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Applying Species Distribution Modelling to a Data Poor, Pelagic Fish Complex: The Ocean Sunfishes

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Running head: Distribution and seasonal movements of ocean sunfishes

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Abstract

Aim

Conservation management of vulnerable species requires detailed knowledge of their spatial and temporal distribution patterns. Within this context species distribution modelling (SDM) can provide insights into the spatial ecology of rarely encountered species and is used here to explore the distribution pattern of ocean sunfishes (*Mola mola* and *M. ramsayi*). Both species are prone to high levels of bycatch and are classified respectively as Globally Vulnerable and Not Assessed by the IUCN; although their overall range and drivers of distribution remain poorly defined. Here, we constructed suitable habitat models for *Mola* spp. on a global scale and considered how these change seasonally to provide a much needed baseline for future management.

Location

Global.

Methods

Sighting records collected between 2000 and 2015 were used to build SDMs and provided the first global overview of sunfish seasonal distribution. *Post-hoc* analyses provided a quantitative assessment of seasonal changes in total range extent and latitudinal shifts in suitable habitat.

Results

Mola is a widely distributed genus; however, sightings exhibited significant spatial clustering most notably in coastal regions. SDMs suggested that *Mola* presence was strongly dependant on sea surface temperatures with highest probability of presence between 16 and 23°C. The models identified significant variation in seasonal range extent with latitudinal shifts throughout the year; although large areas of suitable year-round habitat exist globally.

Main conclusions

We provided the first assessment of *Mola* distribution on a global scale, with evidence of a wide latitudinal range and significant clustering in localised ‘hotspots’ (notably between 40-50°N). By assessing the results of SDMs alongside evidence from published satellite tagging studies, we suggest that the species within the genus *Mola* are highly mobile, acting as facultative seasonal migrants. By identifying key suitable habitat alongside potential movement paths, this study provides a baseline that can be used in active conservation management of the genus.

Introduction

Conservation management efforts are dependent on a detailed understanding of the spatial distribution, biogeography and ecology of target species (Ferrier et al., 2002; Ricklefs, 2004; Rushton et al., 2004). For widespread or cryptic species this can pose significant challenges (Pearson et al., 2007; Rissler & Apodaca, 2007). Species distribution models (SDMs, also known as ecological niche models, species-habitat models or predictive habitat models) assess the complex relationship between species occurrence records and environmental variation, even from limited datasets, and offers insight into habitat suitability both spatially and temporally (Elith & Leathwick, 2009; Franklin, 2009). For little known oceanic species, such methods can provide a key starting point in understanding complex, wide-ranging distribution patterns and the mechanisms driving environmental tolerances (Elith et al., 2006).

One such family of oceanic taxa, the ocean sunfishes (or Molidae), are often described as rare, inactive drifters (Pope et al., 2010), however recent studies have revealed high density aggregations in coastal waters (e.g. Silvani et al., 1999; Pope et al., 2010; Syväranta et al., 2012), sustained long distance swimming of ~48 km per day (e.g. Cartamil & Lowe, 2004; Nakamura et al., 2015; Thys et al., 2015) and repeated deep-diving to mesopelagic depths foraging for gelatinous prey (e.g. Cartamil & Lowe, 2004; Nakamura et al., 2015). Such observations suggest that this is an active, highly motile taxon (Cartamil & Lowe, 2004), with a broad trophic niche (e.g. Harrod et al., 2013; Nakamura & Sato, 2014; Sousa et al., 2016a) and capable of travelling significant distances in a directed manner (see review, Pope et al., 2010). This suggests that *Mola* may have more complex ecology than previously thought (Syväranta et al., 2012), which poses broader implications for sustainable management. Such insight is important in light of current bycatch levels (Silvani et al., 1999; Cartamil & Lowe, 2004; Pope et al., 2010), such as the reported capture of > 36 000 individuals per annum in

Mediterranean drift gillnets (Petersen & McDonell, 2007). Bycatch numbers coupled with impacts of large-scale target fisheries, led to a recent IUCN Red List classification of *Mola mola* (L. 1758) as globally Vulnerable (Jing et al., 2010) and Data Deficient in Europe (see Table 1, Appendices). This Red Listing represents a tentative first step towards future management strategies and highlights areas of sunfish ecology that require further research, such as knowledge of their distribution and movements, which currently restricts management and conservation efforts.

Anecdotal evidence collated in a review by Pope et al. (2010) suggested that the Molidae (see Table 1. Appendices) have a pan-global distribution within temperate and tropical latitudes, although limited sighting records and inherent difficulties in species identification have led to problems in delineating species-specific ranges and seasonal movement patterns. Recent high-profile reports of ocean sunfishes at high latitudes, such as in Alaska (Dobbyn, 2015), have led many media outlets to speculate as to why these species are “suddenly” appearing so far north. However, without baseline data on the range extent of ocean sunfishes, it is difficult to know whether they have undergone recent expansion and, if so, what might be driving such changes. Although taken to be widespread (Cartamil & Lowe, 2004), it is not yet known if ocean sunfishes adhere consistently to a migratory paradigm (whether obligate or facultative). Evidence from multiple studies, using satellite tags and accelerometer derived dead-reckoning (e.g. Sims et al., 2009; Dewar et al., 2010; Nakamura et al., 2015; Thys et al., 2015), suggests that *Mola* in temperate and subtropical regions may move to equatorial latitudes during autumn, for example, into UK and Japanese waters. However, other studies using satellite tracking (Hays et al., 2009) and dietary analysis (Harrod et al., 2013) suggest year-round, or at least long-term, residence in some regions, including in Mediterranean and South African waters. The results from these studies support suggestions of distinct, local populations with differing drivers of distribution; however, there is a paucity of evidence across wide spatio-temporal scales.

From a broader conservation perspective, the IUCN states that creating a "comprehensive, objective global approach for evaluating the conservation status of [all] species [is important in order to] inform and catalyse action for biodiversity conservation" (IUCN, 2016). In line with this statement, this study uses SDM to provide an initial assessment of the global distribution pattern of a vulnerable marine genus that is plagued with species-specific identification problems. We present basic life history information for the genus *Mola* and its seasonal range extent in relation to key predictive environmental parameters. This study provides an objective evidence base critical to providing a full IUCN Red Listing, upon which international management decisions can be founded.

Materials and Methods

Data sources and manipulation

Global sightings of *Mola* were collected from public databases, published papers and fisheries logs (see Appendix S1). A total of 14 953 sightings, recorded between the years 1758 and 2015, were compiled before specific criteria were set for standardising the dataset. This study aimed to assess the distribution of the genus *Mola* which currently contains two species. *Mola* is easily distinguishable from other genera in the Molidae (*Ranzania* and *Masturus*, see Table 1. Appendices), due to its differing morphology, and therefore potential for confusion is limited. We accept that misidentification is possible, but by maintaining a conservative approach to data acquisition (i.e. by removing records not identified to genus), we have tried to mitigate this risk. Any incomplete records (missing location or date of observation) were removed. All sighting locations were converted to decimal degrees, and mapped using ARCGIS 10.3.1 (ESRI, California, USA) and all locations that erroneously fell on land were removed. Although the sightings dataset extended over 257 years, 79% of sightings occurred between 2000 and 2015. Therefore only this subset of 5 419 sightings was retained for further analysis. These sightings were divided into each quarter of the year (Jan-Mar, Apr-May, Jun-Aug and Sep-Dec) and matched with recent climate data available through online data sharing platforms.

Environmental parameters

Climate data with near global oceanic coverage described surface oceanography at a resolution of one decimal degree delineated as a cellular matrix. The most recently collected dynamic parameters were selected and of these, sea surface temperature, nitrate, oxygen and chlorophyll concentration were averaged over three month periods suited to generating seasonal summaries (Jan-Mar, Apr-May, Jun-Aug and Sep-Dec). The datasets included sea surface temperature averaged from 2005 to 2012 (NOAA, 2015), nitrate and oxygen concentrations averaged from 1955 to 2012 (NOAA, 2015) and chlorophyll concentration averaged from 2002 to 2012 (NASA, 2012). Despite the extensive coverage provided by satellite data, the limitations of this dataset must be acknowledged; such as the lower quality data from nearshore or frequently clouded environments (Smith et al., 2013). Of all the parameters included, bathymetry was the only static variable recorded from a 2002-2003 global survey (NASA, 2003). If climatic data were missing from the decimal degree cell in which a sighting was recorded, it was removed from the analysis (leaving n = 4 985 sightings).

Data validation

Since all *Mola* data collected were ‘presence only’ sightings, we implemented a bias file as a proxy of survey effort to indicate the likelihood of being encountered and recorded, as presence-absence models perform better than presence only models (Elith et al., 2006). Since true absence data were not available, we followed established methods to construct a 'bias file' (e.g. Phillips et al., 2009; Aguirre-Gutierrez et al., 2013: Pokharel et al., 2016). This process requires the identification of a suitable proxy species (termed a target group) for which further presence data were available (e.g. Ponder et al., 2001: Anderson, 2003). We chose to use the leatherback turtle, *Dermochelys coriacea* (Vandelli, 1761) as it is suggested to inhabit similar environments to ocean sunfishes (Hays et al., 2009). Moreover, the species is an active predator of gelatinous zooplankton and conforms to the seasonal migration paradigm suggested for sunfishes (see Pope review, 2009), while being subject to similar sea surface and coastal observation biases (Houghton et al., 2006; Hays et al., 2009). Leatherback turtle sightings data were downloaded from the Global Biodiversity Information Facility sightings database (GBIF, 2015). The use of target group data has been reported to provide a considerable improvement in model performance, providing more realistic data than taking pseudo-absences from sites that have not been sampled at all (e.g. Phillips, 2009; Mateo et al., 2010; Aguirre-Gutierrez et al., 2013). The rationale here is that leatherback sightings provided a proxy for recorder presence with the inference that ocean sunfish sightings would have been recorded concurrently if present. Correspondingly, these locations were used to generate ocean sunfish pseudo-absence data (n = 434) to train SDMs.

Statistical Analysis & SDMs

The distribution of *Mola* was mapped globally and a minimum convex hull containing all sightings created to satisfy the IUCN Red List range map requirements. Owing to the cryptic speciation within *Mola*, such range mapping was constrained to genus level.

A cluster analysis of sightings was performed using a Clark-Evans nearest neighbour test (Clark & Evans, 1954) using the R x64 3.2.2 (R Development Core Team, 2008) package 'spatstat' (Baddeley et al., 2015). The degree of grouping was determined using a correction cumulative distribution function and a Monte Carlo test to provide a probability value.

Climatic data were tested for collinearity using Pearson's correlation, before SDMs were produced using the R package 'Biomod2' (Thuiller et al., 2015). Seven SDM types were assessed including: surface range envelopes (SRE, quant = 0.025), classification tree analysis (CTA, CV.tree = 50), random forest (RF), multiple adaptive regression splines (MARS), flexible discriminant analysis (FDA), generalised linear models (GLM, type = simple) and generalised additive models (GAM, spline = 3). The models were designed with an 80:20 data split for training and testing and run with a 5 000 fold cross validation. All models used in Biomod2 were run using the default settings recommended by Thuiller et al. (2010). Using this model design, the seasonal distribution of *Mola* was predicted using matched sightings and environmental data from each quarter of the year.

Model evaluation statistics were calculated including the Kappa value (*k*), true skill statistic (TSS) and area under the curve (AUC) of the receiver operating characteristic (ROC). These evaluation metrics are frequently used to evaluate SDM performance, although AUC values have recently been criticised for overestimating performance by including large areas of absence data (Lobo et al. 2008; Leach et al. 2015). Popular alternatives also have limitations, such as TSS which is calculated from sensitivity and specificity, which themselves can contain misleading commission errors (Leach et al. 2015). The Kappa value provides a more objective measure of prediction accuracy, although this can also produce commission errors (Leach et al. 2015), but it provides accepted thresholds used in model evaluation. Here, we present each evaluation metric for all models however, the final evaluation of model accuracy used Kappa.

The optimal SDM was selected from those with a Kappa > 0.4 (see Table 2), as this threshold has been widely used in a range of published work (Landis et al., 1977; Altman, 1990; Allouche et al., 2006; Leach et al. 2015). The random forest model was the single best approximating model selected for further analysis and re-run with 100% of the sightings data to predict the seasonal probability of *Mola* presence globally.

To assess the seasonal range extent of *Mola*, the proportion of cells predicted with a probability of presence > 0.7 was calculated and tested with a 4-sample test for equality of proportions without continuity correction. As the distribution data were strongly skewed, non-parametric tests were used. Due to uneven sampling, data were divided into Northern and Southern Hemispheres and the predicted range extent of *Mola* examined by plotting box and whisker diagrams of the latitudinal range divided by season and compared statistically using a Kruskal-Wallis test. To assess if individual *Mola* move seasonally in accordance with the model predictions, the latitude of all sightings were plotted against the Julian day of the year on which they were recorded and fitted with a locally weighted scatterplot smoothing curve (LOESS).

Results

Mola observations were distributed globally (Fig. 1a and b) but with significant clustering ($z = 0.335$, $p < 0.05$), with aggregations in North American and European coastal waters predominately between 20-60°N, and peaking at 50°N (Fig. 2).

Nitrate and oxygen concentrations were significantly correlated ($r = 0.88$, $p < 0.001$), and since nitrate is used here as a proxy for productivity, it was removed to avoid leverage in statistical models. The random forest model had the highest model evaluation statistic values (mean values of 5 model runs: Kappa = 0.63, TSS: 0.72, ROC: 0.93) and were thus chosen as the optimal SDM technique.

Random forest LOESS curves suggested *Mola* presence was associated with shallow, temperate (7-23°C), relatively low productivity (chlorophyll < 125mg/m^3), oxygen rich (>

4ml/L) coastal waters (Fig. 3a-d). However, cells predicted to have a probability of presence > 0.7 were widespread in all seasons resulting in a pan-global distribution in surface waters (Fig. 4a and b); but with lowest occurrence in polar and equatorial waters. The extent of suitable habitat (defined as the percentage suitable ocean surface) varied significantly between seasons ($\chi^2_{df=3} = 591.2$, $p < 0.001$; Table 3). The latitudinal range of *Mola* also varied significantly in both Northern (tested individually) across all seasons ($\chi^2_{df=3} = 1690.5$, tabulated $\chi^2_{df=3} = 8.81e^{-11}$, $p < 0.001$) and Southern Hemispheres ($\chi^2_{df=3} = 3121.2$, tabulated $\chi^2_{df=3} = 8.81e^{-11}$, $p < 0.001$). Seasonal differences in latitudinal range reflected movement patterns, with the latitude of individual sightings varying temporally in both the Northern and Southern Hemispheres with animals shifting to more northerly latitudes in both hemispheres between April and October (Figs. 5a and b).

Discussion

This study used detailed records from public sightings databases, alongside fisheries surveys and museum archives which provided global coverage of a Data Deficient genus (IUCN, 2016). Although public sightings are widely used in broad-scale ecological studies, such data come with caveats, such as potential misidentification of cryptic species, incorrect data entry or regions of limited data availability. Despite such restrictions, such citizen science initiatives offer extensive coverage well beyond the budget and feasibility of most research projects. One of the best known examples, the North American Christmas Bird Count, has been running for over 100 years, with millions of person hours contributed to survey effort (Bibby, 2003; Audubon, 2008). With careful interpretation and strict data processing, substantial quantities of data can be collated over wide spatial and temporal scales, to the same quality as those collected by experts (Danielsen et al., 2014).

When applying SDM to sightings data, we must be aware of the limitations of the dataset in question, choose ecologically relevant variables (Mac Nally, 2000) and use appropriate methods (Elith & Leathwick, 2009). However, despite potential pitfalls and limitations, SDM have become important tools for predicting species distribution patterns and subsequent conservation management (Kremen et al., 2007; Wiens & Graham, 2005; Evans et al., 2015). In this study, SDM enabled us to delineate the range extent of ocean sunfishes, quantify distinct local clustering and describe seasonal changes in range extent accompanied with intra-annual movement patterns consistent with being a facultative seasonal migrant.

Distribution patterns

To date, there are two recognised species within *Mola: Mola mola* (L. 1758) and *Mola ramsayi* (Giglioli, 1883). Alongside these two species, recent papers have reported differences between the Atlantic and Pacific *M. mola* populations based on genetic and morphological studies (e.g. Bass et al., 2005; Yoshita et al., 2009; Gaither et al., 2016). Despite these discoveries, a formal classification of cryptic species is yet to be published, and the species taxonomy of *Mola* remains in flux (see review by Pope, 2009). In light of the current pressures faced by the ocean sunfishes, this study provides baseline information on *Mola* spatial ecology, which can be further refined to species-specific level as discrepancies over speciation resolve themselves over time.

Our study revealed that the genus *Mola* has a wide habitat range (see Fig. 1b) with confirmed sightings records extending 128° of latitude from approximately 70°N near Altenfjord, Norway to -58°S in the Beagle Canal, Chile (sightings contributed by Lukas Kubicek, *pers. comm.*). When compared to the latitudinal range extents of > 10 000 other marine species (Strona et al., 2012), this range would appear in the top 15 range extents (maximum reported range 150° latitude). However, within this range, our analysis suggests that *Mola* frequently aggregate and cluster in specific regions rather than being distributed randomly. Such clustering may be partly an artefact of sighting bias in coastal regions and known hotspots, particularly in North American and Europe. Nonetheless, the findings presented here align well with anecdotal evidence that *Mola* occur in patchily distributed, high density aggregations, particularly in coastal waters (e.g. Silvani et al., 1999; Sims & Southall, 2002; Houghton et al., 2006).

Several regions globally have already been identified as hosting annual aggregations of *Mola mola*, suggested to be shoals of juveniles (< 1 m); for example in Camogli, Italy (Syväranta et al., 2012) and California, USA (Cartamil & Lowe, 2004; Thys et al., 2015), whilst our analysis may help predict other areas with high density populations. We are aware that limited data availability such as sparse information from equatorial regions, may have a partial effect on our habitat suitability predictions, but this is likely reduced by our implementation of a bias file. To the best of our knowledge, we have defined the full range extent of *Mola* (Fig. 1b), however, as sightings were likely subject to significant observer bias. Indeed, the predicted presence from SDMs (Fig. 4b) may be of greater use to characterise the actual range extent *Mola* populations whilst predicted probability values are likely correlated with density.

Environmental drivers of *Mola* distribution

The Random Forest model provided the most reliable approximation of *Mola* distribution. Sea surface temperature and an indicator of regional productivity (chlorophyll *a* concentration) have been proposed as primary drivers of *Mola* movements (e.g. Thys et al., 2015; Sims et al., 2009). *Mola* habitat suitability increased gradually with chlorophyll *a* concentration until reaching a threshold of approximately 140 mg m^{-3} with habitat suitability declining rapidly at higher concentrations. Many studies comment on *Mola* range limitation in terms of minimum temperatures, and indeed we found sightings of *Mola* to be absent from waters below 7°C. However, our data suggested that *Mola* have a similarly-defined upper thermal threshold, of approximately 23°C, beyond which habitat suitability declined rapidly. In the Atlantic, *M. mola* were found to spend ~99% of their time in water temperatures between 10 - 19°C over a three month period (Sims et al., 2009), with a similar thermal preference of 16 - 17°C suggested from Pacific studies (Nakamura et al., 2015). The suggested thermal preference of approximately 16°C is further supported by our results, with habitat suitability peaking at this value. Interestingly, the warmest ambient water conditions recorded by external data loggers on free swimming *M. mola*, was 22°C (Nakamura et al., 2015) with internal body temperatures ranging from 12 - 21°C; considerably narrower than external ambient water temperatures experienced by the fish (3 - 22°C). More recently, a study on spatial occupancy of tagged *M. mola* in the North East Atlantic suggested movements were strongly related to water temperature on regional scales with an "escape" from regional maxima of approx. 25°C (Sousa et al., 2016b). By combining such evidence alongside the modelled thermal response curves, we suggest that the genus *Mola* may have an upper thermal tolerance limit of approximately 23°C, although occasional forays above this temperature may occur as demonstrated by the recording of an individual *M. ramsayi* at a maximum of 27.5°C (Thys et al., 2016). Further support for a thermal optimum of 16°C can be derived from a recent study comparing optimum temperatures for performance in the wild to maximum temperature experiences in fish species' ranges (Payne et al., 2016a). If a thermal optimum of 16°C is aligned with the expected response curve, then an upper thermal limit of 23°C would be expected from this genus (Payne et al., 2016b). The thermal limits identified in our study may, therefore, reflect a loss of performance beyond such limits, at a genus level, although further research will be required to confirm species specific responses.

From *post-hoc* analysis of the range extent of *Mola*, it appears that presence is also associated with dissolved oxygen levels between 5 and 7 ml/L. However, Thys et al. (2015) recently suggested that *M. mola* may be able to tolerate very low oxygen levels after observing individuals within ocean hypoxic zones at 60 m. Following periods exposed to such conditions, it is likely that individuals may need to recover in well-oxygenated waters (Cartamil & Lowe, 2004). To date, *Mola mola* and *Mola ramsayi* have been observed at maximum depths of 844 m (Potter & Howell, 2011) and 483 m respectively (Phillips et al., 2015), suggesting that mesopelagic ranging of sunfishes is perhaps more common than previously thought (Phillips et al., 2015). However, although the *Mola* are capable of deep water ranging, large schools of small *Mola* spp. are often noted in coastal areas, possibly a reflection of their mixed diet at this life stage (e.g. Syväranta et al., 2012; Harrod et al., 2013; Nakamura & Sato, 2014). The increased availability of benthic prey and discards in coastal waters may function as a driver of seasonal abundance in shallow water in the genus *Mola* (Harrod et al., 2013).

Seasonal movements

We identified large areas of suitable habitat available year-round for *Mola*, however, our results also suggested that the total suitable sea surface area and latitudinal position of varied significantly between seasons (see Fig. 5a). The predictive models (see Fig. 4) suggested that *Mola* thermal tolerance enables movement to higher latitudes in the Northern Hemisphere during the boreal spring to late summer, before retreating further south over the boreal autumn and winter months. Within the confines of this study, we were only able to model *Mola* presence in surface waters, however, these latitudinal movements may correspond to shifts in deep prey fields (Angel & Pugh, 2000; Houghton et al., 2008). Our predicted seasonal movement of *Mola* supports evidence from tagging studies in the northwest and northeast Atlantic (e.g. Sims et al., 2009; Potter & Howell, 2011; Sousa et al., 2016b), and northeast and northwest Pacific (e.g. Dewar et al., 2010; Thys et al., 2015), which identified seasonal movements of individuals driven by temperature and patchily distributed prey. However, despite a range of tagging studies providing data across the Northern Hemisphere, there are relatively few data available from the Southern Hemisphere on *Mola* movements. From the SDMs, we suggest that a similar pattern occurs in the Southern Hemisphere, where *Mola* are able to move to maximum southern latitudes during the austral spring to late summer and then retreat towards the equatorial regions during the austral winter (Fig. 5a and b). These broad scale movements reflect the migration patterns of many species, in accordance with the seasonal migratory paradigm, where warmer temperatures during summer months enable range extensions poleward, and which then contract as the seasons change; example species include bluefin tuna (Lutcavage et al., 1999), swordfish (Sedberry et al., 2001) and loggerhead turtles (Mansfield et al., 2009).

Our data suggest that although the average latitudinal position of *Mola* in surface waters varied over the seasons, much of the world's oceans remain suitable for *Mola* year-round, with a wide latitudinal range. It is apparent, therefore, that *Mola* cannot be classified as obligate migrants, owing to discrepancies in distribution between populations. Although the species within this study were all considered to be *Mola mola,* the more common of the two *Mola* species, inferred differences in movement strategy between populations may be due to misidentification and behavioural differences between *M. mola* and the lesser studied *M. ramsayi* (Pope et al., 2010). *Mola ramsayi* is morphologically very similar to *M. mola* (Bass et al., 2005), identified by 16 fin rays with 12 closely spaced ossicles, compared to the 12 fin rays and 8 broadly spaced ossicles and reduced band of denticles prior to the clavus of *M. mola* (Fraser-Brunner, 1951; Thys et al., 2013). *Mola ramsayi* was initially suggested to be the Southern Hemisphere species (Fraser-Brunner, 1951), however, individuals have since been identified in the Northern Hemisphere, including the Sea of Oman (Al Ghais, 1994), the Indian waters of Chennai (Mohan et al., 2006) and even co-occurring with *M. mola* (Bass et al., 2005). Further molecular genetic analyses are required to confirm species identification and to assess the movement ecology of these species (Pope et al., 2010).

Alongside the predicted distribution patterns modelled here, the average position of *Mola* raw sightings was consistent with the concept of seasonal migration. However, outliers to this pattern do exist, supported by evidence of prolonged residency (e.g. Hays et al., 2009; Harrod et al., 2013). Since this study only assessed *Mola* surface distribution, it does not provide information on depth distribution, however several studies suggest that *Mola* spends a significant proportion of time (up to 30%) in surface waters less than 10 m deep (Potter & Howell, 2010). Although sightings data alone will be insufficient to fully determine the seasonal distribution patterns of marine species (Southall et al., 2005), the frequent sightings of *Mola* in surface waters is related to their universal basking behaviour at the sea surface (Norman & Fraser, 1938). We suggest that the surface prediction of *Mola* distribution will provide a useful measure of their global distribution.

Although the results of this study do not provide direct evidence of a reciprocal migration, they do support the suggestion that some populations move latitudinally as suitable conditions shift over the course of the year. Such long distance movements may be restricted to populations near the latitudinal limits of their distribution; however, further study is required to test this assertion. Taken together, these results suggest that the genus *Mola* contains populations subject to differing drivers of distribution and, therefore, we propose they may be classed as facultative seasonal migrants.

Conclusions

This study provides a first assessment of the spatio-temporal global biogeography of the genus *Mola*. Taken together, our results suggest that the genus is globally distributed with significant clustering in specific locations, influenced by sea surface temperatures ranging from ~7 to 23°C. Based on SDMs, we suggest that populations act as facultative seasonal migrants with differing regional drivers of distribution. Although this study was able to consider the potential influence of productivity (using the proxy variable of chlorophyll concentration), future work may be able to assess smaller regions which have better data availability. Further studies on the ontogenetic shifts in the diet of ocean sunfishes are also required to integrate SDMs with international databases of putative prey items to explore the life history significance of shallow water and offshore habitats in more detail.

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Supporting information

Appendix S1 Data sources table of global sunfish sightings

Biosketch

Natasha Phillips is a PhD researcher at the University of Belfast interested in the movement ecology, diet and energetics of ocean sunfishes (family Molidae).

Editor and Handling Editor

Michelle Gaither and Şerban Procheş

Author contributions:

NDP, JDRH, TT, NR and CH conceived the ideas. TT and CM collected data. NDP and JH led the writing. HJW, SP, NR, NP advised on analysis. NDP analysed the data.

Tables

Table 1. IUCN Red List designation for ocean sunfishes on both global and European scales.

		IUCN Red Listing	
Species	**Common name**	**Global Scale**	**European Scale**
Mola mola (L. 1758)	Ocean sunfish	Vulnerable	Data Deficient
Mola ramsayi (Giglioli 1883)	Southern ocean sunfish	Not Assessed	Not Assessed
Masturus lanceolatus (Liénard 1840)	Sharptail sunfish	Least Concern	Not Assessed
Ranzania laevis (Pennant 1776)	Slender sunfish	Least Concern	Data Deficient

Table 2. Evaluation metrics Kappa, true skill statistic (TSS) and receiver operating characteristic (ROC) values for all species distribution models (mean value of five model runs ± standard deviation). All models were performed in R, using package "Biomod2".

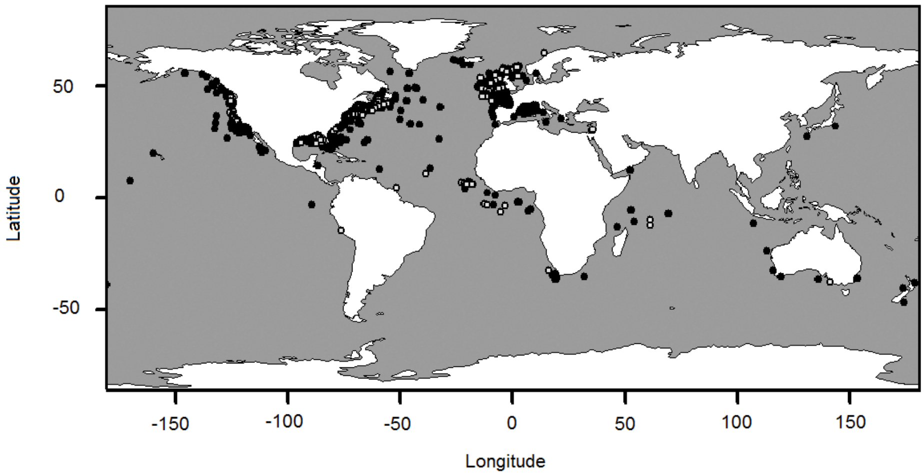
SDM type	Kappa Value	TSS Value	ROC Value
Surface Range Envelope	0.14 ± 0.01	0.19 ± 0.02	0.60 ± 0.01
Classification Tree Analysis	0.42 ± 0.03	0.62 ± 0.08	0.83 ± 0.05
Random Forest	0.63 ± 0.04	0.72 ± 0.04	0.93 ± 0.02
Multiple Adaptive Regression Splines	0.36 ± 0.04	0.48 ± 0.07	0.81 ± 0.04
Flexible Discriminant Analysis	0.31 ± 0.03	0.41 ± 0.04	0.76 ± 0.05
Generalised Linear Model	0.25 ± 0.01	0.35 ± 0.05	0.71 ± 0.03
Generalised Additive Model	0.35 ± 0.05	0.45 ± 0.07	0.79 ± 0.04

Table 3. Analysis of random forest species distribution models to consider the extent of suitable habitat for *Mola* using the seasonal predicted probability of genus presence in each grid cell.

	Season			
	Jan-Mar	**Apr-Jun**	**Jul-Sep**	**Oct-Dec**
Mean predicted probability of *Mola* presence across all cells (± standard deviation)	0.49 ± 0.50	0.50 ± 0.50	0.44 ± 0.50	0.51 ± 0.50
Total number of cells modelled	41,009	41,369	41,579	41,369
No. cells predicted as suitable (p>0.7)	19,914	21,094	18,257	21,270
% of ocean surface predicted as suitable	48.56	50.99	43.91	51.42

Figures

Figure 1a. Global distribution of presence sightings of *Mola* (black) and pseudo-absences provided by sightings of leatherback turtles (grey) used in the species distribution model. **b.** Minimum convex hull range extent of *Mola* sightings data from 2000-2015. The origin of the base map is a spheroid WGS 1984 projection.



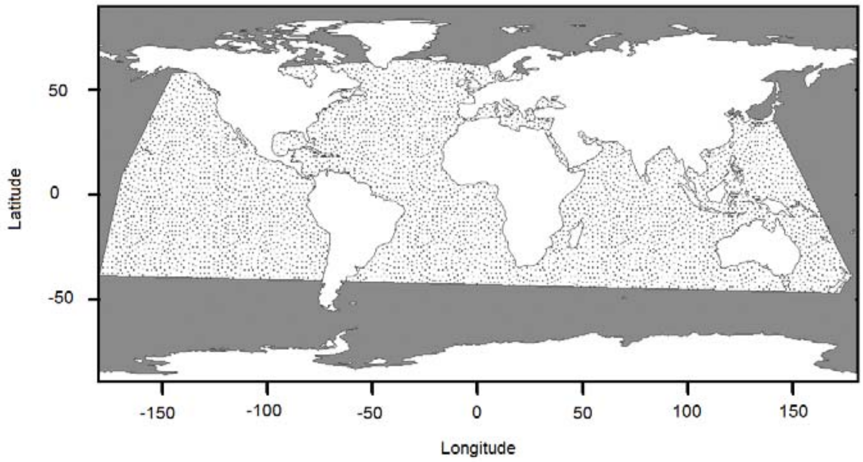


Figure 2. Frequency distribution of *Mola* sightings by latitude. The data showed a significant bias toward the Northern Hemisphere, particularly between 40-50º N. The origin of the base map is a spheroid WGS 1984 projection.

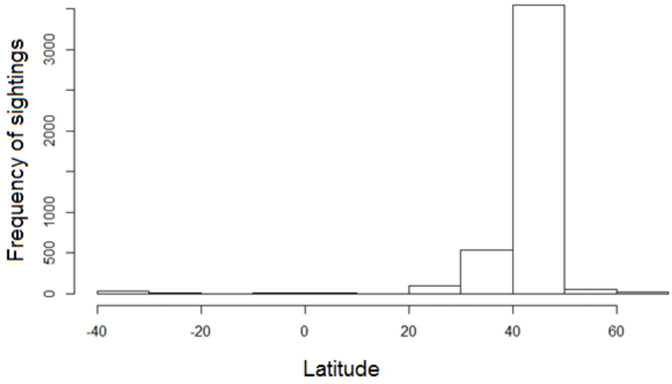
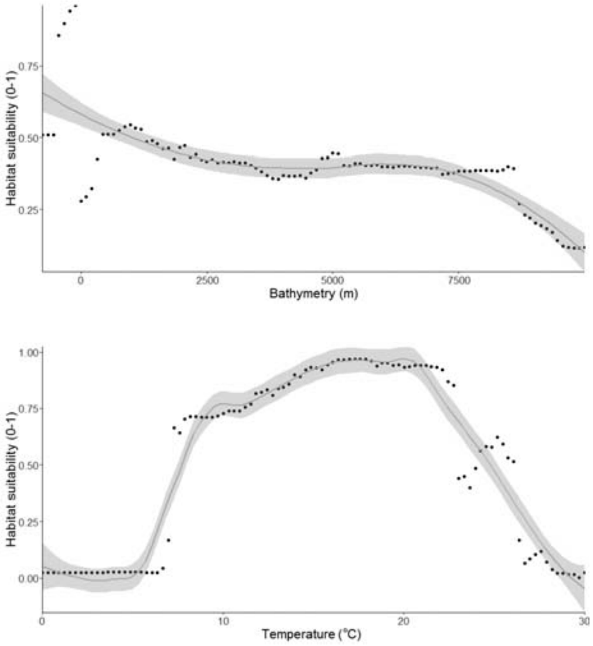


Figure 3. Species response curves for each climatic variable included in the final species distribution models (SDM) for *Mola* showing range suitability at the sea surface (0-1) against: a) bathymetry, b) sea surface temperature, c) chlorophyll concentration, and d) dissolved oxygen concentration.



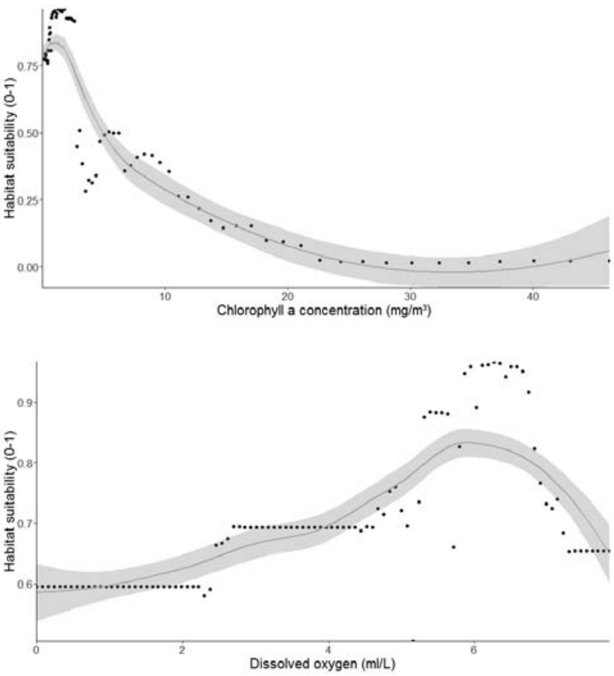


Figure 4a. Seasonal range suitability at the sea surface for *Mola* from species distribution model (SDM) outputs for i) January to March, ii) April to June, iii) July to September and iv) October to December. Probability of presence shaded from 0 < 0.1 (white) to 0.9 < 1 (black) at 0.1 intervals. **b.** predicted presence of *Mola* (probability >0.7). Predicted presence (black) and predicted absence (grey). The origin of the base maps is a spheroid WGS 1984 projection.

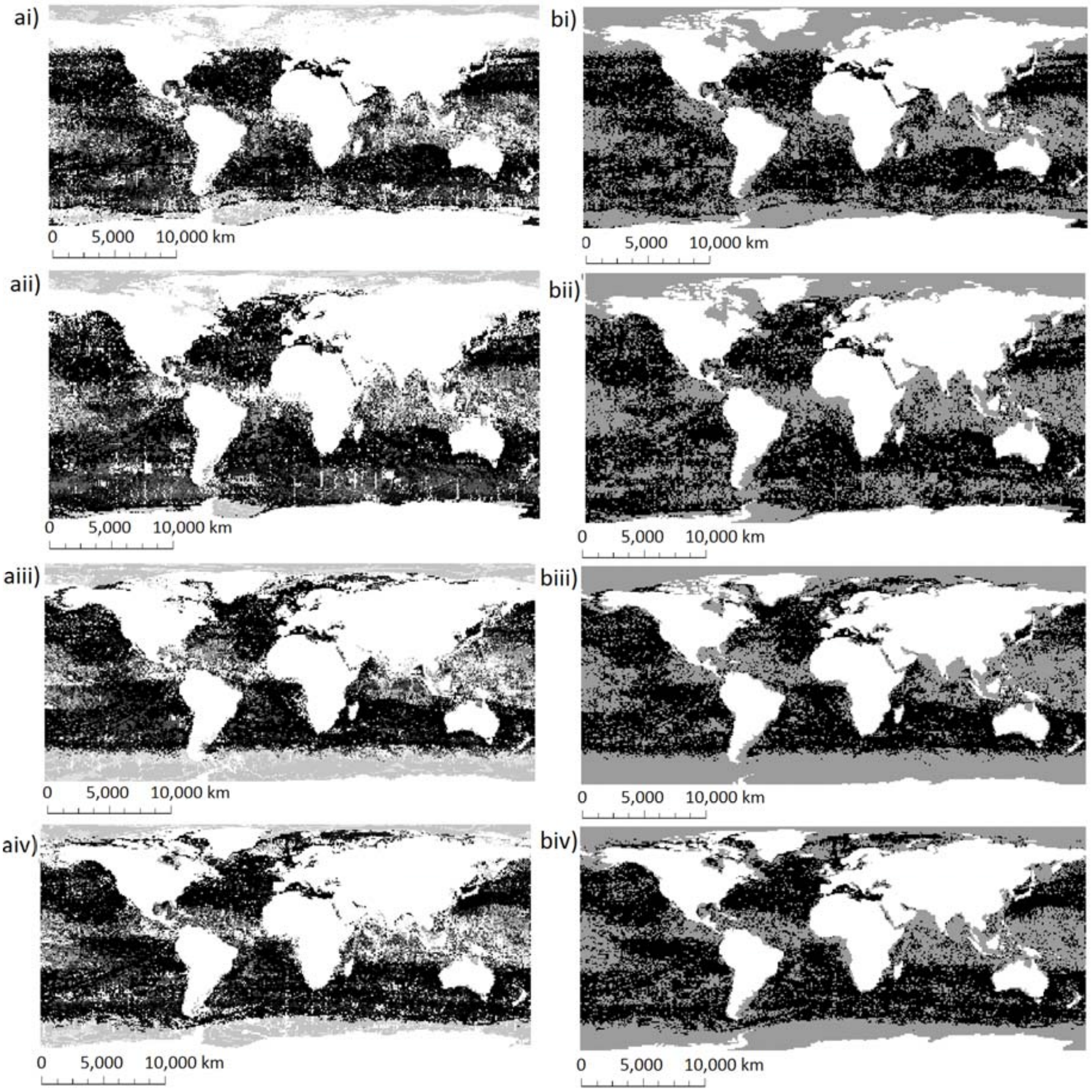
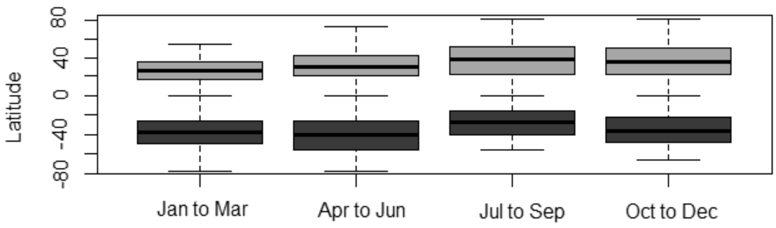
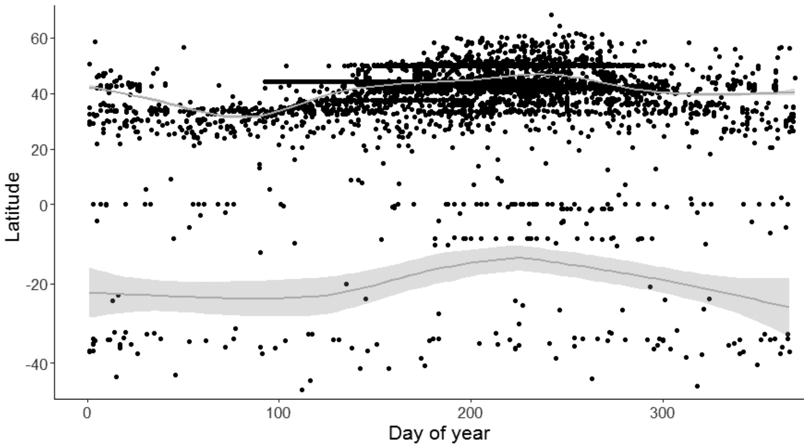


Figure 5a. Seasonal predicted latitudinal range of *Mola* in both hemispheres (outliers removed). **b.** Intra-annual variation in latitude of sightings data plotted by day of year with locally weighted scatterplot smoothing curve (LOESS) curve and 95% confidence interval for both hemispheres.




60
40
20
0
-20
-40
Latitude
0
100
200
300
Day of year