Seasonal variations in the abundance and body size distribution of the ocean sunfish *Mola mola* in coastal waters off southern Portugal

Miguel Baptista[1,2,3], Ana Couto[1,2], José Ricardo Paula[1], Joana Raimundo[3], Nuno Queiroz[2] and Rui Rosa[1]

[1]Laboratório Marítimo da Guia, MARE – Marine and Environmental Sciences Centre, Faculdade de Ciências da Universidade de Lisboa, Av. Nossa Senhora do Cabo, 939, 2750 -374 Cascais, Portugal; [2]CIBIO/InBIO, Universidade do Porto, Campus Agrário de Vairão, 4485-661 Vairão, Portugal and [3]Divisão de Oceanografia Ambiental e Bioprospecção, IPMA – Instituto Português do Mar e da Atmosfera, Av. Brasília, 1449-006 Lisbon, Portugal

Abstract

The present work expands the existing knowledge on *M. mola* ecology by assessing, for the first time, its abundance (and body size distribution) in the southern waters of Portugal and relating the associated temporal variations with environmental variables. There were significant seasonal differences in abundance, with peaks in spring and autumn and lower values throughout the summer. Ocean sunfish abundance was positively correlated with sea surface temperature and chlorophyll a, indicating that a combination of both temperature and productivity dictates spatial use. Complementarily, the absence of a relationship between abundance and water transparency may reveal a strategy in spatial use favouring a medium-term steady food supply over short-term improved feeding opportunities. Specimens ranged between 31.8 and 230.0 cm (total length), with 98% of all individuals measuring between 31.8 and 59.9 cm. As the vast majority of specimens analysed were immature, seasonal differences in abundance should not be related to spawning.

Introduction

The ocean sunfish *Mola mola* (Linnaeus, 1758) is a widely distributed species, being found in waters stretching from 75°N (Norway and North America) to 55°S (South America and New Zealand; AquaMaps, 2016). While standing out from other fish due to its uncommon morphology, *M. mola* has been subject historically to a lack of academic interest. In fact, only in the last two decades has the scientific community truly directed its attention to this animal, in an attempt to unveil the mysteries surrounding its life (e.g. Sims & Southall, 2002; Cartamil & Lowe, 2004; Houghton *et al.*, 2006; Watanabe & Sato, 2008; Hays *et al.*, 2009; Syväranta *et al.*, 2012; Kang *et al.*, 2015; Nakamura *et al.*, 2015; Sousa *et al.*, 2016a; Breen *et al.*, 2017). A number of satellite tracking studies were performed on *M. mola*, providing solid evidence of the existence of seasonal migratory movements in distinct geographic regions (e.g. Sims *et al.*, 2009a; Dewar *et al.*, 2010; Potter *et al.*, 2011; Thys *et al.*, 2015). In the northern hemisphere, northward movements are performed in late winter–spring and southward movements are performed in late summer–autumn (Sims *et al.*, 2009a; Dewar *et al.*, 2010; Potter *et al.*, 2011; Thys *et al.*, 2015; Sousa *et al.*, 2016b). Though valuably contributing to the knowledge on habitat usage preferences, satellite tracking studies are inherently expensive. For this reason, analysis is generally limited to a relatively small number of specimens (i.e. 3–25 specimens; Sims *et al.*, 2009a; Dewar *et al.*, 2010; Potter *et al.*, 2011) whose behaviour may not be representative of that of the population. As such, the use of satellite tracking data to infer population-wise temporal habitat preferences may be inappropriate. Long-term collection of abundance data in a given area, on the other hand, allows for the recognition of seasonal patterns in habitat usage at the population level (Yozzo & Smith, 1995; Prista, 2013; Licandro *et al.*, 2015). A few satellite tracking studies have been performed on *M. mola* off southern Portugal (Sims *et al.*, 2009a, 2009b; Sousa *et al.*, 2016a, 2016b), but information on the seasonal patterns of spatial use at the population level in this general area is lacking.

Mola mola holds an overall low commercial value globally (Fulling *et al.*, 2007) and directed fisheries are largely restricted to Asian waters (Sagara & Ozawa, 2002; Liu *et al.*, 2009; Kang *et al.*, 2015). Nonetheless, high bycatch rates are reported worldwide and severe localized declines have been documented, leading the International Union for Conservation of Nature (IUCN) to recently categorize this species as 'vulnerable' (Liu *et al.*, 2015). A quite recent drastic reduction in Portuguese landings of this fish from 12 metric tonnes in 1999 to about zero in 2009 (Liu *et al.*, 2015) may indicate a severe decline in the standing stock of *M. mola* inhabiting Iberian Atlantic waters. As accurate knowledge on basic biological

and ecological traits of any species is vital to the delineation of conservation measures and therefore its preservation, the IUCN recommends further research on the life of this fish.

In this context, the present work aimed to study, for the first time, the seasonal variation in the abundance and body size distribution of *M. mola* in southern waters of Portugal. Furthermore, the relationships between *M. mola* abundance and sea surface temperature (SST), chlorophyll a (chl *a*), upwelling and water transparency were also examined.

Materials and methods

Data collection

This study was carried out in southern Portugal, off Olhão, at a set-net targeting tuna (Tunipex). *Mola mola* abundance data (number of specimens entering the net per day as bycatch) were collected between April and November 2014. More specifically, data collection occurred throughout the months of April (5 days of sampling), May (5 days), June (18 days), July (3 days), August (10 days), September (24 days), October (12 days) and November (11 days). Additionally, whenever possible, size-related data were also obtained from the set-net daily bycatch. Due to the inherent difficulties in accurately measuring all individuals comprising the set-net daily bycatch, as noted by Nakamura (2014), crude total length (TL) measurements were mostly obtained, allowing for the assignment of specimens into 20 cm TL size classes.

Environmental data

Animal spatial usage is usually linked to the pursuit of favourable thermal and foraging conditions (Polovina *et al.*, 2001; Stensholt, 2001; Kumari & Raman, 2010; Binder *et al.*, 2011). As such, the existence of a relationship between *M. mola* abundance and environmental variables linked to thermal and foraging conditions was assessed.

In situ measurements of SST and water transparency (Secchi depth) were performed daily by Tunipex collaborators. Satellite-derived daily chl *a* data were obtained from AquaMODIS with a spatial resolution of ∼4 km. A 7-day moving average was calculated and used as a proxy for primary productivity. Finally, an upwelling index (i.e. difference between coastal and offshore SST) was calculated using remotely sensed nocturnal SST (Aqua-MODIS, http://oceancolor.gsfc.nasa.gov/; Krug *et al.*, 2012; Couto *et al.*, 2017).

Statistical analysis

The seasonal variation in *M. mola* abundance and the relationship between abundance and environmental variables were analysed using a negative binomial regression under generalized linear models (GLM) to account for overdispersion. Selection for best model was performed using Akaike Information Criterion (AIC) which balances the quality of model fitness to data and the complexity of the model (Quinn & Keough, 2002). Presence of outliers was assessed using Cook's distance approach (Zuur *et al.*, 2010). No outliers were identified. The assumptions of each model were tested following Zuur *et al.* (2010); independence and absence of residual patterns were verified by plotting residuals against fitted values and normality was tested with the quantile-quantile (Q-Q) plot.

To understand the relationship between *M. mola* abundance and environmental variables (i.e. SST, chl *a* (7-day moving average), upwelling index and water transparency), we applied a multistep strategy (Sikkink *et al.*, 2007). To correct for heterogeneity of variance in this model, data were analysed using generalized

Table 1. Summary of the generalized least squares (GLS) model relating the abundance of *Mola mola* in a tuna set-net off southern Portugal in 2014 to the independent variables kept in the final model

	β	SD	P
Sea surface temperature (°C)	8.926	3.926	0.026
Chlorophyll *a* (7-day moving average; mg m^{-3})	40.777	19.236	0.038
Water transparency (Secchi depth; m)	5.7	3.302	0.089

β, slope; SD, standard deviation; P, P-value.

least squares (GLS) as proposed by Zuur *et al.* (2010). The independent variables kept in the final model are shown in Table 1. Finally, the performance of the GLS model was evaluated by calculating the concordance index (C-index; Harrell *et al.*, 1984) using the Hmisc package (Harrell, 2006) that estimates the probability of concordance between predicted and observed responses (Swets, 1988).

Statistical analysis was performed in R (version 3.4.3; R Core Team, 2017) and data exploration and model validation used the HighstatLibV10 R library from Highland Statistics (Zuur *et al.*, 2009).

Results

Abundance and environmental variables

Mola mola were present in southern waters of Portugal throughout the studied period (April–November 2014). There were, however, significant seasonal differences in abundance (GLM Analysis of Deviance, df = 15, F = 9.77 P < 0.001). Two peaks were observed, one in the spring (median value of 115 specimens/day in early (days 1–15) May) and the other in the autumn (148 specimens/day in early September and 150 specimens/day in early October; Figure 1). Abundance was generally low throughout the summer, mostly below 40 specimens/day, yet, the lowest abundance values were found in early November with a median value of one specimen/day.

The GLS model revealed statistically significant relationships between *M. mola* abundance and two environmental variables. Positive relationships were found with SST (which ranged between 14 and 22°C; β = 8.93, SD = 3.93, P = 0.026) and chl *a* (7-day moving average; 0.2–2.4 mg m^{-3}; β = 40.78, SD = 19.24, P = 0.038; Table 1). No significant relationship was found between *M. mola* abundance and water transparency (which ranged between 4 and 17 m; Table 1).

Body size

Measured ocean sunfish specimens ranged between 31.8 and 230 cm TL, with the second largest animal registering 120.3 cm TL. The use of crude TL measurements for the assignment of fish into different size classes is a relevant limitation of the present study and may not allow for the accurate description of biologically relevant features. Nonetheless, some patterns became available in the present study. Overall, 98% of all sampled specimens measured between 31.8 and 59.9 cm TL. Specimens larger than 80 cm were extremely rare, accounting for less than 0.7% of sampled *M. mola*. There was an apparent seasonal shift in size distribution around the 40 cm TL mark. Size class '40–59.9 cm' was more abundant between April and June (75% of total specimens), while class '20–39.9 cm' attained slightly greater numbers between September and November (60% of total specimens; Figure 2).
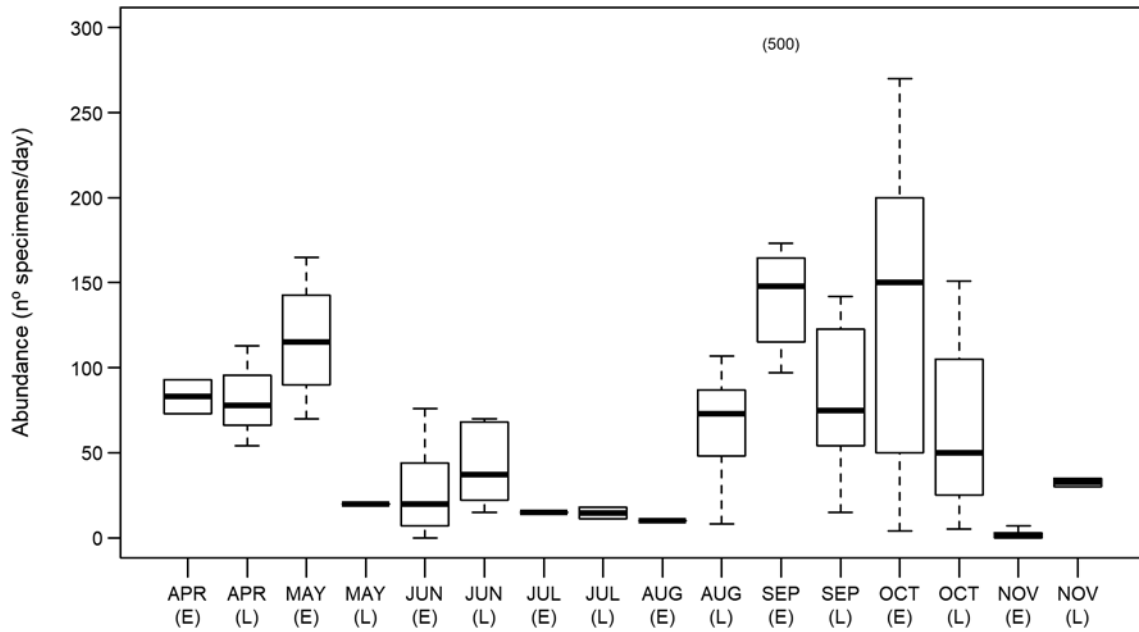
Fig. 1. *Mola mola* abundance between April and November 2014, in the studied location – Tunipex S.A. set-net, off Olhão, Portugal. Box-plot shows median and 25 and 75 percentiles, whiskers indicate the range. Data is pooled over fortnight periods. The number of days in which data was collected varied among fortnights: early April (2 days), late April (3 days), early May (4 days), late May (1 day), early June (13 days), late June (5 days), early July (1 day), late July (2 days), early August (1 day), late August (9 days), early September (12 days), late September (12 days), early October (5 days), late October (7 days), early November (9 days) and late November (2 days). E, early (days 1–15); L, late (days 16–30/31, depending on month). The number 500 in parentheses indicates a day (8 September 2014) when 500 specimens entered the set-net.
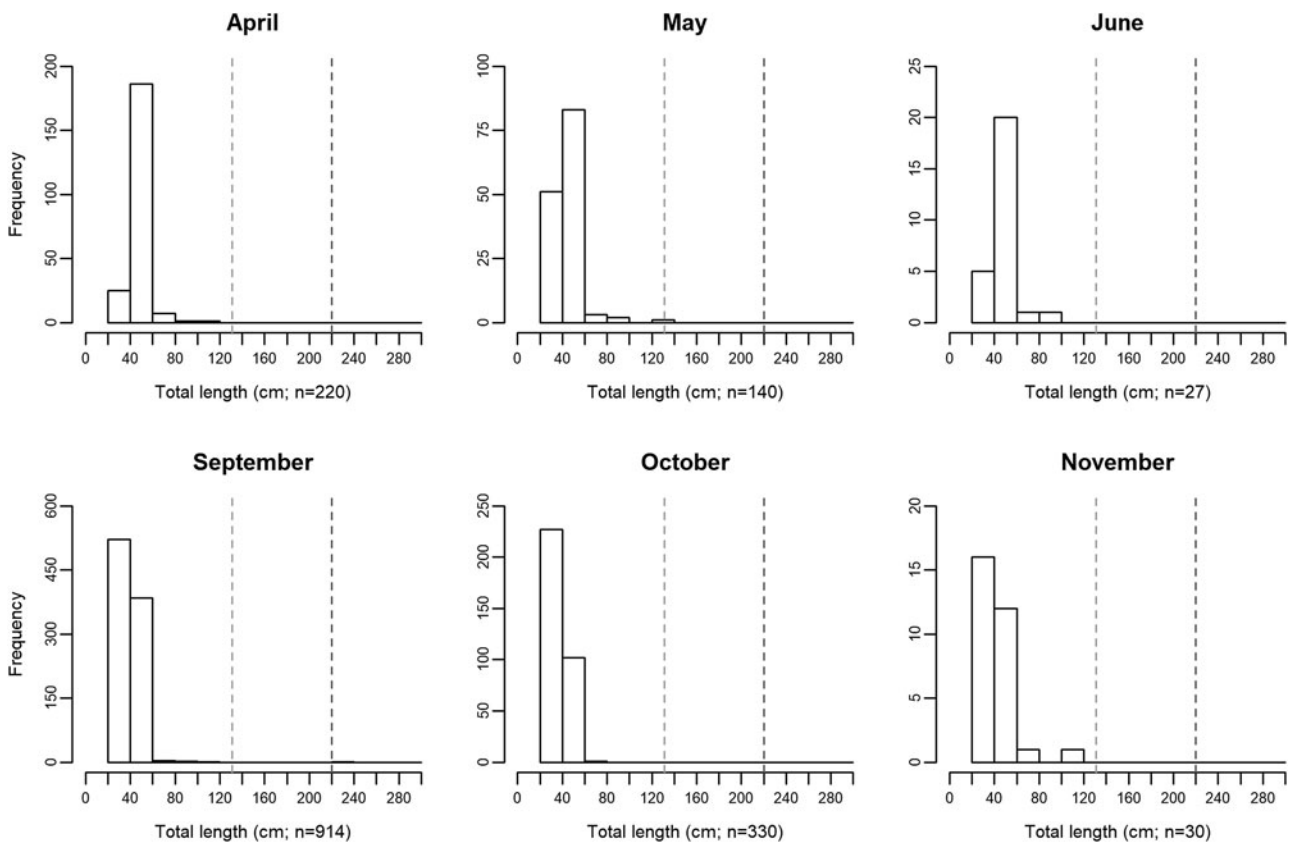

Fig. 2. Monthly changes in *Mola mola* body size distribution between April and November, 2014, in the studied location – Tunipex S.A. set-net, off Olhão, Portugal. The vertical dashed lines indicate size at maturity for males (131 cm; light grey) and females (220 cm; dark grey) obtained from Kang *et al.* (2015).

Discussion

Seasonal changes in abundance and body size distribution

Information on seasonal variations in habitat use provides critical data needed when planning for species conservation, stock management and establishment of marine protected areas (West *et al.*, 2009; Chapman *et al.*, 2012). The present study showed that the presence of *Mola mola* in southern waters of Portugal is recurrent between April and November (study period). Moreover, ocean sunfish probably occur in the area throughout the year

since SST in this area generally varies between 13 and 23°C year-round (Tunipex, 2017), a range of temperatures in which ocean sunfish are found worldwide (Sims et al., 2009a; Dewar et al., 2010; Potter et al., 2011; Thys et al., 2015; Sousa et al., 2016b). Interestingly and contrarily to other large migratory fish such as bluefin tuna (Thunnus thynnus), meagre (Argyrosomus regius) and basking shark (Cetorhinus maximus) that show only one peak of abundance in this area (mid-summer for tuna, late-summer for meagre and mid-spring for basking shark; Prista, 2013; Santos et al., 2016; Couto et al., 2017), M. mola revealed two peaks – spring and autumn (greater values being registered in early May and both early September and early October). More so, the existence of spring and autumn abundance peaks is recurrent in this area (Poço, personal communication, 24 August 2017), and agrees with the seasonal latitudinal movements reported for ocean sunfish in the region (Sims et al., 2009a; Sousa et al., 2016b). This finding is indicative of the relevance of southern waters of Portugal in the migratory ecology of M. mola in the North-east Atlantic. A comprehensive number of studies performed on the horizontal movements of mostly ≤150 cm TL M. mola (e.g. Hays et al., 2009; Potter et al., 2011; Thys et al., 2015; Sousa et al., 2016b) has allowed for the identification of migration patterns that appear confined to coastal areas (Thys et al., 2015). Indeed, movement ranges generally do not exceed 500 km away from shoreline and fish largely remain within 300 km of the shore. Migratory movements of smaller ocean sunfish (≤150 cm TL) seem therefore dependent on coastal proximity and while the use of alternative more oceanic migration routes is not viable, the presently studied area should be pivotal in the northward-southward migration pattern described for the species in the North-east Atlantic (Sims et al., 2009a, 2009b; Sousa et al., 2016b). Seasonal changes in abundance are sometimes related to reproductive processes and, in the presently studied general area, episodes of greater bluefin tuna abundance occur as a result of migration into the Mediterranean Sea for spawning (Santos et al., 2016). Regarding M. mola, however, as the overwhelming majority (∼99.9%) of specimens inhabiting the southern waters of Portugal were immature (see Figure 2; Nakatsubo et al., 2007; Kang et al., 2015), the presently revealed seasonal differences in abundance should not be related to spawning (Dewar et al., 2010). Conversely, the presence of smaller M. mola in the studied area has been attributed to its value as a developmental habitat for this species (Sousa et al., 2016b). A seasonal shift in size distribution around the 40 cm TL mark was apparent in the present study, with slightly greater numbers of smaller specimens later in the year. While sampling limitations (i.e. usage of crude TL measurements for size class assignment) do not allow solid conclusions to be drawn from this pattern, it resembles that observed by Sawai et al. (2011) in north-eastern Japanese waters. Future work should attempt to assess the actual existence of a seasonal size shift as increases in the relative abundance of smaller sized fish are most likely indicative of recruitment success and a shift in habitat use. In loggerhead turtles (resembling ocean sunfish in regard to seasonality and habitat use; Kenney, 1996), smaller juveniles were found to occupy oceanic habitats whereas larger ones occupy coastal habitats (Bowen et al., 2004). It is possible that young ocean sunfish adopt a similar strategy in spatial use, initially inhabiting oceanic waters and switching to a more coastal habitat upon reaching 20 cm TL, size of the smallest specimens observed in coastal waters (Silvani et al., 1999; Thys et al., 2015).

Relationships between abundance and environmental variables

Typically, migration patterns follow seasonal changes in temperature and productivity as animals seek favourable thermal and foraging conditions (Polovina et al., 2001; Stensholt, 2001; Kumari & Raman, 2010; Binder et al., 2011). As fluctuations in the abundance of an organism at a given location are in all likelihood related to seasonal migratory movements, a relationship between abundance and those environmental factors should also be verified. Accordingly, the present investigation found SST and chl a (a widely recognized indicator of productivity; e.g. Breen et al., 2017; Couto et al., 2017) as determinants of M. mola abundance in southern waters of Portugal (Table 1). Mola mola abundance was positively correlated with both environmental variables. In the studied area, greater abundance was found upon higher SSTs (between 18.0 and 21.5°C). While in agreement with the work of Fulling et al. (2007) where greater ocean sunfish presence was verified at SSTs around 20.5°C, the presently obtained results differ from those of Hahlbeck et al. (2017) and Nakamura & Sato (2014) who observed higher M. mola abundance associated with SSTs below 17–18°C. The discrepancy in these observations provides an indication that the relationship between spatial use and temperature is not straightforward. Indeed, even though abundance was shown to increase with temperature (Table 1), abundance peaks took place under differing SST scenarios: spring (April–May; 16.46 ± 1.54°C) and autumn (September–October; 20.63 ± 1.39°C; Figure 3). Conversely, chl a was also found as a determinant of M. mola abundance in the southern waters of Portugal (Table 1). Chlorophyll a is widely recognized as an indicator of productivity (Sims et al., 2003; Breen et al., 2017; Couto et al., 2017) and an association between predators and productive areas is frequently observed (Polovina et al., 2001; Kumari & Raman, 2010) as these areas should provide enhanced foraging opportunities. Concomitantly, M. mola abundance peaks coincided with the seasons exhibiting regular occurrence of phytoplankton blooms in the North Atlantic – spring and autumn (Lalli & Parsons, 2006; Longhurst, 2007). While M. mola has not been shown to seek highly productive areas, it appears to avoid oligotrophic areas (Sousa et al., 2016b), being mostly associated with chl a concentrations in the range 0.5–2.5 mg m^{-3} (Phillips et al., 2017). Accordingly, in the present work, greater M. mola abundance was observed above 0.6 mg m^{-3}. Curiously, no effect of chl a was found on M. mola abundance in western USA coastal waters (Hahlbeck et al., 2017). It is possible that the implementation of different methodologies and/or consideration of diverse spatial and temporal scales may explain the contrasting results. The presently found relationship between abundance and productivity in southern waters of Portugal, is indicative of the relevance of this general area (i.e. Gulf of Cadiz), as a feeding ground for ocean sunfish during their seasonal migratory movements in the North-east Atlantic. Additionally, the observed association of M. mola abundance with both temperature and productivity provides an indication that a combination of these environmental factors dictates spatial use, in agreement with the hypothesis put forth by Thys et al. (2015) regarding seasonal migrations. The visual acuity of juvenile M. mola (42–46 cm TL) was found to be similar to that of adult cetaceans (Kino et al., 2009). Additionally, 95% of feeding events by ocean sunfish take place during the day (Nakamura et al., 2015). Such observations point to vision as playing an important role in the foraging ecology of M. mola and as such, it would make sense that this animal attempted to maximize prey capture chances by actively seeking high visibility waters. Surprisingly, however, water transparency was found to have no effect on M. mola abundance and therefore spatial use. As both productivity and water transparency provide information on potential foraging success, the apparent disregard for the latter may indicate a strategy in M. mola spatial use favouring a medium-term steady food supply over short-term improved feeding opportunities.
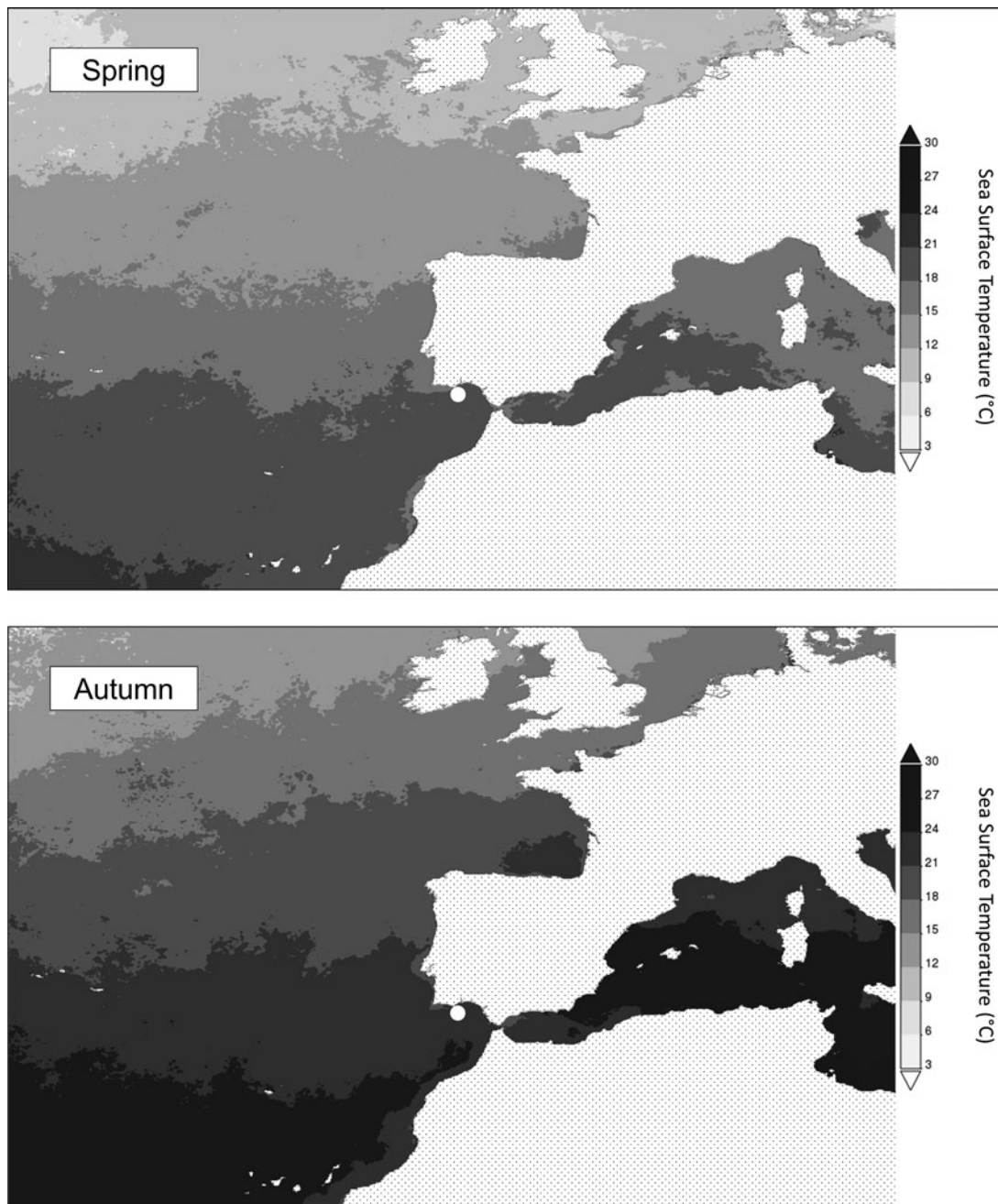
Fig. 3. MODIS Aqua average sea surface temperature in the studied location and surrounding areas in the spring (April–May) and autumn (September–October) of 2014. Data obtained from Giovanni (Acker & Leptoukh, 2007). The white filled circle indicates the studied location.

Concluding remarks

The present study supports the notion of seasonal latitudinal movements in the North-eastern Atlantic and highlights the importance of southern waters of Portugal (and potentially Gulf of Cadiz) in the migratory ecology of *M. mola*. As the vast majority of specimens inhabiting the studied area were immature, such horizontal movements should not be related to spawning. Instead, the observed relationship between *M. mola* abundance and both temperature and productivity provides indication that a combination of these environmental factors dictates spatial use. Complementarily, the absence of a relationship between abundance and water transparency may reveal a strategy in spatial use favouring a medium-term steady food supply over short-term improved feeding opportunities.

Author ORCIDs. (iD) Miguel Baptista, 0000-0001-8833-4766.

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