


Climate-induced vulnerability of fisheries in the Coral Triangle: Skipjack Tuna thermal spawning habitats

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Abstract

We investigated projected changes in sea surface temperature (SST) and the associated impacts on spawning habitat for skipjack tuna (*Katsuwonus pelamis*) in the Coral Triangle region (CT). A multimodel aggregate of SST CMIP5 models for the CT region, based on a comprehensive skill validation assessment, was used to identify the five best performing of 36 models tested for inclusion in a regional multimodel ensemble. Monthly 1° SST multimodel aggregate projections for the CT region under RCP8.5 show that increases in SST, as high as 2.8°C (mean value), will likely occur by the end of this century. Using these estimates of SST change, we applied three parameterizations of skipjack tuna spawning temperatures to assess the potential for change in spawning habitat within the CT region. The three spawning temperature parameterizations were as follows: (a) a square-wave function derived from catch data with boundaries at 26 and 30°C; (b) a symmetric Gaussian function derived from the SEAPODYM models; and (c) an asymmetric Gaussian function that modifies the SEAPODYM curve in (b) to include the results of relevant physiological experiments. All three parameterizations show similar geographic patterns, with the amount of favourable spawning habitat decreasing throughout the central, equatorial CT region and increasing at higher latitudes. However, the three parameterizations show marked differences in the modelled magnitude of change, with an asymmetric Gaussian function (ASGF) showing a regionwide average of 66.1% decline in favourable spawning habitat between 2015 and 2099. These projected changes in tuna spawning habitats are likely to have important consequences on local and regional fisheries management in the CT region.

KEYWORDS

climate, Coral Triangle, habitats, skipjack, spawning, temperature, trends

1 | INTRODUCTION

1.1 | Climate change in the Coral Triangle region

The Coral Triangle region (CT, 12°S–22°N and 94°E–163°E) is the most biologically diverse marine ecosystem on the planet, covering ~6 million km² of ocean, consisting of more than 30,000 islands across six countries (Indonesia, Malaysia, the Philippines, Papua New

Guinea, Timor-Leste and the Solomon Islands) in the Asia-Pacific region. An estimated 120 million people live within the CT region, of which approximately 2.25 million are fishers who depend on sustainable fisheries for their livelihoods (Dunning, 2014).

Seafood caught in the CT region feeds tens of millions of people and sustains local economies, but growing seafood consumption (Asian Development Bank, 2014a) and fully exploited fish populations (Garcia, 2009) highlight the importance of seafood stocks to

fishers' livelihoods and food security (Asian Development Bank, 2014b). The region is home to 76% of the world's reef-building coral species and six of the seven known species of marine turtles (Salinger et al., 2013). It is recognized as the global centre of marine biodiversity and a global priority for conservation (Hoeksema, 2007). The biodiversity and natural productivity of the CT region are under threat from coastal development, destructive fishing, overfishing, a high market demand for rare and threatened species, and climate change (Asian Development Bank, 2014c). The impacts of climate change on coastal areas of the CT region and pelagic species that utilize this habitat are active areas of investigation with large uncertainties.

Approximately 30% of the CO₂ released into the atmosphere since the industrial revolution has been absorbed by the world's oceans (Sabine et al., 2004). Climate change will result in ocean warming (Sampayo, Ridgeway, Bongaerts, & Hoegh-Gulberg, 2008; Wilkinson, 2008), ocean acidification (Kleypas, 1999; Raven et al., 2005), sea level rise (Church et al., 2013), decreased ocean productivity (Behrenfeld et al., 2006; Polovina, Howell, & Abecassis, 2008), and increasing frequency and intensity of storms (Webster, Holland, Curry, & Chang, 2005). These changes will have direct and indirect effects on ecologically and economically important natural resources and may threaten local fisheries, especially in small island communities that depend heavily on ocean resources for both nutrition and livelihoods. Studies of climate impacts on fisheries around the world have increased rapidly in recent years, following the contributions to the assessment reports of the Intergovernmental Panel on Climate Change (IPCC) and the development of a broad set of projection models bundled into the Climate Model Intercomparison Project phase 5 (CMIP5, <http://cmip-pcmdi.llnl.gov/cmip5/>). This suite of CMIP5 models allows us to test a diversity of projections against each other and to develop regional multimodel aggregates by lessening the uncertainty. While marine ecosystem models are increasingly used for prediction to support high stakes decision-making, it is imperative that the models' capabilities are tested and understood under a rigorous model skill assessment (Jolliff et al., 2009; Stow, Roessler, Borsuk, Bowen, & Reckhow, 2003; Stow et al., 2009).

1.2 | Tuna populations in the Coral Triangle region

The CT region supports large, commercially important tuna fisheries for skipjack tuna (*Katsuwonus pelamis*), bigeye tuna, and yellowfin tuna. Tuna fisheries are a multibillion-dollar global industry, with annual trade and tuna catch in Indonesia, Papua New Guinea, the Philippines, Fiji, and the Solomon Islands reaching 1 billion U.S. dollars and 991,482 metric tons (Western and Central Pacific Fisheries Commission 2014 yearbook). Tuna species are characterized as being the faster-growing fish species reaching constant population numbers close to the maximum that the environment can carry while achieving large body sizes (Murua, Rodriguez-Marin, Neilson, Farley, & Juan-Jordá, 2017). The ecological success of tuna species, relative to most other fish species, is associated with an ensemble of specializations as their swimming mechanisms (Dewar & Graham, 1994),

radically different thermal biology (Zhang, Farkas, & Hale, 2001), increased rate functions and a markedly different cardiac physiology (Graham & Dickson, 2004).

The most common and heavily fished tuna species, skipjack tuna, account for at least 60% of the legally caught tuna landed worldwide (International Seafood Sustainability Foundation, 2009; Western and Central Pacific Fisheries Commission 2014). Skipjack is the fastest-growing tuna species, growing more than 1 m in length, weighing up to 18 kg in average, and reaching longevity of up to 10 years (Froese & Pauly, 1994). However, they require relatively rapid swimming to generate hydrodynamic lift to account for the fact they are denser than seawater due to missing gas bladder (Graham & Dickson, 2004). This need for swimming, associated with search for food, and optimal nursery areas are consistent with skipjack's highly migratory patterns and their wide distribution from oceanic to epipelagic areas of tropical and subtropical waters of the Atlantic, Indian and Pacific Oceans (IUCN Red List, <http://maps.iucnredlist.org/map.html?id=170310>). Adult skipjack tuna feed on fish, crustaceans, cephalopods, and molluscs and often mix with juvenile individuals of other tuna species forming large schools along convergence zones, upwelling areas, and near thermal fronts, but not necessarily islands (Boehlert & Mundy, 1994), reaching depths of about 260 m during the day, but limited to near-surface waters at night (Collette & Nauen, 1983).

Skipjack tuna reproduce through broadcast spawning year-around in equatorial waters, and from late spring to early fall in subtropical waters, especially around midnight (Hunter, Macewicz, & Sibert, 1986), with relative batch fecundity from 40 to 130 eggs/g body-weight (Collette & Nauen, 1983; Stequert & Ramcharrun, 1995). Each tuna spawning event can generate about 100,000 to 2 million eggs per adult female and varies with the size of the female (Matsumoto, Skillman, & Dizon, 1984). Females mature at 41–42 cm fork length, while males mature at a slightly large size, 42–43 cm fork length (Stequert & Ramcharrun, 1996). Adults have an overall thermal range from 14.7 to 30°C (Barkley, Neill, & Gooding, 1978; Collette & Nauen, 1983), with higher occurrence between 20.0 and 29.0°C (Sund, Blackburn, & Williams, 1981). Efforts to characterize the optimal spawning habitat for tunas have used data from wild catches, from physiological experiments, and from modelling efforts (e.g., Collette, 2010; Lehodey, Senina, & Murtugudde, 2008; Schaefer, 2001; Ueyanagi, 1969). Larvae are more abundant in offshore waters (Boehlert & Mundy, 1994), and higher occurrences follow the 30–50 m range, with a few larvae found at depths between 60 m (Matsumoto, 1976; Schaefer, 2001) and 90 m (Boehlert & Mundy, 1994). Data from the western North Pacific (Ueyanagi, 1969) and from the Hawaiian Islands area (Matsumoto et al., 1984) show that the minimum and maximum temperatures for skipjack tuna larvae occur at 22.1 and 30°C, respectively. While optimal spawning temperatures have been described at >24°C (Collette, 2010; Schaefer, 2001), with high larval occurrence at >25°C (Collette & Nauen, 1983), and especially at around 29°C and in some regions at hottest waters surveyed (Matsumoto et al., 1984; Ueyanagi, 1969).

While these catch data effectively parameterize the lower edge of a spawning window and define an approximate peak, they leave greater uncertainty about the highest thermal temperatures for

successful spawning. The state-of-the-art models describing climate effects on skipjack populations (SEAPODYM, Lehodey et al., 2008; Lehodey, Senina, Calmettes, Hampton, & Nicol, 2013; Lehodey, Senina, Nicol, & Hampton, 2015) have modelled this thermal spawning window using a symmetric Gaussian probability of spawning. This parameterization allows significant levels of spawning at temperatures as high as 36°C. Under laboratory conditions, skipjack caught in Hawaii have shown a median survival threshold of 33°C (Dizon, Neill, & Magnuson, 1977). Although we do not have similar laboratory estimates of larval thermal thresholds in skipjack, physiological experiments for yellowfin tuna suggest that at temperatures above 33°C, yellowfin yolk-sac larvae are malformed and unlikely to survive (Wexler, Margulies, & Scholey, 2011). Yellowfin and skipjack are both tropical tunas, with similar thermal ranges of adult occurrence, successful spawning and similar diet (Dragovich & Potthoff, 1972).

To achieve a better understanding of the effects of changing ocean temperatures on skipjack thermal spawning habitat in the CT region, we applied three different parameterizations of skipjack spawning probability with SST: (a) a square-wave range, (b) a symmetric Gaussian, and (c) an asymmetric Gaussian with a steeper decline at higher temperatures to the results from a regional, multimodel aggregate temperature ensemble, based on the Representative Concentration Pathways 8.5 (RCP 8.5) scenario from IPCC Assessment Report.

2 | MATERIALS AND METHODS

2.1 | Multimodel skill validation assessment for predicted (forecasts of) sea surface temperatures in the Coral Triangle region

Available global Earth System Models (ESMs) fields of sea surface temperature (SST) from the IPCC (<http://www.ipcc.ch/>) and the CMIP 5 (<http://cmip-pcmdi.llnl.gov/cmip5/>) were used to generate a regional multimodel projections aggregate for the CT region. Monthly SST fields from 46 CMIP5 models covering both historical (1861–2005) and the RCP8.5 (2006–2099) scenarios were used to generate the CT region SST multimodel aggregate. The RCP 8.5 scenario represents “business-as-usual” where CO₂ concentrations could increase to 1,000 ppm by 2100 (IPCC, 2014). Model fields were remapped to a 1° latitude by 1° longitude grid as part of a collaboration with the International Pacific Research Center at the University of Hawaii, using a bilinear interpolation method (Jones, 1999; <http://apdrc.soest.hawaii.edu/datadoc/cmip5.php>).

A comprehensive skill validation assessment (SVA) was developed to estimate the accuracy of all available CMIP5 model SSTs with a spatial grid of 1 × 1 degree. Ten of the models were removed from this analysis because data errors (e.g., extreme values) or time discrepancies existed. As an observational data set against which to test, we used the NOAA/NCEP Reynolds monthly Optimally Interpolated (Reynolds-OI) SST product (Reynolds, Rayner, Smith, Stokes, & Wang, 2002), at 1° latitude by 1° longitude grid. The Reynolds-OI was generated using both in situ SSTs from ships

and buoys and satellite-derived SSTs from the NOAA Advanced Very High-Resolution Radiometer (AVHRR). The satellite-derived SSTs come from the Multichannel SST products that have been constructed operationally from the five-channel AVHRR by NOAA's National Environmental Satellite, Data and Information Service. We compared this observational data series to 36 SST models' simulations bounded within the CT region and generated SVA scores (Figure 1).

The SVA was based on side-by-side statistical comparisons of observations and the SST simulations from the 36 models for the period December 1981 to July 2014. The SVA was constructed using six indices to provide an assessment that captures distinct aspects of model performance (following Stow et al., 2009): (a) correlation coefficient [*r*], (b) root-mean-squared error [RMSE], (c) reliability index [RI], (d) average error (bias) [AE], (e) average absolute error [AAE] and (f) modelling efficiency [ME]. The strength of the linear relationship between predicted and observed values is represented by *r*. The size of the discrepancies between predicted and observed values is measured using the RMSE, AE, and AAE. The AE is a measure of combined model bias; however, this measure can be misleading when similar negative and positive discrepancies can cancel each other. The AAE and the RMSE both consider the magnitude rather than the direction as the main AE limitation. Together, these three statistics provide an indication of model prediction accuracy (Stow et al., 2009). The average factor by which model simulations differ from observations is computed by the RI (Leggett & Williams, 1981), while the ME measures how well a model simulate relative to the average of the observations (Loague & Green, 1991; Nash & Sutcliffe, 1970).

To identify the suite of CMIP5 RCP 8.5 SST models most representative of the observations, we applied the above-described SVA approach to three variables: (a) time series of spatially averaged monthly fields, (b) the monthly climatology derived from over the whole test period (1981–2014), and (c) trend slope and the y-intercept of a linear regression. We then summarized the results by taking the mean of the normalized statistics in (a), (b) and (c) above and reported the mean of these three values as the final SVA score for a model or an ensemble. Then, we sorted models from high to low SVA (Figure 1b) and generated a series of 35 multimodel aggregates that varied according to the number of top-ranked models included; that is, we first generated an average of the best-performing two models, then the best three, the best four, etc., until the final multimodel average that included all 36 models evaluated. We then re-evaluated each resulting multimodel average and assigned each an SVA score (Figure 1c), and selected the best-performing multimodel aggregate by calculating the arithmetic average of results of the best five models.

2.2 | Identifying Skipjack Successful spawning habitat

We compared the monthly spatial distribution of successful spawning habitat for skipjack tuna at “present” and “end of the

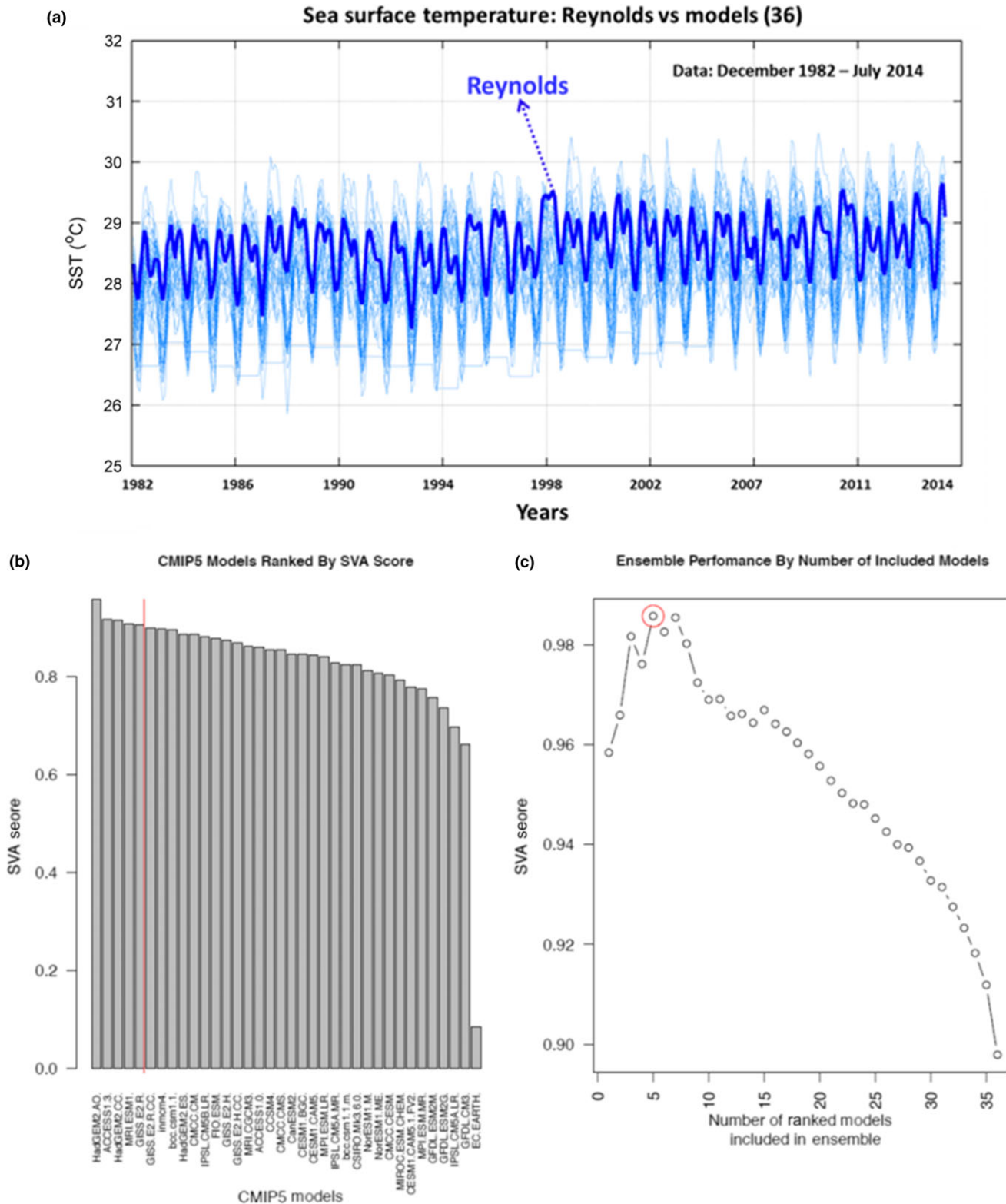


FIGURE 1 Coral Triangle Region Sea Surface Temperature Skill Validation Assessment (SVA) on: (a) Observations (Reynolds monthly Optimally Interpolated [bold line] and 36 IPCC CMIP5 SST models [thin lines] used in the SVA), (b) normalized SVA scores from 36 models, respect to observations, and (c) ensemble performance by number of included models from (b) [Colour figure can be viewed at wileyonlinelibrary.com]

century” (2099) SST conditions. We used the monthly and 1° latitude by 1° longitude gridded SST multimodel mean (MMM) assemblage for the CT region, generated with the five models that

performed best in the regional SVA (Figure 1), under the RCP8.5 scenario. Figure 2 reveals a significant increase in SST between present and projected conditions. We analysed the extent of

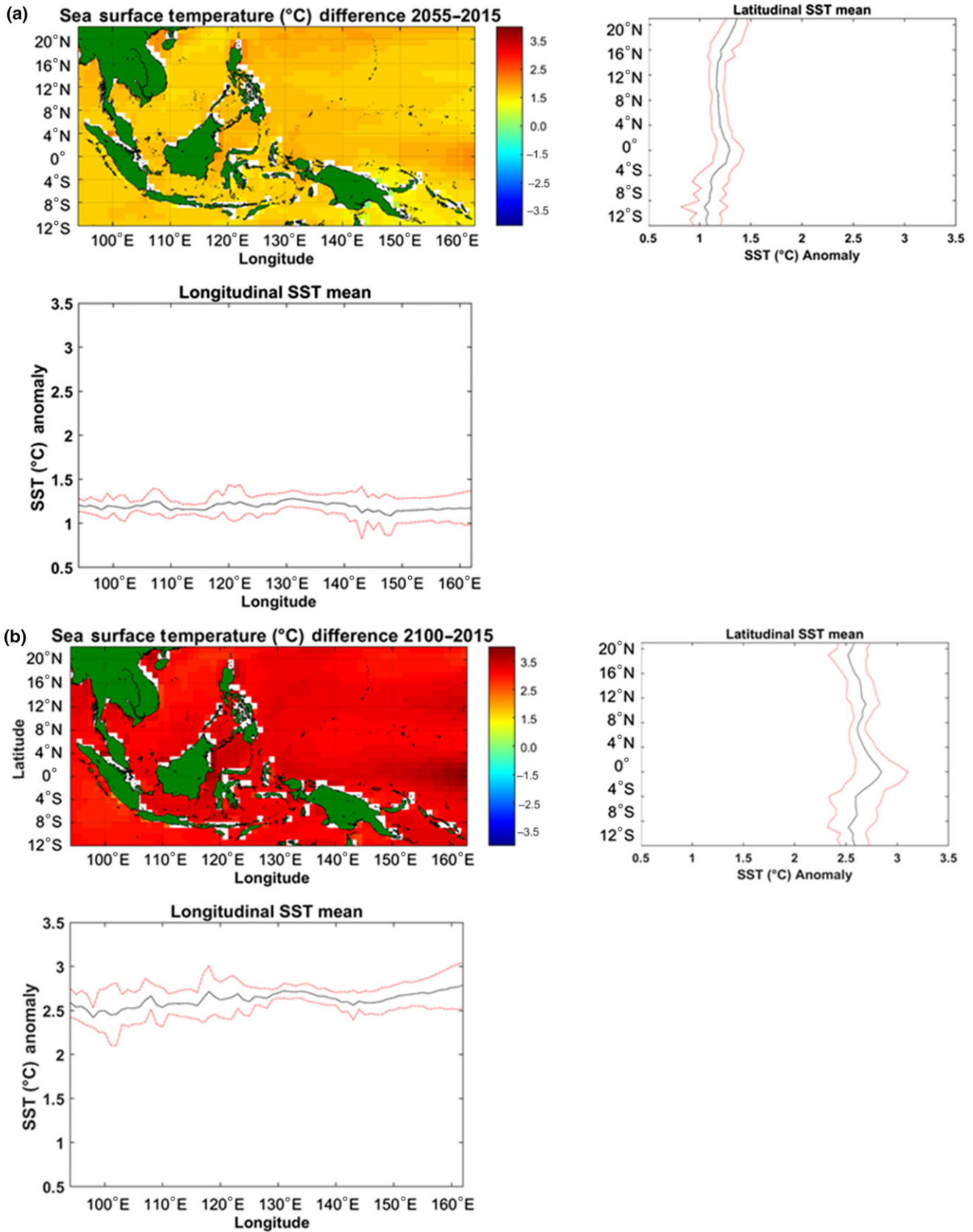


FIGURE 2 Sea surface temperature differences between 2055 and 2015 (top three panels), and 2099 and 2015 (bottom three panels). Colour plots show the spatial distribution of the sea surface temperature differences. Line plots show the mean (central line) and standard deviation (outside lines) of the sea surface temperature differences associated with each latitude and longitude [Colour figure can be viewed at wileyonlinelibrary.com]

skipjack thermal spawning habitat from these model results using three different parameterizations of skipjack spawning sensitivity to temperature (Figure 3): (a) a square-wave function (SQF), with 26.0 and 30.0°C temperature ranges (Forsbergh, 1989; Schaefer, 2001), (b) a symmetric Gaussian function (SYF), with a mean of 29.5°C and a standard error of 3.5°C (Lehodey et al., 2013), and (c) an asymmetric Gaussian function (ASGF), with a mean of 29.5°C and standard errors of 3.5°C (lower) and 1.5°C (upper) limits.

Using these three parameterizations, we show the impact of distinct physiological assumptions ranging from: (a) a coarse thermal range defined by catch data (Forsbergh, 1989; Schaefer, 2001), (b) the probability distribution used in the SEAPODYM model following Lehodey et al. (2013) assumptions and (c) a modified probability distribution which includes the upper thermal limits suggested by physiological experiments (Dizon et al., 1977; Wexler et al., 2011).

To assist interpretation of the spatial extent of habitats of a given quality, we have defined areas with a calculated probability of successful spawning >90% as optimal spawning habitat, >50% as favourable spawning habitat and >10% as possible spawning habitat. Note that results from the SQF characterize habitat binomially, that is, YES spawning, or NO spawning, rather than as a continuous estimate of habitat quality.

3 | RESULTS

3.1 | Skill validation assessment

We used regional SST projections for the CT region derived from the IPCC CMIP5 climate models to identify the potential impacts of climate change on spawning habitat for skipjack tuna. We obtained estimates of the models' accuracy, with respect to observations for the period December 1981 to July 2014, after we applied an SVA to the RCP 8.5 SST model outputs available.

Most individual models tested performed well when compared to the observational record. Ten models of the 36 tested had SVA scores >0.9, 29 had scores >0.8, and only seven showed scores below 0.8 (Figure 1b). However, when we tested multimodel aggregates that incrementally included the top-ranked individual models, ensemble performance increased rapidly upon the inclusion of more models, up to five. This performance held reasonably steady until seven to eight models and then rapidly declined (Figure 1c). For our projections, we used the five-model ensemble that presented the highest normalized SVA scores of all tested multimodel aggregate (Figure 1c).

The CT region MMM ensemble reveals a significant increase in SST between the present (2015) and 2055 (Figure 2a) and 2099 (Figure 2b) conditions. The Celebes Sea, the Java Sea and the South China Sea will experience the strongest effect with maximum SST values of up to 33.2°C; 2.8°C higher than present mean conditions (Figure 2).

3.2 | Skipjack optimal spawning temperature

We applied three distinct parameterizations for skipjack spawning temperatures for the CT region MMM aggregate results to estimate the effect of SST changes in skipjack spawning habitat (Figure 3). The results of the three different skipjack spawning temperature parameterizations showed highly distinct magnitudes and timing of changes in skipjack spawning habitat but broadly similar spatial patterns (Figures 4 and 5).

The three parameterizations differ dramatically in projected magnitude and timing of effects in the CT region for the 2015–2099 SST conditions (Figure 4). The SQF projects the most extreme effects, showing an 82.8% decline in spawning habitat in the CT region by 2099 (Figure 4a–c). The SEAPODYM-derived SYF projections show a regional decline of 65.5% by 2099 strictly for “optimal” spawning habitat conditions, that is, those with >90% probability of successful spawning (Figure 4a). The decline shown in SYF is only for “optimal” habitat, while the projected extents of “favourable” spawning habitat (>50% probability) and “possible” spawning habitat (>10%) show minimal impact (Figure 4b,c). However, when using a distribution of thermal spawning habitat modified to include relevant physiological data on high-temperature stress (i.e., under ASGF assumptions), “optimal,” “favourable” and “possible” spawning habitat all show meaningful declines, respectively, showing regionwide reductions in extent of 80.5%, 66.1% and 10.9% by 2099 (Figure 4).

The time-course and immediacy of change also differ among parameterizations. Again, SQF shows the most extreme case, with changes occurring as early as 2025. SYF, in contrast, only shows changes in “optimal” habitat, and the downward trend starts around 2050. However, in ASGF, the timing of changes in “optimal,” “favourable” and “possible” habitat mirrors the eventual magnitudes. We see regional declines in “optimal” habitat as early as 2025, as shown by the SQF; declines in “favourable” habitat beginning around 2050; and a decline in “possible” habitat occurring as late as 2080.

Despite the stark differences in magnitude and timing, each of the three parameterizations shows similar spatial patterns of spawning habitat change, with spawning habitat declining in near-equatorial latitudes and increasing to some degree in higher latitudes.

Based on SQF assumptions, skipjack tuna are able to spawn across most of the CT region under observed temperature conditions in 2010 (Figure 5a, top row). The coldest water temperatures (<26°C) occurred at high latitudes during February in the northern portions of the region. Warm water conditions (>30°C) occurred during June over areas with shallow bathymetry along the equator between West Papua, Malacca Strait, the Sulu Sea, west of Philippines, south of the Kepulauan Riau and the Gulf of Thailand. Favourable spawning conditions at thermal conditions between 27 and 30°C present a strong contrast between conditions projected to occur in 2040, 2070 and 2099, as most of the CT region will be subject to SSTs >30°C especially by 2099 (Figure 5a, bottom row). Skipjack spawning conditions under SQF, between 26°C and 30°C (Collette & Nauen, 1983; Forsbergh, 1989; Schaefer, 2001; Sund et al., 1981), will shift by the end of the century to higher northern

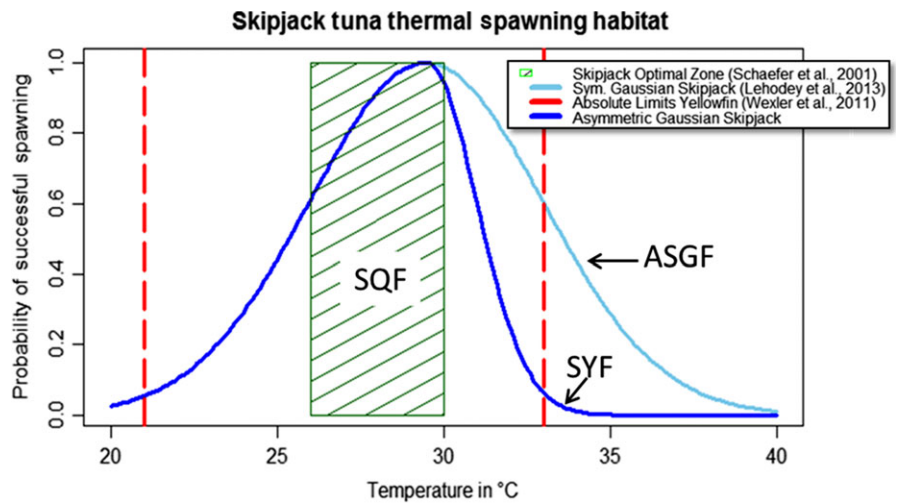


FIGURE 3 Thermal functions for Tuna spawning habitat: square-wave function (SQF, dashed box), the symmetric function (SYF, dark blue line) and the asymmetric function (ASGF, light line) [Colour figure can be viewed at wileyonlinelibrary.com]

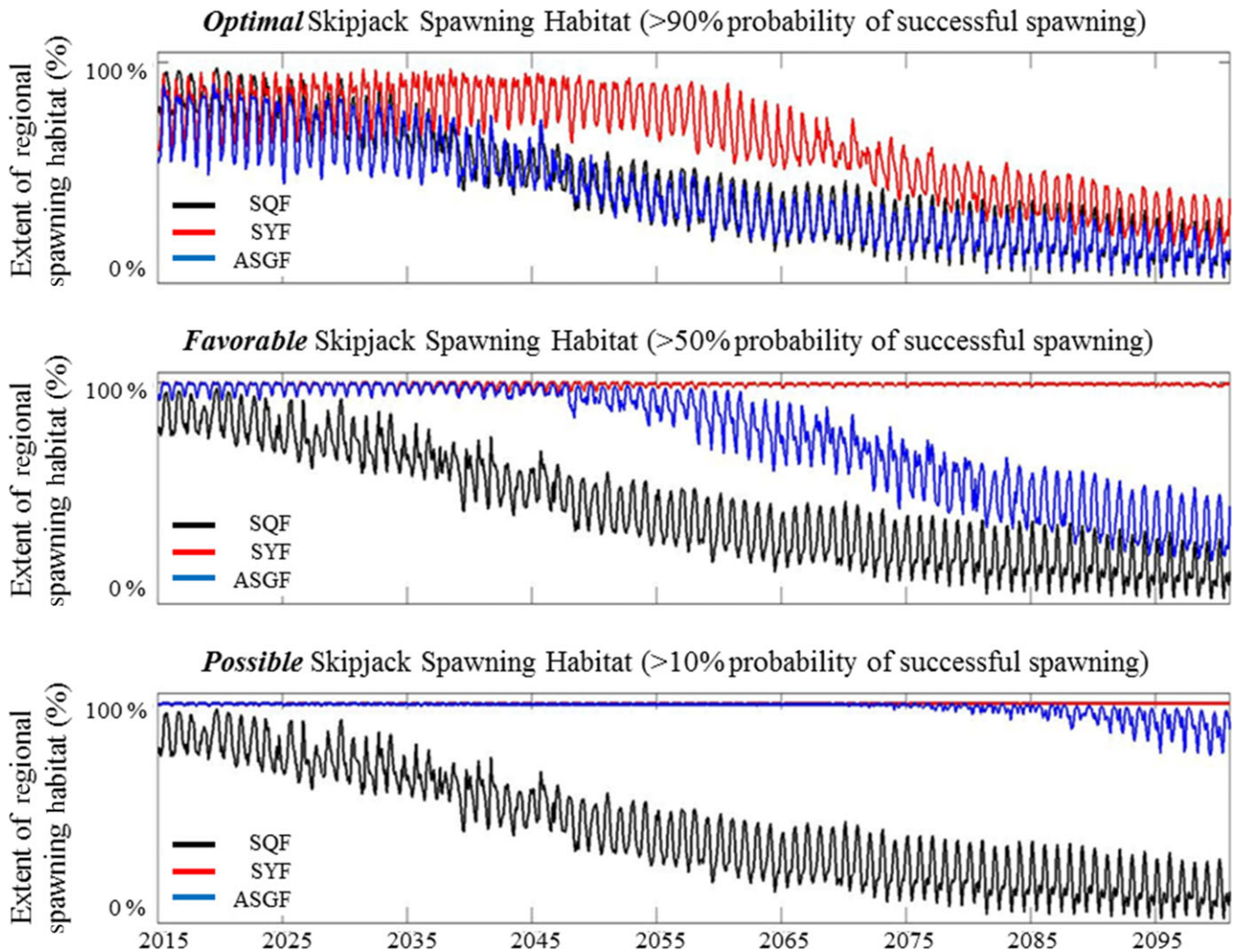


FIGURE 4 Change in regional extent of skipjack spawning habitat across all three spawning temperature parameterizations (SQF, SYF, ASGF) at three levels of favourability: (a) optimal spawning habitat, >90% probability of successful spawning; (b) favourable spawning habitat, >50% probability; and (c) possible spawning habitat, >10% probability. Note the square-wave function (SQF) is a yes/no output and therefore shows the same result for all three levels of favourability [Colour figure can be viewed at wileyonlinelibrary.com]

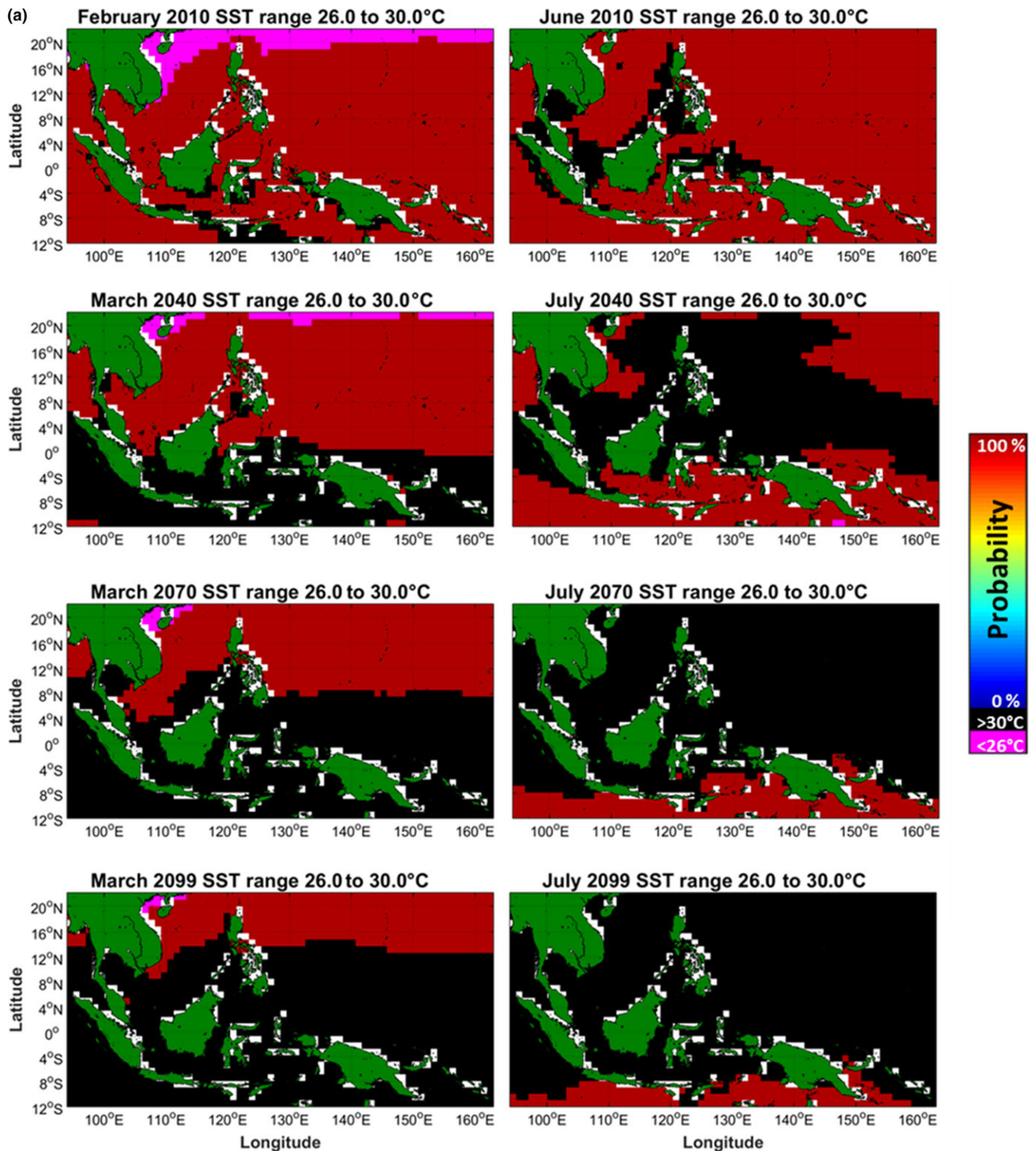


FIGURE 5 (a) Square-wave function (SQF) with boundaries at 26 and 30°C. (b) Symmetric function (SYF) with mean SST of 29.5°C and standard error of 3.5°C of the spawning temperature function (Lehodey et al., 2013). (c) Asymmetric function (ASGF) with mean SST of 29.5°C and two standard errors of 3.5°C (first half of curve) and 1.5°C (second half of curve) of the spawning temperature function (proposed in this analysis) [Colour figure can be viewed at wileyonlinelibrary.com]

latitudes during the boreal summer and to lower latitudes during the Northern Hemisphere winter.

Under the SYF parameterization, present-day SST conditions in the central area of the CT region show probabilities above 70% for successful spawning year-round. Medium-to-low successful spawning

probabilities are found at higher latitudes during minimum (February) and maximum (July) temperatures with a mean change between present SST conditions and the end of the century of 2.5–2.8°C. By 2099, the region between the equator and 12°S, and the Beibu Gulf will likely show lower probabilities of successful spawning in

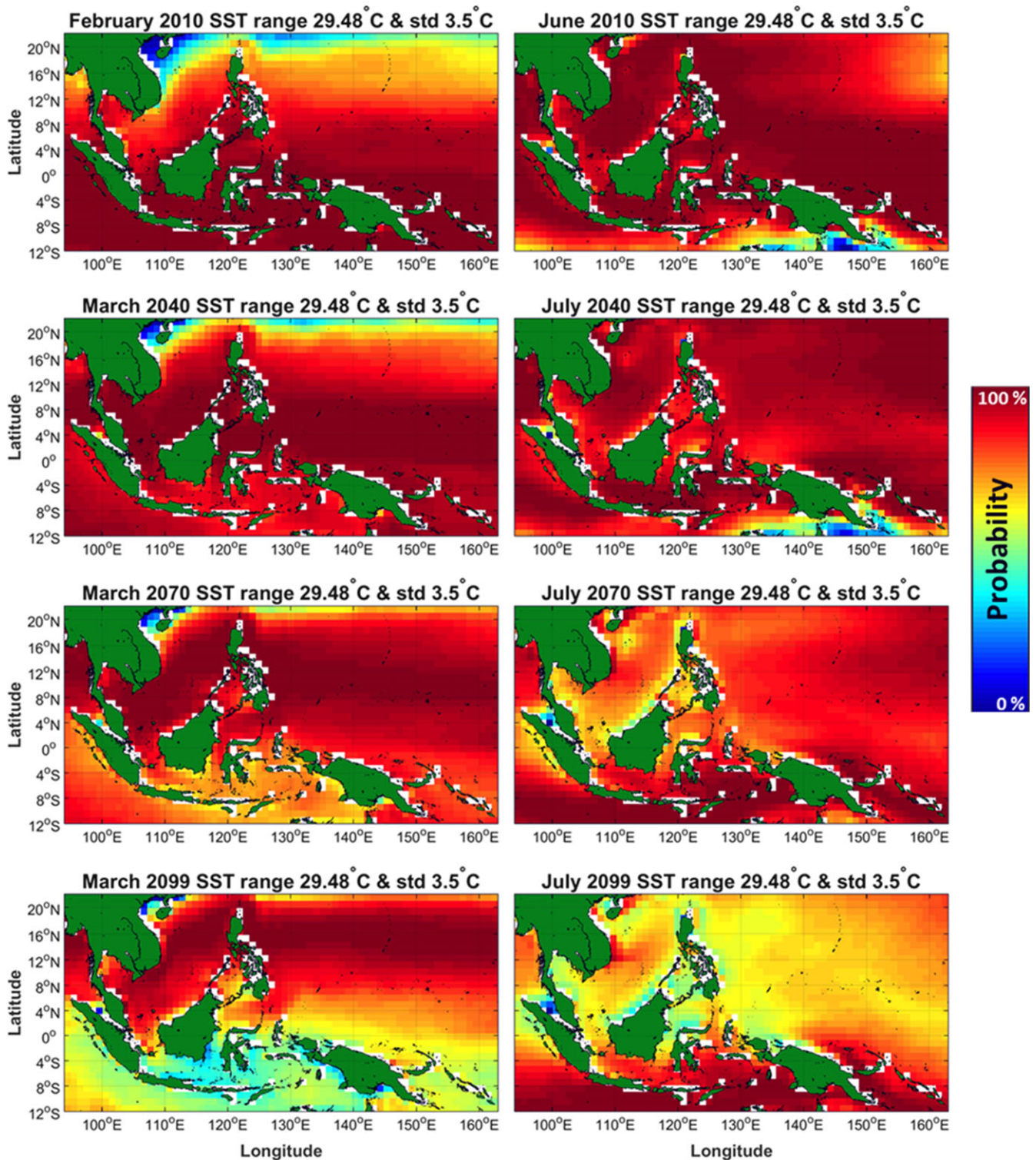


FIGURE 5 (Continued)

January, February and March (down to about 50% probability of successful spawning), while areas from 8°N to 20°N will show higher probabilities of successful spawning. These conditions will shift during the months of June, July and August. Greater seasonal variability in spawning probabilities between present conditions and future projections for the CT region is associated with the SST

range used to define the lower and upper boundaries in the SYF (Figure 5b).

Finally, under the ASGF parameterization, present-day SST conditions show similar spawning probabilities with the SYF results. However, significant changes from high to low spawning probabilities happen from 2040 to 2099, with strong seasonal variability

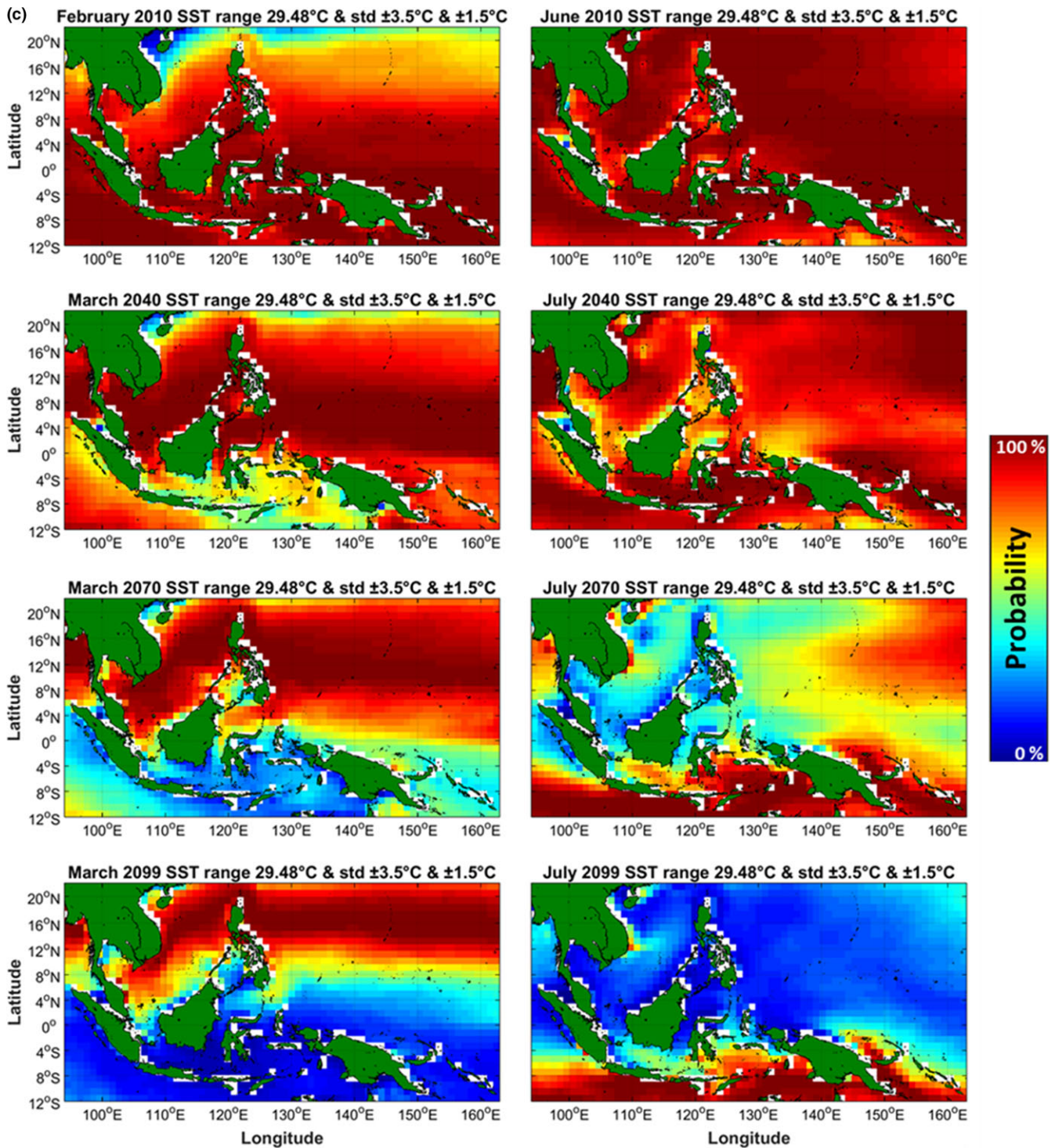


FIGURE 5 (Continued)

(Figure 5c). By 2099, however, the ASGF parameterization probabilities below 30% for successful spawning during July, with the exception of highest probabilities projected in the south Indonesia/Indian Ocean, Timor Sea, Arafura Sea, Bismarck Sea, and the Solomon Sea. Higher spawning probabilities are projected to occur between February, March, and April in the China Sea, West Philippine Sea and the Andaman Sea, with the exception of the Gulf of Tonkin-Vietnam (highest spawning in July). This projected seasonal change in the

high/low probability of spawning may have strong and direct effects in skipjack tuna adult distribution and selection of spawning areas.

4 | DISCUSSION

Our ability to project future changes in climate depends on the strengths and limitations of global climate models. No current model

is superior to others in all respects, but different models have different strengths and weaknesses (Bader et al., 2008). This forecasting challenge is greatly compounded when attempting to project species or ecosystem responses to changes in the physical environment (Muhling et al., 2015; Rose et al., 2010). Here, we have demonstrated a set of approaches in which we showcase strategies for managing both a range of physical and physiological possibilities in projecting skipjack tuna spawning habitat.

4.1 | CMIP5 Coral Triangle region skill validation

In high-stakes fisheries management decision-support applications, information regarding model accuracy or “skill” is essential for decision-makers to consider when weighing forecasts and the possible outcomes of alternative management actions aimed at achieving sustainable fisheries. It is then imperative that a rigorous model skill assessment is conducted so that the model's capabilities are tested and understood. In this study, we developed an SVA for the CT region using satellite and in situ observations of SST and an extensive suite of 36 available CMIP5 climate models to generate a summary of predictions representing the best regional MMM projection for SST from present to 2099. Having this opportunity to compare long-term SST observations time series to climate models provided the possibility to better estimate climate change effects on skipjack tuna spawning habitats based on thermal conditions. Based on our results, the severity and rate of change in SST conditions will not be uniform across the CT region, and it is evident from the results that significant shifts in spawning conditions will likely occur from now to the end of the century in the CT region.

4.2 | Physiological assumptions are critical, especially at upper thermal range

While our regional MMM assessment of SST shows significant, spatially variable change across the CT region, the relative impact of that change on skipjack tuna spawning depends highly on the assumptions of temperatures assumed to be associated with skipjack spawning. We employed three distinct ranges of skipjack tuna spawning, two specifically suggested in the literature (SQF, Schaefer, 2001; SYF, Lehodey et al., 2013), and a third that we proposed based on modifying the current standard with relevant physiological experimental results (ASGF; Wexler et al., 2011; Dizon et al., 1977).

The three parameterizations' distributions differ most along the upper range of skipjack tuna spawning temperatures, which is the range we have the least direct observational data. The SST models suggest that temperatures in the CT region will rise into ranges rarely observed today (Figure 2), and the effect on skipjack tuna spawning critically depends on the response in these upper thermal ranges. The impacts of these differences are borne out in the distinct results from each of these parameterizations, with the two parameterizations with lower thermal thresholds for cessation of spawning (i.e., SQF, ASGF; Figure 3) showing much greater impacts

on skipjack tuna spawning habitat than the high-temperature-tolerating SYF model (Lehodey et al., 2013; Figures 3, 4, and 5a–c).

Asymmetric thermal performance curves are a common feature of the thermal physiology of ectotherms and tend to show a gradual rise to optimal performance with increasing temperatures and rapid decline in performance at higher temperatures (e.g., Deutsch et al., 2008). While adult tuna are remarkable for their ability to maintain internal temperatures through their thermoregulation (Graham, 1973), tuna larvae are classically ectothermic, and successful tuna spawning requires the survival of tuna larvae (Lehodey et al., 2008). The current gold-standard parameterization of skipjack spawning temperatures is a component of the comprehensive SEAPODYM model (Lehodey et al., 2008, 2013), and while its symmetrical Gaussian function fits observed data well at lower temperatures, it allows substantial successful spawning at temperatures shown experimentally to be fatal for both skipjack tuna adults (Dizon et al., 1977) and larvae (Wexler et al., 2011). To both maintain the good lower temperature fit of the SEAPODYM parameterization and to better fit experimental expectations at higher temperatures, we proposed an asymmetric Gaussian function (ASGF, Figure 3) in which the probability of spawning is near zero in 34°C waters.

4.3 | Patterns of Tuna spawning change in the Coral Triangle region

Under all three parameterizations, current temperature data suggest that the majority of the CT region provides good potential skipjack tuna spawning habitat (Figure 5a–c, left columns). The only regions highlighted as too cold include the northern Philippines and the northern portion of the South China Sea during boreal winter and regions south of Sumatra, Java, and south-east Papua New Guinea during the austral winter. As the parameterizations largely agree on the lower limits for spawning, these patterns are consistent across the models. In the SQF parameterization, a few present-day regions have temperatures likely too warm to provide favourable spawning habitat, including around the Halmahera Sea near West Papua, portions of the Java Sea, Savu Sea and coastal waters between Borneo and Malaysia (Figure 5a,c).

For the 2099 projections, the three parameterizations differ markedly on the magnitudes and timing of predicted changes in regional probability for successful skipjack tuna spawning, but all three show patterns of decline in equatorial latitudes and a lesser extent of potential increases at higher latitudes within the region (Figures 4 and 5). If, as we suspect, the ASGF better represents the skipjack tuna larval thermal habitat distribution (Dizon et al., 1977; Forsbergh, 1989; Wexler et al., 2011), then it is likely that the distribution, abundance and survival of skipjack tuna larvae will be dramatically affected within the CT region.

Under the parameterizations that assume stronger high-temperature effects on spawning (SQF and ASGF), we project a major reduction in spawning habitat across the equatorial latitudes of the region (Figures 4 and 5). More specifically, SQF projects an 82.8% region-wide reduction in all spawning habitat, while ASGF projects similar

reductions in “optimal” habitat of 80.5% regionwide by 2099, and a 66.1% decline in “favourable” spawning habitat 2099. Both of these patterns are subject to seasonal variability in central latitudes of the CT region (Figures 4 and 5), but the overall regional trends are clear. Under the distribution that allows spawning at the highest temperatures (SYF), areas within the centre of the CT region are still likely to see a 30%–50% reduction in successful spawning probability, with a regionwide 65.5% reduction in the extent of “optimal” spawning habitat between 2015 and 2099.

The three parameterizations are largely consistent with the spatial patterns of habitat change. They project that in the equatorial latitudes spawning will decline to vary degrees. In the central latitudes of the CT region, spawning will be highly variable by season, and at high latitudes of the CT region, spawning will increase, at least seasonally. The areas of highest probability of successful skipjack tuna spawning will shift northwards in a band stretching from the Andaman Sea through much of the South China Sea, the Philippines and westward during the boreal winter. During the austral winter, the highest skipjack tuna spawning will likely occur in areas spanning the southern coasts of Sumatra, Java and across to Papua New Guinea (south of ~6°S).

4.4 | Caveats

Although we used SVA to discover the models that best-matched hindcast temperatures in the study region, the selection of models that performed well in matching “old” data provide no guarantee that these models will continue to perform well under the new conditions running until 2099. It is also important to note that in none of these scenarios we did allow for acclimation or adaptation of successful skipjack tuna spawning over time. While potential acclimation or adaptation may occur, our current knowledge of skipjack tuna larval thermal performance is minimal, and we know even less about the degree to which tuna can modify it through an acquired elevation in thermal tolerance or a heritable increase in thermal tolerance.

We should also be clear that we investigated the effects of a single parameter, SST, on successful skipjack tuna spawning and that subsurface temperature was not part of this study. While this relatively narrow view of habitat may be inappropriate in other taxa and life stages, there is a broad consensus that temperature is the most direct determinant on larval tuna survival (Brill & Bushnell, 2001; Brill, Lowe, & Cousins, 2000). Unlike adults, larvae have little ability to maintain internal temperatures distinct from their surrounding water and have the narrowest thermal tolerances of any tuna life stage (Lehodey et al., 2008). As larvae tend to remain in surface water (Schaefer, 2001), sea surface temperature values serve as a good proxy for larval habitat and the threat posed by changing oxygen concentrations is less relevant (e.g., Pörtner & Kunst, 2007). Although the act of successful spawning through yolk-sac larvae is our main focus, food availability is a secondary concern and extending the model to examine larval food availability may provide further benefit to our conclusions. As other studies on climate change impacts on skipjack tuna abundance and spatial distribution (Dueri,

Bopp, & Maury, 2014) recognize that the primary driver of habitat changes is ocean warming and that the main goal of our funded project through USAID Philippines is to study the SST effects on economically important fisheries in the CT region, here we only considered to estimate the associated impacts of thermal changes on spawning habitat for skipjack tuna. Other possible oceanographic conditions (e.g., oxygen concentrations, salinity and stratification) affecting the distribution, abundance, survival and migration of skipjack should be taken into account in future analysis. Furthermore, it would be fundamental to work closer with local fisheries management agencies from the CT region to have a better understanding and more reliable information on skipjack catch and life stages within the CT region.

4.5 | Climate change effects on Tuna habitat

Climate change is already having profound effects on marine life, with increasing ocean temperatures, bleaching of corals, sea level rise, ocean stratification increase leading to a decrease in vertical mixing, and acidifying oceans (Raven et al., 2005). Changes in ocean temperature conditions will have important implications on modifications of phytoplankton yearly growth cycles and the consecutive effect on the entire food chain. These modifications and the expected changes in SST can produce significant shifts in the distribution, abundance and survival of ecologically and economically important fish species (Yoon, Watanabe, Ueno, & Kishi, 2015). Here, we show that under any of the scenarios we examined, important changes in skipjack tuna spawning habitat are expected. Our results coincide with Dueri et al. (2014) in that skipjack tuna habitat will deteriorate in most tropical waters and improve at higher latitudes. Furthermore, metabolic rates, growth and reproduction as well as shifts associated with predatory habits, migration, growth, reproduction and mortality rates will affect skipjack and other tuna species. Even under the most favourable scenario we examined, these changes will be severe enough to dramatically impact the skipjack tuna fisheries of the 12 nations that occur within these waters.

Changes in SST conditions will have a strong effect on the future availability of fisheries resources for food security and livelihoods and will cause economic disruptions in local and regional economies across the CT region. It is, therefore, essential to have a better understanding of thermal vulnerability of economically important marine species, such as skipjack in the CT region, for effective management responses that aim to support and enhance the resilience of resources, and in turn protect human communities by providing for sustainable livelihoods, food security and sustainable fisheries.

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