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Phillips, N. D., Reid, N., Thys, T., Harrod, C., Payne, N. L., Morgan, C. A., White, H. J., Porter, S., & Houghton, J. D. R. (2017). Applying species distribution modelling to a data poor, pelagic fish complex: the ocean sunfishes. *Journal of Biogeography*. <https://doi.org/10.1111/jbi.13033>

Published in:
Journal of Biogeography

Document Version:
Peer reviewed version

Queen's University Belfast - Research Portal:
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Original Article

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

Keywords: Biogeography, Environmental Niche Models, Marine, Migration, *Mola*, sunfishes, Spatial Ecology

24 **Abstract**

25

26 **Aim**

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

36

37 **Location**

38 Global.

39

40 **Methods**

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

45

46 **Results**

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

52

53 **Main conclusions**

54 We provided the first assessment of *Mola* distribution on a global scale, with evidence of a
55 wide latitudinal range and significant clustering in localised 'hotspots' (notably between 40-
56 50°N). By assessing the results of SDMs alongside evidence from published satellite tagging
57 studies, we suggest that the species within the genus *Mola* are highly mobile, acting as

58 facultative seasonal migrants. By identifying key suitable habitat alongside potential
59 movement paths, this study provides a baseline that can be used in active conservation
60 management of the genus.

61 **Introduction**

62 Conservation management efforts are dependent on a detailed understanding of the spatial
63 distribution, biogeography and ecology of target species (Ferrier et al., 2002; Ricklefs, 2004;
64 Rushton et al., 2004). For widespread or cryptic species this can pose significant challenges
65 (Pearson et al., 2007; Rissler & Apodaca, 2007). Species distribution models (SDMs, also
66 known as ecological niche models, species-habitat models or predictive habitat models)
67 assess the complex relationship between species occurrence records and environmental
68 variation, even from limited datasets, and offers insight into habitat suitability both spatially
69 and temporally (Elith & Leathwick, 2009; Franklin, 2009). For little known oceanic species,
70 such methods can provide a key starting point in understanding complex, wide-ranging
71 distribution patterns and the mechanisms driving environmental tolerances (Elith et al.,
72 2006).

73 One such family of oceanic taxa, the ocean sunfishes (or Molidae), are often described as
74 rare, inactive drifters (Pope et al., 2010), however recent studies have revealed high density
75 aggregations in coastal waters (e.g. Silvani et al., 1999; Pope et al., 2010; Syväranta et al.,
76 2012), sustained long distance swimming of ~48 km per day (e.g. Cartamil & Lowe, 2004;
77 Nakamura et al., 2015; Thys et al., 2015) and repeated deep-diving to mesopelagic depths
78 foraging for gelatinous prey (e.g. Cartamil & Lowe, 2004; Nakamura et al., 2015). Such
79 observations suggest that this is an active, highly motile taxon (Cartamil & Lowe, 2004), with
80 a broad trophic niche (e.g. Harrod et al., 2013; Nakamura & Sato, 2014; Sousa et al., 2016a)
81 and capable of travelling significant distances in a directed manner (see review, Pope et al.,
82 2010). This suggests that *Mola* may have more complex ecology than previously thought
83 (Syväranta et al., 2012), which poses broader implications for sustainable management. Such
84 insight is important in light of current bycatch levels (Silvani et al., 1999; Cartamil & Lowe,
85 2004; Pope et al., 2010), such as the reported capture of > 36 000 individuals per annum in

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

93 Anecdotal evidence collated in a review by Pope et al. (2010) suggested that the Molidae
94 (see Table 1. Appendices) have a pan-global distribution within temperate and tropical
95 latitudes, although limited sighting records and inherent difficulties in species identification
96 have led to problems in delineating species-specific ranges and seasonal movement patterns.
97 Recent high-profile reports of ocean sunfishes at high latitudes, such as in Alaska (Dobbyn,
98 2015), have led many media outlets to speculate as to why these species are “suddenly”
99 appearing so far north. However, without baseline data on the range extent of ocean
100 sunfishes, it is difficult to know whether they have undergone recent expansion and, if so,
101 what might be driving such changes. Although taken to be widespread (Cartamil & Lowe,
102 2004), it is not yet known if ocean sunfishes adhere consistently to a migratory paradigm
103 (whether obligate or facultative). Evidence from multiple studies, using satellite tags and
104 accelerometer derived dead-reckoning (e.g. Sims et al., 2009; Dewar et al., 2010; Nakamura
105 et al., 2015; Thys et al., 2015), suggests that *Mola* in temperate and subtropical regions may
106 move to equatorial latitudes during autumn, for example, into UK and Japanese waters.
107 However, other studies using satellite tracking (Hays et al., 2009) and dietary analysis
108 (Harrod et al., 2013) suggest year-round, or at least long-term, residence in some regions,
109 including in Mediterranean and South African waters. The results from these studies support

110 suggestions of distinct, local populations with differing drivers of distribution; however, there
111 is a paucity of evidence across wide spatio-temporal scales.

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

121

122 **Materials and Methods**

123 **Data sources and manipulation**

124 Global sightings of *Mola* were collected from public databases, published papers and
125 fisheries logs (see Appendix S1). A total of 14 953 sightings, recorded between the years
126 1758 and 2015, were compiled before specific criteria were set for standardising the dataset.
127 This study aimed to assess the distribution of the genus *Mola* which currently contains two
128 species. *Mola* is easily distinguishable from other genera in the Molidae (*Ranzania* and
129 *Masturus*, see Table 1. Appendices), due to its differing morphology, and therefore potential
130 for confusion is limited. We accept that misidentification is possible, but by maintaining a
131 conservative approach to data acquisition (i.e. by removing records not identified to genus),
132 we have tried to mitigate this risk. Any incomplete records (missing location or date of
133 observation) were removed. All sighting locations were converted to decimal degrees, and
134 mapped using ARCGIS 10.3.1 (ESRI, California, USA) and all locations that erroneously fell

135 on land were removed. Although the sightings dataset extended over 257 years, 79% of
136 sightings occurred between 2000 and 2015. Therefore only this subset of 5 419 sightings was
137 retained for further analysis. These sightings were divided into each quarter of the year (Jan-
138 Mar, Apr-May, Jun-Aug and Sep-Dec) and matched with recent climate data available
139 through online data sharing platforms.

140

141 **Environmental parameters**

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

156

157 **Data validation**

158 Since all *Mola* data collected were ‘presence only’ sightings, we implemented a bias file as a
159 proxy of survey effort to indicate the likelihood of being encountered and recorded, as

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

178

179 **Statistical Analysis & SDMs**

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

183 A cluster analysis of sightings was performed using a Clark-Evans nearest neighbour test
184 (Clark & Evans, 1954) using the R x64 3.2.2 (R Development Core Team, 2008) package

185 'spatstat' (Baddeley et al., 2015). The degree of grouping was determined using a correction
186 cumulative distribution function and a Monte Carlo test to provide a probability value.

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

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

208 The optimal SDM was selected from those with a Kappa > 0.4 (see Table 2), as this
209 threshold has been widely used in a range of published work (Landis et al., 1977; Altman,

210 1990; Allouche et al., 2006; Leach et al. 2015). The random forest model was the single best
211 approximating model selected for further analysis and re-run with 100% of the sightings data
212 to predict the seasonal probability of *Mola* presence globally.

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

223

224 **Results**

225 *Mola* observations were distributed globally (Fig. 1a and b) but with significant clustering (z
226 $= 0.335$, $p < 0.05$), with aggregations in North American and European coastal waters
227 predominately between 20-60°N, and peaking at 50°N (Fig. 2).

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

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

235 4ml/L) coastal waters (Fig. 3a-d). However, cells predicted to have a probability of presence
236 > 0.7 were widespread in all seasons resulting in a pan-global distribution in surface waters
237 (Fig. 4a and b); but with lowest occurrence in polar and equatorial waters. The extent of
238 suitable habitat (defined as the percentage suitable ocean surface) varied significantly
239 between seasons ($\chi^2_{df=3} = 591.2$, $p < 0.001$; Table 3). The latitudinal range of *Mola* also
240 varied significantly in both Northern (tested individually) across all seasons ($\chi^2_{df=3} = 1690.5$,
241 tabulated $\chi^2_{df=3} = 8.81e^{-11}$, $p < 0.001$) and Southern Hemispheres ($\chi^2_{df=3} = 3121.2$, tabulated
242 $\chi^2_{df=3} = 8.81e^{-11}$, $p < 0.001$). Seasonal differences in latitudinal range reflected movement
243 patterns, with the latitude of individual sightings varying temporally in both the Northern and
244 Southern Hemispheres with animals shifting to more northerly latitudes in both hemispheres
245 between April and October (Figs. 5a and b).

246

247 **Discussion**

248 This study used detailed records from public sightings databases, alongside fisheries surveys
249 and museum archives which provided global coverage of a Data Deficient genus (IUCN,
250 2016). Although public sightings are widely used in broad-scale ecological studies, such data
251 come with caveats, such as potential misidentification of cryptic species, incorrect data entry
252 or regions of limited data availability. Despite such restrictions, such citizen science
253 initiatives offer extensive coverage well beyond the budget and feasibility of most research
254 projects. One of the best known examples, the North American Christmas Bird Count, has
255 been running for over 100 years, with millions of person hours contributed to survey effort
256 (Bibby, 2003; Audubon, 2008). With careful interpretation and strict data processing,
257 substantial quantities of data can be collated over wide spatial and temporal scales, to the
258 same quality as those collected by experts (Danielsen et al., 2014).

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

267

268 **Distribution patterns**

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

278 Our study revealed that the genus *Mola* has a wide habitat range (see Fig. 1b) with confirmed
279 sightings records extending 128° of latitude from approximately 70°N near Altenfjord,
280 Norway to -58°S in the Beagle Canal, Chile (sightings contributed by Lukas Kubicek, *pers.*
281 *comm.*). When compared to the latitudinal range extents of > 10 000 other marine species
282 (Strona et al., 2012), this range would appear in the top 15 range extents (maximum reported
283 range 150° latitude). However, within this range, our analysis suggests that *Mola* frequently

284 aggregate and cluster in specific regions rather than being distributed randomly. Such
285 clustering may be partly an artefact of sighting bias in coastal regions and known hotspots,
286 particularly in North American and Europe. Nonetheless, the findings presented here align
287 well with anecdotal evidence that *Mola* occur in patchily distributed, high density
288 aggregations, particularly in coastal waters (e.g. Silvani et al., 1999; Sims & Southall, 2002;
289 Houghton et al., 2006).

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

301

302 **Environmental drivers of *Mola* distribution**

303 The Random Forest model provided the most reliable approximation of *Mola* distribution.
304 Sea surface temperature and an indicator of regional productivity (chlorophyll *a*
305 concentration) have been proposed as primary drivers of *Mola* movements (e.g. Thys et al.,
306 2015; Sims et al., 2009). *Mola* habitat suitability increased gradually with chlorophyll *a*
307 concentration until reaching a threshold of approximately 140 mg m⁻³ with habitat suitability
308 declining rapidly at higher concentrations. Many studies comment on *Mola* range limitation

309 in terms of minimum temperatures, and indeed we found sightings of *Mola* to be absent from
310 waters below 7°C. However, our data suggested that *Mola* have a similarly-defined upper
311 thermal threshold, of approximately 23°C, beyond which habitat suitability declined rapidly.
312 In the Atlantic, *M. mola* were found to spend ~99% of their time in water temperatures
313 between 10 - 19°C over a three month period (Sims et al., 2009), with a similar thermal
314 preference of 16 - 17°C suggested from Pacific studies (Nakamura et al., 2015). The
315 suggested thermal preference of approximately 16°C is further supported by our results, with
316 habitat suitability peaking at this value. Interestingly, the warmest ambient water conditions
317 recorded by external data loggers on free swimming *M. mola*, was 22°C (Nakamura et al.,
318 2015) with internal body temperatures ranging from 12 - 21°C; considerably narrower than
319 external ambient water temperatures experienced by the fish (3 - 22°C). More recently, a
320 study on spatial occupancy of tagged *M. mola* in the North East Atlantic suggested
321 movements were strongly related to water temperature on regional scales with an “escape”
322 from regional maxima of approx. 25°C (Sousa et al., 2016b). By combining such evidence
323 alongside the modelled thermal response curves, we suggest that the genus *Mola* may have an
324 upper thermal tolerance limit of approximately 23°C, although occasional forays above this
325 temperature may occur as demonstrated by the recording of an individual *M. ramsayi* at a
326 maximum of 27.5°C (Thys et al., 2016). Further support for a thermal optimum of 16°C can
327 be derived from a recent study comparing optimum temperatures for performance in the wild
328 to maximum temperature experiences in fish species’ ranges (Payne et al., 2016a). If a
329 thermal optimum of 16°C is aligned with the expected response curve, then an upper thermal
330 limit of 23°C would be expected from this genus (Payne et al., 2016b). The thermal limits
331 identified in our study may, therefore, reflect a loss of performance beyond such limits, at a
332 genus level, although further research will be required to confirm species specific responses.

333 From *post-hoc* analysis of the range extent of *Mola*, it appears that presence is also
334 associated with dissolved oxygen levels between 5 and 7 ml/L. However, Thys et al. (2015)
335 recently suggested that *M. mola* may be able to tolerate very low oxygen levels after
336 observing individuals within ocean hypoxic zones at 60 m. Following periods exposed to
337 such conditions, it is likely that individuals may need to recover in well-oxygenated waters
338 (Cartamil & Lowe, 2004). To date, *Mola mola* and *Mola ramsayi* have been observed at
339 maximum depths of 844 m (Potter & Howell, 2011) and 483 m respectively (Phillips et al.,
340 2015), suggesting that mesopelagic ranging of sunfishes is perhaps more common than
341 previously thought (Phillips et al., 2015). However, although the *Mola* are capable of deep
342 water ranging, large schools of small *Mola* spp. are often noted in coastal areas, possibly a
343 reflection of their mixed diet at this life stage (e.g. Syväranta et al., 2012; Harrod et al., 2013;
344 Nakamura & Sato, 2014). The increased availability of benthic prey and discards in coastal
345 waters may function as a driver of seasonal abundance in shallow water in the genus *Mola*
346 (Harrod et al., 2013).

347

348 **Seasonal movements**

349 We identified large areas of suitable habitat available year-round for *Mola*, however, our
350 results also suggested that the total suitable sea surface area and latitudinal position of varied
351 significantly between seasons (see Fig. 5a). The predictive models (see Fig. 4) suggested that
352 *Mola* thermal tolerance enables movement to higher latitudes in the Northern Hemisphere
353 during the boreal spring to late summer, before retreating further south over the boreal
354 autumn and winter months. Within the confines of this study, we were only able to model
355 *Mola* presence in surface waters, however, these latitudinal movements may correspond to
356 shifts in deep prey fields (Angel & Pugh, 2000; Houghton et al., 2008). Our predicted
357 seasonal movement of *Mola* supports evidence from tagging studies in the northwest and

358 northeast Atlantic (e.g. Sims et al., 2009; Potter & Howell, 2011; Sousa et al., 2016b), and
359 northeast and northwest Pacific (e.g. Dewar et al., 2010; Thys et al., 2015), which identified
360 seasonal movements of individuals driven by temperature and patchily distributed prey.
361 However, despite a range of tagging studies providing data across the Northern Hemisphere,
362 there are relatively few data available from the Southern Hemisphere on *Mola* movements.
363 From the SDMs, we suggest that a similar pattern occurs in the Southern Hemisphere, where
364 *Mola* are able to move to maximum southern latitudes during the austral spring to late
365 summer and then retreat towards the equatorial regions during the austral winter (Fig. 5a and
366 b). These broad scale movements reflect the migration patterns of many species, in
367 accordance with the seasonal migratory paradigm, where warmer temperatures during
368 summer months enable range extensions poleward, and which then contract as the seasons
369 change; example species include bluefin tuna (Lutcavage et al., 1999), swordfish (Sedberry et
370 al., 2001) and loggerhead turtles (Mansfield et al., 2009).

371 Our data suggest that although the average latitudinal position of *Mola* in surface waters
372 varied over the seasons, much of the world's oceans remain suitable for *Mola* year-round,
373 with a wide latitudinal range. It is apparent, therefore, that *Mola* cannot be classified as
374 obligate migrants, owing to discrepancies in distribution between populations. Although the
375 species within this study were all considered to be *Mola mola*, the more common of the two
376 *Mola* species, inferred differences in movement strategy between populations may be due to
377 misidentification and behavioural differences between *M. mola* and the lesser studied *M.*
378 *ramsayi* (Pope et al., 2010). *Mola ramsayi* is morphologically very similar to *M. mola* (Bass
379 et al., 2005), identified by 16 fin rays with 12 closely spaced ossicles, compared to the 12 fin
380 rays and 8 broadly spaced ossicles and reduced band of denticles prior to the clavus of *M.*
381 *mola* (Fraser-Brunner, 1951; Thys et al., 2013). *Mola ramsayi* was initially suggested to be
382 the Southern Hemisphere species (Fraser-Brunner, 1951), however, individuals have since

383 been identified in the Northern Hemisphere, including the Sea of Oman (Al Ghais, 1994), the
384 Indian waters of Chennai (Mohan et al., 2006) and even co-occurring with *M. mola* (Bass et
385 al., 2005). Further molecular genetic analyses are required to confirm species identification
386 and to assess the movement ecology of these species (Pope et al., 2010).

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

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

405

406 **Conclusions**

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

417

418 **Acknowledgements**

419 The authors would like to acknowledge the generous contribution of all those who collected
420 and provided data for this study (for full list please see Appendix S1), particularly the
421 thousands of citizen scientists globally, without whom this work would not be possible. Many
422 thanks also to Lawrence Eagling for proof-reading the manuscript on several occasions.
423 N.D.P was funded by The Fisheries Society of the British Isles.

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541 California Current System. *Journal of Experimental Marine Biology and Ecology*, **471**,
542 64–76.

543 **Supporting information**

544 Appendix S1 Data sources table of global sunfish sightings

545

546 **Biosketch**

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

549

550 **Editor and Handling Editor**

551 Michelle Gaither and Şerban Procheş

552

553 **Author contributions:**

554 NDP, JDRH, TT, NR and CH conceived the ideas. TT and CM collected data. NDP and JH

555 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.

Species	Common name	IUCN Red Listing	
		Global Scale	European Scale
<i>Mola mola</i> (L. 1758)	Ocean sunfish	Vulnerable	Data Deficient
<i>Mola ramsayi</i> (Giglioli 1883)	Southern ocean sunfish	Not Assessed	Not Assessed
<i>Masturus lanceolatus</i> (Liénard 1840)	Sharptail sunfish	Least Concern	Not Assessed
<i>Ranzania laevis</i> (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 \pm standard deviation). All models were performed in R, using package “Biomod2”.

SDM type	Kappa Value	TSS Value	ROC Value
Surface Range Envelope	0.14 \pm 0.01	0.19 \pm 0.02	0.60 \pm 0.01
Classification Tree Analysis	0.42 \pm 0.03	0.62 \pm 0.08	0.83 \pm 0.05
Random Forest	0.63 \pm 0.04	0.72 \pm 0.04	0.93 \pm 0.02
Multiple Adaptive Regression Splines	0.36 \pm 0.04	0.48 \pm 0.07	0.81 \pm 0.04
Flexible Discriminant Analysis	0.31 \pm 0.03	0.41 \pm 0.04	0.76 \pm 0.05
Generalised Linear Model	0.25 \pm 0.01	0.35 \pm 0.05	0.71 \pm 0.03
Generalised Additive Model	0.35 \pm 0.05	0.45 \pm 0.07	0.79 \pm 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 <i>Mola</i> presence across all cells (\pm standard deviation)	0.49 \pm 0.50	0.50 \pm 0.50	0.44 \pm 0.50	0.51 \pm 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.

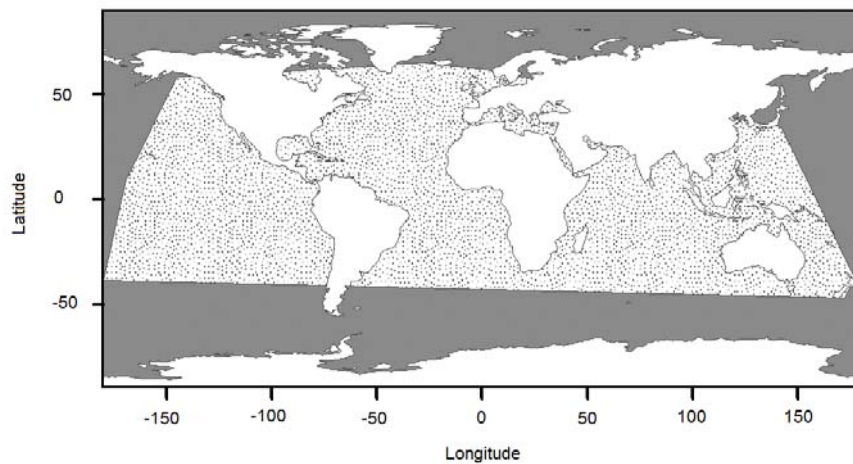
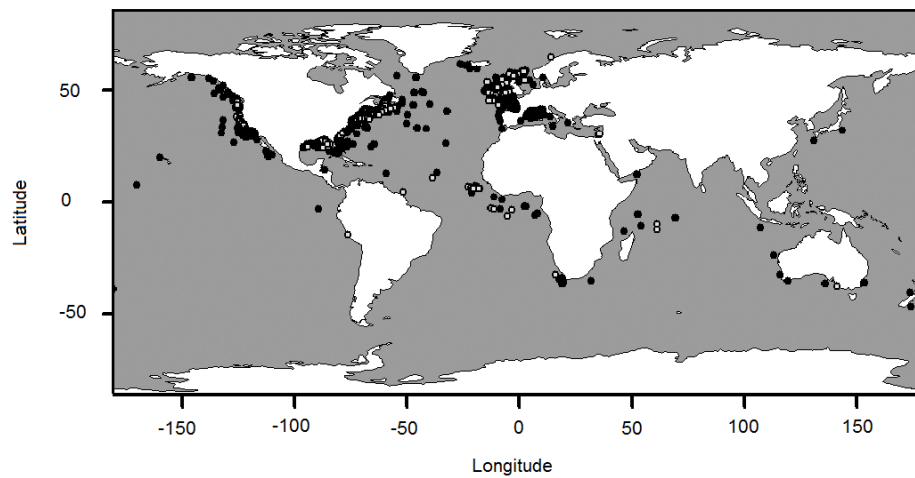


Figure 2. Frequency distribution of *Mola* sightings by latitude. The data showed a significant bias toward the Northern Hemisphere, particularly between 40-50° N. The origin of the base map is a spheroid WGS 1984 projection.

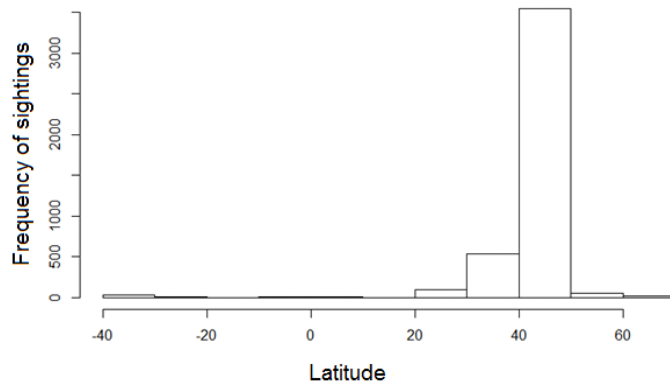
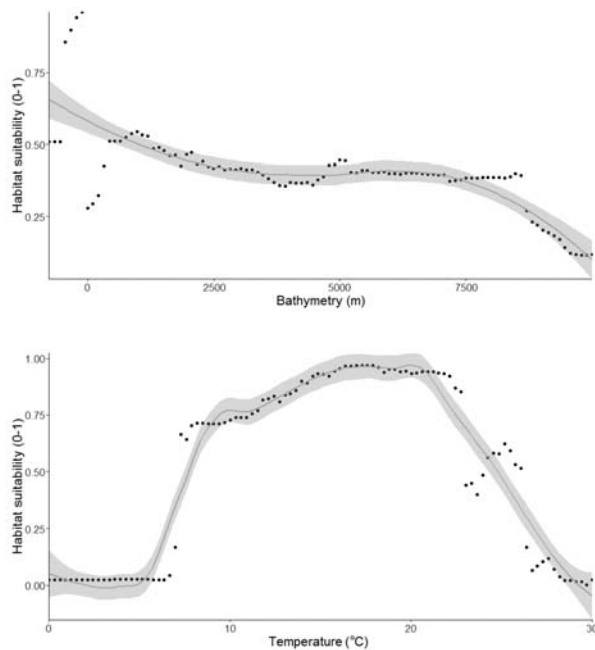


Figure 3. Species response curves for each climatic variable included in the final species distribution models (SDM) for *Mola* showing range suitability at the sea surface (0-1) against: a) bathymetry, b) sea surface temperature, c) chlorophyll concentration, and d) dissolved oxygen concentration.



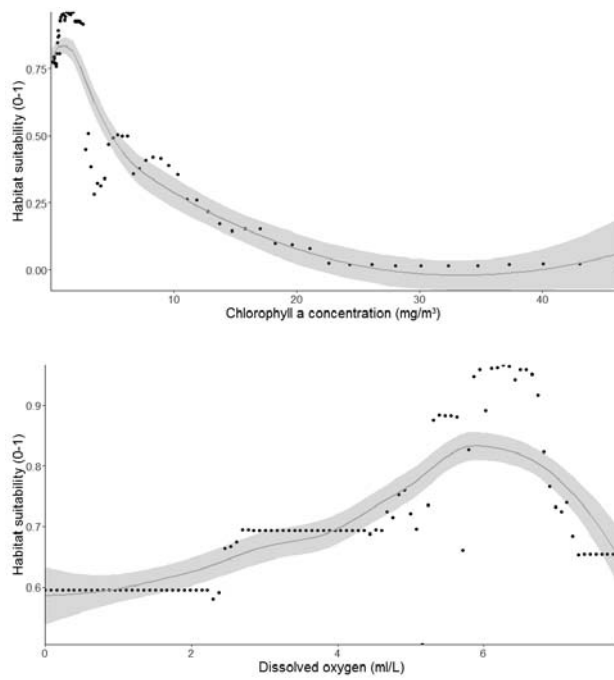


Figure 4a. Seasonal range suitability at the sea surface for *Mola* from species distribution model (SDM) outputs for i) January to March, ii) April to June, iii) July to September and iv) October to December. Probability of presence shaded from $0 < 0.1$ (white) to $0.9 < 1$ (black) at 0.1 intervals. **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.

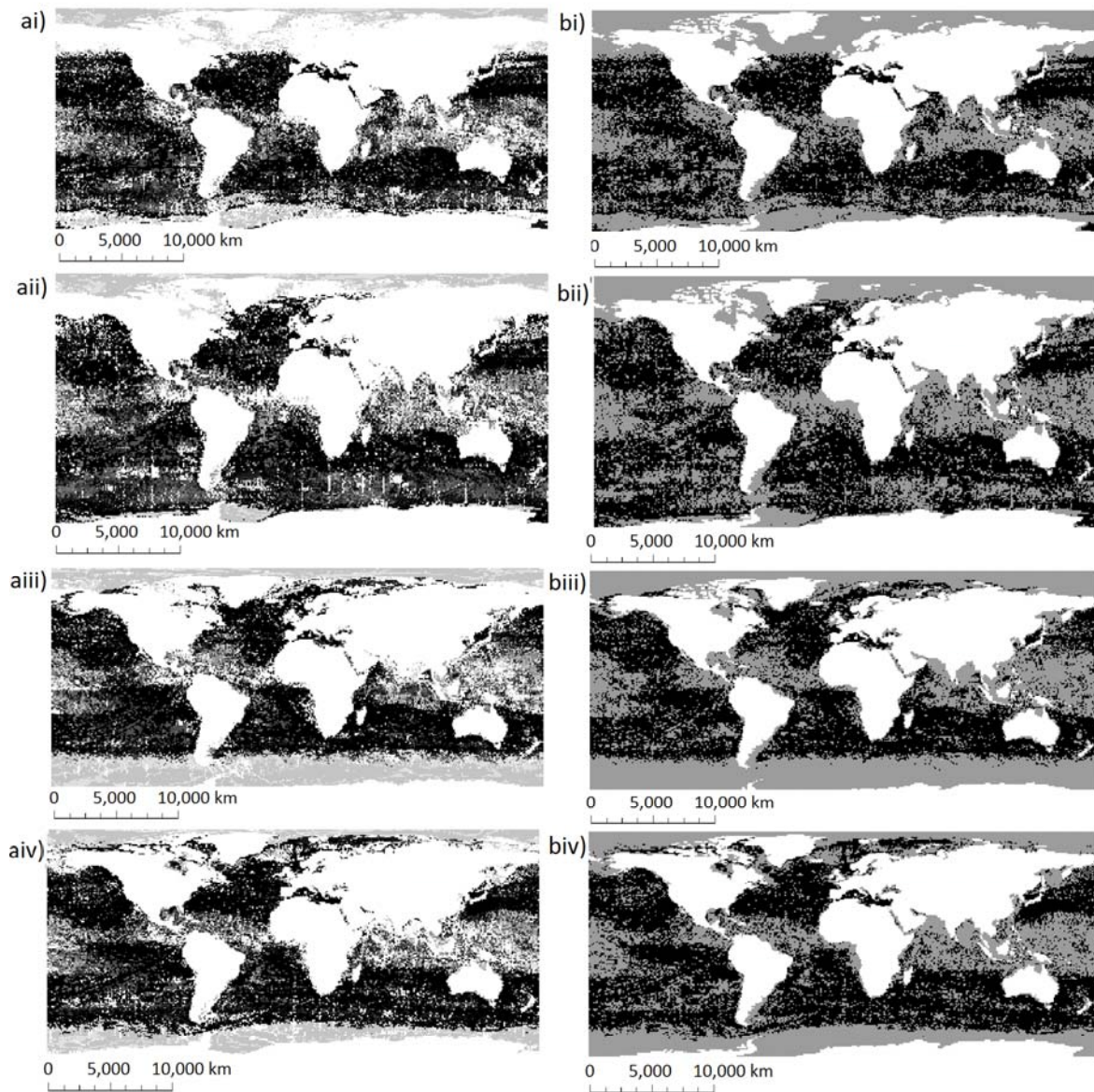


Figure 5a. Seasonal predicted latitudinal range of *Mola* in both hemispheres (outliers removed). **b.** Intra-annual variation in latitude of sightings data plotted by day of year with locally weighted scatterplot smoothing curve (LOESS) curve and 95% confidence interval for both hemispheres.

