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Worldwide distributions of tuna larvae: revisiting hypotheses on environmental requirements for spawning habitats

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ABSTRACT: Tuna are among the most ubiquitous oceanic predators, and range globally from the equator to temperate regions (0 to 55° latitude). While the distribution of adult fish has been mapped from fishing records, the extent of tuna spawning and larval habitats is less well understood. We compiled and analyzed data on the global distributions of larval occurrence for 7 major oceanic tuna species to investigate environmental predictors of larval habitat. Our results showed that tuna larvae occur within the adults' distributional range, but were restricted to lower latitudes and higher water temperatures than adults, largely consistent with Schaefer's 'temperature hypothesis'. Temperature requirements explained much of the variation in larval occurrence, though temperature by itself tended to over-predict the extent of larval habitats. We also demonstrate that tuna larvae have an elevated probability of occurrence at intermediate values of eddy kinetic energy, generally supporting Bakun's 'ocean triad hypothesis', which relates tuna larval habitats to mesoscale oceanographic activity. However, some deviations in this pattern were also observed, such as for albacore. Regions of suitable larval habitats were most commonly found in western boundary currents, where warm water masses coincide with intermediate eddy kinetic energy. Bluefin tuna species are exceptional though, in that their spawning habitats tended to be much more confined than predicted from oceanographic conditions. Our results provide support for a combination of the 2 hypotheses to explain global environmental requirements for tuna larvae. We have identified oceanographic parameters that can easily be measured by remote sensing and features that should be considered when determining areas of critical habitat for tuna larvae.

KEY WORDS: Spawning habitat · Global · Spatial distribution · Large predators · Tuna · Larvae · Thunnus · Temperature hypothesis · Ocean triad hypothesis

INTRODUCTION

Tuna (family Scombridae, tribe Thunnini) are large predators that inhabit the marine pelagic environment. As valuable economic resources worldwide, most tuna species are heavily fished, and scientists have raised concerns about the sustainable exploitation of most stocks (Allen 2010, Collette et al. 2011, Juan-Jordá et al. 2011). Tunas are typically considered tropical and warm-water fishes (e.g. skipjack tuna *Katsuwonus pelamis*, bigeye tuna *Thunnus obesus*, and yellowfin tuna *Thunnus albacares*), though some species have adapted to colder waters, such as the Atlantic bluefin tuna *Thunnus thynnus* (Fromentin &

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Fonteneau 2001). As with other top predators, their global diversity and distribution is subject to long-term environmental changes, with temperature being a key factor in determining their distribution (Worm et al. 2005, Boyce et al. 2008, Tittensor et al. 2010). In addition, exploitation may have an effect on species distributions, with global range contractions detected in a number of species, particularly the bluefin tuna species (Worm & Tittensor 2011). However, not all species are suffering range contractions; for example, skipjack tuna appear to have undergone a range expansion in the Pacific Ocean.

Although our understanding of the distribution and diversity patterns of adult and juvenile tuna has continued to increase, we know less about the extent of spawning areas and the distribution of larvae. Though adult tuna can be wide-ranging, many species have spatially restricted spawning grounds. Two hypotheses have been postulated to explain the worldwide distributions of these spawning grounds: (1) that they are constrained by water temperature and are restricted to areas >24°C (Schaefer 2001) and (2) that spawning generally occurs in areas with mesoscale oceanographic features, such as fronts and eddies (Bakun 2006). The first hypothesis, called from here onwards the 'temperature hypothesis', relates the restricted spawning and larval habitats to a narrower thermal tolerance of larvae compared to that of adult tuna (Boyce et al. 2008). Physiological adaptations and enhanced mobility of adult tunas have allowed evolutionary niche expansions to a broad range of latitudes (Graham & Dickson 2004), yet all tuna species spawn in warm waters. The second hypothesis, known as the 'ocean triad hypothesis', links physical processes with favorable habitats for reproduction. Specifically, it posits that larval growth and survival are dependent on mechanisms that enhance local food supply and retain larvae within a favorable habitat, such as in upwelling areas and around mesoscale eddies (Bakun 2006). Though both hypotheses have been formulated to explain worldwide patterns of tuna spawning distributions, they remain largely untested. The temperature hypothesis is based primarily on gonad data from adult catches of different species, as well as some limited larval sampling (Schaefer 2001 and references therein). The ocean triad hypothesis is based on the larval distribution of albacore in the North Pacific and Atlantic bluefin tuna (Bakun 2006 and references therein, 2013). Because they are based on limited information within specific geographical regions, it has been difficult to determine the generality of these 2 hypotheses on a global scale.

In order to test these hypotheses more generally, we analyzed the global distribution of larvae for 7 common tuna species. Tuna species tend to share similar life history at early developmental stages, despite widely differing life-history traits as adults, such as body size, age at maturity and longevity. All tuna species spawn pelagic eggs that hatch into larvae within a couple of days (~3 mm long), grow fast and develop foraging and swimming organs, then metamorphose into juveniles during the first month of life (Kaji et al. 1996, Miyashita et al. 2001, Margulies et al. 2007). Though spawning areas are usually more restricted than the areas where the larvae are found (Planque et al. 2007), larval distributions offer useful empirical information. Early life stages will be influenced by local environmental and oceanographic conditions that ultimately determine the distribution and survivorship of the larvae. Therefore, an investigation of larval habitats may help to understand the applicability of the 2 above-mentioned hypotheses.

Our aim was to evaluate whether the available larval distribution data support either hypothesis, or both. Worldwide data on larval occurrence (presence–absence) obtained from an extensive exploration of the literature were correlated with sea-surface temperature measurements to test the temperature hypothesis and with eddy kinetic energy fields to test the ocean-triad hypothesis. The statistical significance and trends obtained from the models relating these 2 variables to larval occurrence within and between species were used to test the support for both hypotheses and elucidate the processes that may drive larval distributions. Global patterns in larval species richness and inferred ranges based on these larval distributions were then compared to those for adults to assess the commonalities and differences between adult and larval tuna habitats.

MATERIALS AND METHODS

Mapping larval ranges

This study focused on the 7 oceanic tuna species which support major international fisheries: skipjack tuna, yellowfin tuna, albacore *Thunnus alalunga*, bigeye tuna, southern bluefin tuna *Thunnus maccoyii*, Atlantic bluefin tuna and Pacific bluefin tuna *Thunnus orientalis*. We assembled and reviewed scientific articles and grey literature on larval surveys from across the world that reported the presence of at least 1 tuna species. The search terms used on

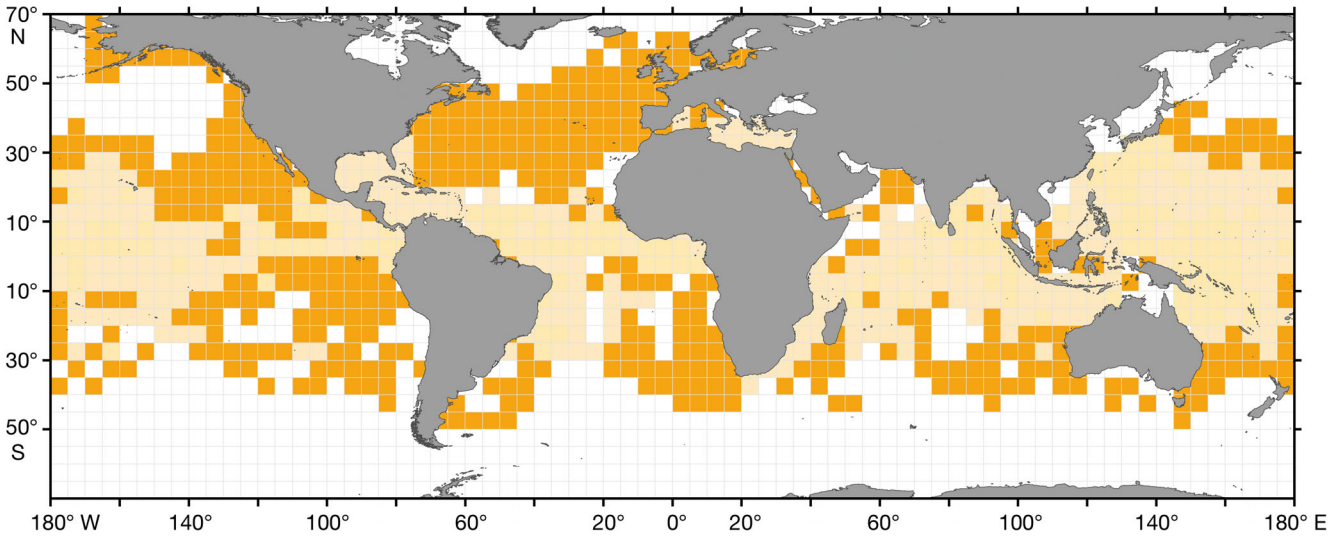

Fig. 1. Tuna larvae habitat. A total of 1678 grid cells, excluding land cells, between 70°S and 70°N were mapped according to the available information on the presence or absence of tuna larvae for every species. Cells where at least 1 tuna larval occurrence has been reported at the species level are shown in light orange. Sampled cells where no tuna larvae were obtained from geo-referenced icthyoplankton surveys are shown in dark orange. Areas with missing data are shown in white

Google Scholar were 'alalunga and larv*', which produced ~1450 results, 'albacares and larv*' with ~2070 results, 'Thunnus obesus and larv*' with ~1050 results, 'maccoyii and larv*' with ~955 results, 'pelamis and larv*' with ~682 results, 'thynnus and larv*' with ~3190 results and 'Thunnus orientalis and larv*' with ~625 results. After removing articles not dealing with tuna larvae and repeated references we retained 150 articles. From these, 92 reported geo-referenced tuna larval catches (see Supplement 1 at www.int-res.com/articles/suppl/m501p207_supp.pdf).

From each article we extracted the location of the sampled stations where occurrences of larvae identified to the species level were reported and the sampling season of the year (January to March, April to June, July to September, October to November). We used studies where the latitude and longitude coordinates were specifically reported or where the coordinates could be estimated after digitalizing the maps where larval occurrences were shown. A total of 1678 grid cells of 5° × 5° between 70°S and 70°N, excluding those on land, were mapped according to the data on the presence or absence of tuna larvae for every species (Fig. 1).

The larvae were identified to species level using morphological characters including body shape, pigmentation, meristic counts and body measurements. In most studies, difficulties in the taxonomic identification were addressed by (1) grouping individuals that were not accurately identified into a *Thunnus* spp. group and (2) establishing a minimum larval length above which larvae were considered to be accurately identified, since most difficulties appeared for the small larvae. Data from these 2 groups were not included in the database. A tag with the references used for taxonomical descriptions reported in the articles was included in the database. A discussion of the particularities for the identification of each species is included in the 'Discussion' section.

Absence data were obtained from geo-referenced absences reported from cruises targeting tuna larvae and historical icthyoplankton surveys where all larvae were taxonomically identified but tuna larvae had not been reported (ICES eggs and larval data, http://eggsandlarvae.ices.dk [accessed 2012]; Ichthyoplankton Cruise Database, National Oceanic and Atmospheric Administration (NOAA), http://access.afsc.noaa.gov/icc/index.cfm [accessed 2012]). The rest of the cells were non-sampled areas.

Global maps of larval catch locations were represented in geographic coordinates by using the WGS-1984 datum and geocentric ellipsoid projection, which minimized distortion at high latitudes, with 5° × 5° grid squares, plotted using the Geographical Information System software ArcMap 9.2 (ESRI).

Environmental data

We included environmental data, namely the seasonal sea-surface temperature (SST) obtained from satellite remote sensing and the eddy kinetic energy

(EKE) calculated from satellite-altimetry derived sea-surface height anomalies for each grid cell. This mostly captures the energy contained in mesoscale eddies. Prominent signals in sea-surface height make satellite altimetry effective in observing ocean eddies on a global scale (Fu et al. 2010).

Monthly means of SST and sea-surface current velocity derived from altimetry (latitudinal *U* and longitudinal *V* components) at a spatial resolution of 0.25° were provided by the Coast Watch Program from the NOAA Satellite and Information Service, www.nesdis.noaa.gov/. EKE values were calculated from the geostrophic velocity components as the sum of the square of each component *U* and *V* divided by 2. Both monthly EKE and SST values were averaged at each 5° × 5° cell of the analysis grid to obtain seasonal (3 mo) data. Details of the satellite data acquisition are provided in Supplement 2 at www.int-res.com/articles/suppl/m501p207_supp.pdf.

The area of each cell was calculated as the ocean surface encompassed within each cell, using ArcMap 9.2. Data were used for mapping, as well as modeling, after filtering out cells without SST or EKE data. Standardized data on larval densities were not available for comparison across studies and oceans; hence, we were forced to focus on larval presence records only. Furthermore, larval sampling cruises were not routinely recorded over the years in different areas, so we have combined different sampling years, with the earliest cruises dating from the 1920s and the latest from the 2000s. The obtained database including the larval data and environmental variables is available by contacting the corresponding author.

Modeling

The spatial distribution of tuna larvae was modeled using a nonparametric regression approach (generalized additive model, GAM, with a binomial link function). For each species the response variable was larval presence or absence for a given location at a given season. The covariates included in the analyses to predict the larval occurrences were the seasonal SSTs (testing the temperature hypothesis) and the seasonal EKEs (testing the ocean triad hypothesis) for a given location. Therefore, the presence/absence of bluefin tuna species (Atlantic bluefin tuna, Pacific bluefin tuna and southern bluefin tuna) in the different cells was estimated as:

$$P_{species,s,i,j} = a + s_1(SST_{s,i,j}) + s_2(EKE_{s,i,j}) + \varepsilon \quad (1)$$

where $P_{species,s,i,j}$ is the probability of finding tuna larvae of a given species (species) in each season (s) in a particular cell (i,j are the latitude and longitude corresponding to each 5° cell). The s_1 and s_2 are unidimensional smoothing functions, typically with a thin plate regression spline (Wood 2006); therefore, the relationships were modeled as splines with no *a priori* assumption of linearity, *a* is the model intercept and ε is the error.

For yellowfin tuna, skipjack tuna, albacore and bigeye tuna larvae that showed a wide latitudinal distribution, the model included an additional variable to remove the effect that latitudinal position (i.e. cell area) may have had on the species presence. Therefore, the presence/absence in the different cells was estimated as:

$$P_{species,s,i,j} = a + s_0(area_{i,j}) + s_1(SST_{s,i,j}) + s_2(EKE_{s,i,j}) + \varepsilon \quad (2)$$

where all terms are as in Eq. (1) including a new unidimensional smoothing function s_0 associated with the area of that cell. We used a binomial distribution to model the larval data because we had presence/absence data. The variable selection criteria were based on the confidence region for the smoothing effect, the percentage of deviance explained and the unbiased risk estimator (UBRE; Wood 2006). The degrees of freedom for each variable are shown as an indicator of the departure from linearity. GAMS were fitted using the 'mgcv' library in the R statistical software (www.r-project.org).

Stepwise backwards selection by eliminating non-significant variables was used to select the best model. Tuna larvae are generally very patchily distributed and the de-correlation scale is on the order of 1 to 10s of kilometers (Satoh 2010), removing the need to include a spatial autocorrelation term, given the large size of the grid cells (~550 × 550 km at the equator).

Adult ranges

The global distribution of larval grounds was compared to contemporary adult spatial ranges extracted from Worm & Tittensor (2011) on a 5° × 5° grid with individual maps for every species. Adult ranges were mapped using observed occurrences for adult tuna from both a multi-decadal database of global Japanese longline fisheries and the United Nations Food and Agriculture Organization (FAO) Tuna Catch

Atlas (Worm & Tittensor 2011). The adult and larval species richness was calculated as the sum of the number of species occurring within each 5° × 5° cell.

Temperature tolerances

Histograms showing the probability density functions (Scott 1992) of observed larval occurrences at the different SSTs were computed for each species using the function 'hist' in the R statistical software (www.r-project .org). The upper and lower limits of temperature tolerances for spawning were estimated as the maximum and minimum water temperatures in which larval occurrences of each species were found from these density functions. Average temperatures for positive presences of larval tuna were calculated. The temperature limits constraining thermal habitats for adults were derived from the tolerance data compiled by Boyce et al. (2008).

RESULTS

Tuna larvae were generally confined to a much narrower spatial range than adults (Figs. 2 & 3). In general, tuna larvae were found to occupy latitudes between 30°S and 30°N (with the exception of the Mediterranean Sea where larvae are found upwards of 35°N), whereas adults were found to have a much larger range, from 60°S to 60°N (Figs. 2 & 3). The Atlantic bluefin tuna larvae were found only in semi-enclosed seas: the Mediterranean Sea and the Gulf of Mexico (Fig. 2a). The Pacific bluefin tuna larvae were confined to the area between Japan and the Philippines (Fig. 2b). Southern bluefin tuna larvae were found only in the tropical East Indian Ocean (Fig. 2c). Skipjack, yellowfin and bigeye tuna were, in contrast, distributed throughout the tropics in every ocean, both as adults and larvae (Fig. 3a–c), while albacore larvae were also found at higher latitudes in the Mediterranean Sea with low occurrences in the equatorial zone (Fig. 3d).

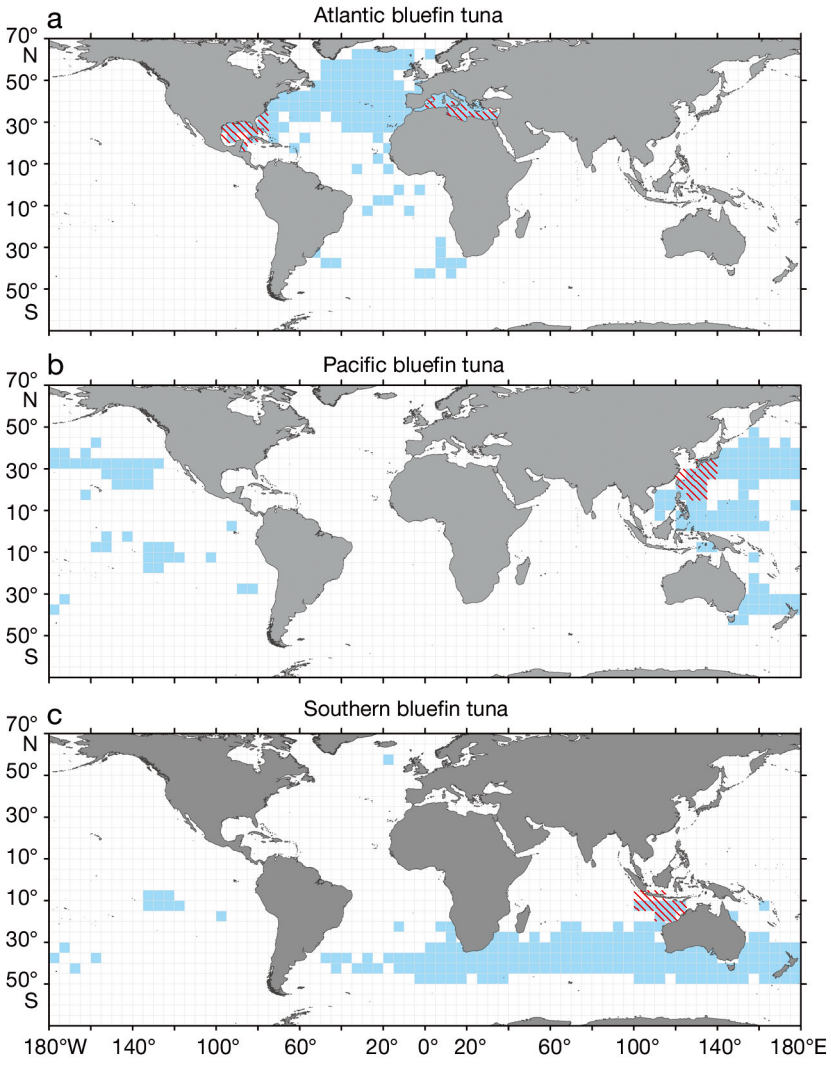

Fig. 2. Larval versus adult habitat for (a) Atlantic bluefin tuna, (b) Pacific bluefin tuna and (c) southern bluefin tuna. The presence of larvae (red hatching) and adults (blue squares) are mapped; larval habitats may also contain spawning locations

The probability of larval occurrence was positively and linearly related to temperature in Atlantic bluefin tuna (Fig. 4a) and southern bluefin tuna (Fig. 4b) larvae, but did not significantly explain the occurrence of Pacific bluefin tuna (Table 1). The probability of larvae occurring in a cell increased with EKE, linearly in Atlantic bluefin tuna (Fig. 4c), and plateauing around intermediate values of 0.01 to 0.06 $m^2 s^{-2}$ in Pacific bluefin tuna (Fig. 4d), but were not significant in explaining the occurrence of southern bluefin tuna (Table 1).

The model fit including both variables, SST and EKE, was significant for skipjack, yellowfin, albacore and bigeye tuna (Table 2). The probability of larval occurrence was positively related to temperature, with larvae having a higher probability of occurrence

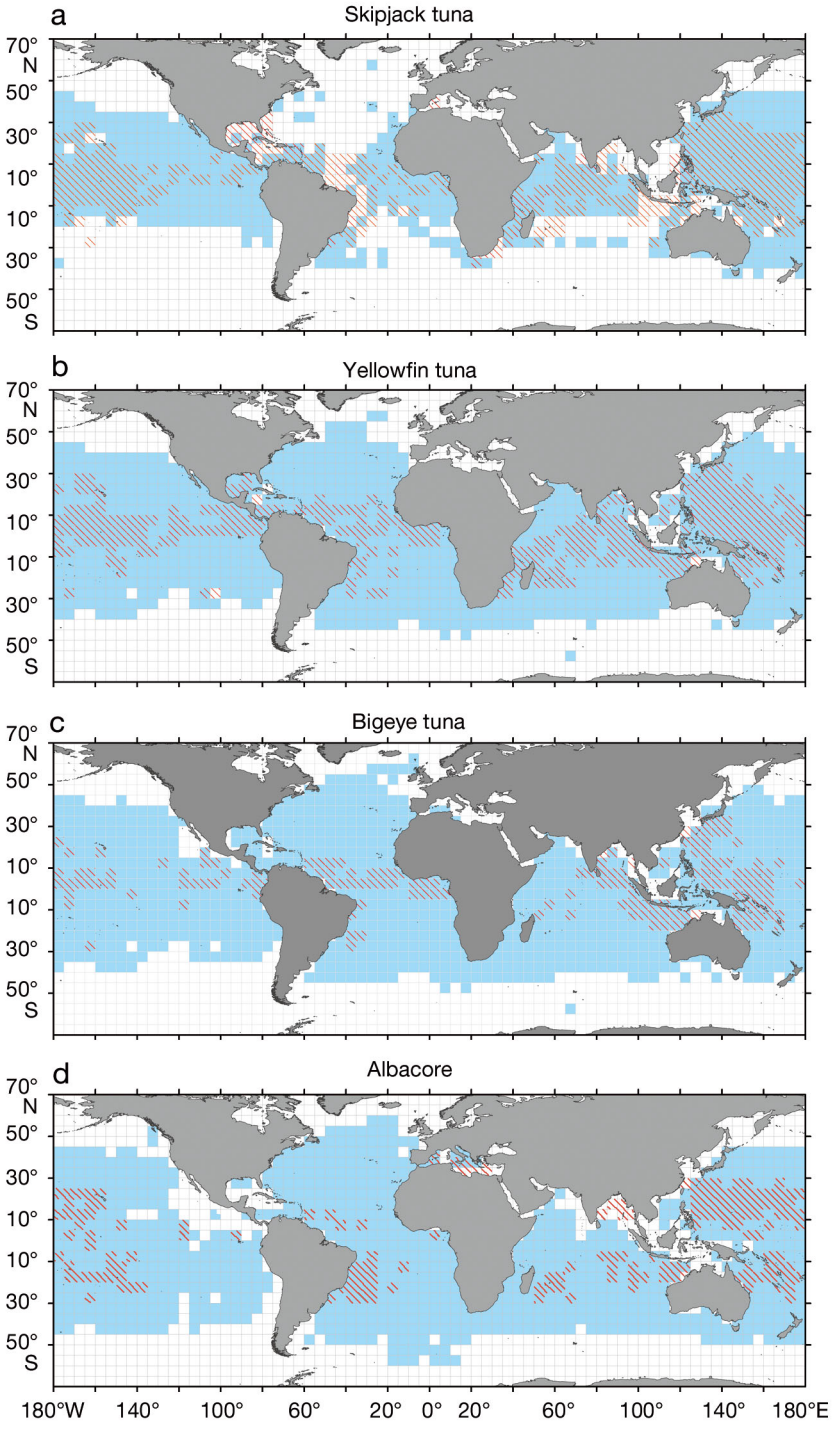

Fig. 3. Larval versus adult habitat for (a) skipjack tuna, (b) yellowfin tuna, (c) bigeye tuna and (d) albacore. The presence of larvae (red hatching) and adults (blue squares) are mapped; larval habitats may also contain spawning locations

when temperatures were >20°C in the 4 species (Fig. 5a–d). Larval occurrences increased with EKE, plateauing around intermediate values of 0.01 to 0.06 m^2 s^{-2}, then decreasing slightly for skipjack (Fig. 5e), yellowfin (Fig. 5f) and bigeye (Fig. 5g). In contrast, the probability of albacore larvae occurring in a cell was negatively and linearly related to EKE (Fig. 5h).

The model predicted very low larval occurrences for the 3 bluefin tunas in all areas (Fig. 6a–c). Within this range, the spatial distributions captured by the model suggest a predominance of larvae of the 3 species in the tropical East Indian Ocean, the Gulf of Mexico and along the Japanese coast (Fig. 6a–c). Therefore, the predictive power of the model was insufficient to separate the observed spatial patterns for each bluefin tuna species (Table 1), but suggested that specific areas of predominance for the 3 species share common characteristics in terms of SST and EKE (Fig. 6a–c). In general, they were characterized by intermediate to high values of EKE and seasonally warm SST (see Figs. 8 & 9). Plausible larval habitats for Pacific and southern bluefin tuna were over-predicted in the eastern Indian Sea and some equatorial areas which probably show similar characteristics to the more confined regions. Atlantic bluefin tuna larvae were also present in the Mediterranean Sea, but no predictions were obtained for this area, since EKE values were not available.

Spatial patterns of skipjack and yellowfin tuna were predicted well by the model, with larvae distributed broadly throughout the tropics (Fig. 7a,b). Their predicted distributions matched the areas having the highest temperatures through the entire year or seasonally at northern and southern latitudes and having predominantly intermediate to high EKE values (Figs. 8 & 9). Bigeye tuna were predicted to occur in every ocean, being distributed in the equatorial area, but predicted probabilities of occurrence were lower than those for skipjack and yellowfin tuna (Fig. 7c). The prediction for albacore matched well with the absence of larvae in the equatorial zone, predominantly in areas with lower EKE and higher temperature, which, in addition, was also found at northern latitudes (Figs. 7d, 8 & 9).

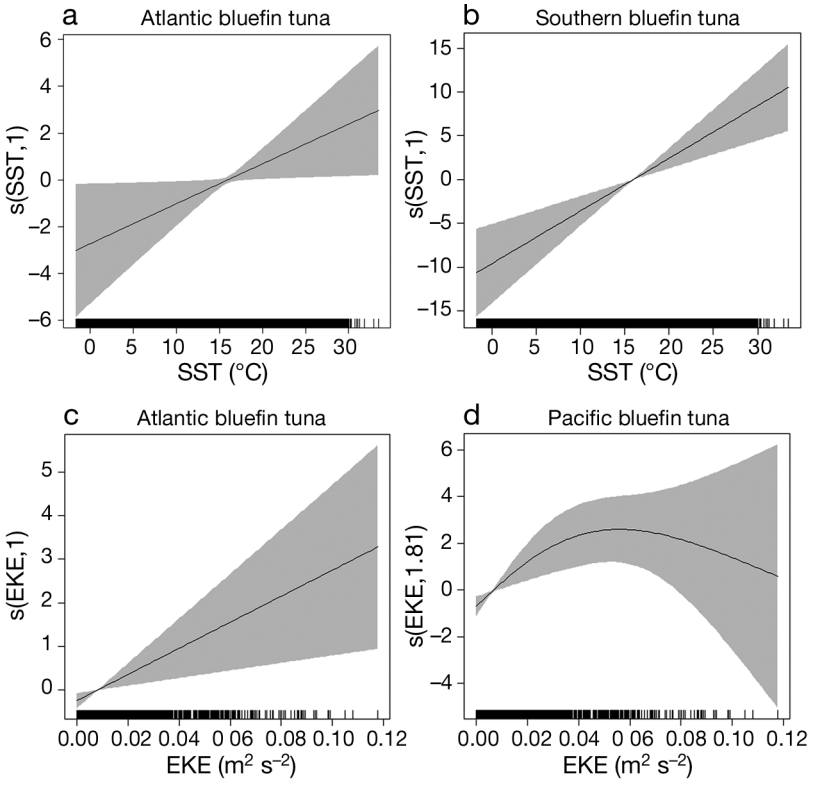

Fig. 4. Environmental drivers in bluefin tuna species. Shown are significant partial effects of eddy kinetic energy (EKE) and sea-surface temperature (SST) on the presence of larvae of (a,c) Atlantic bluefin tuna, (b) southern bluefin tuna and (d) Pacific bluefin tuna. Effects were estimated from a generalized additive model; for full results see Table 1. Fitted values <0 indicate a negative effect of the variable on larval occurrence; positive values indicate a positive effect. Fitted regression lines (solid) and 95% confidence intervals (grey areas) are shown. Marks on the *x*-axis indicate the density of actual measurements for that variable

Table 1. Model results of the relationship between the presence/absence of Atlantic bluefin tuna, Pacific bluefin tuna and southern bluefin tuna with respect to SST and eddy kinetic energy (EKE). For each variable, we included the estimated degrees of freedom (indicative of departure from linearity) and their probability. The deviance explained and the unbiased risk estimator (UBRE) of the model are reported

Variable	df	Prob	Deviance explained (%)	UBRE score
Atlantic bluefin tuna				
SST	1	0.005		
EKE	1	0.03		
Total model			14	−0.98
Pacific bluefin tuna				
SST	1.8	0.12		
EKE	1.8	0.001		
Total model			20	−0.98
Southern bluefin tuna				
SST	1	<0.001		
EKE	1.4	0.003		
Total model			21	−0.93

Temperature tolerances

Tuna larvae preferred warmer waters and tended to have narrower temperature tolerances, on average, than adults (Table 3). All species showed similar maximum temperature tolerances of ≥28.5°C, but different minima: <22°C in skipjack tuna, yellowfin tuna, albacore, bigeye tuna and Pacific bluefin tuna and >24°C in Atlantic bluefin tuna and southern bluefin tuna (Fig 10, Table 3). Observed cells with positive occurrences of tuna larvae were usually in the upper range of the tolerance of temperatures for all species (Fig. 10). Maximum probabilities of occurrence of larvae for most of the species were predominantly in SSTs between 27.4 and 27.8°C, whereas Atlantic and Pacific bluefin tuna were, on average, found at slightly colder temperatures (26.5 and 25.3°C, respectively). The species with the widest adult range in temperature tolerances were bluefin and bigeye tuna, as determined by Boyce et al. (2008). For albacore and southern bluefin tuna, the larval thermal range was found to extend above the upper thermal range of adults (25.2°C compared to 30°C in albacore, 28.4°C compared to 30.2°C in southern bluefin tuna). Atlantic bluefin tuna, skipjack tuna and yellowfin tuna had slightly higher upper tolerance limits for adults than for larvae.

DISCUSSION

Our results show that tuna larvae are confined to a much narrower range of habitat than adult fish. Both SST and EKE were found to be major predictors for the spatial distribution of tuna larvae, but the trends of the 2 environmental predictors differed among species. We found a significant positive effect of temperature in all of the species analyzed. According to our results, the lower temperature tolerance for tuna larvae appears to be 20°C, at least for some species, though most positive occurrences were observed in warmer temperatures. Therefore, the conjecture that the boundaries of tuna spawning grounds are located between the 24°C isotherms (Schaefer 2001) may

Table 2. Model results of the relationship between the presence/absence of skipjack tuna, yellowfin tuna, albacore and bigeye tuna with respect to the cell of the area (area), sea-surface temperature (SST) and eddy kinetic energy (EKE). For each variable, we included the estimated degrees of freedom (indicative of departure from linearity) and their probability. The deviance explained and the unbiased risk estimator (UBRE) of the model are reported

Variable	df	Prob	Deviance explained (%)	UBRE score
Skipjack tuna				
SST	1	0.005		
Area	1.9	<0.001		
SST	2	<0.001		
EKE	2	<0.001		
Total model			39.6	0.28
Yellowfin tuna				
Area	3.1	<0.001		
SST	1.9	<0.001		
EKE	1.9	<0.001		
Total model			38.9	−0.70
Albacore				
Area	2.3	<0.001		
SST	1.9	<0.001		
EKE	1	<0.001		
Total model			29.3	−0.78
Bigeye tuna				
Area	3	0.1		
SST	1.8	<0.001		
EKE	1.8	<0.001		
Total model			32	−0.81

need to be revisited. However, temperature alone resulted in an over-prediction of plausible larval habitats for all species, especially the bluefin tuna species.

The probability of finding larvae in relation to EKE was homogeneous for skipjack, yellowfin and bigeye tuna. According to our results, tuna larvae are not typically found in areas of low EKE, and have the highest probability of occurrence at intermediate values of EKE. This supports the ocean triad hypothesis (Bakun 2006). Tuna larval habitat is related to the occurrence of mesoscale oceanographic activity. However, albacore showed the completely opposite pattern. Their larvae are distributed above and below 10°N and 10°S, avoiding the equatorial waters, a spatial pattern that is well modeled when the negative influence of EKE in the occurrence of albacore larvae is taken into account. Despite the 4 species being distributed in the Pacific, Indian and Atlantic Oceans, the species could separate their habitats based on their different preferences for areas characterized by different EKE values, especially albacore compared to skipjack, yellowfin and bigeye tuna.

The observed correlations with warm water masses and intermediate EKE suggest a general predominance of suitable larval habitats in the western boundary currents compared to eastern. However, the global patterns in larval distribution were easier

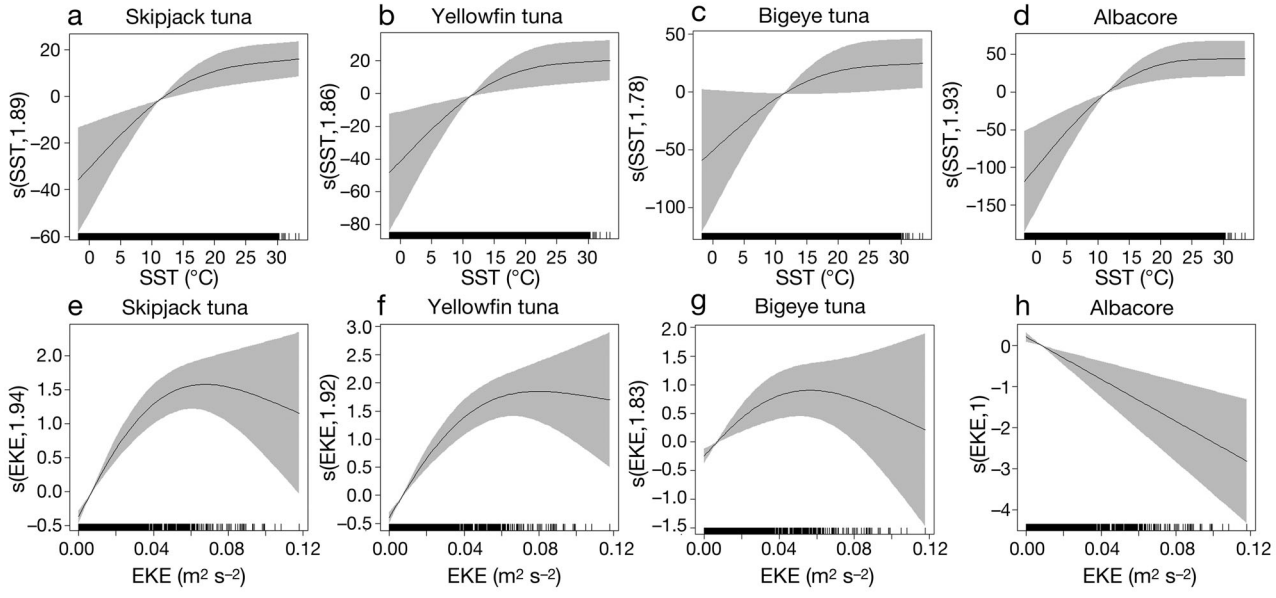

Fig. 5. Environmental drivers in skipjack tuna, yellowfin tuna, bigeye tuna and albacore. Shown are significant partial effects of SST and eddy kinetic energy (EKE) on the presence of larvae of (a,e) skipjack tuna, (b,f) yellowfin tuna, (c,g) bigeye tuna and (d,h) albacore. Effects were estimated from a generalized additive model; for full results see Table 2. Fitted values <0 indicate a negative effect of the variable on larval occurrence; positive values indicate a positive effect. Fitted regression lines (solid) and 95% confidence intervals (grey areas) are shown. Marks on the *x*-axis indicate the density of actual measurements for that variable

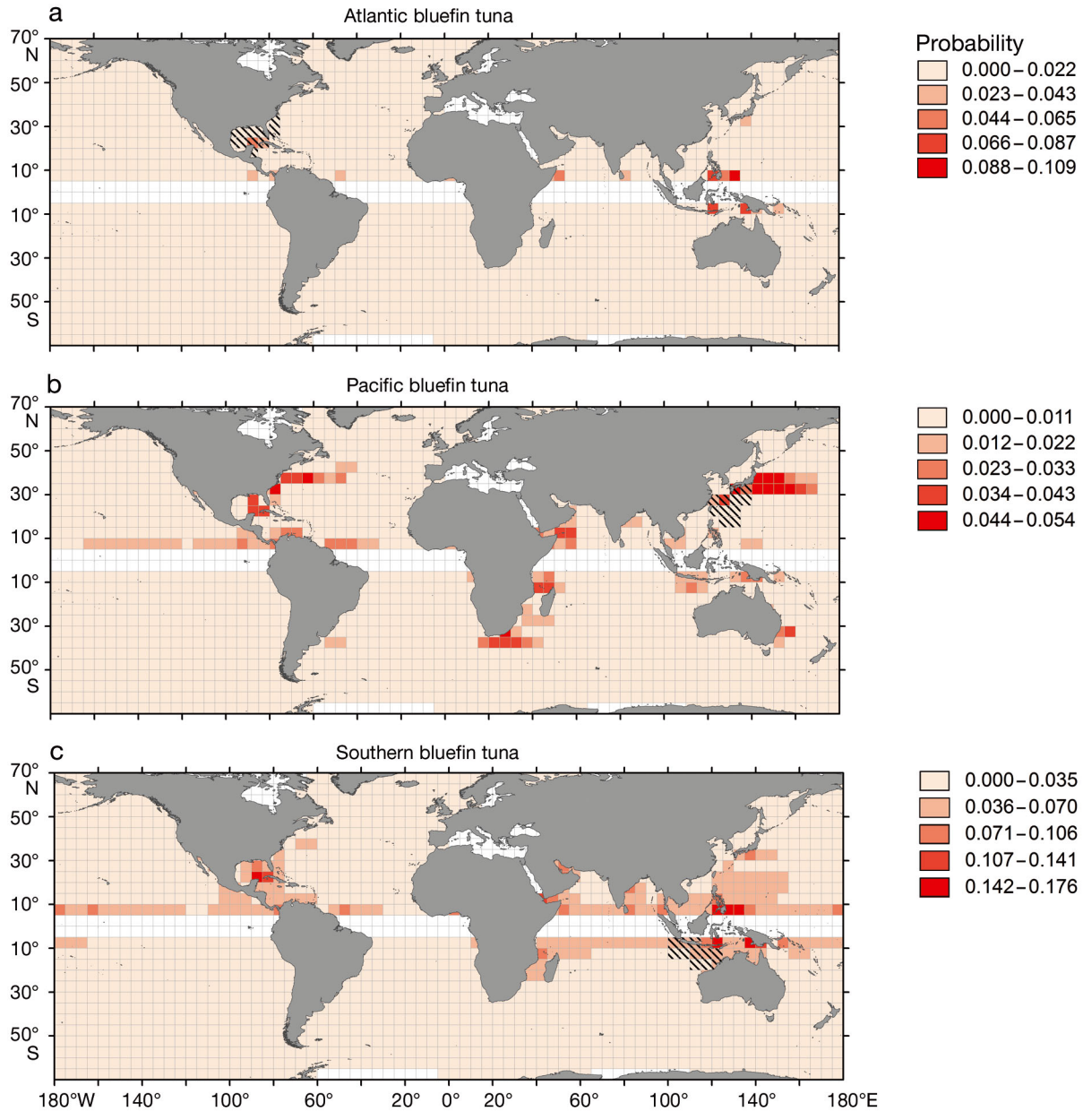

Fig. 6. Predicted versus observed distribution of larvae in bluefin tuna species. The probability of occurrence of larvae for (a) Atlantic bluefin tuna, (b) Pacific bluefin tuna and (c) southern bluefin tuna is color coded; predicted values were derived from a generalized additive model including SST and EKE as predictor variables when significant. The observed occurrences of the larvae are superimposed as cross-hatching. White cells had no associated probability of occurrence since EKE values were missing and therefore were not included in the model. Note the scale is magnified and different for the 3 species to emphasize spatial patterns compared to Fig. 7

to predict in skipjack and yellowfin tuna than in bluefin tuna species, where spawning areas and larval habitats appear much more spatially constrained. Broader larval distributions were found for species that mature early in life and do not attain a large size, in contrast to the larger tuna species, which mature at an older age and have a narrower distribution as larvae (Fromentin & Fonteneau 2001), a pattern that correlates with tropical versus temperate tuna. In general, temperature has a consistent and dominant role in structuring broad-scale marine diversity patterns (Tittensor et al. 2010). In addition, oceanographic discontinuities have been suggested to limit the range distribution of marine species by acting as a boundary, but also through their influence on larval dispersal and recruitment (Gaylord & Gaines 2000).

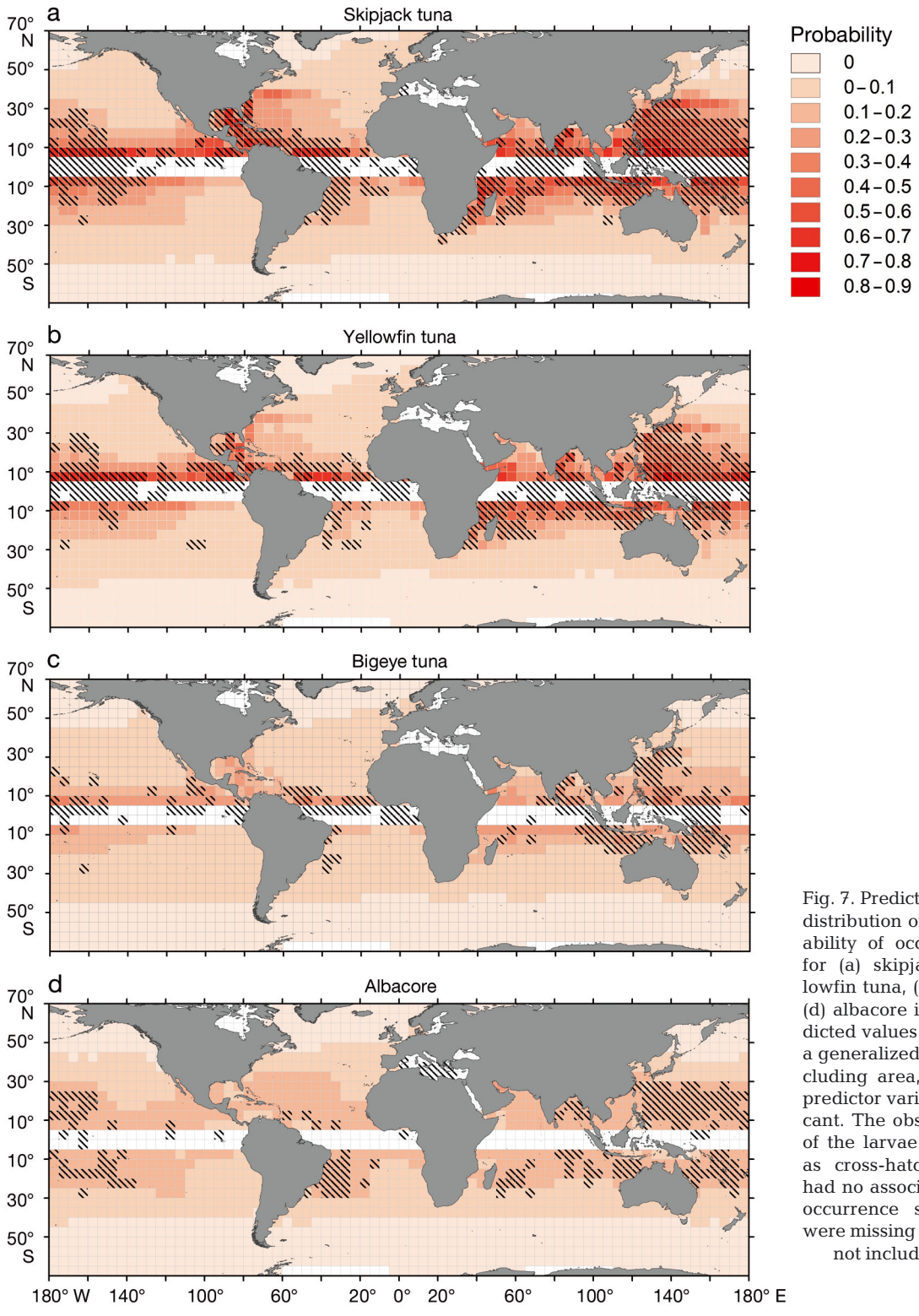

Fig. 7. Predicted versus observed distribution of larvae. The probability of occurrence of larvae for (a) skipjack tuna, (b) yellowfin tuna, (c) bigeye tuna and (d) albacore is color coded; predicted values were derived from a generalized additive model including area, SST and EKE as predictor variables when significant. The observed occurrences of the larvae are superimposed as cross-hatching. White cells had no associated probability of occurrence since EKE values were missing and therefore were not included in the model

The data

In general, it is very difficult to obtain empirical data to test worldwide spawning distributions for tuna species. We were able to compile geo-referenced records of larval presence and absence across all oceans, providing a globally comprehensive dataset of tuna larval occurrence. However, the number of studies remains restricted and the dataset has some limitations. The combined database shows good spatial coverage,

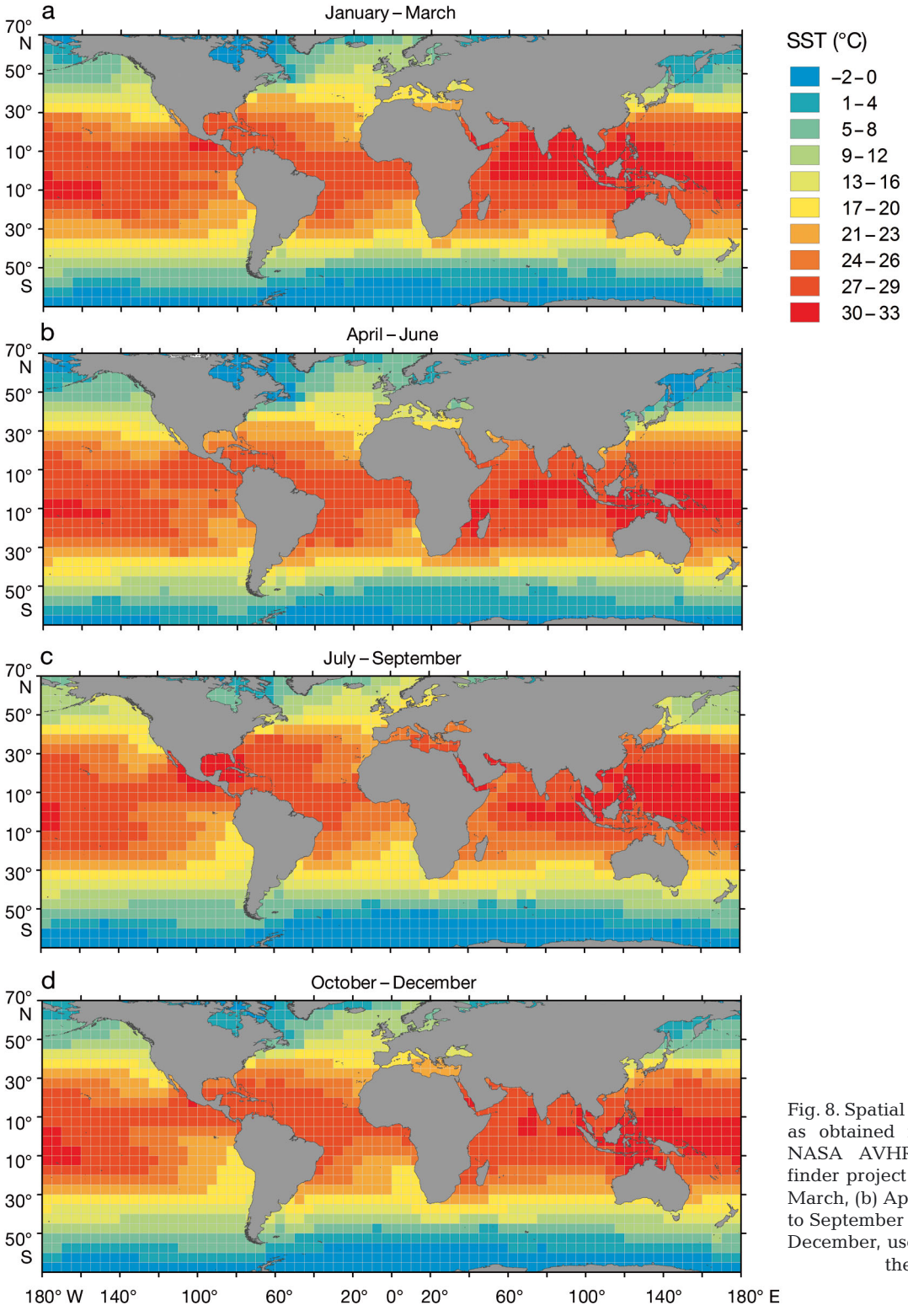

Fig. 8. Spatial distribution of SST as obtained from the NOAA/NASA AVHRR Oceans Pathfinder project for (a) January to March, (b) April to June, (c) July to September and (d) October to December, used as predictors in the model

though individual surveys were very fragmented spatially and temporally and were not coordinated internationally. Surveys often covered restricted areas within the limits of the main spawning areas, a common issue in icthyoplankton surveys (Bernal et al. 2007). In addition, variations in the migration patterns of Atlantic bluefin tuna to foraging grounds have occurred in the last decade (Fromentin & Powers 2005), and changes in adult ranges have also occurred over a longer time-scale (Worm & Tittensor 2011). If such

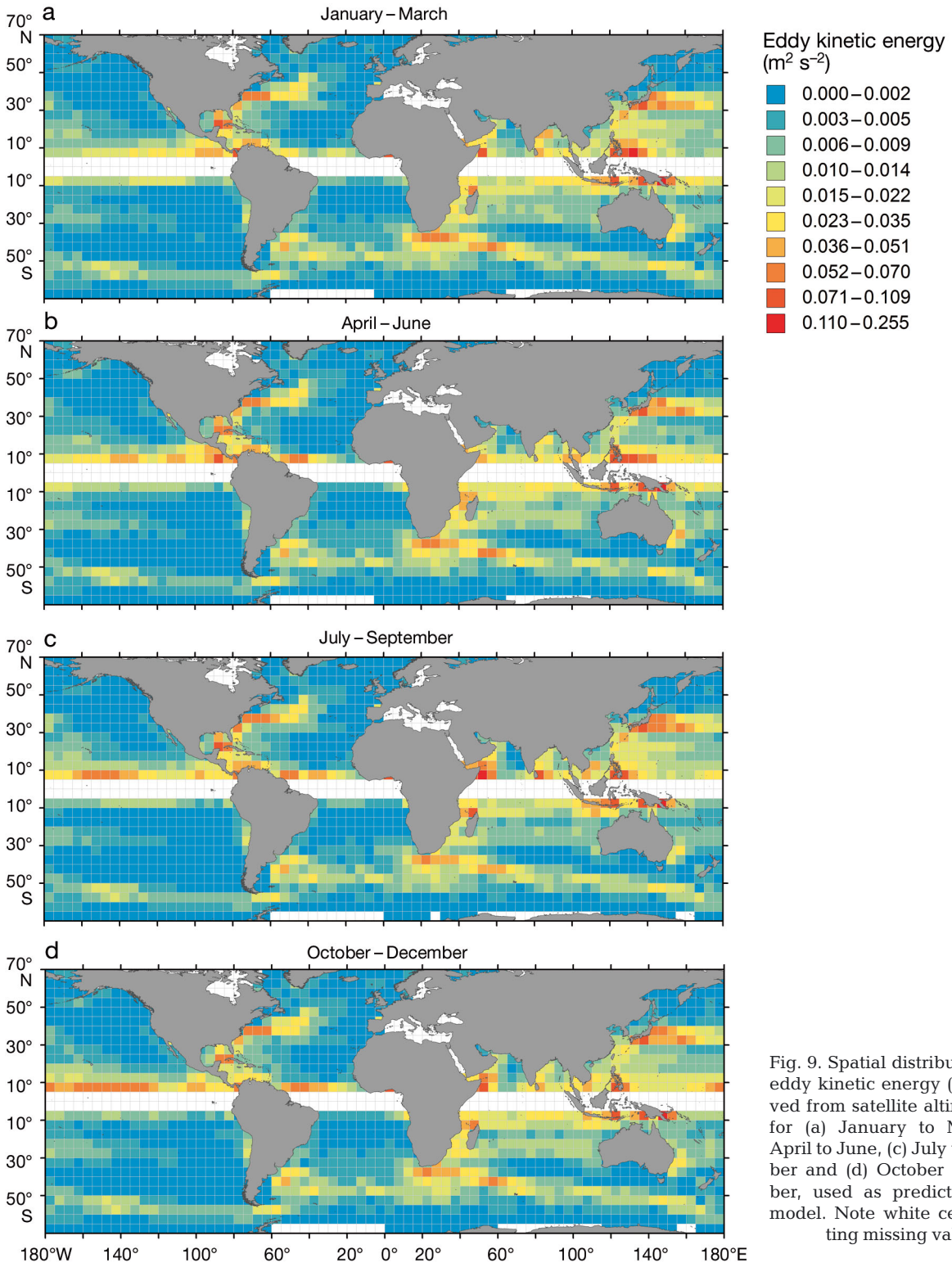

Fig. 9. Spatial distribution of the eddy kinetic energy (EKE) derived from satellite altimeter data for (a) January to March, (b) April to June, (c) July to September and (d) October to December, used as predictors in the model. Note white cells indicating missing values

variations occur relative to spawning migrations they will not be reflected in the data.

The analysis of presence–absence data provides information on where the tuna species occur, but does not provide information on patterns of relative abundance (Cope & Haltuch 2012). The main cons using presence–absence data were that we were able to explore the areas of highest occurrence of tuna larvae, but not the areas of highest density. The main pros were that we were able to compile infor-

Table 3. Ambient water temperature tolerances (°C) for adult and larval stages of selected tuna species (see Fig. 10 for larval data and Boyce et al. 2008 for adult data).

Species	—Adults—		——— Larvae ———		
	Min.	Max.	Min.	Max.	Mean (±SD)
Skipjack tuna	14.7	33	19.2	30.2	27.6 (1.72)
Yellowfin tuna	7	31	20.2	30.2	27.8 (1.5)
Albacore	7	25.2	21.7	30	27.4 (1.59)
Bigeye tuna	3	29	21.7	30.2	27.9 (1.43)
Atlantic bluefin tuna	2.8	31	24.7	28.5	26.48 (1.07)
Pacific bluefin tuna	2.8	28.4	21.7	28.9	25.3 (2.7)
Southern bluefin tuna	5	28.4	24.8	30.2	27.7 (1.54)

mation from different sources together, despite differences in data standardization in the reported larval densities.

Larval tuna identification at species level can be problematic when based on morphological descriptions, especially in the Gulf of Mexico (Richards et al. 1990). We have carefully reviewed the basis for taxonomical descriptions in the articles used as data sources for our analyses. Some species benefit from periodical sampling during long time series (e.g. Atlantic and Pacific bluefin tuna), particular morphological traits (skipjack tuna), or larval laboratory-rearing experiments (Atlantic and Pacific bluefin tuna, yellowfin tuna). Molecular analyses have confirmed identifications in some areas for some species and, in the future, could be a useful tool to validate identifications. We have digitalized the data providing a tag with the taxonomical clues used for identification. Future validations using molecular methods could be integrated into the database. The main aspects of the identification found in the review are discussed below for each species.

Larval tuna identification at species level

Due to extensive experimental work on the culturing of both Atlantic bluefin tuna and Pacific bluefin tuna, the developmental larval stages of these 2 species are very well described, and can be readily distinguished. Morphological descriptions of the larval developmental stages for both species have been provided from experiments and field sampling (Yabe et al. 1966, Alemany 1997, Olivar & Fortuño 1991, Kaji et al. 1996, Miyashita et al. 2001). For these species there are 3 major datasets from field samplings in the Gulf of Mexico (e.g. Muhling et al. 2010), the Japanese spawning area (e.g. Nishikawa et al. 1985, Kimura et al. 2010) and the Balearic Sea (e.g. Alemany et al. 2010). The data underlying the analyses

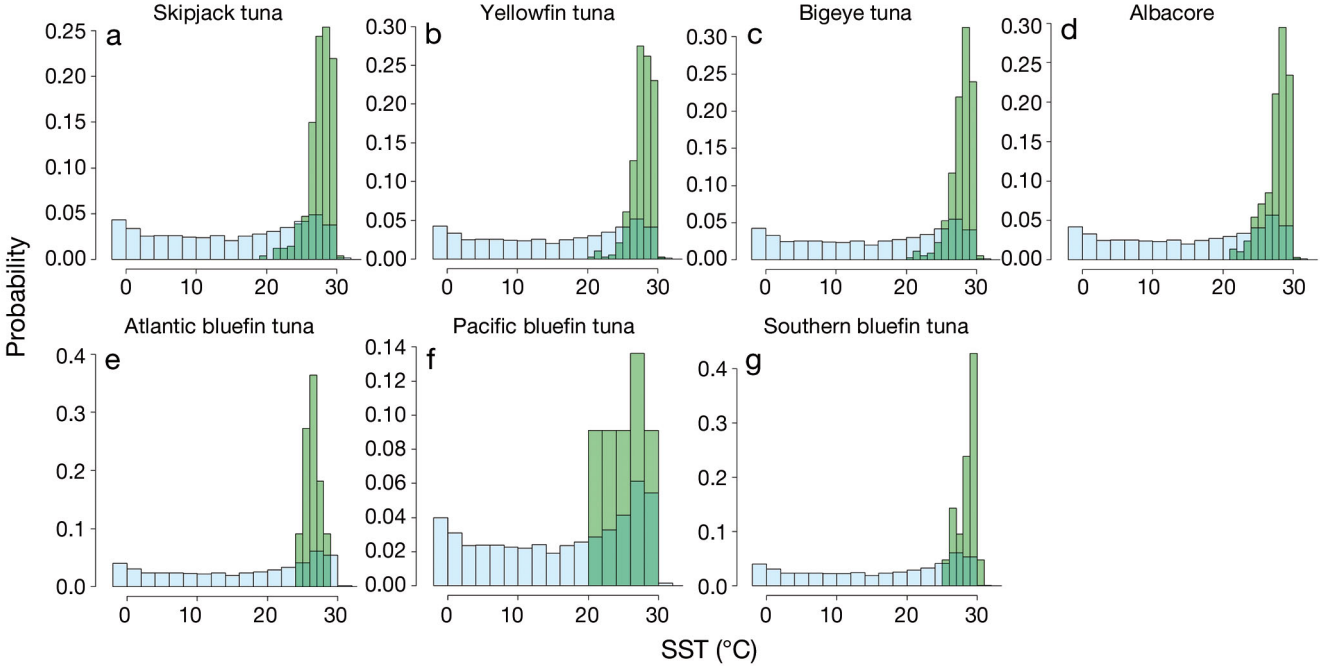

Fig. 10. Histograms showing the probability density functions of observed larval occurrences at the different SSTs computed for (a) skipjack tuna, (b) yellowfin tuna, (c) bigeye tuna, (d) albacore, (e) Atlantic bluefin tuna, (f) Pacific bluefin tuna and (g) southern bluefin tuna. Blue: observed larval absence; green: observed larval presence

are therefore based on 3 datasets targeting Atlantic and Pacific bluefin tuna of a very good temporal and spatial resolution; therefore, occurrences have been validated over years.

The spatial distribution of southern bluefin tuna larvae was obtained from Nishikawa et al. (1985) and periodic regional surveys (e.g. Davis et al. 1990a,b, 1991). The larvae were identified according to Nishikawa et al. (1985) and Nishikawa & Rimmer (1987). In regional surveys identifications were conducted mostly on individuals >3.5 mm to avoid misidentification (e.g. Davis et al. 1991). Similar descriptions of southern bluefin tuna were also provided by Yabe et al. (1966). The area described based on the larval data is the only known spawning area off Australia in the Indian Ocean (south of Indonesia); this was confirmed with data from ovaries analyzed in adults (e.g. Farley & Davis 1998).

The morphological description by Matsumoto (1958), confirmed by Matsumoto et al. (1972), Collette et al. (1984), Olivar & Fortuño (1991), Alemany (1997) and Richards (2006), is used in most oceans to identify skipjack tuna. This species has a forebrain pigment that helps to separate them from *Thunnus* species (Richards 2006). The use of molecular markers is rare but has confirmed skipjack identifications based on morphological traits in the Pacific Sea (Paine et al. 2008) and the Gulf of Mexico (Richardson et al. 2010). This species benefits from the most extensive sampling at large and regional scales.

Identifications of yellowfin tuna also benefit from the descriptions of individuals cultured in the laboratory (e.g. Margulies et al. 2007). This species can usually be identified using the works by Matsumoto (1958) and Matsumoto et al. (1972). Molecular identification has confirmed occurrences in the Strait of Florida (Richardson et al. 2006, Llopiz et al. 2010), the Panama Bight (Wexler et al. 2007) and the Pacific Ocean (Paine et al. 2008).

Matsumoto et al. (1972) is usually used for species identification of bigeye tuna and to determine its distribution in regional studies in the Pacific and Indian Oceans. Bigeye tuna larvae have been reported in the Gulf of Mexico (Nishikawa et al. 1985, Estévez et al. 1993), but further molecular analyses did not identify bigeye tuna in the Strait of Florida (Richardson et al. 2006). Therefore, we have disregarded their presence in the Gulf of Mexico in our database. The rest of the data for bigeye tuna worldwide comes primarily from Nishikawa et al. (1985), based on around 6000 net tow samplings and some regional sampling (Richards & Simmons 1971, Conand & Richards 1982, Lirdwitayaprasit et al. 2008). This is a challenging species since few data are available, even for adults, and so we should be cautious in our interpretations of the results.

Albacore larvae have been described by Matsumoto et al. (1972), Alemany (1997) and Richards (2006). Albacore can be confounded with yellowfin tuna in smaller larval size categories (Matsumoto et al. 1972). This may be a problem where both species co-occur, but not in the Mediterranean where only albacore is present and readily identified (Alemany 1997). Therefore, in some areas, it is usually included in the group *Thunnus* sp.

The temperature hypothesis

Temperature is a key factor in determining the distributions of adult tuna (Worm et al. 2005, Boyce et al. 2008, Tittensor et al. 2010), as well as of larvae (present study). Though both Atlantic bluefin tuna and southern bluefin tuna had higher minimum tolerances than the other species, all tuna species were shown to have narrower thermal tolerances during spawning than foraging. Spawning temperature preferences for tuna species could be linked to the physiological thresholds for adult spawning and larval development. Physiological temperature limits for biological processes such as gonad development and egg development obtained from experiments (Sawada et al. 2005, Margulies et al. 2007, Masuma et al. 2008) matched the spatially observed larval temperature tolerance limits well. An increase of water temperatures before and during spawning is needed for the adult tunas to release eggs (Margulies et al. 2007). No laboratory incubations exist that estimate the percentage of hatched tuna eggs with temperature or viable embryos. The temperature effects on metabolism have not been specifically studied in tuna larvae; however, higher temperatures are expected to increase metabolic costs, as has been observed in scombrid larvae (Giguère et al. 1988).

Regarding favorable temperatures for growth, the compilation of data from different tuna species suggests increasing growth rates with temperature (Reglero et al. 2011), but further studies are needed at the species level. Larval temperature preferences in the Gulf of Mexico, the Japanese Sea and the Mediterranean Sea support our results (Alemany et al. 2010, Muhling et al. 2010), though eggs and larvae can also be caught at 20 to 21°C in the Balearic Sea (Reglero et al. 2013). Maximum temperature thresholds are >30°C according to our analyses.

The ocean triad hypothesis

The ocean triad hypothesis suggests tuna spawning generally occurs in areas with mesoscale oceanographic features such as fronts and eddies (Bakun 2006). We have used EKE as a proxy of mesoscale activity and frontal density (Pascual et al. 2006). Though EKE has been used in several studies to model the spatial distribution of adult tuna (e.g. Worm et al. 2005, Zainuddin et al. 2008), it has not been used to estimate larval habitats. We found tuna larvae were more likely to occur in areas with intermediate EKE values of >0.02 m^2 s^{-2}, supporting the hypothesis that larvae are more likely to occur in areas where mesoscale activity is observed. The probability of larval occurrence was linear and positively related to EKE in Atlantic bluefin tuna, but linear and negatively related in albacore. A preference for similar ranges of EKE has been reported for adult breeding Atlantic bluefin tuna distributions in the Gulf of Mexico (Teo et al. 2007), and mesoscale activity is commonly found in areas with larvae (Muhling et al. 2013).

The EKE values with the highest probability of occurrence for tuna larvae, combined with optimal temperatures, were associated with warm western boundary currents: the Gulf Stream and the Brazil Current in the North and South Atlantic, respectively, the Kuroshio Current in the North Pacific, the East Australia Current in the South Pacific and the Agulhas Current in the Indian Ocean. In contrast, eastern boundary currents have EKE values <0.01 to 0.02 m^2 s^{-2} and are associated with colder temperatures. Tuna larvae also preferred intermediate EKE values that were associated with the south and north equatorial currents, respectively.

The spatial patterns for the larval occurrences of the 3 bluefin tuna species in this study suggest these species share similar characteristics in their habitats. Atlantic bluefin tuna larvae are present in enclosed seas such as the Gulf of Mexico and the Mediterranean Sea. EKE obtained from sea-surface height anomalies may be a good indicator of mesoscale activity in most of the oceans. But in such confined areas mesoscale structures can be induced by topography or occur at a smaller scale than the grid size used in this study.

The ecological processes that could explain the general preference of tuna larvae for areas with intermediate mesoscale activity are difficult to elucidate. In general, tuna species show a preference for mesoscale structures, with moderate activity to spawn, but avoid high EKE (Teo et al. 2007, Reglero et al. 2012, Muhling et al. 2013); one factor involved could be the opportunity to disperse during the larval stage. It has been shown that Pacific bluefin tuna larvae entering anticyclonic eddies after hatching increase their chances of successfully arriving in nursery regions (Kitagawa et al. 2010). Regions of high EKE could be less suitable for spawning if larvae end up in less optimal areas for later growth and survival as a result of the influence of strong currents on transport. The preference of albacore for regions with low EKE values may be an adaptation to separate their larval habitat from that of the other species.

Bakun (2006) proposed that eddies are associated with high productivity, increasing the chances of larval survival. At broad scales, tuna deposit eggs and, therefore, larvae into oligotrophic, low-productivity areas (e.g. Mediterranean Sea). Therefore, local food enrichment driven by eddies or frontal structures may help larvae to survive. Peaks of food abundance during both the planktivorous and the piscivorous stages of larval development may be a determinant of survival in these oligotrophic areas (Reglero et al. 2011). If intermediate EKE values associated with mesoscale structures influence the spatial distribution of feeding resources, this may increase larval survival. This aspect has rarely been analyzed in the literature to date. A trade-off between predation and food availablity may be the reason why larvae prefer mesoscale structures within broad-scale oligotrophic areas. Thus, there would be low food availability and, consequently, low predator abundances, as suggested by the so-called 'loophole hypothesis' (Bakun & Broad 2003, Irigoien et al. 2007). The loophole hypothesis has been partially tested for bluefin tuna in the Balearic Sea (Reglero et al. 2011), but needs to be tested for other species and locations in the future.

CONCLUSIONS

We tested 2 hypotheses regarding environmental spawning requirements for tuna, and our results provide support for a combination of the 2 hypotheses in most tuna species. The distributional range in tunas during the larval phase was related to temperature (temperature hypothesis), though with a lower limit (20°C) than the 24°C traditionally used to delineate tuna spawning-ground boundaries (Schaefer 2001). We also showed that temperature alone resulted in an overestimation of plausible spawning grounds. Intermediate intensity mesoscale processes (ocean

triad hypothesis) were also found to be an important factor in global larval distribution patterns. A combination of the 2 hypotheses (areas delineated both by temperature >20°C and with an intermediate EKE) provided the greatest explanatory power for most larval distributions, except for in the 3 bluefin tuna species, which had more restricted spawning locations, and albacore, which preferred low EKE values. The mechanisms linking larval development and survival in relation to the 2 variables (SST and EKE) remain speculative, but likely are related to the speed of development, larval retention and locally enhanced productivity.

There is very limited scientific information on the spatio-temporal spawning patterns of tuna species (Schaefer 2001) and strong uncertainties in our knowledge of many biological parameters, including reproduction, of tuna species. This study provides the first compilation of published data for tuna larvae on a broad spatial scale. Its availability for the research community could hopefully result in further collaborative research that would help to disentangle global drivers in tuna distributions.

Identification of the oceanographic parameters that drive the location of larval habitats for different tuna species and production of distributional maps may be useful tools in the implementation of high seas marine protected areas (HSMPA). One constraint on the implementation of HSMPAs is limited knowledge regarding the biodiversity of oceanic species and the identification of the parameters that should be measured (UNEP-WCMC 2008). Here we have identified oceanographic parameters (mesoscale eddies and SST) that can easily be measured by remote sensing and features (eastern boundary currents, semi-enclosed seas) that should be considered when determining areas of critical habitat for tuna larvae.

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