


# Small scale temporal patterns of recruitment and hatching of Atlantic horse mackerel (L.) at a nearshore reef area

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## Funding information

Fundação para a Ciência e Tecnologia (FCT), Grant/Award Number: SFRH/BD/72970/2010, SFRH/BPD/23743/2005, POCTI/MAR/57934/2004; MATRIX, Grant/Award Number: PTDC/MAR/115226/2009; REEFFISH, Grant/Award Number: PTDC/MAR-EST/4356/2012; Pluriannual Programmes, Grant/Award Number: PEST-OE/MAR/UI0331/2011; CCMAR, Grant/Award Number: Multi/04326/2013; MARE, Grant/Award Number: OE/MAR/UI0331/2011, UID/MAR/04292/2013

## Abstract

Atlantic horse mackerel (*Trachurus trachurus*, Linnaeus, 1758) is a highly exploited species, common throughout the North-East Atlantic. As a pelagic-neritic fish it typically occurs over the shelf from the surface to 200 m deep on sandy bottoms. Most research has focused on distributions of adults or early life stages (eggs and larvae) of this species in offshore waters and only a few studies have reported the occurrence of early stages near the coast. However, these nearshore environments might be important for the early growth and survival of the Atlantic horse mackerel. In addition, little is known on how environmental processes might affect the early stages of this species. Here, we monitored weekly recruitment of horse mackerel to artificial substrates (SMURFS) deployed near the coast at both the surface and near the bottom, and back-calculated hatching cohorts. The relationship of both recruitment and hatching patterns with environmental factors was investigated. From a total of 2,515 fish, 2,490 (99%) recruited to surface SMURFS. A GAM and GAMM analysis of the recruitment and hatching patterns, respectively, revealed a strong relationship with the lunar cycle and upwelling. Both recruitment and hatching showed lunar periodicity, with peaks near the new moon and revealed to be influenced negatively by upwelling. This study suggests that the nearshore environment might be an important nursery area for post-larval and early juvenile Atlantic horse mackerel.

## KEYWORDS

hatching, juvenile, lunar pattern, recruitment, *Trachurus trachurus*, upwelling

## 1 | INTRODUCTION

Marine fish can have highly variable recruitment patterns, which can strongly affect population dynamics (reviewed by e.g., Cury & Roy, 1989; Pepin & Myers, 1991; Doherty, 2002; Carr & Syms, 2006). Various interacting biotic and abiotic processes at multiple scales can cause this variability. Abiotic factors include, for example, sea surface temperature (SST; Daskalov, 1999; Jenkins & King, 2006), upper ocean stability (including wind and current speeds and direction or tides; Roy, Cury, Fontana, & Belvèze, 1989; Milicich, 1994; Caselle, Kinlan, & Warner, 2010), nutrient availability (Caselle, Carr, Malone,

Wilson, & Wendt, 2010; Meekan, Carleton, McKinnon, Flynn, & Furnas, 2003), or the lunar phase (Sponaugle & Cowen, 1994; Victor, 1982).

Atlantic horse mackerel (*Trachurus trachurus*, Linnaeus, 1758) is a highly exploited species common throughout the North-East Atlantic, from the Norwegian Fjords to South Africa (Lockwood & Johnson, 1977; Smith-Vanith, 1986). In 2015, 137,304 tonnes of this species were captured by the European fishing industry (FAO, 2017). In Portugal, it was the second most important marine fish species in 2015 in terms of landed biomass. Given its economic importance, this species has been the subject of intensive research (e.g., Abaunza et al.,

2008; Macer, 1977; Smith-Vanith, 1986) revealing its pelagic-neritic distribution, typically occurring over the shelf from the surface to 200 m depth over sandy bottoms. Most research has focused on deeper offshore waters and adult phases, with few exceptions that measured larvae and egg distribution (e.g., Berenbeim, 1974; Farinha & Borges, 1994; Farinha & Lopes, 1996). There is evidence that eggs and larvae concentrate near the shelf-edge (Farinha & Borges, 1994; Farinha & Lopes, 1996), and that immature fish can be distributed over the shelf closer to the coast, at least in Southwest Portugal (Borges & Gordo, 1991).

Despite the general absence of studies focusing on nearshore occurrence, larvae and early stages of *Trachurus* species have been observed several times in nearshore rocky reefs at the Arrábida Marine Park (Portugal) (Beldade, Borges, & Gonçalves, 2006; Borges, Ben-Hamadou, Chícharo, Ré, & Gonçalves, 2007; Borges, Vaz, Serrão, & Gonçalves, 2009), indicating the potential importance of this area to the early life of this pelagic fish.

Additionally, little is known on how environmental processes might affect early life stages of Atlantic horse mackerel (Trenkel et al., 2014). The few published studies found (i) no significant correlation between larval abundance and SST in the Celtic Sea (Fives et al., 2001), (ii) a negative correlation between upwelling during the winter spawning season and the yearly recruitment to the fishery in Portugal (Santos, Borges, & Groom, 2001) and (iii) a positive relationship between lower coastal SST (indicating upwelling and mild weather patterns) during spring and summer and higher annual recruitment in the whole Iberian Peninsula (Lavín, Moreno-Ventas, Ortiz de Zárate, Abaunza, & Cabanas, 2007).

Atlantic horse mackerel recruitment (i.e., the transition from the larval to the juvenile stage) has not yet been directly investigated, as previous studies used an annual estimate of the number of recruits entering the fishery as a proxy for recruitment. The present study addresses this knowledge gap by aiming to: (i) measure the occurrence and recruitment patterns of Atlantic horse mackerel at small temporal (weekly) resolution nearshore and (ii) investigate the impact of environmental processes on recruitment and hatching patterns.

## 2 | MATERIALS AND METHODS

### 2.1 | Sampling

Sampling sites were located at the Arrábida Marine Park (hereafter AMP) in central Portugal (Figure 1), which is part of the Western Iberian upwelling ecosystem, a wind-driven eastern boundary upwelling system (Cunha, 1993; Fiúza, Macedo, & Guerreiro, 1982; Moita, 2003; Wooster, Bakun, & McLain, 1976). A southern oriented steep coast protects the AMP from prevailing northerly and north-westerly winds and waves (Beldade, Erzini, & Gonçalves, 2006), allowing frequent sampling in the nearshore areas.

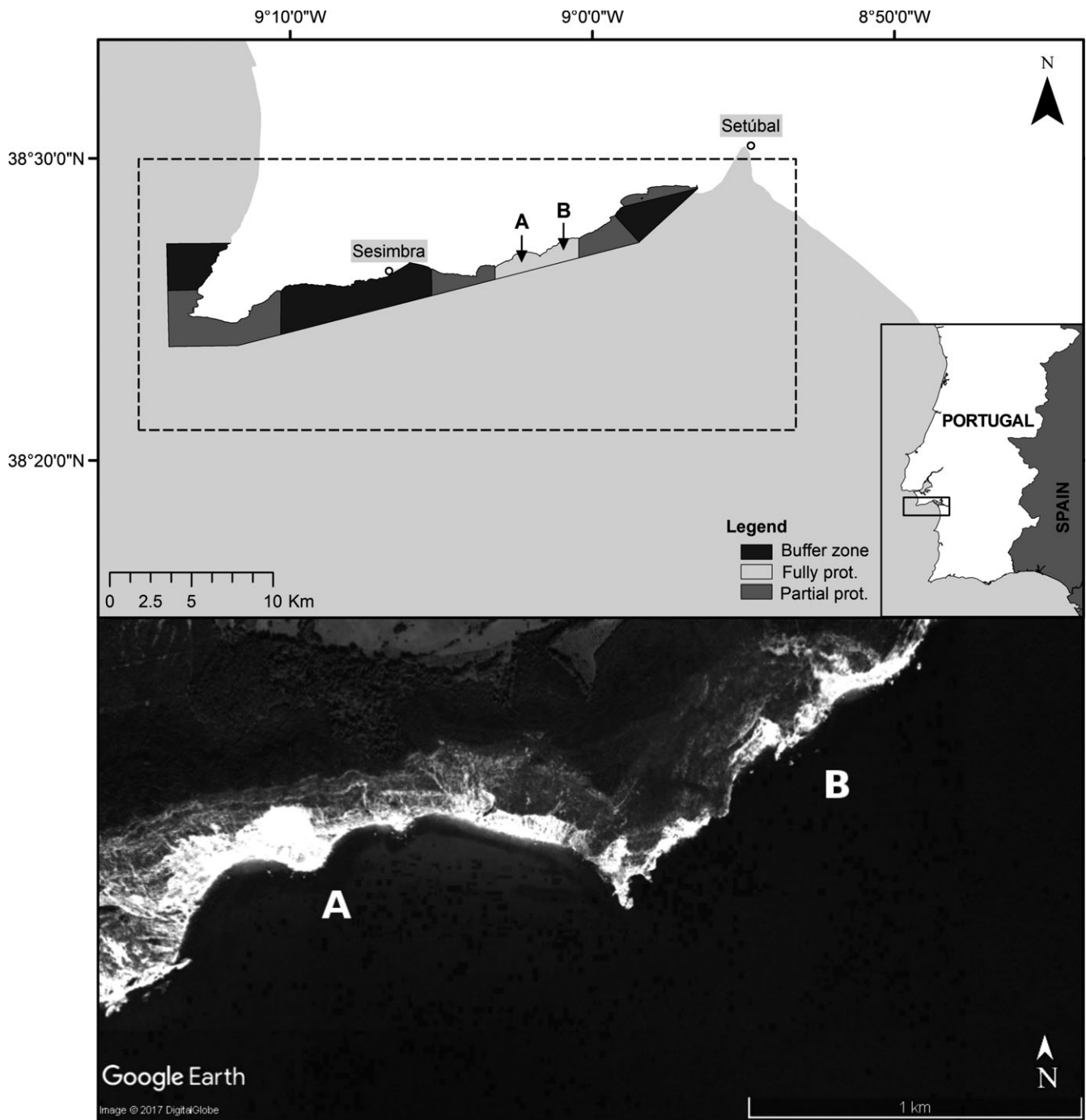
In this study, recruitment refers to the arrival of fish to the nearshore and the approximately concurrent metamorphosis to the juvenile stage. Given that juvenile Atlantic horse mackerel show thigmotactic behaviour (Deudero, Merella, Morales-Nin, Massutí, &

Alemany, 1999; Massutí, Morales-Nin, & Deudero, 1999), standard monitoring units for recruitment of fish (SMURFs; Ammann, 2004; Wilson, Broitman, Caselle, & Wendt, 2008) were used here to monitor nearshore aggregation of this pelagic species. SMURFs can successfully sample ready-to-settle fish in the nearshore (Caselle, Kinlan et al., 2010; Tavernetti, Morgan, & Yu, 2009; White & Caselle, 2008). SMURFs were made out of a cylindrical frame of green gardening fence (1.0 × 0.35 m diameter) and filled with plastic fencing to imitate algae, as applied in several recruitment studies in California (Ammann, 2004; Caselle, Carr et al., 2010; Wilson, Broitman, Caselle, & Wendt, 2008). These collectors were deployed in two bays with similar rocky reef habitat, within the fully protected area of the AMP (Figure 1). The sampling sites A (38°26′45.35″N, 9°2′18.44″W) and B (38°26′57.68″N, 9°1′19.09″W) were located approximately 1.5 km apart and around 100 m seaward from the nearest reef (Figure 1).

In each site, three mooring lines were deployed from a small boat over sandy bottom at a water depth of around 12 m in site A and 15 m in site B. On each line, two SMURFs were attached, one just below the surface (1–3.5 m depending on the tide) and one close (~40 cm) to the bottom, resulting in a total of 6 replicate SMURFs per site (Figure S1 for further details). Sampling was performed weekly from the 29th of June till the 27th of September in 2011, comprising 14 weeks of sampling. SMURFs were collected by two scuba divers using a benthic ichthyofaunal net for coral/kelp environments (BINCKE net; Anderson & Carr, 1998; Ammann, 2004). Once onboard, SMURFs were cleared over the net with repeated washings and the sample was transferred first to a bucket and then into a sieve before being preserved in 80% ethanol. In the laboratory, after sorting and species identification, total (TL) and standard length (SL) were measured to the nearest 0.01 cm. A subsample of 297 fish was aged from sagittal otolith analysis to build a length-age relationship, well described by the Gompertz growth function ( $R^2 = .72$ ; see Van Beveren, Klein, Serrão, Gonçalves, & Borges, 2016 for further details on the otolith data analysis). This function was then used to back-calculate dates of hatching.

### 2.2 | Environmental factors

For the time period between the earliest back-calculated hatching date (10 May 2011) and the end of the sampling period (27 September 2011; Figures 2a,b), daily data were compiled for the study area (Figure 1) for the following environmental parameters: sea surface temperature (SST), concentration of Chlorophyll a (Chla), eastward and northward current velocity (U- and V component, respectively), wind speed and direction, upwelling, moon phase and tidal amplitude (Table 1). For daily raster data (SST, Chla and currents), a daily average was calculated for the study region (Figure 1; extent: -9.25, -8.50, 38.50, 38.35). Hourly wind speed and direction data was averaged per day. The upwelling index was calculated as the difference between offshore SST measured from an offshore area of similar size located two degrees further offshore at the same latitude and the SST in the sampling area (Santos et al., 2001; Relvas et al., 2009).

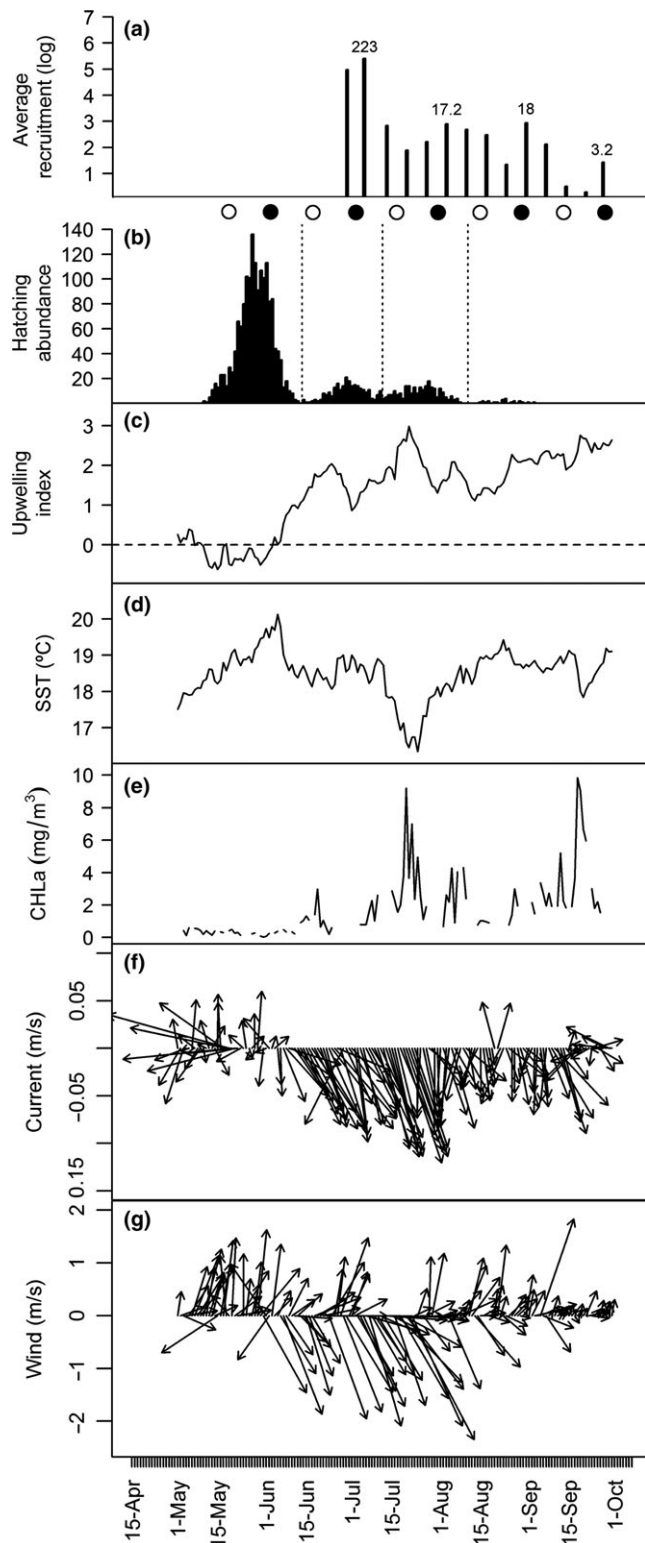


**FIGURE 1** Map of the study site (Arrábida Marine Park) on the top, with indications of the protection zones, the two sampling sites A and B, and the area (dashed frame) for which satellite data of environmental parameters was averaged and a detailed satellite image of the sampling area on the bottom. Country maps were provided by the Portuguese Institute of Hydrography and the satellite image by Google Earth

Positive values indicate upwelling conditions and negative values describe relaxation from upwelling. For the model analysis lunar illumination was categorized in order to distinguish between first and third quarter moon: full moon (75%–100%), new moon (0%–25%) and first and third quarter moon shared 25%–75% illumination. In this study site, each lunar cycle included two tidal cycles, with spring tides occurring on the same day, or 1 day after full and new moon.

### 2.3 | Data analyses

Bottom SMURFs collected very few fish (0.99% of the total catch) and therefore only data from surface SMURFs were analysed. Fish sampled with a SL < 25 mm (Figure S2; Van Beveren et al., 2016) were considered recruits and selected for data analysis. A Kruskal–Wallis test was used to compare the non-normally distributed



**FIGURE 2** (a) Weekly averaged recruit abundance of *T. trachurus* (log-transformed with untransformed numbers on peaks); estimated daily hatching intensity (b: with dashed lines separating hatching cohorts and circles indicate lunar phase; full moon, white; new moon, black); daily time series of the upwelling index (c), SST (d), CHLa concentration (e) surface currents (f) and wind (g). See Table 1 for more details on units and source of environmental variables

abundance of recruits among SMURF replicates in each site. A Wilcoxon rank sum test was used for site (A, B) comparisons. To analyse the weekly recruitment patterns as a function of daily environmental parameters, the latter were averaged over the 7 days preceding sampling, to capture the environmental conditions during the time over which fish arrived to SMURFs (due to the weekly nature of sampling).

Data exploration of the explanatory variables was performed by following the protocol of Zuur, Ieno, and Elphick (2010). Both a multiple pairwise scatterplot with Pearson correlation and a Variance Inflation Factor (VIF) analysis was used to test for collinearity and to choose which explanatory variables were included in the models (Zuur et al., 2010). A Pearson correlation of  $R^2 = .6$  was used as a threshold. Accordingly, wind variables were correlated with current components, which were highly correlated between each other and CHLa was correlated with the upwelling index. The modelling included as continuous variables, SST and the upwelling index and U current, due to their higher correlation with the response variables compared to the wind variables. Selected categorical variables were moon phase, site (only in recruitment models) and hatching cohort (only in hatching models).

A generalized additive model (GAM) was used on the recruitment and hatching data. Since an auto-correlation analysis (ACF) performed on the model residuals revealed temporal dependence of the hatching time series, a generalized additive mixed model (GAMM; Wood, 2006; Zuur, Ieno, Walker, Saveliev, & Smith, 2009) was used here. A dependence structure was included to the GAMM by using the factor hatching cohort as a random intercept. Models were set up using a negative-binomial error structure and a log link function (Wood, 2006). The Akaike Information Criterion (AIC) and a graphical validation of model residuals were used to select the best model (Zuur et al., 2009). The data exploration and all statistical analyses were carried out with R (version 3.1.0; R-Core-Team, 2009) and test results were evaluated at the  $p < .05$  level. The GAM and GAMM models were analysed using the mgcv library (version 1.8-1; Wood, 2011) in R.

### 3 | RESULTS

A total of 2490 Atlantic horse mackerel were collected with surface SMURFs. Standard length ranged from 6.1 mm to 48.56 (mean  $SD = 15.5$  mm; Figure S2) and 2,126 out of 2,209 measurable fish were post-larvae and/or recruits (96.2%; 6.1 mm–25.0 mm SL). Fish morphology ranged from late stage larvae to juvenile (Di Padoa, 1956; Russell, 1976). In several weekly samples, the great majority of fish aggregated to just one or two of the six surface SMURFs, but no spatial preference was detected (Figure S3). Abundance of recruits was not significantly different among replicate SMURFs within sites A and B (Kruskal–Wallis test,  $\chi^2 = 0.38$ ,  $p$  value = n.s.,  $n = 42$  and  $\chi^2 = 1.99$ ,  $p$  value = n.s.,  $n = 42$ , respectively), or between the two sites (Wilcoxon rank sum test,  $W = 893$ ,  $p$  value = n.s.,  $n = 84$ ).

Fish recruited every week at both sites but the majority of recruitment (72%) occurred during the first two sampling weeks

**TABLE 1** Environmental variables

Variable	Unit	Spa. res.	Temp. res.	Type	Dataset/Source	Reference
SST	°C	~6 km	Daily	RS + DO	Copernicus Marine environment monitoring service (marine.copernicus.eu)	OSTIA <sup>a</sup> ; Donlon et al. (2012)
CHLa	mg/m <sup>3</sup>	~4 km	Daily	RS		Gohin et al. (2008)
U and V current	m/s	~3 km	Daily	MO		IBI <sup>b</sup> ; Sotillo et al. (2015)
Wind speed	m/s	NA	Hourly	DO	Local weather station	NA
Wind direction	°	NA	Hourly			NA
Moon phase	%	NA	Daily	MO	Portuguese calendar	NA
Tidal amplitude	m	NA	Daily	MO	Hydrographic Institute	NA

Listed are the unit, original spatial and temporal resolution (Spa. and Temp. res., respectively), the type (RS, remote sensing; DO, direct observation; MO, model), source and reference of the dataset.

<sup>a</sup>Operational Sea Surface Temperature and Sea Ice Analysis (OSTIA) run by the UK Met Office combines remote sensed satellite data provided by the GHRSSST project with in situ observations, to determine through an Optimal Interpolation procedure global daily sea surface temperature (SST; Donlon et al., 2012).

<sup>b</sup>IBI (Iberian Biscay Irish) Ocean Analysis and Forecasting system run by Puertos del Estado and Mercator Ocean is based on an eddy-resolving NEMO model application driven by meteorological and oceanographic forcing (Madec, 2008; Sotillo et al., 2007, 2015).

(Figure 2a). Despite a sharp decrease in recruitment after the first 2 weeks, three smaller peaks were observed at the beginning and end of August and at the end of September (Figure 2a). Standard length of fish collected during recruitment peaks was very similar, but on subsequent weeks, off-peak samples tended to have older and larger fish (Figure 3). Sampling dates during which the collected fish were generally smaller (samples with lowest median and smaller variability of SL) likely indicate the arrival of a new recruitment group. Accordingly, four recruitment groups were identified during the sampling period (Figure 3).

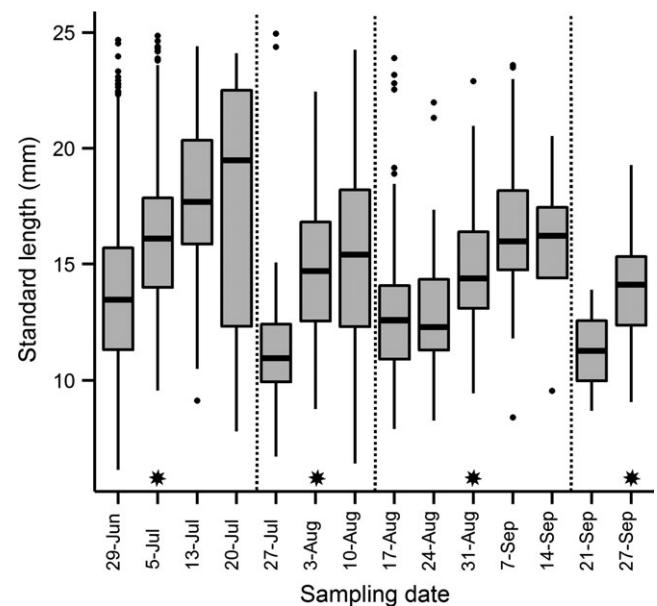
Estimated back-calculated hatching dates of recruits occurred from 10 May through 3 September, with a decrease in hatching frequency over time (Figure 2b). Three clear hatching cohorts (i.e., peaks separated by days on which no or only few hatching occurred) were detected, with a fourth one that was less distinct and had few individuals (Figure 2b). Overall, SL of recruits decreased from the first to the fourth hatching cohort, with fish hatched in the first cohort recruiting at significantly larger sizes than fish from the third cohort ( $\chi^2 = 23.85$ ;  $df = 3$ ;  $p < .0001$ ;  $n = 2,126$ ; post-hoc: first versus third cohort:  $\chi^2 = 5.94$ ;  $p < .001$ ; Figure 4). Fish belonging to different recruitment groups could have hatched within the same hatching cohort (Figure 5) and, inversely fish from the same recruitment group could belong to different hatching cohorts.

The sampling encompassed four tidal cycles, while during the estimated hatching period five tidal cycles occurred (Figures 2a,b). The tidal range extended from 1 m to 3.5 m. From the beginning of sampling through early June, the upwelling index was around or below 0, indicating a period of respectively relaxation or downwelling (Figure 2c). From early June onwards, the upwelling index steadily increased. Prior to early June, SST increased from approximately 17–20°C, then decreased to 16°C by the end of July and increased again, stabilizing around 19°C until the end of the sampling period (Figure 2d). CHLa peaked similarly to the upwelling index in mid July and mid September (Figure 2e). A similar temporal pattern as for SST was observed for the surface currents in the marine park, as from the start of June currents changed from less stable

conditions including days with northward currents, to almost exclusively south and south-eastward currents (Figure 2f).

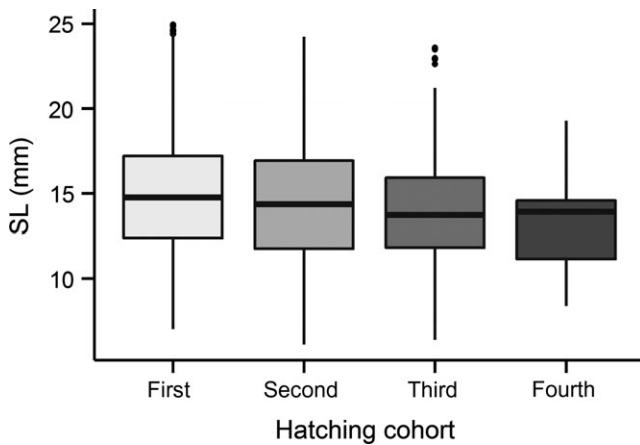
After a stepwise forward and backward selection process, the GAM model containing the factor moon phase, and variables upwelling (UP\_INDEX) and U current component (U) as smoothing functions was the one with the lowest AIC (523.1) and explained the largest part of the deviance in recruitment of *T. trachurus* (71.7%; Table 2). No strong residual pattern was observed and no autocorrelation was detected (Figure S4a,b). Adding factor SITE lowered the fit of the model and the factor was also not significant.

Lunar phase had a strong influence on the recruitment of Atlantic horse mackerel, with higher numbers of recruits collected after the third quarter and new moon phases (Figures 2a and 6a). Results of the smoothed variables indicated that recruitment decreased with

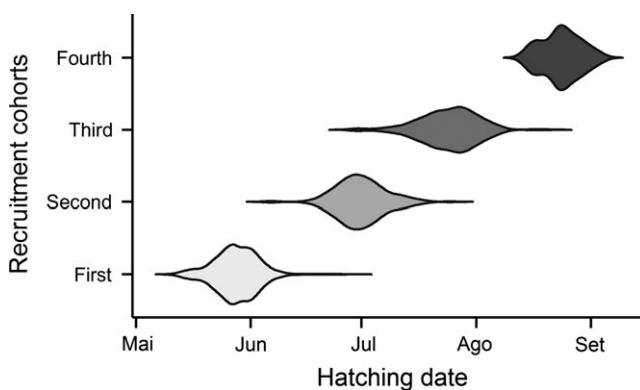


**FIGURE 3** Length distribution of weekly sampled recruits. Stars indicate weeks of peak recruitment and dashed lines separate recruitment groups





**FIGURE 4** Length distribution of recruits for each hatching cohort



**FIGURE 5** Hatching period of recruitment groups; areas are scale-independent

increasing upwelling index (Figure 7a). Recruitment decreased with decreasing east-west current component ( $U$ ) and was higher at positive values (Figure 7b).

The optimal combination of environmental variables for the hatching pattern models included moon phase, hatching cohort, upwelling index (UP\_INDEX) and SST with a smoothing function (Table 2). Including the factor cohort as a random effect lead to a much better fit than the model without this dependence structure (AIC = 284.1 vs. AIC = 292.4; likelihood ratio test:  $p < .005$ ; Table 2) and eliminated the residual autocorrelation (Figure S5 D vs. B). No clear patterns were observed when plotting model residuals against fitted values and against environmental variables.

Most of the recruited fish hatched during third quarter and new moon periods (Figures 2b and 6b). The hatching abundance was negatively related to the upwelling index (Figure 7c). A non-linear relationship was found between SST and hatching (Figure 7d).

## 4 | DISCUSSION

This study recorded for the first time recruitment of post-larval and early juvenile Atlantic horse mackerel to the nearshore (~100 m off-shore), suggesting that this species is using shallow water rocky reefs

as nursery areas. The detection of such behaviour is innovative, given that high larvae and egg abundances of this species were usually detected above the shelf edge (Álvarez et al., 2012; Farinha & Borges, 1994; Farinha & Lopes, 1996; Fives et al., 2001) and because only few studies have occasionally noted the occurrence of newly hatched larvae in the nearshore (Borges, Beldade, & Gonçalves, 2007; Borges, Ben-Hamadou et al., 2007; Sabatés, Zabala, & García-Rubies, 2003). Our results indicate that Atlantic horse mackerel utilises the nearshore during their early growth period and clearly associates with floating structures. A thigmotactic behaviour has also been observed for other carangid species (e.g., Dempster & Kingsford, 2004; Masuda & Tsukamoto, 2000; Masuda, Yamashita, & Matsuyama, 2008), and, in particular, for Atlantic horse mackerel in the Mediterranean by Deudero et al. (1999) and Massutí et al. (1999), who studied the functioning of fish aggregating devices (FADs). In contrast to our study, FADs were installed further off-shore (4–7 nautical miles) and had only sampled Atlantic horse mackerel larger than 36 mm (average fork length = 64 mm). This might indicate that post-larval and early juvenile stages may use the nearshore as a nursery area before moving to deeper waters, their main adult habitat (Borges & Gordo, 1991; Lloris & Moreno, 1995; Sousa, Azevedo, & Gomes, 2005).

We show that *T. trachurus* have a clear depth preference, as 99% of individuals aggregated in surface collectors. This confirms previous studies on vertical distribution which recorded eggs and larvae predominantly at the surface (Berenbeim, 1974; Southward & Barrett, 1983; Coombs, Conway, & Halliday, 1996; Borges, Beldade et al., 2007). Our results also indicate that Atlantic horse mackerel forms schools during the larval and post-larval phase, consisting of different size and age individuals which had likely hatched on different days. Therefore, the pelagic larval duration (PLD) might be variable in this species. These schools are assumed to be distributed patchily as the number of recruits varied largely among SMURFs without any clear pattern, and no significant relationship between sampling site and recruitment intensity. Possible reasons could be variation in small-scale flow patterns (Breitburg et al., 1995) and sweepstake recruitment (e.g., Moberg & Burton, 2000; Selkoe, Gaines, Caselle, & Warner, 2006), but to clarify this further, oceanographic and genetic analysis would be needed.

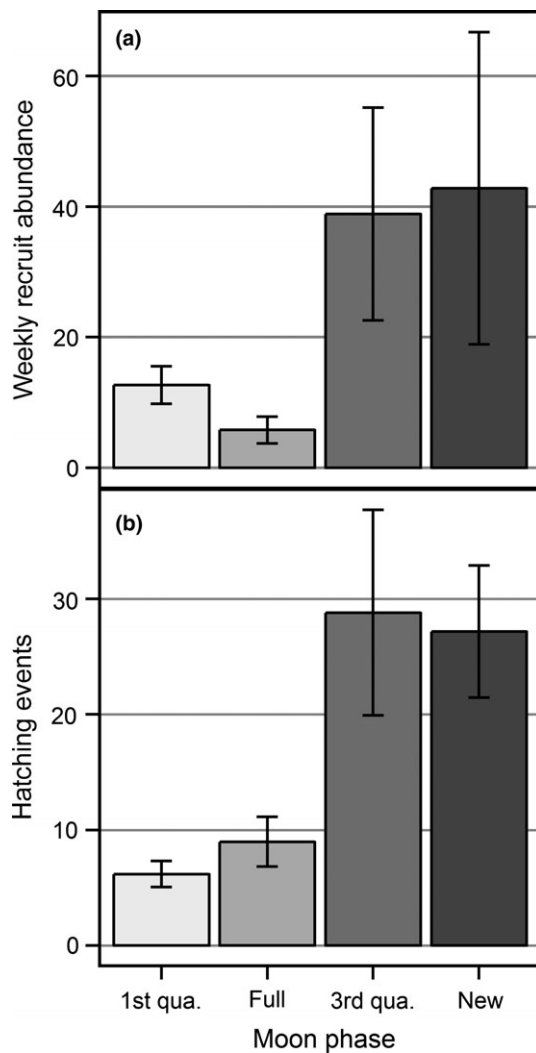
The strong decrease in recruit abundance over the sampling period can be hypothesized to be associated with the end of the spawning season, but in this region this is known to extend to the summer and autumn (Arruda, 1984; Barraca, 1964; Borges, Dinis, & Monteiro, 1977; Borges & Gordo, 1991). The decrease and weekly variability in recruit abundance might also be caused by variability in oceanographic conditions affecting larval survival and dispersal. Other factors contributing to larval natural mortality, such as predation pressure, starvation and disease or maternal effects, have not been analysed in this study and are not discussed here.

Despite differences in abundance, recruitment peaks followed a clear cyclic pattern with a roughly monthly periodicity corresponding to a lunar pattern. Most fish recruited during the waning (third quarter) and new moon periods. For many fish species, lunar periodicity

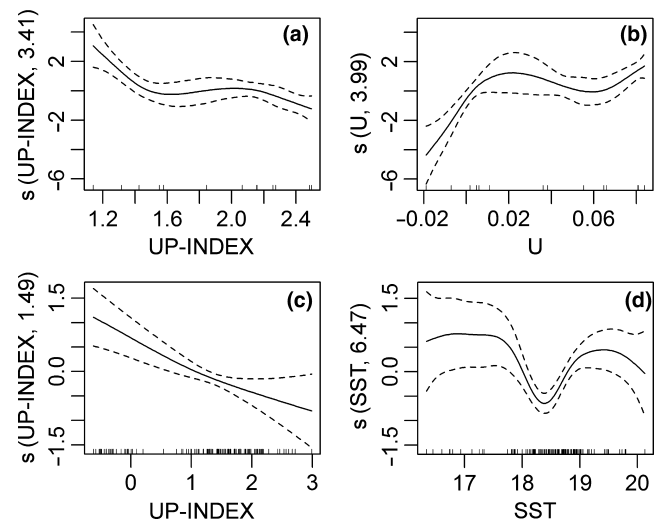
**TABLE 2** Model results of the GAM of the recruitment data and of the GAMM of the hatching data with and without random effect

Data	Model type	Dev. expl.	$r^2$ adj.	AIC	log Lik. (df)	Predictors	df/edf	$\chi^2/F$	p
Recruitment	GAM	71.7	0.46	523.08	248.41 (13.13)	fMOON	3.00	19.6	<.001
						UP_INDEX	3.41	41.4	<.001
						U	3.99	34.4	<.001
Hatching	GAMM	–	0.75	295.21	–138.6 (9)	fMOON	3.00	13.3	<.001
						UP_INDEX	1.00	168.0	<.001
						SST	3.75	12.8	<.001
Hatching	GAMM with random effect	–	0.40	284.14	–132.07 (10)	fMOON	3.00	17.9	<.001
						UP_INDEX	1	13.5	<.001
						SST	6.41	7.0	<.001

The following information is provided for each model: Dev. expl., explained deviance;  $r^2$  adj., adjusted  $r^2$ ; AIC, Akaike Information Criterion. For each predictor factor moon phase (fMOON), upwelling index (UP\_INDEX), U current component (U) and SST are listed: degrees of freedom (df) or effective degrees of freedom (edf) for smoothed variables, Chi-square statistics ( $\chi^2$ ) for GAM and F statistics for GAMM models (F), and significance value (p).

**FIGURE 6** Mean recruit abundance (a) and mean hatching intensity (b) at each moon phase; error bars indicate SE

in recruitment has been established. Moreover, the type of moon phase influencing recruitment (e.g., full, new, quarter moons) is species-specific and likely context-dependent depending on tidal flow

**FIGURE 7** Estimated smoothing curves and 95% confidence bands (dashed lines), illustrating the influence of upwelling (a) and U current component (b) on recruit abundance and upwelling (c) and SST (d) on hatching intensity

and light levels. Two potential explanations for lunar recruitment patterns have been proposed; predator avoidance theory, and the other related with reef sound. Predator avoidance due to low light levels has been documented (Robertson, Green, & Victor, 1988; Sponaugle & Cowen, 1994) and although not tested here, it could explain the higher recruit abundances recorded, from the third quarter phase onwards, when both moon illumination and the time when the moon is visible over the horizon progressively decrease, until a minimum light is reached during new moon. A second, new area of research which is still in its infancy, is reef soundscape. Maximal sound intensity created by biological processes occurs during new moon in both tropical (Staaterman et al., 2014) and temperate reefs (Radford, Jeffs, Tindle, & Montgomery, 2008), which might increase the ability of fish to detect and to orient to reefs.

The hatching pattern of those fish that survived the larval phase and recruited to SMURFS showed a clear lunar cycle with distinct

hatching cohorts. A lunar spawning pattern around new and full moon has also been described for other carangid species such as *Trachurus declivis* (Jordan, 1994), *Caranx melampygus*, *Caranx ignobilis* (Johannes, 1978), and only around full moon for *Caranx mate* and *Carangoides fulvoguttatus* (Johannes, 1978). Nevertheless, all of these species, with the exception of *T. declivis*, are carangids with tropical and nearshore distributions. Spawning around a specific moon phase might facilitate the aggregation of fish and increase the fertilization success (Graham & Castellanos, 2005; Johannes, 1978; Whaylen, Pattengill-Semmens, Semmens, Bush, & Boardman, 2004).

In addition to a lunar pattern, upwelling was negatively correlated to recruitment and hatching. This supports the study of Santos et al. (2001), which revealed a negative correlation between upwelling and the overall yearly recruitment of the Atlantic horse mackerel to the fishery in Portugal. In our study, when summer upwelling intensified, hatching decreased rapidly, but this result can also indicate that fewer individuals survived the pelagic larval phase. Although the upwelling index was found to be highly positively correlated with CHLa concentration, the negative correlation of both hatching and recruitment with upwelling could be driven by upwelling generated turbulence and offshore advection (Fiúza et al., 1982; Rossi et al., 2013) in spite of an increase of phyto- and zooplankton production (Cunha, 1993; Moita, 2003).

Intensified offshore advection of surface water (offshore Ekman transport; Relvas et al., 2007) can transport larval fish offshore (Rodríguez, Barton, Hernández-León, & Arístegui, 2004; Rodríguez et al., 1999; Rodríguez, Hernández-León, & Barton, 1999) and potentially increase larval mortality (Bakun & Parrish, 1980; Parrish, Bakun, Husby, & Nelson, 1983). This could partially explain the decrease of recruitment, as the majority of fish recruiting after the first peak had hatched during upwelling conditions. Indeed, in our study stronger south and south-eastward (i.e., offshore) currents occurred when upwelling started.

Earlier studies on other pelagic fish species, suggested that they have developed a reproductive strategy that benefits from upwelling patterns (Bakun, 1996; Cubillos, Arcos, Bucarey, & Canales, 2001; Cury & Roy, 1989; Cushing, 1974; Lasker, 1978; Roy et al., 1989). Future studies should explore this hypothesis for Atlantic horse mackerel.

Fish collected in weeks following each of the four observed recruitment peaks were larger and older than fish that settled during peaks. This could be due to several reasons: (i) these fish belonged to the previous recruitment pulse of fish arriving to the nearshore, and kept growing locally; (ii) they have spent more time offshore before arriving to the nearshore, i.e., delayed recruitment, or (iii) all fish might have arrived to the nearshore at the same time, but some delayed their arrival to the SMURFs. The ability to delay recruitment is known for reef fish species (e.g., Cowen, 1991; McCormick, 1999; Victor, 2007). In general, when comparing hatching cohorts, the size of recruits decreased over the sampling period. Additionally, fish of the first hatching cohort had a higher growth rate than fish of the following cohorts

(Van Beveren et al., 2016). We hypothesise that environmental conditions prevailing during larval growth might have caused these differences. The first cohort developed during a period of downwelling conditions and at the start of upwelling, whereas fish of the later cohorts grew only during increasing upwelling conditions with increasing CHLa concentration. On average, the temperature was higher during the larval growth of the first cohort than for the other cohorts and this might have led to a faster larval growth and to a larger size at recruitment of the first cohort (McCormick & Molony, 1995; Sponaugle, Grorud-Colvert, & Pinksard, 2006; Takahashi & Watanabe, 2004). Meekan et al. (2003) observed that larval growth was higher during absence of upwelling, when water temperatures were higher and prey abundance lower, concluding that temperature was more important for larval growth than prey abundance. Our results were similar, as fish of the second and third hatching cohorts were smaller and had a lower growth rate despite higher CHLa concentration (Van Beveren et al., 2016).

The large majority of fish from the first hatching cohort with faster larval growth recruited to our SMURFs during the first and highest recruitment peak. Similar results were found in other species with faster larval growth and higher rate of survival (Hare & Cowen, 1997; Houde, 1987; Takahashi, Sassa, & Tsukamoto, 2012; Wilson & Meekan, 2002) being associated with higher recruit abundance (Fontes, Santos, Afonso, & Caselle, 2011; Jenkins & King, 2006; Robert, Castonguay, & Fortier, 2007; Shima & Findlay, 2002; Watanabe, Kurita, Noto, Oozeki, & Kitagawa, 2003).

In summary, this first study of fine scale recruitment patterns of Atlantic horse mackerel revealed a clear relationship between the lunar cycle and the upwelling regime with both spawning and recruitment to nearshore environments. These processes could be driving population fluctuations and hence be key to inform management of such an important commercial species. In addition, this study suggests that nearshore areas might be important nursery grounds for the growth of post-larval and juvenile Atlantic horse mackerel.

## ACKNOWLEDGEMENTS

We wish to thank G. Franco, H. Folhas, A. Rebelo and F. Pessanha for help during sampling campaigns. We thank R. Coelho for advice on the statistical analysis. We thank the local company Secil for providing local wind data and for co-funding project BIOMARES (EU-LIFE 06 NAT/P/000192) and its subsequent programs. This study had the support of Fundação para a Ciência e Tecnologia (FCT), through a PhD grant (SFRH/BD/72970/2010) for MK, a post doc fellowship (SFRH/BPD/23743/2005) for RB and through the projects (POCTI/MAR/57934/2004), MATRIX (PTDC/MAR/115226/2009), REEFISH (PTDC/MAR-EST/4356/2012), the Pluriannual Programmes (R&D Unit 331/94, PEST-OE/MAR/UI0331/2011), and the strategic project Multi/04326/2013 granted to CCMAR, and PEst-OE/MAR/UI0331/2011 and UID/MAR/04292/2013 granted to MARE.



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## REFERENCES

- Abaunza, P., Murta, A. G., Campbell, N., Cimmaruta, R., Comesaña, A. S., Dahle, G., ... Zimmermann, C. (2008). Stock identity of horse mackerel (*Trachurus trachurus*) in the Northeast Atlantic and Mediterranean Sea: Integrating the results from different stock identification approaches. *Fisheries Research*, *89*, 196–209. <https://doi.org/10.1016/j.fishres.2007.09.022>
- Álvarez, I., Catalán, I. A., Jordi, A., Palmer, M., Sabatés, A., & Basterretxea, G. (2012). Drivers of larval fish assemblage shift during the spring-summer transition in the coastal Mediterranean. *Estuarine, Coastal and Shelf Science*, *97*, 127–135. <https://doi.org/10.1016/j.ecss.2011.11.029>
- Ammann, A. J. (2004). SMURFs: Standard monitoring units for the recruitment of temperate reef fishes. *Journal of Experimental Marine Biology and Ecology*, *299*, 135–154. <https://doi.org/10.1016/j.jembe.2003.08.014>
- Anderson, T. W., & Carr, M. H. (1998). BINKCE: A highly efficient net for collecting reef fishes. *Environmental Biology of Fishes*, *51*, 111–115. <https://doi.org/10.1023/A:1007355408723>
- Arruda, L. M. (1984). Sexual-maturation and growth of *Trachurus-trachurus* (L) along the Portuguese coast. *Investigacion Pesquera*, *48*, 419–430.
- Bakun, A. (1996). *Patterns in the Ocean: Ocean processes and marine population dynamics*. San Diego, CA: University of California Sea Grant, in cooperation with Centro de Investigaciones Biológicas de Noroeste, La Paz, Baja California Sur, Mexico, 323 pp.
- Bakun, A., & Parrish, R. H. (1980). Environmental inputs to fishery population models for eastern boundary current regions. In G. D. Sharp (Ed.), *Workshop on the effects of environmental variation on the survival of larval pelagic fishes*. Lima, Peru: IOC Workshop Report.
- Barraca, I. F. (1964). Quelques aspects de la biologie et de la pêche de chinchard, *Trachurus trachurus* (L.) de la côte Portugaise. *Notas e Estudos do Instituto do Biología Marítima*, *29*, 1–21.
- Beldade, R., Borges, R., & Gonçalves, E. J. (2006). Depth distribution of nearshore temperate fish larval assemblages near rocky substrates. *Journal of Plankton Research*, *28*, 1003–1013. <https://doi.org/10.1093/plankt/fbl035>
- Beldade, R., Erzini, K., & Gonçalves, E. J. (2006). Composition and temporal dynamics of a temperate rocky cryptobenthic fish assemblage. *Journal of the Marine Biological Association of the United Kingdom*, *86*, 1221–1228. <https://doi.org/10.1017/S0025315406014226>
- Berenbeim, D. Y. (1974). On regularities in the variability of the spawning terms of horse mackerel (*Trachurus trachurus*) within the spawning area. *ICES CM 1974, J14*, 9. (mimeo).
- Borges, R., Beldade, R., & Gonçalves, E. (2007). Vertical structure of very nearshore larval fish assemblages in a temperate rocky coast. *Marine Biology*, *151*, 1349–1363. <https://doi.org/10.1007/s00227-006-0574-z>
- Borges, R., Ben-Hamadou, R., Chicharo, M. A., Ré, P., & Gonçalves, E. J. (2007). Horizontal spatial and temporal distribution patterns of nearshore larval fish assemblages at a temperate rocky shore. *Estuarine, Coastal and Shelf Science*, *71*, 412–428. <https://doi.org/10.1016/j.ecss.2006.08.020>
- Borges, F., Dinis, H., & Monteiro, C. (1977). Resultats preliminaires sur la ponte, composition des tailles et etat du stock du chinchard (*Trachurus trachurus* L.) de la côte continentale portugaise. *ICES Cooperative Research Report, CM, J14*, 22.
- Borges, M. F., & Gordo, L. S. (1991). Spatial distribution by season and some biological parameters of horse mackerel (*Trachurus trachurus* L.) in the Portuguese continental waters (Division IXa). *ICES CM, H54*, 17.
- Borges, R., Vaz, J., Serrão, E. A., & Gonçalves, E. J. (2009). Short-term temporal fluctuation of very-nearshore larval fish assemblages at the Arrábida Marine Park (Portugal). 10th International Coastal Symposium, 2009 Lisbon. *Journal of Coastal Research, SI 56*, 376–380.
- Breitburg, D. L., Palmer, M. A., & Loher, T. (1995). Larval distributions and the spatial patterns of settlement of an oyster reef fish: Responses to flow and structure. *Marine Ecology Progress Series*, *125*, 45–60.
- Carr, M. H., & Syms, C. (2006). Recruitment. In L. G. Allen, D. J. Pondella, & M. H. Horn (Eds.), *The ecology of marine fishes: California and adjacent waters* (pp. 411–427). Berkeley and Los Angeles: University of California Press.
- Caselle, J. E., Carr, M. H., Malone, D. P., Wilson, J. R., & Wendt, D. E. (2010). Can we predict interannual and regional variation in delivery of pelagic juveniles to nearshore populations of rockfishes (Genus *Sebastes*) using simple proxies of ocean conditions? *California Cooperative Oceanic Fisheries Investigations Reports*, *51*, 91–105.
- Caselle, J. E., Kinlan, B. P., & Warner, R. R. (2010). Temporal and spatial scales of influence on nearshore fish settlement in the Southern California Bight. *Bulletin of Marine Science*, *86*, 355–385.
- Coombs, S. H., Conway, D. V. P., & Halliday, N. C. (1996). The vertical distribution of eggs and larvae of horse mackerel (*Trachurus trachurus*). *ICES CM*, *S48*, 10.
- Cowen, R. K. (1991). Variation in the planktonic larval duration of the temperate wrasse *Semicossyphus pulcher*. *Marine Ecology Progress Series*, *69*, 9–15. <https://doi.org/10.3354/meps069009>
- Cubillos, L. A., Arcos, D. F., Bucarey, D. A., & Canales, M. T. (2001). Seasonal growth of small pelagic fish off Talcahuano, Chile (37°S, 73°W): A consequence of their reproductive strategy to seasonal upwelling? *Aquatic Living Resources*, *14*, 115–124. [https://doi.org/10.1016/S0990-7440\(01\)01112-3](https://doi.org/10.1016/S0990-7440(01)01112-3)
- Cunha, M. E. (1993). Spatial variation of the zooplankton biomass in relation to the hydrographic conditions off the Portuguese Coast. *ICES CM 1993, L63*, 1–23.
- Cury, P., & Roy, C. (1989). Optimal environmental window and pelagic fish recruitment success in upwelling areas. *Canadian Journal of Fisheries and Aquatic Sciences*, *46*, 670–680. <https://doi.org/10.1139/f89-086>
- Cushing, D. H. (1974). The natural regulation of fish populations. In T. F. R. Harden-Jones (Ed.), *Sea fisheries research* (pp. 399–412). New York, NY: John Wiley and Sons.
- Daskalov, G. (1999). Relating fish recruitment to stock biomass and physical environment in the Black Sea using generalized additive models. *Fisheries Research*, *41*, 1–23. [https://doi.org/10.1016/S0165-7836\(99\)00006-5](https://doi.org/10.1016/S0165-7836(99)00006-5)
- Dempster, T., & Kingsford, M. J. (2004). Drifting objects as habitat for pelagic juveniles fish off New South Wales, Australia. *Marine and Freshwater Research*, *55*, 675–678. <https://doi.org/10.1071/MF04071>
- Deudero, S., Merella, P., Morales-Nin, B., Massutí, E., & Alemany, F. (1999). Fish communities associated with FADs. *Scientia Marina*, *63*, 199–207. <https://doi.org/10.3989/scimar.1999.63n3-4199>
- Di Padoa, E. (1956). *Carangidae, Fauna e Flora del Golfo di Napoli, Monogr. 38 (3ª Puntata), Parte III. Stazione Zoologica di Napoli*. pp. 548–561.
- Doherty, P. J. (2002). Variable replenishment and the dynamics of reef fish populations. In P. F. Sale (Ed.), *Coral reef fishes: Dynamics and diversity in a complex ecosystem* (pp. 327–355). San Diego, CA: Academic Press. <https://doi.org/10.1016/B978-012615185-5/50019-0>
- Donlon, C. J., Martin, M., Stark, J. D., Roberts-Jones, J., Fiedler, E., & Wimmer, W. (2012). The operational sea surface temperature and sea ice Analysis (OSTIA) system. *Remote Sensing of Environment*, *116*, 140–158. <https://doi.org/10.1016/j.rse.2010.10.017>
- FAO (2017). *Fisheries and aquaculture information and statistics service [Online]*. Retrieved from [www.fao.org](http://www.fao.org) [Accessed 06.04.2016].

- Farinha, A., & Borges, M. F. (1994). Daily egg production of horse mackerel (*Trachurus trachurus* L) in Portuguese area (DIV. IXa). *ICES CM*, H:19, 1–9.
- Farinha, A., & Lopes, P. D. C. (1996). Horizontal and vertical distribution of planktonic phases of *Trachurus trachurus* (L.) and *Sardina pilchardus* (Walbaum), off Northwestern Portuguese coast. *ICES CM*, S:28, 1–9.
- Fiúza, A. F. G., Macedo, M. E., & Guerreiro, M. R. (1982). Climatological space and time variation of the Portuguese coastal upwelling. *Oceanologica Acta*, 5, 31–40.
- Fives, J. M., Acevedo, S., Lloves, M., Whitaker, A., Robinson, M., & King, P. A. (2001). The distribution and abundance of larval mackerel, *Scomber scombrus* L., horse mackerel, *Trachurus trachurus* (L.), hake, *Merluccius merluccius* (L.), and blue whiting, *Micromesistius poutassou* (Risso, 1826) in the Celtic Sea and west of Ireland during the years 1986, 1989 and 1992. *Fisheries Research*, 50, 17–26. [https://doi.org/10.1016/S0165-7836\(00\)00239-3](https://doi.org/10.1016/S0165-7836(00)00239-3)
- Fontes, J., Santos, R. S., Afonso, P., & Caselle, J. E. (2011). Larval growth, size, stage duration and recruitment success of a temperate reef fish. *Journal of Sea Research*, 65, 1–7. <https://doi.org/10.1016/j.seares.2010.05.001>
- Graham, R. T., & Castellanos, D. W. (2005). Courtship and spawning behaviors of carangid species in Belize. *Fishery Bulletin*, 103, 426–432.
- Gohin, F., Saulquin, B., Oger-Jeanneret, H., Lozac'h, L., Lampert, L., Lefebvre, A., ... Bruchon, F. (2008). Towards a better assessment of the ecological status of coastal waters using satellite-derived chlorophyll-a concentrations. *Remote Sensing of Environment*, 112, 3329–3340.
- Hare, J. A., & Cowen, R. K. (1997). Size, growth, development, and survival of the planktonic larvae of *Pomatomus saltatrix* (Pisces: Pomatomidae). *Ecology*, 78, 2415–2431. [https://doi.org/10.1890/0012-9658\(1997\)078\[2415:SGDASO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1997)078[2415:SGDASO]2.0.CO;2)
- Houde, E. D. (1987). Fish early life dynamics and recruitment variability. *American Fisheries Society Symposium*, 2, 17–29.
- Jenkins, G. P., & King, D. (2006). Variation in larval growth can predict the recruitment of a temperate, seagrass-associated fish. *Oecologia*, 147, 641–649. <https://doi.org/10.1007/s00442-005-0336-5>
- Johannes, R. E. (1978). Reproductive strategies of coastal marine fishes in the tropics. *Environmental Biology of Fishes*, 3, 65–84. <https://doi.org/10.1007/BF00006309>
- Jordan, A. R. (1994). Age, growth and back-calculated birthdate distributions of larval jack mackerel, *Trachurus declivis* (Pisces: Carangidae), from eastern Tasmanian coastal waters. *Marine and Freshwater Research*, 45, 19–33. <https://doi.org/10.1071/MF9940019>
- Lasker, R. (1978). The relation between oceanographic conditions and larval anchovy food in the California Current: Identification of factors contributing to recruitment failure. *Rapports et Procès-verbaux des Réunions*, 173, 212–230.
- Lavin, A., Moreno-Ventas, X., Ortiz de Zárate, V., Abaunza, P., & Cabanas, J. M. (2007). Environmental variability in the North Atlantic and Iberian waters and its influence on horse mackerel (*Trachurus trachurus*) and albacore (*Thunnus alalunga*) dynamics. *ICES Journal of Marine Science*, 64, 425–438. <https://doi.org/10.1093/icesjms/fsl042>
- Lloris, D., & Moreno, T. (1995). Distribution model and association in three pelagic congeneric species (*Trachurus* spp.) present in the Iberic Mediterranean Sea. *Scientia Marina*, 59, 399–403.
- Lockwood, S. J., & Johnson, P. O. (1977). *Horse Mackerel Trachurus trachurus*. Laboratory Leaflet No. 38. Lowestoft, UK: Ministry of Agriculture, Fisheries and Food, Directory of Fisheries Research.
- Macer, C. T. (1977). Some aspects of the biology of the horse mackerel [*Trachurus trachurus* (L.)] in waters around Britain. *Journal of Fish Biology*, 10, 51–62. <https://doi.org/10.1111/j.1095-8649.1977.tb04041.x>
- Madec, G. (2008). *NEMO Ocean General Circulation Model Reference Manual v. 3.4. Note du Pôle de modélisation*. Paris, France: Institut Pierre-Simon Laplace (IPSL).
- Massuti, E., Morales-Nin, B., & Deudero, S. (1999). Fish fauna associated with floating objects sampled by experimental and commercial purse nets. *Scientia Marina*, 63, 219–227. <https://doi.org/10.3989/scimar.1999.63n3-4229>
- Masuda, R., & Tsukamoto, K. (2000). Onset of association behavior in striped jack, *Pseudocaranx dentex*, in relation to floating objects. *Fishery Bulletin*, 98, 864–869.
- Masuda, R., Yamashita, Y., & Matsuyama, M. (2008). Jack mackerel *Trachurus japonicus* juveniles use jellyfish for predator avoidance and as a prey collector. *Fisheries Science*, 74, 276–284. <https://doi.org/10.1111/j.1444-2906.2008.01522.x>
- McCormick, I. M. (1999). Delayed metamorphosis of a tropical reef fish (*Acanthurus triostegus*): A field experiment. *Marine Ecology Progress Series*, 176, 25–38. <https://doi.org/10.3354/meps176025>
- McCormick, I. M., & Molony, W. B. (1995). Influence of water temperature during the larval stage on size, age and body condition of a tropical reef fish at settlement. *Marine Ecology Progress Series*, 118, 59–68. <https://doi.org/10.3354/meps118059>
- Meekan, M. G., Carleton, J. H., McKinnon, A. D., Flynn, K., & Furnas, M. (2003). What determines the growth of tropical reef fish larvae in the plankton: Food or temperature? *Marine Ecology Progress Series*, 256, 193–204. <https://doi.org/10.3354/meps256193>
- Milicich, M. J. (1994). Dynamic coupling of reef fish replenishment and oceanographic processes. *Marine Ecology Progress Series*, 110, 135–144. <https://doi.org/10.3354/meps110135>
- Moberg, P. E., & Burton, R. S. (2000). Genetic heterogeneity among adult and recruit red sea urchins, *Strongylocentrotus franciscanus*. *Marine Biology*, 136, 773–784. <https://doi.org/10.1007/s002270000281>
- Moita, T. (2003). Distribution of chlorophyll a and *Gymnodinium catenatum* associated with coastal upwelling plumes off central Portugal. *Acta Oecologica*, 24, 125–132. [https://doi.org/10.1016/S1146-609X\(03\)00011-0](https://doi.org/10.1016/S1146-609X(03)00011-0)
- Parrish, R. H., Bakun, A., Husby, D. M., & Nelson, C. S. (1983). Comparative climatology of selected environmental processes in relation to Eastern boundary current pelagic fish reproduction. In G. D. Sharp & J. Csirke (Eds.), *Proceedings of the expert consultation to examine changes in abundance and species composition of neritic fish resources*. FAO Fish. Rep; pp. 731–777.
- Pepin, P., & Myers, R. A. (1991). Significance of egg and larval size to recruitment variability of temperate marine fish. *Canadian Journal of Fisheries and Aquatic Sciences*, 48, 1820–1828. <https://doi.org/10.1139/f91-215>
- Radford, C. A., Jeffs, A. G., Tindle, C. T., & Montgomery, J. C. (2008). Temporal patterns in ambient noise of biological origin from a shallow water temperate reef. *Oecologia*, 156, 921–929. <https://doi.org/10.1007/s00442-008-1041-y>
- R-Core-Team (2009). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Relvas, P., Barton, E. D., Dubert, J., Oliveira, P. B., Peliz, Á., da Silva, J. C. B., & Santos, A. M. P. (2007). Physical oceanography of the western Iberia ecosystem: Latest views and challenges. *Progress in Oceanography*, 74, 149–173. <https://doi.org/10.1016/j.jpocan.2007.04.021>
- Relvas, P., Luis, J., & Santos, A. M. P. (2009). Importance of the mesoscale in the decadal changes observed in the northern Canary upwelling system. *Geophysical Research Letters*, 36, L22601. <https://doi.org/10.1029/2009GL040504>.
- Robert, D., Castonguay, M., & Fortier, L. (2007). Early growth and recruitment in Atlantic mackerel *Scomber scombrus*: Discriminating the effects of fast growth and selection for fast growth. *Marine Ecology Progress Series*, 337, 209–219. <https://doi.org/10.3354/meps337209>
- Robertson, D. R., Green, D. G., & Victor, B. C. (1988). Temporal coupling of production and recruitment of larvae of a Caribbean Reef fish. *Ecology*, 69, 370–381. <https://doi.org/10.2307/1940435>
- Rodríguez, J. M., Barton, E. D., Hernández-León, S., & Aristegui, J. (2004). The influence of mesoscale physical processes on the larval fish

- community in the Canaries CTZ, in summer. *Progress in Oceanography*, 62, 171–188. <https://doi.org/10.1016/j.pocean.2004.07.006>
- Rodríguez, J. M., Hernández-León, S., & Barton, E. D. (1999). Mesoscale distribution of fish larvae in relation to an upwelling filament off Northwest Africa. *Deep Sea Research Part I: Oceanographic Research Papers*, 46, 1969–1984. [https://doi.org/10.1016/S0967-0637\(99\)00036-9](https://doi.org/10.1016/S0967-0637(99)00036-9)
- Rossi, V., Garçon, V., Tassel, J., Romagnan, J.-B., Stemmann, L., Jourdin, F., ... Morel, Y. (2013). Cross-shelf variability in the Iberian Peninsula Upwelling System: Impact of a mesoscale filament. *Continental Shelf Research*, 59, 97–114. <https://doi.org/10.1016/j.csr.2013.04.008>
- Roy, C., Cury, P., Fontana, A., & Belvéze, H. (1989). Stratégies spatio-temporelles de la reproduction des clupéidés des zones d'upwelling d'Afrique de l'Ouest. *Aquatic Living Resources*, 2, 21–29. <https://doi.org/10.1051/alr:1989003>
- Russell, R. (1976). Carangidae. In Russel, R. (Ed.), *The eggs and planktonic stages of British marine fishes* (pp. 197–202). London: Academic Press.
- Sabatés, A., Zabala, M., & García-Rubies, A. (2003). Larval fish communities in the Medes Islands Marine Reserve (North-west Mediterranean). *Journal of Plankton Research*, 25, 1035–1046. <https://doi.org/10.1093/plankt/25.9.1035>
- Santos, A. M. P., Borges, M. D. F., & Groom, S. (2001). Sardine and horse mackerel recruitment and upwelling off Portugal. *ICES Journal of Marine Science*, 58, 589–596. <https://doi.org/10.1006/jmsc.2001.1060>
- Selkoe, K. A., Gaines, S. D., Caselle, J. E., & Warner, R. R. (2006). Current shifts and kin aggregation explain genetic patchiness in fish recruits. *Ecology*, 87, 3082–3094. [https://doi.org/10.1890/0012-9658\(2006\)87\[3082:CSAKAE\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[3082:CSAKAE]2.0.CO;2)
- Shima, J. S., & Findlay, A. M. (2002). Pelagic larval growth rate impacts benthic settlement and survival of a temperate reef fish. *Marine Ecology Progress Series*, 235, 303–309. <https://doi.org/10.3354/meps235303>
- Smith-Vanith, W. F. (1986). Carangidae. In P. J. P. Whitehead, M. L. Bauchot, J. C. Hureau, J. Nielsen, & E. Tortonese (Eds.), *Fishes of the North-eastern Atlantic and the Mediterranean* (pp. 815–844). Paris, France: UNESCO.
- Sotillo, M. G., Cailleau, S., Lorente, P., Levier, B., Aznar, R., Reffray, G., ... Alvarez-Fanjul, E. (2015). The MyOcean IBI Ocean Forecast and Reanalysis Systems: Operational products and roadmap to the future Copernicus Service. *Journal of Operational Oceanography*, 8, 63–79. <https://doi.org/10.1080/1755876X.2015.1014663>
- Sotillo, M. G., Jordi, A., Ferrer, M. I., Conde, J., Tintoré, J., & Álvarez-Fanjul, E. (2007). The ESEOO regional ocean forecasting system. *Proceedings of the seventeenth International Offshore and Polar Engineering Conference*. 1716–1722.
- Sousa, P., Azevedo, M., & Gomes, M. C. (2005). Demersal assemblages off Portugal: Mapping, seasonal, and temporal patterns. *Fisheries Research*, 75, 120–137. <https://doi.org/10.1016/j.fishres.2005.03.012>
- Southward, A. J., & Barrett, R. L. (1983). Observations on the vertical distribution of zooplankton, including post-larval teleosts, off Plymouth in the presence of a thermocline and a chlorophyll-dense layer. *Journal of Plankton Research*, 5, 599–618. <https://doi.org/10.1093/plankt/5.4.599>
- Sponaugle, S., & Cowen, R. K. (1994). Larval durations and recruitment patterns of two Caribbean gobies (Gobiidae): Contrasting early life history in demersal spawners. *Marine Biology*, 120, 133–143.
- Sponaugle, S., Grorud-Colvert, K., & Pinkard, D. (2006). Temperature-mediated variation in early life history traits and recruitment success of the coral reef fish *Thalassoma bifasciatum* in the Florida Keys. *Marine Ecology Progress Series*, 308, 1–15. <https://doi.org/10.3354/meps308001>
- Staaterman, E., Paris, C. B., DeFerrari, H. A., Mann, D. A., Rice, A. N., & D'Alessandro, E. K. (2014). Celestial patterns in marine soundscapes. *Marine Ecology Progress Series*, 508, 17–32. <https://doi.org/10.3354/meps10911>
- Takahashi, M., Sassa, C., & Tsukamoto, Y. (2012). Growth-selective survival of young jack mackerel *Trachurus japonicus* during transition from pelagic to demersal habitats in the East China Sea. *Marine Biology*, 159, 2675–2685. <https://doi.org/10.1007/s00227-012-2025-3>
- Takahashi, M., & Watanabe, Y. (2004). Growth rate-dependent recruitment of Japanese anchovy *Engraulis japonicus* in the Kuroshio-Oyashio transitional waters. *Marine Ecology Progress Series*, 266, 227–238. <https://doi.org/10.3354/meps266227>
- Tavernetti, R., Morgan, S., & Yu, Q. (2009). Effect of biological fouling on passive collectors used to estimate fish recruitment. *Journal of Fish Biology*, 75, 699–706. <https://doi.org/10.1111/j.1095-8649.2009.02307.x>
- Trenkel, V. M., Huse, G., MacKenzie, B. R., Alvarez, P., Arrizabalaga, H., Castonguay, M., ... Speirs, D. C. (2014). Comparative ecology of widely distributed pelagic fish species in the North Atlantic: Implications for modelling climate and fisheries impacts. *Progress in Oceanography*, 129, Part B, 219–243. <https://doi.org/10.1016/j.pocean.2014.04.030>
- Van Beveren, E., Klein, M., Serrão, E. A., Gonçalves, E. J., & Borges, R. (2016). Early life history of larvae and early juvenile Atlantic horse mackerel *Trachurus trachurus* off the Portuguese west coast. *Fisheries Research*, 183, 111–118. <https://doi.org/10.1016/j.fishres.2016.05.018>
- Victor, B. C. (1982). Daily otolith increments and recruitment in two coral-reef wrasses, *Thalassoma bifasciatum* and *Halichoeres bivittatus*. *Marine Biology*, 71, 203–208. <https://doi.org/10.1007/BF00394631>
- Victor, B. C. (2007). *Coryphopterus kuna*, a new goby (Perciformes: Gobiidae: Gobiinae) from the western Caribbean, with the identification of the late larval stage and an estimate of the pelagic larval duration. *Zootaxa*, 1526, 51–61.
- Watanabe, Y., Kurita, Y., Noto, M., Oozeki, Y., & Kitagawa, D. (2003). Growth and survival of Pacific Saury *Cololabis saira* in the Kuroshio-Oyashio transitional waters. *Journal of Oceanography*, 59, 403–414. <https://doi.org/10.1023/A:1025532430674>
- Whaylen, L., Pattengill-Semmens, C. V., Semmens, B. X., Bush, P. G., & Boardman, M. R. (2004). Observations of a Nassau grouper, *Epinephelus striatus*, spawning aggregation site in Little Cayman, Cayman Islands, including multi-species spawning information. *Environmental Biology of Fishes*, 70, 305–313. <https://doi.org/10.1023/B:EBFI.0000033341.57920.a8>
- White, J. W., & Caselle, J. E. (2008). Scale-dependent changes in the importance of larval supply and habitat to abundance of a reef fish. *Ecology*, 89, 1323–1333. <https://doi.org/10.1890/07-0840.1>
- Wilson, J. R., Broitman, B. R., Caselle, J. E., & Wendt, D. E. (2008). Recruitment of coastal fishes and oceanographic variability in central California. *Estuarine, Coastal and Shelf Science*, 79, 483–490.
- Wilson, D. T., & Meekan, M. G. (2002). Growth-related advantages for survival to the point of replenishment in the coral reef fish *Stegastes partitus* (Pomacentridae). *Marine Ecology Progress Series*, 231, 247–260. <https://doi.org/10.3354/meps231247>
- Wood, S. N. (2006). *Generalized additive models: An introduction with R*. Chapman and Hall. Boca Raton, FL: CRC Press.
- Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society (B)*, 73, 3–36. <https://doi.org/10.1111/j.1467-9868.2010.00749.x>
- Wooster, W. S., Bakun, A., & McLain, D. R. (1976). The seasonal upwelling cycle along the eastern boundary of the North Atlantic. *Journal of Marine Research*, 34, 131–141.
- Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, 1, 3–13. <https://doi.org/10.1111/j.2041-210X.2009.00001.x>

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R. Statistics for biology and health*. New York, NY: Springer. <https://doi.org/10.1007/978-0-387-87458-6>

#### SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

**How to cite this article:** Klein M, Beveren EV, Rodrigues D, et al. Small scale temporal patterns of recruitment and hatching of Atlantic horse mackerel (L.) at a nearshore reef area. *Fish Oceanogr.* 2018;27:505–516. <https://doi.org/10.1111/fog.12269>