suggested that the islands of the archipelago would play a role in creating an ‘island mass effect’ where habitat heterogeneity results in increased oceanic productivity, and that geographic features present in the BIOT MPA would act as natural aggregation points for tuna and other highly-mobile pelagic species (Koldewey et al., 2010). The central hotspot for large yellowfin tuna presented in this study may represent one such aggregation point due to its proximity to the atolls. Previous studies have suggested that the reserve is not an area of significance for large, mature yellowfin tuna within the Indian Ocean (Kaplan et al., 2014), however, with yellowfin tuna stocks in the Indian Ocean considered *overfished and subject to overfishing* (IOTC, 2017), it is essential that the conservation potential of the BIOT MPA for yellowfin tuna is determined. The ecological effects of large pelagic MPAs are still to be comprehensively reviewed, and theoretical models predicting the decrease of movement rates within MPAs (Mee et al., 2017) are yet to be validated. If individuals do not remain in the BIOT MPA for long periods of time, and the MPA does not protect a large proportion of the tuna population, then overall stocks are unlikely to increase in biomass. Calls have been made for specific movement studies to be performed in the MPA to determine the residency of pelagic species (Kaplan et al., 2014), and tagging studies have been able to provide this information for tuna in Hawaii (Adam, Sibert, Itano, & Holland, 2003; Itano & Holland, 2000). Sibert and Hampton showed that both yellowfin and skipjack tuna can travel thousands of nautical miles after being tagged, but most individuals travelled less than 200Nmi (Sibert & Hampton, 2003). To date, yellowfin tuna have only been tagged opportunistically in the BIOT MPA and whilst individuals have remained within the MPA boundaries, it is unclear whether the species remains resident over long periods of time (Carlisle et al., 2019). The central hotpot for large yellowfin tuna identified in this study could provide a focal area from which a long-term tagging studies can take place to determine how tuna use the MPA throughout the year.

In BIOT, illegal fishing has decimated reef shark populations (Graham, Spalding, & Sheppard, 2010) and sharks represented 80% of the total catch by weight of illegal fishing records from arrested vessels between 2006 and 2015 (Martin, Moir Clark, Pearce, & Mees, 2013; Moir Clark, Duffy, Pearce, & Mees, 2015). Whilst the catch of tuna by illegal fishing vessels in BIOT may not represent a major threat to tuna populations within the MPA, the identified hotspot for large yellowfin tuna may indicate an area of high productivity that represents important habitat for other endangered, threatened or protected pelagic species. Sharks are known to be associated with tuna fisheries across the world (Gilman et al. 2008, Amandè et al. 2010, Torres-Irineo et al. 2014, Hutchinson et al. 2015) and in the Western Indian Ocean, at least 50 non-target species have been recorded as bycatch in the tuna purse seine fishery (Romanov, 2002). The silky shark (*Carcharhinus falciformis*) is the most commonly caught bycatch species in the Indian Ocean (Amandè, Chassot, Chavance, & Pianet, 2008), with the majority of bycatch coming from log- and FAD-accociated sets (Amande et al., 2008; Romanov, 2002). Further research should explore available bycatch records to determine whether there were any apparent bycatch hotspots within BIOT and how bycatch in the area compared to the rest of the Indian Ocean. The areas of high predicted presence of tuna identified in this study should be investigated as potential hotspots for other pelagic species and enforcement should be increased in the areas to reduce the impact of illegal fishing on shark populations in the MPA. Given the distance between areas of high predicted presence for each tuna species, there may be a need for greater monitoring and enforcement resources to provide adequate protection within the MPA. The development satellite monitoring techniques should be considered by management for the delivery of effective management of this large MPA (Pimm et al., 2015).

As the environmental data used in this study were based on monthly averages and were not collected simultaneously with the catch data, it is difficult to draw meaningful conclusions from relationships between the two (Brill, 1994). However, the variables that are significant in the GAMs have been shown to impact tuna distribution in previous studies. The importance of temperature as a determinant of tuna distribution has been shown in numerous studies (Arrizabalaga et al., 2015; Barkley, Neill, & Gooding, 1978; Brill & Lutcavage, 2001; Mugo et al., 2010; Zagaglia et al., 2004) and the range of water temperatures in this study is within the established ranges of preferred water temperatures for skipjack and yellowfin (Arrizabalaga et al., 2015; Barkley et al., 1978). Our results do show similar trends to those found in recent studies (Arrizabalaga et al., 2015), however whereas surface temperature is a significant variable for skipjack tuna, it is temperature at 50m that impacts the presence of yellowfin tuna in this study. As the Indian Ocean warms (Rao et al., 2012), it is important that any study looking to model the impact of climate change on tuna distribution considers the water temperature at multiple depths.

Despite some authors showing that salinity is not an important variable for tuna (Sund, Blackburn, & Williams, 1981), recent studies have suggested that salinity can in fact be an important determinant of distribution (Arrizabalaga et al., 2015; Maury et al., 2001; Reygondeau et al., 2012). Although this study only contained a limited range of salinity values, our results also suggest that salinity can be an important variable for tuna presence and abundance and should therefore be considered in future modelling studies particularly when modelling climate change impacts on tuna distribution. Whilst findings here for large yellowfin tuna do not follow the same trends as those found by Maury et al. (2001), the presence of small yellowfin tuna do show a similar trend to that found for the relationship between salinity and young yellowfin tuna in the Atlantic Ocean (Maury et al., 2001). Furthermore, despite the far greater spatial scale of their study, the impacts of salinity on the catch per unit effort of yellowfin tuna found by Arrizabalaga et al. (2015) do show a similar trend to results for the presence of large yellowfin tuna in this study. The reason why salinity levels impact tuna distribution remains unknown, however, some authors have suggested that salinity influences tuna distribution through its impact on dissolved oxygen in the water (Maury et al., 2001). Further research into this is required and models of the future environmental conditions in BIOT should be made so that potential impacts of climate change can be predicted, and management plans can be made.

Whilst drifting-FADs do have the potential to impact the distribution of tuna (Hallier & Gaertner, 2008; Marsac et al., 2000), we included FAD-associated catches in our analysis to ensure that we did not ignore vital information on the catch of skipjack tuna, which are targeted through the use of FADs (Fonteneau et al., 2000). Increased presence of skipjack and small yellowfin tuna, which are commonly associated with drifting-FADs (Fonteneau et al., 2000), is linked to faster water velocity in the westward direction in this study. This finding is in line with results from Lopez et al. (2017), who found that for tuna associated with FADs in the Atlantic Ocean, presence and abundance was significantly impacted by FAD bearing, with highest presence related to a westward direction of movement (Lopez et al., 2017). During the winter monsoon season (January and February) the South Equatorial Countercurrent runs from west to east above the atolls in BIOT (Schott, Xie, & McCreary Jr, 2009), suggesting that the predominant direction of water movement during the purse seine fishing season would have been to the east. The increased abundance of large yellowfin tuna with faster eastward water velocity suggests that the current may be producing favourable habitat for mature yellowfin tuna. This could be due to increased prey density, or increased oxygen levels in the water being introduced as a result of the stronger current. Whilst far less numerous than artificial FADs, natural flotsam will still act as aggregation points for fish within the MPA and impact their distribution accordingly.

The predicted distributions of skipjack and large yellowfin tuna do not overlap, with each group having the highest predicted presence in areas where predicted presence for the other group is low. Spatial niche separation is not apparent between the two groups in the Indian Ocean (Olson et al., 2016), therefore, it may be important to consider the potential impact of market dynamics and fishing fleet behaviour on the results (Branch et al., 2006). Contrasting spatial distributions may reflect the targeting for one group over the other in certain locations. Absence of a tuna group in a recorded catch may not represent a genuine absence, as fish may have been discarded due to the individuals being too small for markets or not worth retaining given the storage capacity of the vessel (Ardill, Itano, & Gillett, 2011). Vessels were only required to report the landed catch, which could have impacted the recorded abundance of tuna caught in a set. The logbook data used in this study did not have information of bycatch or discards and zero-catch was therefore treated as a true absence. Future studies should attempt to use bycatch and discard data, if available, and combine these with the fishery landed catch data to give a better representation of species distributions. As fishing vessels were not permitted to fish within 12Nmi (22km) of land (Dunne et al., 2014), future research should also consider investigating tuna presence within 12Nmi of land in the BIOT MPA to fully understand their distribution.

Although the models had low explained deviances, this is in line with other similar studies using GAMs (Becker et al., 2010; Forney et al., 2012; Lopez et al., 2017; Mannocci et al., 2014). As the binomial models achieved greater explained deviance than the lognormal model, it appears that predictions of presence are more robust than predictions of abundance from fisheries data. The low explained deviances may be due to the use of indirect predictors rather than potentially causal ones such as prey distribution (Mannocci et al., 2014) and the inclusion of prey distribution has been shown to improve the fits of distribution models for other marine predators (Benoit-Bird et al., 2013; Tickler, Letessier, Koldewey, & Meeuwig, 2017; Wirsing, Heithaus, & Dill, 2007), suggesting that the distributions of mobile predators, such as tuna, can be strongly influenced by prey availability. Furthermore, the low explained deviance may be caused by the absence of potentially important environmental variables such as dissolved oxygen and chlorophyll-a concentration. Yellowfin and skipjack tuna require areas of high oxygen concentration (Barkley et al., 1978; Gooding, Neill, & Dizon, 1981; Potier et al., 2014; Romena, 2001) and chlorophyll-a concentration is often used as a proxy for net primary productivity in a water body when investigating the presence of tuna (Brill & Lutcavage, 2001; Zagaglia et al., 2004). It was not possible to acquire dissolved oxygen concentration and chlorophyll-a data at sufficient resolution spanning the time scale required for this study, but future studies using more recently collected fisheries data should include both chlorophyll-a and dissolved oxygen concentration in analyses.

In conclusion, historical fisheries data do have a part to play in the design and management of MPAs. As one of the largest MPAs on the planet, the BIOT MPA requires high levels of enforcement to ensure the protection of species within its boundaries. Results from this study suggest that there is a key hotspot for large yellowfin tuna within the BIOT MPA, and that distribution of skipjack is highly variable. Results also suggest that skipjack were most often targeted by fishers in November, after which yellowfin became the target until February. As this is likely to closely reflect the presence of each species in the MPA, management should consider focusing on the protection of specific areas in different months. Further research of tuna outside of the fishing season is required to determine the residency of these species within the MPA throughout the year, this will determine how resources can be employed effectively to manage the protected area. The results from this study can provide crucial starting points for such research.

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Table 1. The estimated degrees of freedom and chi-squared score of terms used in binomial generalised additive models for the presence/absence of skipjack, large yellowfin and small yellowfin tuna. (BATH: depth; Slope: slope of change in depth; UGO: geostrophic eastward sea water velocity; VGO: geostrophic northward sea water velocity; SST: sea surface temperature; TO.50: sea water temperature at 50m; SOS: sea surface salinity; SO.50: sea water salinity at 50m; *: p<0.05; **: p<0.005; ***: p<0.001)

	Skipjack		Large yellowfin		Small yellowfin	
Adjusted r^2	0.280		0.235		0.108	
Deviance explained (%)	24.6		20.9		11.9	
Residual d.f	2021.27		2028.59		2043.11	
n	2082		2082		2082	
Variable	**d.f**	χ^2	**d.f**	χ^2	**d.f**	χ^2
Longitude, latitude	38.72	154.76***	36.88	146.87***	28.06	99.09***
Season	2.95	102.11***	2.88	108.96***	2.44	26.85***
Month	2.61	38.04***	2.30	16.43***	0.80	9.99***
BATH	2.76	4.93	-	-	0.33	0.751
Slope	2.60	3.22	2.59	3.83	-	-
UGO	2.99	57.74***	3.00	57.88***	1.06	13.50***
VGO	-	-	-	-	-	-
SST	2.11	8.49**	-	-	-	-
TO.50	-	-	0.72	2.52*	2.27	8.78**
SOS	2.22	11.34**	2.05	7.69**	-	-
SO.50	2.78	10.15**	2.00	5.64*	2.93	24.10***

Table 2. The estimated degrees of freedom and F score of terms used in lognormal generalised additive model for the abundance of skipjack, large yellowfin and small yellowfin tuna. (BATH: Bathymetry; Slope: slope of change in bathymetry; UGO: geostrophic eastward sea water velocity; VGO: geostrophic northward sea water velocity; SST: sea surface temperature; TO.50: sea water temperature at 50m; SOS: sea surface salinity; SO.50: sea water salinity at 50m; *: $p<0.05$; **: $p<0.005$; ***: $p<0.001$)

	Skipjack		Large yellowfin		Small yellowfin	
Adjusted r^2	0.060		0.104		0.089	
Deviance explained (%)	7.22		12.7		11.7	
Residual d.f	915.12		1224.79		389.26	
n	928		1257		403	
Variable	**d.f**	**F**	**d.f**	**F**	**d.f**	**F**
Longitude, latitude	-	-	17.8	0.475***	-	-
Season	2.76	3.92**	2.71	3.59**	1.87	1.84*
Month	1.00	5.66***	2.45	12.78***	-	-
BATH	2.80	4.01**	-	-	1.95	1.55
Slope	0.73	1.14*	1.28	1.01	-	-
UGO	1.01	4.66***	1.66	1.51*	-	-
VGO	1.50	7.82***	2.79	5.07***	0.64	1.00*
SST	-	-	1.61	0.55	2.45	2.09
TO.50	-	-	0.88	2.38**	1.54	0.70
SOS	2.09	5.22***	-	-	1.93	2.27*
SO.50	-	-	-	-	2.37	2.77*

FIGURE LEGENDS

Figure 1 The location of the British Indian Ocean Territory (BIOT). The shaded polygon represents the 640,000km^2 BIOT Marine Protected Area, atolls are shown in the insert with the grey outlines indicating underwater features.

Figure 2 Two-dimensional kernel density showing the overall frequency of purse seine fishing sets in the British Indian Ocean Territory (black polygon) and surrounding waters.

Figure 3 Partial plots showing the response of significant environmental variables on the binomial presence/absence generalised additive models of free-schooling skipjack, large yellowfin and small yellowfin tuna. Plots show the smooth fit of each significant variable (95% confidence intervals in dashed lines) with the y-axis representing the smooth’s contribution to the model on the scale of the linear predictor with the degrees of freedom of that variable in the y-axis label. The “rug” above the x-axis shows the distribution of the observed values.

Figure 4 Partial plots showing the response of significant environmental variables on the lognormal generalised additive models for the abundance skipjack, large yellowfin and small yellowfin tuna. Plots show the smooth fit of each significant variable (95% confidence intervals in dashed lines), the y-axis representing the smooth’s contribution to the model on the scale of the linear predictor with the degrees of freedom of that variable in the y-axis label. The “rug” above the x-axis shows the distribution of the observed values.

Figure 5 Spatial predictions from binomial generalised additive models (GAM) showing the predicted probability of presence for a) skipjack, b) large yellowfin and c) small yellowfin tuna in the British Indian Ocean Territory Marine Protected Area (black polygon) and surrounding waters.

Figure 6 Spatial predictions from overall delta generalised additive models (GAM) showing the predicted relative abundance of a) skipjack, b) large yellowfin and c) small yellowfin tuna in the British Indian Ocean Territory Marine Protected Area (black polygon) and surrounding waters.