Pelagic habitat and offspring survival in the eastern stock of Atlantic bluefin tuna

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In this manuscript, we test how an understanding of geographical variation in larval fitness in relation to temperature and habitat use could be a useful method to improve our understanding of recruitment and develop better indices of annual recruitment. On the basis of the assumption that growth and survival of tuna larvae are influenced by temperature, we have developed a potential larval survival index for Atlantic bluefin tuna (*Thunnus thynnus*) by combining empirical data from egg and larval rearing experiments with temperature data from hydrodynamic models. The experiments were designed to test the full range of temperature variability that bluefin larvae would experience in the field and provide a mechanistic understanding of the processes driving egg and larval survival. We then developed a biological model using the temperature-related growth expressions and a size-dependent survival function for the larvae. The biological model was applied to a time-series of spatially explicit temperature data for the western Mediterranean from the Strait of Gibraltar to 6°E, which includes the major recognized bluefin tuna eastern stock spawning area, the Balearic Sea. Our results show that areas with high probabilities of larval survival coincide with those that would be considered as optimal based on other data sources (ichthyoplankton surveys, spawning female locations from commercial fisheries data, and adult tracking data). However, evidence of spawning has been found in areas with suboptimal thermal habitats, as predicted by the model, which we discuss regarding sampling effort and salinity fronts. There was a good match between the survival index and recruitment indices from standardized CPUE fisheries data. These results have implications for our understanding of the recruitment process of the eastern stock of Atlantic bluefin tuna, since they suggest that the combined effects of temporal and spatial variability of the environment drive recruitment success, which has important implications for the management of the species.

Keywords: Atlantic bluefin tuna, fish larvae recruitment, Mediterranean Sea, spawning stock, temperature

Introduction

The environments in which fish reproduce usually provide favourable food conditions for the larvae, suitable temperatures for egg and larval development, and/or suitable retention areas (Mullon *et al.*, 2002). Given the difficulties in directly studying both spawning and recruitment processes for many species, particularly large pelagic fish, a knowledge of the effects of environmental variability on egg and larval growth and survival rates can be used alternatively to forecast spawning locations, reproductive output, and/or recruitment strength. Most fisheries assessment models and much of fisheries theory is predicated on a relationship between the number of spawners and the eventual recruits that they produce. Although there is strong evidence for environmentally driven recruitment (Vert-Pre *et al.*, 2013; Szuwalski *et al.*, 2015), environmental information is rarely included in stock assessments of large pelagic fish. Understanding and monitoring the physical and biological processes that control recruitment, the ecological cornerstone of determining fish population dynamics, is essential for improving current fisheries stock assessments. Particularly, there is a need to take into account geographical variability in offspring fitness if spatial management decisions are to be taken in the future (Berger *et al.*, 2017).

Atlantic bluefin tuna (*Thunnus thynnus*) are managed by the International Commission for the Conservation of Atlantic Tunas (ICCAT) as two separate stocks: an eastern and a western stock. As with most assessed fish, estimates of recruitment and the functional shape of the stock–recruit relationship are major sources of uncertainty. There is no consensus among experts on which type of stock–recruit relationship to use, and trends in recruitment for the two stocks have been suggested to be correlated either with spawning biomass or environmental variability (e.g. see references in Porch and Lauretta, 2016). For the eastern stock, the functional form of the stock–recruit relationship remains elusive, as evidenced by the clear asynchronous fluctuation between spawning biomass and recruitment at a multidecadal scale (Anonymous, 2017; Figure 1), with high spawning biomass being associated with low recruitment events until the 1990s, low spawning biomass associated with high recruitment events during the 1990–2000s, and again high spawning biomass associated with low recruitment events since 2008. On the other hand, the increasing trend in annual recruitment from the 1970s to the early 2000s has been related to increasing summer temperatures in the Balearic Sea (Harford *et al.*, 2017), which suggests a significant environment–recruitment relationship. However, the scenario seems to be more complex since estimates from the latest assessment show that recruitment is decreasing despite the continual warming trend (Anonymous, 2017; Figure 1). This scenario suggests a potential density-dependent control at large temporal scales that, in combination with large-scale increasing trends in water temperature due to climate warming in the Mediterranean, may explain long-term fluctuations in recruitment. However, short-term variations, particularly the interannual variation that has occurred in the last decade, challenge the hypothesis of a direct thermal influence on interannual variability in recruitment (Figure 1).

The current challenge to developing a model of the recruitment dynamics of Atlantic bluefin tuna is to understand the mechanistic influence of regional environmental drivers that link spatial patterns of larval performance to interannual variability in recruitment. We applied laboratory-derived, temperature-dependent growth and survival relationships for Atlantic bluefin tuna eggs and larvae to temperature records from the western Mediterranean during the spawning season. We then used these data to develop an annual index of potential larval survival in one of the primary spawning areas of the eastern stock of Atlantic bluefin tuna. We tested the hypothesis that thermal conditions which promote growth and survival of Atlantic bluefin eggs and larvae coincide with the location of a major spawning ground around the Balearic Islands in the western Mediterranean basin. Further, we hypothesize that these thermal conditions are associated with temporal variation in annual recruitment. We compared our index to available indices of recruitment from fisheries-dependent data. Our final goal was to produce mechanistic-based knowledge that will allow scientists to include environmental variability and its spatial trends into future stock assessments of Atlantic bluefin tuna.

Material and methods
Study site and time-series

Atlantic bluefin tuna are managed separately as two stocks. The eastern stock is defined as being east of the 45°W meridian (Figure 2a). This study focuses on the western Mediterranean portion of the eastern stock (Figure 2b). The major spawning and breeding area for the eastern stock of Atlantic bluefin tuna (Alemany *et al.*, 2010; Harford *et al.*, 2017) is the Balearic Sea, located in the centre of the western half of the western Mediterranean Sea (Figure 2c). The data analysed in this study were from 2000 to 2014, the same years for which detailed monitoring of the spatial distribution of larvae, spawners, and tracking data of Atlantic bluefin tuna in the western Mediterranean were available for comparison to the model results. This time-series includes years with variability in thermal conditions, recruitment, and spawning-stock biomass (Figure 1).

Time-series of spatially explicit environmental data

The selection of environmental data to use in this study was based on the ability of the available oceanographic models to reproduce the CTD observations collected during 2000–2014. Using data from summer 2004, 72 CTD observations (Alemany *et al.*, 2010) were compared with temperature and salinity fields at 5-m depth from four different oceanographic models to test how well the models represented the spatial variability of these variables. The four different models include two versions of the Mediterranean model available from the Copernicus Marine Service (CMEMS-MED version v02 and sv03, http://marine.copernicus.eu), the GLORYS2V1 version of MERCATOR (https://www.mercator-ocean.fr), and the MEDAR-MEDATLAS summer climatological values. Model data were extracted from the grid-point that contained the CTD station. In this way, it was possible to construct a time-series for each model. The four model time-series were compared with the CTD observations using a Taylor diagram (Taylor, 2001). Dynamic height (DH) was calculated by vertically integrating the specific volume obtained from the CTD data, using 600 m as the level of no motion, as described by Balbín *et al.* (2014). The same methodology was applied to the model and climatological data.
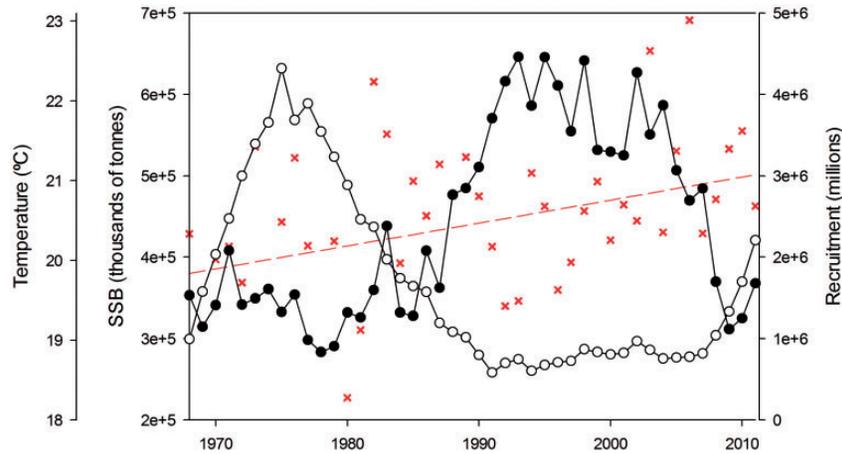
Figure 1. Estimates of spawning-stock biomass in thousands of tonnes (white dots) and recruitment at age 1 in millions of fish (black dots) from the 2017 assessment for the eastern stock of Atlantic bluefin tuna (Anonymous, 2017) and increasing average temperatures in July for the Balearic Sea over the years [crosses and fit (temperature = 0.0288 year − 36.842; $r^2 = 0.16$; $p < 0.01$) as dash line].

Comparison of temperatures from the model data to CTD observations indicates that both of the CMEMS-MED model versions were the best at replicating the spatial pattern of the CTD observations (with a correlation coefficient close to 0.9 and a centred Root-Mean-Square difference around 0.4°) (Supplementary Figure S1). This indicates that the horizontal structure of temperature variability was well replicated. In the case of salinity, the MEDAR-MEDATLAS climatological values were the most strongly correlated with the observations (with a correlation coefficient of 0.6), while the CMEMS-MED models present values of only around 0.4 and a centred Root-Mean-Square difference around 0.3° (Supplementary Figure S2). Therefore, salinity was not well represented in the models and could not be used for calculations of the location of frontal areas. Taylor analysis of DH showed that observations from the MEDAR-MEDATLAS were correlated with observations, with correlation coefficients of 0.65, and for all the other models with correlations coefficients below 0.35 (results not shown). Therefore, the DH of mesoscale structures was not well represented in the models, demonstrating that geostrophic currents derived from the models were not usable for detailed calculations of possible drift effects. As such, only temperature data were well represented by the available models for the period of study (2000–2014) and, therefore, only the temperature model from CMEMS-MED was used.

We compared the average temperature between 1 and 15 June each year from 2002 to 2014 in an area centred in the Balearic Islands (0.5–4.5°E 38.2–40.5°N) using the CMEMS-MED model and satellite data (L4 JPL MUR product, only available since 2002). This comparison shows that the CMEMS-MED model replicates very well the interannual variability of temperature in the area (Supplementary Figure S3). Therefore, the model can be used to model the temporal and spatial variations in temperature.

Given the low capability of the model to represent salinity, we used maps of salinity derived from field cruises to investigate the distribution of larvae and adults relative to this variable within the spatial coverage of the cruises centred in the area around the Balearic Islands instead. Summer surveys carried out during 2001–2005 and 2012–2014 had enough spatial resolution to

resolve the typical regional mesoscale structures, therefore allowing the identification of the location of salinity fronts, while the area covered in 2006 and 2011 was too small (Supplementary Figure S4). No CTD salinity data were available in 2007–2010. Temperature data from SeaBird 911+ and SeaBird 25 CTDs were processed using the Sea-Bird Electronics Data Processing routines, and salinity was calibrated using IAPSO standard seawater and a Guildline 8400A salinometer (see details in Balbín *et al.*, 2014).

Geographical fitness of larval survival and annual survival index

Simulations were conducted to analyse whether the spatio-temporal variability of environmental variables influenced the geographical fitness of larval survival. Specifically, we tested the influence of the spatial and temporal temperature variability on the survival of eggs spawned each day to flexion stage throughout the spawning season. These simulations were conducted without explicitly incorporating any spatial spawning strategy.

Eggs were released daily throughout the western Mediterranean (from 6°W to 6°E). Releases were scaled using a given probability of being released (P) estimated from fitting a polynomial function to the gonadosomatic index of 528 females sampled from the commercial fishery from the Strait of Gibraltar to the Balearic Sea in the western Mediterranean during spring-summer 2003–2014 (Reglero *et al.*, 2018a):

$$P = 28.3156 + 0.0024609\ d^2 - 7.4867e^{-06}\ d^3 - 4.5819\ d^{0.5}$$
(1)

where P is the probability of egg release and d is the day of the year.

Daily probability of egg release was normalized so that release probabilities summed to 1 at the end of each spawning season. We made two assumptions: (i) the same spawning window applies to all years and (ii) the duration of an individual fish's spawning period is independent of the spawner's body size. For each day and position, the eggs hatched into larvae following a
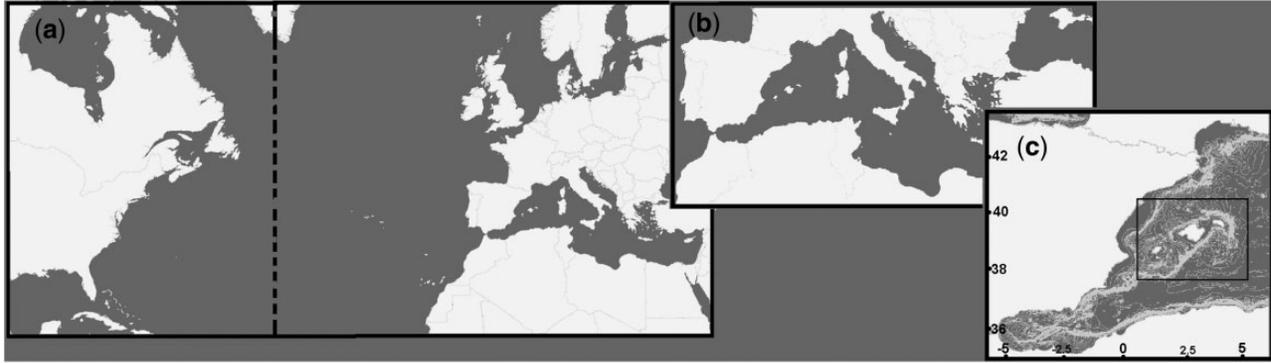
Figure 2. Study area. (a) The distribution of the eastern stock of Atlantic bluefin tuna encompasses the region of the Atlantic eastward from the 45° meridian and the Mediterranean Sea. (b) The western Mediterranean is the area located most west within the Mediterranean Sea. (c) The Balearic Sea is located in the western Mediterranean Sea.

survival function relating hatching success, H, to temperature T (in °C) in a temperature range between 17 and 34°C (Reglero *et al.*, 2018a) formulated as:

$$H = -1.27T^2 + 63.78T - 727.98, \ r^2 = 0.92, \ p < 0.001 \tag{2}$$

The eggs hatched into larvae with an initial average dry weight (W_0) based on measurements of recently hatched larvae in the laboratory ($W_0 = 0.018$ mg DW, ± 0.007 s.d., $n = 27$; Reglero *et al.*, 2018a). Growth from hatching to the post-flexion larval stage was modelled for each daily cohort in each spatial unit as a function of temperature. These models were developed using the maximum potential specific growth rates at each temperature obtained using age–weight relationships from laboratory experiments of Atlantic bluefin tuna larvae (Reglero *et al.*, 2018a). The maximum potential specific growth rates SGR (mg mg^{-1} d^{-1}) increased with temperature (T) and better fit a linear relationship expressed as:

$$SGR = 0.0418T - 0.8355 \ (r^2 = 0.84, \ p < 0.001) \tag{3}$$

The applicable range of temperature on which the relationship is based is 22–29°C (Reglero *et al.*, 2018a).

Mortality (M) was modelled as a function of larval size (W) following the expression (McGurk, 1986 cited in Reglero *et al.*, 2018a):

$$M = 0.00022W^{-0.85} \tag{4}$$

Equations (1)–(4) are used to compute daily larval growth and mortality for the time period from hatching until the larvae reach the flexion stage. This assigns a survival probability to each position and initial day. To visualize the process, the accumulated survival probability for each position was calculated as the time integral of the survival probabilities for each initial day. Using different areas, mean values from these maps were calculated for interannual comparison.

Larval and adult spatial data
Annual geographical larval fitness from our model was compared with the observed spatial distribution of larvae and adult fish in the western Mediterranean. Atlantic bluefin tuna larvae were sampled on cruises conducted during spring and summer during 2001–2014 in an area that covered 180×220 miles around the Balearic Islands with a 10-nautical mile separation between stations (Alemany *et al.*, 2010). During 2001–2005, larvae were collected using Bongo nets with a mouth diameter of 60 cm equipped with 333-μm meshes down to 70 m depth, whereas from 2006 onward, larvae were collected using Bongo nets with a mouth diameter of 90 cm equipped with 500-μm meshes down to 30 m depth (see Alemany *et al.*, 2010; Ingram *et al.*, 2017; Reglero *et al.*, 2018a for more details). Fish larvae from one replicate, preserved in 4% buffered formalin in seawater, were sorted using a stereoscopic microscope, and the total number of Atlantic bluefin tuna larvae was enumerated. We selected only data from stations where presence was positive and data on date, latitude, and longitude were available.

For the location of Atlantic bluefin tuna spawners, position data were obtained from commercial fishing activities (purse-seine and longline) and electronic tagging information. Information on date, latitude, and longitude of the sets of bluefin tuna schools by the purse-seine vessel "La Frau II" was provided by Grup Balfegó for the years 2000–2014. On the basis of previous histological studies (Aranda *et al.*, 2013a), all purse-seine operations in the area were assumed to target schools of actively spawning fish. In contrast, longlines are set over a broader extension in the western Mediterranean and target a more diverse population of Atlantic bluefin tuna in terms of reproductive state (Medina *et al.*, 2007). Hence, GPS positions of longline catches were used only when they captured spawning females. Spawning condition was confirmed by histological analysis when the ovary contained postovulatory follicles and/or migratory-nucleus oocytes and/or hydrated oocytes.

A total of 47 bluefin tuna adults were tagged underwater within the purse-seine nets during regular commercial fishing around the Balearic Islands early in the spawning seasons of 2009 (14 June), 2010 (8 June), and 2011 (9 June) (Aranda *et al.*, 2013b). Another 24 bluefin tuna were tagged, half of them underwater and half onboard the support vessels, in the traps located in the Strait of Gibraltar area early in the 2011 spawning season (Abascal *et al.*, 2016). Fish were tagged with pop-up satellite tags (MK10 and miniPAT; Wildlife Computers, Redmond, WA, USA) attached by a monofilament tether to a dart, which was inserted

into the dorsal musculature at the base of the second dorsal fin. Transmitted information was first processed using the manufacturer software (DAP processor; Wildlife Computers). Tracks were estimated by Collecte Localisation Satellite (CLS) using a Kalman filter/smoother approach constrained by light level, sea surface temperature, and bottom topography as described by Royer and Lutcavage (2008). We only included paths for June and July, which included part of the fish migration to the breeding grounds (only in the case of fish tagged in the tuna traps), the spawning period, and the return to the foraging areas in the Atlantic Ocean.

Time-series of recruitment

Time-series of recruitment were estimated using a fishery-dependent recruitment index employed in the latest assessment for the eastern stock by ICCAT conducted in 2017 (Anonymous, 2017). We split this time-series into two time-series due to changes in fishing gear. The first, 2000–2006, used an age-aggregated index of 2- and 3-year-old fish harvested by the Spanish bait boat fishery, whereas the index after 2006 used an age-aggregated index of 5–6 year olds. We did not consider estimates of recruitment data from VPA outputs, given the uncertainty in the VPA estimates that result in unreliable values for recent dates (Anonymous, 2017).

Results

Geographic patterns of spawning and larval survival may be explained by the role that temperature plays on the early life stages of Atlantic bluefin tuna (Figure 3; Supplementary Figure S5). Potential hatching probabilities were ~40–60% everywhere in the western Mediterranean except in the northern and southern limits (Gulf of Lions and Alboran Sea, respectively) where temperatures were usually lower than 20°C and, therefore, hatching probabilities were very low (Figure 3a–c; Supplementary Figure S5). However, potential larval survival areas were much more restricted than potential hatching areas (Figure 3d–f; Supplementary Figure S5). The area around the Balearic Sea remained optimal for larval survival despite annual differences in temperature, suggesting it to be the best area in the western Mediterranean for bluefin tuna larval survival (Figure 3d–f, Supplementary Figure S5). Latitudes above 41°N and below 36.5°N always had the lowest larval survival; in some cases, no larvae survived (Figure 3d–f, Supplementary Figure S5). Warmer summers enlarged the longitudinal extension of potential areas with enhanced larval survival, whereas colder years shrunk potential larval habitats (Figure 3d and f). As a consequence of optimal thermal conditions for the eggs and larvae, 2003 and 2006 resulted in good year classes from the model, 2005 and 2009–2010 in moderate year classes, and the rest of the years in poor year classes (Figures 3d–f and 4, and Supplementary Figure S5).

The geographic distribution of areas that promote increased larval fitness are consistent with the spatial reproductive strategy of bluefin tuna, as shown by the spatial overlap of larvae and spawning females as well as of modelled data (Figure 3d–f, Supplementary Figure S5). The locations of spawners, as observed from fisheries data, were spatially restricted to the area of the basin around the Balearic Sea as were potential larval habitats predicted by the model and the presence of larvae from ichthyoplankton surveys (Figure 3d–f, Supplementary Figure S5). Tracks of adults indicated movements from the Strait of Gibraltar towards the areas with the highest larval survival (Figure 3f,

Supplementary Figure S5). Spawning was also observed in suboptimal thermal habitats, as predicted by the model, south of the islands despite suitable thermal habitats nearby (Supplementary Figure S5). We could not test these habitats with the data available from observations since ichthyoplankton surveys were only available at local scales (10 s of km), and sampling was conducted mostly south of the islands and rarely north (see sampled stations as dots in Supplementary Figure S4). Nor did industrial and long-line fisheries or electronic tags cover the overall thermal suitable habitats (Figure 3, Supplementary Figure S5). Spatial limitations in sampling effort could be important in explaining distributions at the local scale, such as in 2004 and 2007, when maps suggest that larvae and spawners were distributed in low-quality thermal habitats, although higher-quality habitats were located nearby, or in 2013, with relatively high-quality habitat north of the islands, but with larvae being distributed mostly south (Supplementary Figure S5).

The presence of spawning in suboptimal thermal habitats, yet in relatively stable locations, (in every year, it is observed mainly south of the islands, and seldom or rarely to the north), could also be an indication that the adults use other cues to determine spawning locations at a smaller spatial scale. Besides temperature, characterization of habitat requirements and preferences at the local scale could be influenced by the formation of salinity gradients due to the convergence of less-saline recent Atlantic waters and more-saline-resident Atlantic waters (Supplementary Figure S4). The northernmost area of the Balearic archipelago is usually occupied by resident Atlantic water, whereas the confluence of new and resident Atlantic water usually occurs at the southern border of the surveyed area, south of the islands, as for example in 2002, 2003, 2004, and 2012 or crossing the Mallorca Channel towards Cabrera Island, as in 2001 and 2005 (Supplementary Figure S4). The potential larval survival index from the model and the recruitment index from the bait boat fishery followed a similar trend (Figure 5), suggesting a direct thermal influence on interannual variability in recruitment at the short-term scale in recent years. The strong signal for the 2003 year class both in the model and in the bait boat fishery data is particularly remarkable.

Discussion

Our work corroborates previous hypotheses that the Balearic Sea is an optimal area for Atlantic bluefin tuna egg and larval survival, regardless of interannual variability in summer temperature. Offspring always have a higher chance of surviving to the flexion stage here than in any other region/area of the analyzed western Mediterranean. We have monitored the occurrence of Atlantic bluefin tuna larvae and spawning females in the area since 2000 and have confirmed that bluefin tuna repeatedly spawn in the Balearic Sea, a spatial reproductive strategy that optimizes the chances of survival for the offspring in terms of temperature. The geographic range for best larval survival expands southwestward in warmer years, whereas it is restricted to the Balearic Sea in colder years. This contraction–expansion of potential larval habitat is reflected in the annual survival index, highest in the warmest years and lowest in the coldest years. The index complements previous temperature indices (e.g. Harford et al., 2017), down-scaling the process to a regional index that mechanistically reflects the influence of temperature on eggs and larvae, but also changes in the spatial distribution of suitable spawning areas.
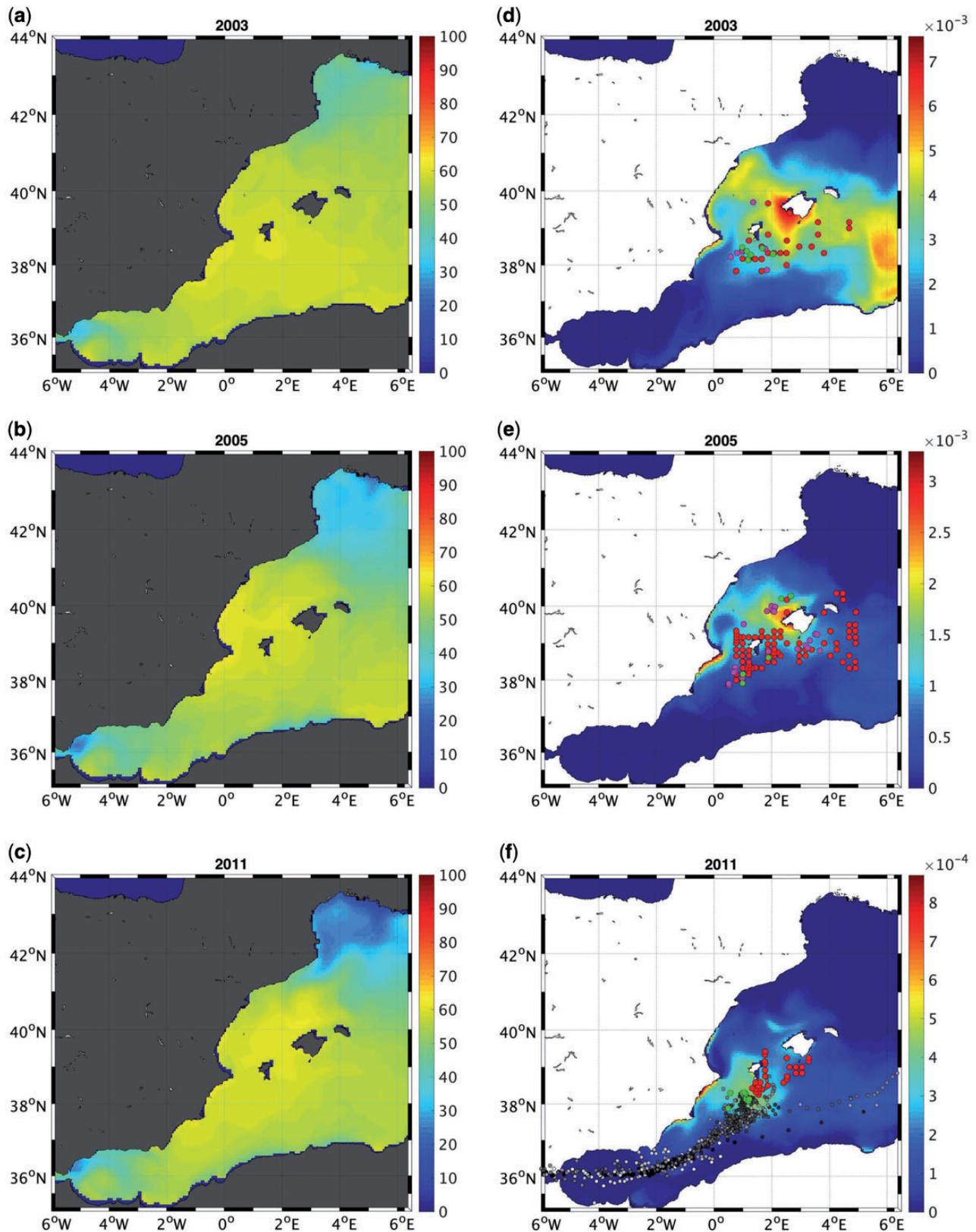
Figure 3. Spatial distribution of the cumulative proportion of eggs successfully hatching for (a) 2003, (b) 2005, and (c) 2011. Spatial distribution of the cumulative proportion of larval survival to the post-flexion stage for (d) 2003 (good larval survival index), (e) 2005 (moderate larval survival index), and (f) 2011 (poor larval survival index). Note the different scales in the figure for each year. Positive locations for the presence of Atlantic bluefin tuna larvae (red dots), spawning females captured by purse-seine (green dots), and by longline (pink dots) are shown on top of the larval survival. Movements of bluefin tuna adults during June–July are shown in grey from tagged fish in 2011.
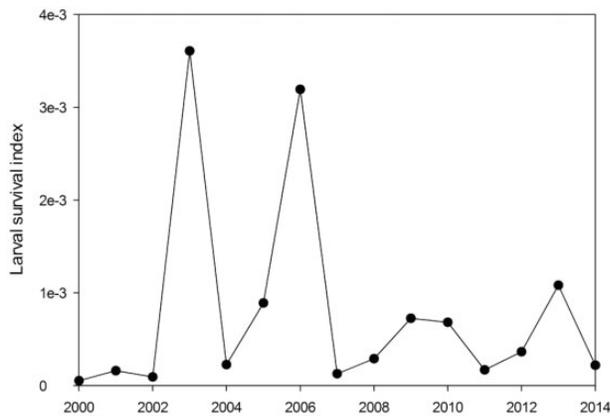
Figure 4. Time-series of the potential larval survival index obtained from the model for 2000–2014.

Figure 5. Variation in recruitment and the potential larval survival index for the eastern stock of Atlantic bluefin tuna. Annual variation in the recruitment corresponds to ages 2–3 (black dots) and ages 5–6 (white dots) estimated from the baitboat index (Anonymous, 2017) (corrected for time lag of 2 and 5 years, respectively) and survival index (crosses). Note data are only available for 2000–2010 within the time-series considered in this study.

The basis for deriving the habitat suitability index in our study was laboratory-derived larval growth and weight-at-age models at different temperatures under the assumption that this relationship reflects growth rates in nature. Results from other laboratory experiments on cultured larval Pacific bluefin (*Thunnus orientalis*) and yellowfin (*T. albacares*) tuna have also shown a clear increase in growth rates with temperature when the effect of temperature was isolated from other variables (Tanaka *et al.*, 2008; Kimura *et al.*, 2010; Wexler *et al.*, 2011), suggesting a potential relationship between growth and temperature. There are very few field-based growth estimates for Atlantic bluefin tuna, and those available have been estimated for a narrow thermal range or age interval either in the Mediterranean (García *et al.*, 2006) or in the Gulf of Mexico (Malca *et al.*, 2017), to indicate how similar laboratory growth rates are to those from field-captured larvae at comparable temperatures. There are indications that growth rates may increase with temperature, although more studies on growth rates are needed before we can use a field-derived relationship to estimate specific growth rates in relation to temperature (see review in Muhling *et al.*, 2017). Potential differences between laboratory estimates and field rates could affect interpretations of time–space variability in thermal habitat survival indices. On the other hand, there could be a situation where thermal conditions of habitat are good or maximal, but other conditions, e.g. poor food availability, in which the habitat index would overestimate survival probability. Timing of spawning in Atlantic bluefin tuna has been shown to be related to both temperature and food abundance for larvae, while competition and predation among tuna larvae, via cannibalism or piscivory, can affect larval survival in a very oligotrophic area (Reglero *et al.*, 2011, 2018a). Nowadays, distribution of food at the basin spatial scale can only be approached from chlorophyll measurements, but since there is no correlation between spatial patterns in chlorophyll and food availability for tuna larvae (Reglero *et al.*, 2017), we cannot yet characterize potential survival habitats regarding food availability.

Long-term average increasing temperatures in the Mediterranean may explain the positive trend in recruitment over long time-series (decadal scale), but may not work in the short-term (interannual scale), particularly in the last decade (Figure 1). Our index shows that thermal conditions in 2003 and 2006 were optimal for Atlantic bluefin tuna egg and larvae
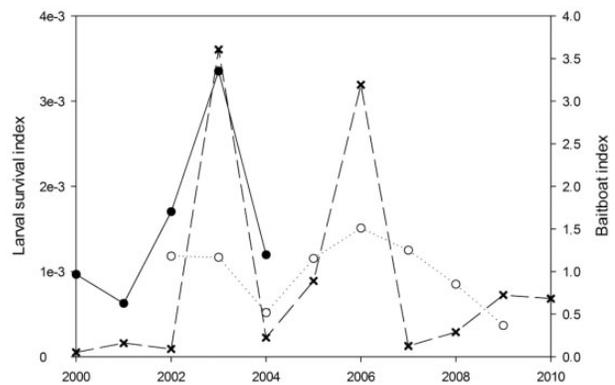
survival compared with other years. The 2003 year class is recognized as one of the strongest, dominating catches from the Japanese longline and the Spanish baitboat fisheries (Rodríguez-Marín *et al.*, 2013; Suzuki *et al.*, 2013; Kimoto and Itoh, 2017), which fits well with optimal environmental conditions in the spawning grounds. Year 2003 was characterized by anomalous warm water that has been considered as a major heat wave in Mediterranean waters. Evidence in the fisheries data for a strong 2006 year class is not as clear. Most of the 2004–2007 year classes were not considered by the ICCAT Bluefin Tuna Working Group to be realistic (Anonymous, 2017). Information on recent recruitment is currently highly uncertain, because no fishery captures eastern bluefin tuna until about age 7 or 8 (Anonymous, 2017), and trends in capture per unit effort (CPUE) for these age classes can be subject to other cumulative sources of variation, other than recruitment. Comparing the model to the Spanish baitboat fisheries index, based on an index of 2- and 3-year-olds in 2000–2004, otherwise 5- and 6-year-olds, suggest an effect of temperature on recruitment. In the case of ages 2–3, the fit between the survival index and the fisheries index is very good, although short, and in the case of ages 5 and 6, there is a match in spite of all the sources of uncertainty in the CPUE standardization and all the factors that are acting between recruitment and the time fish reach that age. There are some difficult data issues with the recruitment data from virtual population analysis (VPA) models used in assessments that reduces the likelihood of a meaningful link between recruitment estimated from the assessment and the new indices we have developed. Therefore, we have not made quantitative use of VPA data (Brooks and Deroba, 2015). Current data availability for this stock limits our understanding of recruitment processes and the ability to resolve which factors drive variations in this species.

There are still some issues that may limit the application of the survival index developed in this study to the entire Mediterranean (Atlantic bluefin tuna eastern stock). The habitat index shown in our study is only for the western Mediterranean, whereas some areas within the eastern and central Mediterranean are also spawning areas for this species (Reglero *et al.*, 2018a). Contributions of other spawning areas to the survival index, as it

is estimated now, are assumed to have constant proportions in all years, which is an untested hypothesis, since egg production that occurs in the different areas has not yet been documented. If the contribution of each region only depends on temperature, then similar temperature regimes across areas would result in similar egg production for a given area. However, spatial contributions of total stock egg production in the different areas have not been tested, and proportions might change from year to year.

It has been shown that salinity and salinity fronts are important in defining bluefin tuna spawning places in the western Mediterranean (Reglero et al., 2012; Alvarez-Berastegui et al., 2014, 2016), and both temperature and salinity should ideally be used for developing recruitment models, so that both effects are incorporated. One procedure could be to use salinity to define the location and size of the more probable spawning area in each year and then, given that region, define its thermal suitability for growth and survival (i.e. a measure of habitat quality) using the relationships derived from the laboratory. In this way, habitat size, location, and quality might be configured more representatively than they are in existing indices and could perhaps explain more variability in recruitment. Unfortunately, hydrographic models were unable to describe salinity variations, and the many CTD data from our extensive fieldwork were only available for a small area within the entire western Mediterranean. Therefore, we currently do not have tools to develop a salinity-derived habitat index.

We have combined different samplings to provide the most accurate spatial spawning distribution in relation to temperature, although some bias occurs due to different sampling efforts. In some years, the only data available were from the fisheries since no larval survey could be conducted (e.g. 2007). Sampling effort during larval surveys is more concentrated southward than north of the islands. Purse-seiners have recently been taking their quota in just a few days or less, so the spatially derived data from the purse-seine fleet provides relatively few data points. Also, in the fisheries data, we have included only those captures where we were assured that the fish were actually spawning, as inferred from ovarian histological analyses. There is quite a demand to link egg–larval ecology to recruitment of this stock that requires continuity in sampling, as the ones used in our study, but also new sampling (e.g. seasonal-repeated surveys, otolith analyses of the survivors) covering a wide spatial and temporal scale. Priorities for this species should be identified in the ICCAT working groups together with stakeholders and scientists.

A critical tool to improve our understanding of geographical fitness in terms of larval growth and survival is the use of realistic hydrodynamic models that simulate realistic drift trajectories coupled to individual-based models that can include behaviour (Fiksen et al., 2007). Limitations to this approach arise from the lack of well-calibrated and validated circulation models at regional scales, the lack of species-specific formulations of growth and survival through ontogeny, the lack of interannual spatial distribution data of both adults and offspring, and the lack of time-series validation of circulation models that generally are updated without maintaining continuity of time-series, which is critical for fisheries studies. To minimize the methodological bias and support the potential operationalization and future implementation of an individual-based model, in the present study, we have ensured: (i) a careful validation of temperature data from the hydrodynamic model in the study area, (ii) the use of growth expressions obtained from laboratory experiments specifically for

Atlantic bluefin tuna and applied to observed temperature records during the spawning season, and (iii) a comparison of model results with field observation data of geographic distributions of larvae and adults.

While circulation models mimic currents well at large spatial and temporal scales, they may perform poorly at the regional spatial and short temporal scales. Our validation shows that available models, with a sufficiently long time-span to be of use for our research, are not capable of accurately reproducing the spatial distribution of different water masses, characterized by their salinity, and mesoscale activity in the area. This limited our ability to (i) reproduce frontal structures and (ii) include drift trajectories to estimate the larval survival index. Bluefin tuna spawning is related to patterns in water masses that explain interannual differences in the spatial distribution of larvae in the area (Alvarez-Berastegui et al., 2016). The circulation models tested did not provide accurate salinity data and, therefore, spatial patterns in salinity and fronts could not be reproduced properly. As such, drift trajectories could not be estimated accurately and, therefore, were not included in the estimation of the potential larval survival index. However, location of the density front in the Balearic Sea, identified from salinity gradients, would signal the best areas for offspring survival. While circulation model outputs may reproduce well general patterns of retention-dispersal in large areas of the Mediterranean, they fail to reproduce detailed interannual patterns in the study area when they strongly depend on mesoscale circulation. Novel multiplatform observing systems, linking modelling capabilities and in situ data, can provide validated high-resolution models for recent years to assess the oceanographic mesoscale scenario in the western Mediterranean (Tintoré et al., 2013; Juzá et al., 2016). Our study represents a trade-off between temporal availability of modelling products and the capability of models to reproduce different environmental variables and key ecological processes.

One common procedure in the literature is to use formulae relating temperature and growth for different species than the primary study species under the assumption that the functions are similar. However, formulae and adaptations to local environments have been shown to be species-specific, and we should be cautious when using expressions that are not specific to the population under study. In our case, we were able to design a set of experiments using Atlantic bluefin tuna and cover the full range of temperature variability observed in the field (Reglero et al., 2018a). On the other hand, we know that surface temperatures are good descriptors of egg and larval habitat for this species, which always occupies the first meters of the water column and show no clear vertical migration patterns (Reglero et al., 2018b). We have assumed the same spawning window for all the years that may result in slightly higher mortalities in years when the water warms later since eggs will be produced, but not survive. Despite the fact that we developed specific growth functions for Atlantic bluefin tuna, we used a size-dependent mortality curve derived from McGurk (1986). One recommendation is to estimate species-specific mortality curves, which will need to be considered in the future.

Directly including environmental variability in stock assessment models or including fisheries-independent recruitment indices are two ways to improve current stock assessment models for the eastern spawning stock of Atlantic bluefin tuna. The index we proposed may be more useful, not as a measure of absolute recruitment, but as a relative index in the stock assessment.

New assessment working groups for this species may need to discuss the best methodology for incorporating observed environmental effects on bluefin tuna growth and survival in current assessments. Survival maps combined with hatching areas would allow the implementation of spatial regulations that would minimize bycatch of bluefin tuna spawners and maximize offspring survival in the western Mediterranean. These could be useful tools if spatial decisions are to be taken for the management of the eastern stock of Atlantic bluefin tuna or if climate change effects in spatial distributions are to be taken into account at different temporal scales (Tommasi *et al.*, 2017).

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Acknowledgements

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