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Modelling the potential impacts of climate change on the distribution of ichthyoplankton in the Yangtze Estuary, China

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Abstract

Aim: Species distribution models (SDMs) are an effective tool to explore the potential distribution of terrestrial, freshwater and marine organisms; however, SDMs have been seldom used to model ichthyoplankton distributions, and thus, our understanding of how larval stages of fishes will respond to climate change is still limited. Here, we developed SDMs to explore potential impacts of climate change on habitat suitability of ichthyoplankton.

Location: Yangtze Estuary, China.

Methods: Using long-term ichthyoplankton survey data and a large set of marine predictor variables, we developed ensemble SDMs for five abundant ichthyoplankton species in the Yangtze Estuary (*Coilia mystus*, *Hypoatherina valenciennei*, *Larimichthys polyactis*, *Salanx ariakensis* and *Chelidonichthys spinosus*). Then, we projected their habitat suitability under present and future climate conditions.

Results: The ensemble SDMs had good predictive performance and were successful in estimating the known distributions of the five species. Model projections highlighted two contrasting patterns of response to future climates: while *C. mystus* will likely expand its range, the ranges of the other four species will likely contract and shift northward.

Main conclusions: According to our SDM projections, the five ichthyoplankton species that we tested in the Yangtze Estuary are likely to respond differently to future climate changes. These projected different responses seemingly reflect the differential functional attributes and life-history strategies of these species. To the extent that climate change emerges as a critical driver of the future distribution of these species, our findings provide an important roadmap for designing future conservation strategies for ichthyoplankton in this region.

KEYWORDS

climate change responses, distribution range shifts, ensemble forecasting, fish larvae, habitat suitability, species distribution modelling

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1 | INTRODUCTION

Ocean warming has been observed in a variety of marine ecosystems and can influence organisms therein in many different ways, such as causing changes in geographical ranges, phenology and species interactions (Belkin, 2009; Cheung et al., 2009; Doney et al., 2012; Poloczanska et al., 2016; Rhein et al., 2014; Vergés et al., 2016; Walsh, Richardson, Marancik, & Hare, 2015). Ichthyoplankton, comprising fish eggs, larvae and juveniles, plays an essential role in the recruitment success, temporal and spatial variations of fish populations, as well as in marine food webs (Miller & Kendall, 2009; Richardson, 2008). Being characterized by weak swimming abilities, ichthyoplankton possess a high intrinsic vulnerability to ambient stimuli, such as predation, starvation and variations in physical conditions; therefore, these planktonic stages should be more sensitive to future climate change than their adult counterparts (Hunter, 1981; Miller & Kendall, 2009; Pankhurst & Munday, 2011). A number of experimental and field studies have demonstrated that climate change will affect various aspects of ichthyoplankton, from their metabolism and phenology to their overall abundance and general distribution (Asch, 2015; Edwards & Richardson, 2004; Hsieh, Kim, Watson, Di Lorenzo, & Sugihara, 2009; Hsieh, Reiss, Hewitt, & Sugihara, 2008; Pankhurst & Munday, 2011; Walsh et al., 2015). For instance, it has been demonstrated that an increase in water temperature leads to higher egg mortality, shorter incubation periods, increased metabolic rates and enhanced developmental rates in ichthyoplankton (reviewed in Pankhurst & Munday, 2011). Moreover, using larval fish data from a 50-year temporal series, Hsieh et al. (2009) found that climate change has led to substantial changes in their distribution and abundance in Southern California. Considering the ecological importance of ichthyoplankton in marine ecosystems and the severity of climate change impacts therein, it is of utmost

importance to understand how future climate change will influence ichthyoplankton for the purpose of better protecting marine fisheries resources (Richardson, 2008; Robinson et al., 2011).

Species distribution models (SDMs) can evaluate habitat suitability for target species, by relating species distribution data to a set of explanatory predictors, such as climatic and topographic variables (Franklin, 2009; Guisan, Thuiller, & Zimmermann, 2017). For example, these models have been used to evaluate habitat suitability under present and future climate scenarios for a wide variety of organisms, including terrestrial (Dyderski, Paż, Frelich, & Jagodziński, 2018), subterranean (Mammola, Goodacre, & Isaia, 2018), freshwater (Capinha, Leung, & Anastácio, 2011) and marine species (Robinson et al., 2011). Future maps of habitat suitability based on these models can effectively be used to make inference-based decisions about conservation strategies, especially for designing future areas of conservation and, ultimately, for the purpose of better protecting and managing marine fisheries resources (Robinson et al., 2011). Thus far, the majority of SDMs applied to marine ecosystems have focused on the adult stage of marine organisms, while limited effort has been devoted to modelling the distribution of ichthyoplankton (but see Pattrick, Strydom, Harris, & Goschen, 2016; Sundblad, Härmä, Lappalainen, Urho, & Bergström, 2009; Vanhatalo, Veneranta, & Hudd, 2012). Moreover, in spite of the pervasive effect of climate change across all components of marine life (Poloczanska et al., 2013), SDMs have seldom, if ever, been employed to examine climate change impacts on ichthyoplankton distributions.

Here, we constructed SDMs for five ichthyoplankton species in the Yangtze Estuary, China (Figure 1), and investigated potential climate-induced changes in their habitat suitability. As the largest estuary in China, the Yangtze Estuary provides a variety of important ecosystem services, including spawning, nursery and foraging habitat for a wide range of fisheries species (Luo & Shen, 1994). This estuary represents a coherent biogeographic

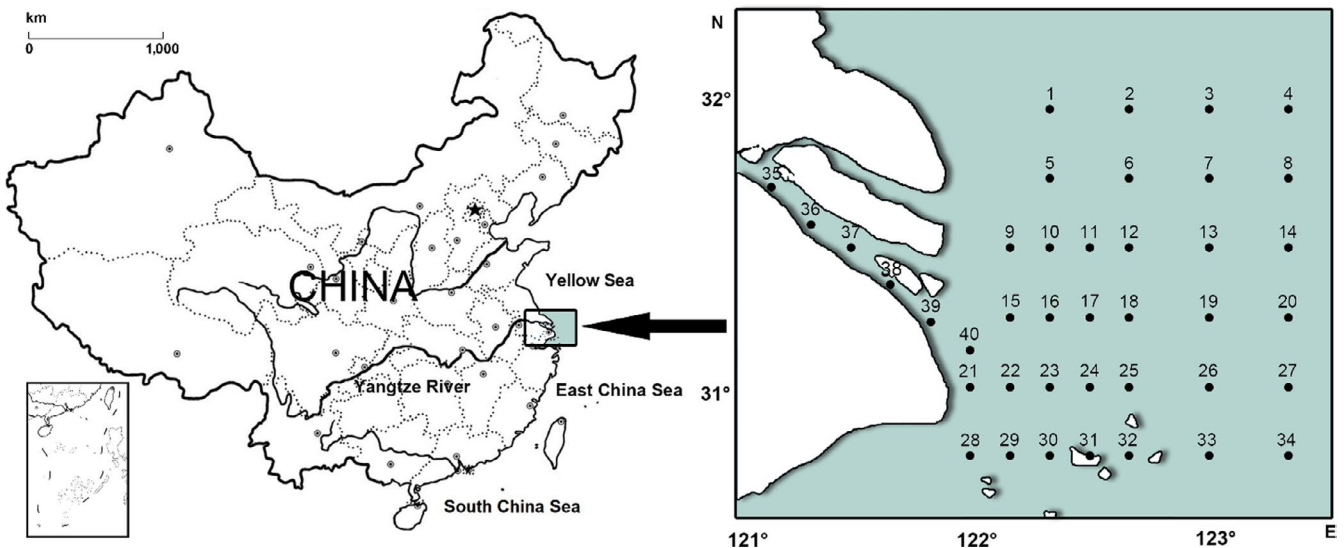


FIGURE 1 Sampling location in the present study. Sampling stations 1–34 and station 40 are in the open sea; sampling stations 35–39 are in the river

area that can be used as a semi-closed model system in which to explore the potential effects of climate change on the distribution of ichthyoplankton species. Indeed, the Yangtze Estuary has experienced an accelerated rate of warming exceeding the global average (Belkin, 2009). Additionally, Yang et al. (2016) pointed out that global warming is expected to cause a poleward shift of the Kuroshio Current, an important warm current in the North Pacific. Therefore, we hypothesize that multiple climate change stressors may cause northward distributional shifts of ichthyoplankton in the Yangtze Estuary. The projections provided by this study have important implications for conservation of the ichthyoplankton resources in the Yangtze Estuary.

2 | MATERIALS AND METHODS

2.1 | Ichthyoplankton sampling

We focused our SDM study on five abundant ichthyoplankton species occurring in the Yangtze Estuary (30.75°N to 32.00°N, 121.00°E to 123.33°): *Coilia mystus* (Linnaeus, 1758) (Engraulidae), *Hypoatherina valencienni* (Bleeker, 1854) (Atherinidae), *Larimichthys polyactis* (Bleeker, 1877) (Sciaenidae), *Salanx ariakensis* (Kishinouye, 1902) (Salangidae) and *Chelidonichthys spinosus* (McClelland, 1844) (Triglidae). *Coilia mystus* is an estuarine migratory and commercially important fish in the Yangtze Estuary which inhabits China's Pacific coastal waters from Hainan province to Liaoning province (He et al., 2008). *Hypoatherina valencienni* is distributed throughout the south-western Pacific and as far north as Japan (Ivantsoff & Kottelat, 1988); this species is a common and sometimes dominant species in the Yangtze Estuary (Zhang, Xian, & Liu, 2015, 2016, 2019). Being one of the target species of bottom trawling (Li, Shan, Jin, & Dai, 2011), *L. polyactis* is an economically important fish resource. In China, this species is mainly distributed in the Bohai Sea, the Yellow Sea and the East China Sea. *Salanx ariakensis* is an annual fish distributed in estuaries and adjacent coasts from the Yellow Sea to the East China Sea (Hua et al., 2009). *Chelidonichthys spinosus* is an offshore warm temperature fish which could be found in China coastline, representing a keystone element in the marine ecosystem food web (Li, Xu, Jiang, & Zhu, 2010).

Forty sampling stations (five stations within the river and thirty-five outside the river mouth) were established in the Yangtze Estuary and monitored between 1999 and 2013 (05/1999, 05/2001, 05/2004, 05/2007, 05/2009, 05/2010, 05/2011, 05/2012 and 05/2013). The spatial distribution of the sampling stations is given in Figure 1. Ichthyoplankton samples were collected by surface tows of a larva net (0.8 m mouth diameter, 2.8 m length, 0.505 mm mesh at the body and 0.505 mm mesh at the cod end) equipped with a flow meter. At each station, the net was towed at a near-surface depth of ~ 0.5 m for 10 min against the tidal flow, at a towing speed of ~2–3 knots. After completion of each tow, the nets were washed and the samples were fixed and preserved in 5% buffered formaldehyde–seawater solution. Ichthyoplankton individuals, whether eggs or larvae, were identified in the laboratory up to the lowest possible

taxonomic level. Occurrence information of each species from the temporal series of surveys was pooled together to increase the sample size.

2.2 | Environmental explanatory variables

Marine ecosystems are exposed to a wide range of environmental change stressors, including ocean warming, acidification and hypoxia (Gruber, 2011; Poloczanska et al., 2013). In addition, the distribution of ichthyoplankton can be influenced by multiple physical or chemical factors, particularly tides, dissolved oxygen and water temperature (Miller & Kendall, 2009; Patrick et al., 2016; Sundblad et al., 2009; Vanhatalo et al., 2012). In the present study, a total of 13 marine predictor variables were initially considered: water depth, distance to shore, pH, annual mean and range of sea surface temperature, annual mean and range of sea surface salinity, annual mean and range of sea surface current velocity, annual mean and range of sea surface dissolved oxygen, and annual mean and range of sea surface primary productivity. All predictors were obtained from the Bio-ORACLE v2.0 dataset (<http://www.bio-oracle.org>; Assis et al., 2018), except data for water depth and distance to shore, which were derived from the Global Marine Environment Datasets (<http://gmed.auckland.ac.nz>; Basher, Bowden, & Costello, 2014). The spatial resolution of all predictors was 5 arcmin, corresponding to 9.2 km at the equator. We checked multicollinearity among these 13 predictor variables by calculating pairwise Pearson's correlation coefficients (r), using an $|r| > 0.70$ to cull collinear predictors (Dormann et al., 2013). According to the results of the collinearity analysis (Figure S1) and data availability under both present and future time periods, four predictors were retained to model habitat suitability for each ichthyoplankton species: distance to shore, annual mean sea surface temperature, annual mean sea surface salinity and annual mean sea surface current velocity.

Projections of annual mean sea surface temperature, salinity and current velocity for the future [time periods 2040–2050 (2050s) and 2090–2100 (2100s)] under four different emission scenarios—representative concentration pathways (RCPs; RCP26, RCP45, RCP60 and RCP85)—were derived from three atmosphere–ocean general circulation models (AOGCMs): CCSM4, HadGEM2-ES and MIROC5 (Assis et al., 2018). Average outputs of the three AOGCMs were used as future climate conditions. These were also retrieved from the Bio-ORACLE v2.0 dataset (Assis et al., 2018). We assume that distance to shore remains constant in future projections.

2.3 | Modelling procedure

An ensemble modelling approach was adopted in this study to reduce uncertainties associated with single modelling algorithms (Araújo & New, 2007; Qiao, Soberón, & Peterson, 2015; Thuiller, Guéguen, Renaud, Karger, & Zimmermann, 2019). The relationships between the ichthyoplankton distribution data and the four selected explanatory variables were estimated via ten modelling algorithms: artificial neural network (ANN), classification tree analysis (CTA),

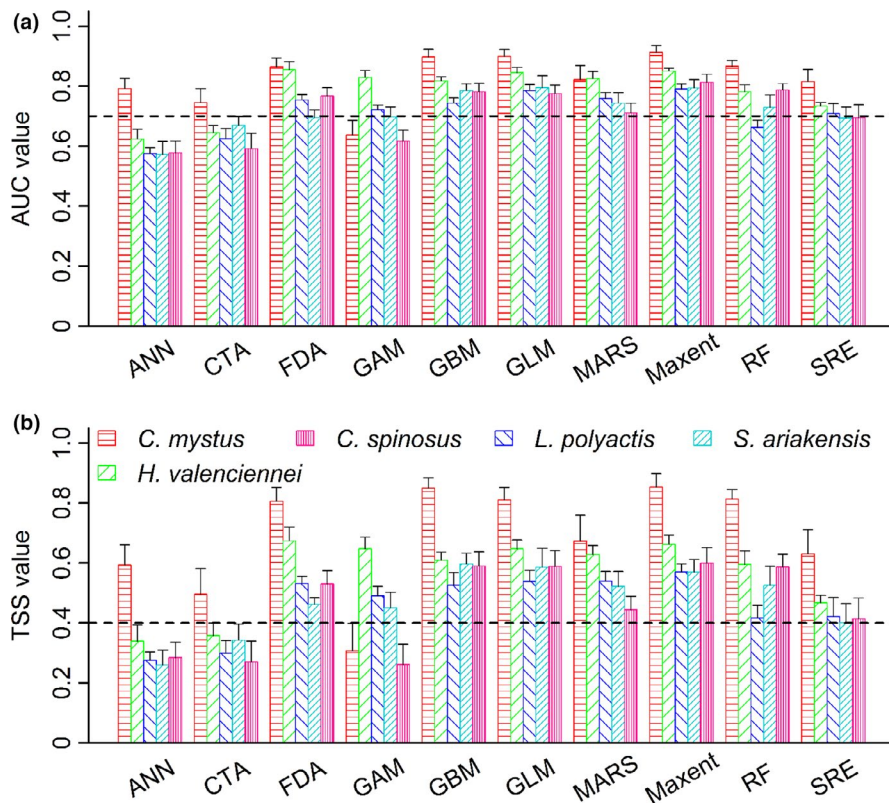


FIGURE 2 Predictive abilities of the ten modelling algorithms for five ichthyoplankton species. (a) the Area Under the receiver operating characteristic Curve (AUC), (b) the True Skill Statistics (TSS). Dashed lines represent cut-off levels for AUC (0.7) and TSS (0.4) used for selecting the algorithms to maintain in the final analyses. Values are expressed as mean \pm standard error

flexible discriminant analysis (FDA), generalized additive model (GAM), generalized boosting model (GBM), generalized linear model (GLM), multiple adaptive regression splines (MARS), maximum entropy (Maxent), random forest (RF) and surface range envelop (SRE). We fitted these ten algorithms with their default parameters using the package *biomod2* (Thuiller, Georges, & Engler, 2014) in the R software environment (version 3.4.3; R Development Core Team, 2017). Binary data (i.e. presence-absence of species) are needed for several SDM algorithms; owing to the small number of true absence records, we used pseudo-absence points instead (Guisan et al., 2017; Thuiller et al., 2014). Pseudo-absence points were randomly sampled from the study region; for each species, the number of pseudo-absences equalled ten times the number of presences (Barbet-Massin, Jiguet, Albert, & Thuiller, 2012; Beaumont et al., 2009). Predictive abilities of the ten algorithms were evaluated using the true skill statistic (TSS; Allouche, Tsoar, & Kadmon, 2006) and the area under the receiver operating characteristic curve (AUC; Swets, 1988) via a fivefold cross-validation technique (Guisan et al., 2017; Thuiller et al., 2014). As with Engler et al. (2011) and Araújo, Pearson, Thuiller, and Erhard (2005), algorithms with values of $TSS \leq 0.4$ and $AUC \leq 0.7$ were disregarded to minimize uncertainty resulting from modelling algorithms with poor predictive ability.

Relative importance of the four explanatory variables was determined by a randomization procedure (see Guisan et al., 2017; Thuiller et al., 2014). Habitat suitability for five ichthyoplankton species in the Yangtze Estuary, under present and future climates, was evaluated using all binary data. Projections of selected single modelling algorithms were ensemble by a committee averaging technique

(Guisan et al., 2017; Thuiller et al., 2014). The projected habitat suitability values range from 0 to 1,000 with 0 representing the lowest occurrence probability (i.e., 0) and 1,000 representing the highest occurrence probability (i.e., 1). For each species, the projected continuous probability maps were converted into binary presence-absence maps by selecting a probability threshold maximizing the TSS value (Franklin, 2009; Guisan et al., 2017; Jiménez-Valverde & Lobo, 2007; Thuiller et al., 2014). In addition to *biomod2* package, different R packages were used in our analyses for data manipulation and exploratory analyses, including *corrplot* (Wei & Simko, 2017), *maptools* (Bivand & Lewin-Koh, 2013), *maps* (Brownrigg, Minka, & Deckmyn, 2018) and *raster* (Hijmans, 2019).

3 | RESULTS

3.1 | Model performances and the importance of explanatory variables

Predictive performances of the ten modelling algorithms varied depending on the ichthyoplankton species considered (Figure 2). Four of the modelling algorithms, namely GBM, GLM, MARS and Maxent, shared a good predictive capacity for all five ichthyoplankton species (Figure 2); these four algorithms were used to estimate relative importance of the predictors and to map ichthyoplankton habitat suitability. Predictive powers of the four selected algorithms were highest for *C. mystus* (Figure 2). The TSS and AUC scores of ensemble models for the five ichthyoplankton species attested good predictive performances, with values of TSS

TABLE 1 Occurrence records used to develop species distribution models (SDMs) for each ichthyoplankton species and predictive abilities of ensemble SDMs

Species	No. records	TSS	AUC
<i>C. mystus</i>	15	0.873 ± 0.013	0.945 ± 0.005
<i>H. valenciennei</i>	32	0.672 ± 0.017	0.883 ± 0.006
<i>L. polyactis</i>	34	0.653 ± 0.015	0.865 ± 0.005
<i>S. ariakensis</i>	26	0.651 ± 0.019	0.867 ± 0.009
<i>C. spinosus</i>	23	0.702 ± 0.021	0.894 ± 0.009

Note: AUC, area under the receiver operating characteristic curve; TSS, true skill statistics. TSS and AUC scores are expressed as mean ± standard error.

above 0.65 and AUC above 0.85 (Table 1). Ensemble SDMs for five ichthyoplankton species exhibited predictive abilities superior to those of single algorithms (Table 1). The four explanatory variables had different importance for explaining the distribution of the five ichthyoplankton species: annual mean salinity was most important for *C. mystus*, annual mean temperature for *H. valenciennei*, *L. polyactis* and *S. ariakensis*, and annual current velocity for *C. spinosus* (Table 2). Response curves indicated that the five ichthyoplankton species have overall similar environmental requirements except *C. mystus*, preferring near shore and low salinity habitats (Figures S2–S5).

3.2 | Habitat suitability under present and future climate scenarios

The predicted habitat suitability for the five ichthyoplankton species was generally consistent with each species' known distribution in the Yangtze Estuary (Figure 3). The predicted climatically suitable areas for *H. valenciennei*, *L. polyactis* and *S. ariakensis* were relatively larger than the areas for *C. mystus* and *C. spinosus* (Figure 3). The species *C. mystus* is predicted to have high habitat suitability close to the mouth of the Yangtze Estuary, while the other four species are expected to have high habitat suitability in the inner estuary (Figure 3). The ensemble of SDM projections suggested that future climate scenarios will have different impacts on habitat suitability for the five ichthyoplankton species: *C. mystus* was consistently projected to expand its range under future climates, while distributions of the other four species will likely contract in the future (Table 3). Given the identical trends

in changes of habitat suitability under the four different emission scenarios (Table 3), projections under the RCP45 scenario—a mid-range emission scenario—were displayed to show the potential climate change impact on the distributions of the ichthyoplankton species.

Projected changes in occurrence probability of the ichthyoplankton species suggest that, among the five species tested here, there will likely be two different responses to climate change in both 2050s (Figure 4) and 2100s (Figure 5). Climates in the 2050s and 2100s will seemingly favour the expansion of *C. mystus* in the Yangtze Estuary, and habitat suitable for this species is predicted to still occur near the estuary mouth (Figure 4a, Figure 5a). In contrast, in addition to their range contractions, the other four species are predicted to shift their distributions northward in response to future climate change, meanwhile losing suitable habitats in the current core of their distribution (Figures 4b–e, 5b–e). Accordingly, owing to changes in the distribution patterns of ichthyoplankton caused by climate change, the biodiversity of ichthyoplankton, as represented by the five species considered, is projected to overall decline in the Yangtze Estuary in the future (Figure 6).

4 | DISCUSSION

In this contribution, we used ensemble SDMs to explore present and future habitat suitability for five ichthyoplankton species in the Yangtze Estuary, the largest estuary in China. Our study represents one of the very few examples of projected climate change impacts on ichthyoplankton distributions. Projections from the present study could contribute to understanding how ichthyoplankton might respond to future climates, with important implications for resource conservation efforts in the Yangtze Estuary.

The ecological importance of ichthyoplankton to marine ecosystems is widely recognized, as well as their great vulnerability to climate change (Asch, 2015; Hsieh et al., 2009; Hunter, 1981; Miller & Kendall, 2009; Pankhurst & Munday, 2011; Poloczanska et al., 2013; Richardson, 2008). Thus, a few previous studies have proposed the potential utility of SDMs in investigating present and future habitat suitability for ichthyoplankton (Dambach & Rödder, 2011; Richardson, 2008). Despite this attention, only few SDM studies to date have focused on planktonic larvae, and these were exclusively devoted to studying the present-day habitat suitability based on a single SDM algorithm (Patrick et al., 2016; Sundblad et

TABLE 2 Relative importance of four predictor variables used to model the distribution of our model species

Species	Distance to shore	Current velocity	Salinity	Temperature
<i>C. mystus</i>	0.254 ± 0.024	0.377 ± 0.029	0.588 ± 0.028	0.344 ± 0.047
<i>H. valenciennei</i>	0.382 ± 0.017	0.279 ± 0.014	0.241 ± 0.021	0.470 ± 0.021
<i>L. polyactis</i>	0.504 ± 0.021	0.109 ± 0.012	0.287 ± 0.020	0.536 ± 0.023
<i>S. ariakensis</i>	0.355 ± 0.019	0.271 ± 0.019	0.201 ± 0.023	0.470 ± 0.025
<i>C. spinosus</i>	0.301 ± 0.032	0.415 ± 0.021	0.140 ± 0.026	0.309 ± 0.033

Note: Results are expressed as mean ± standard error.

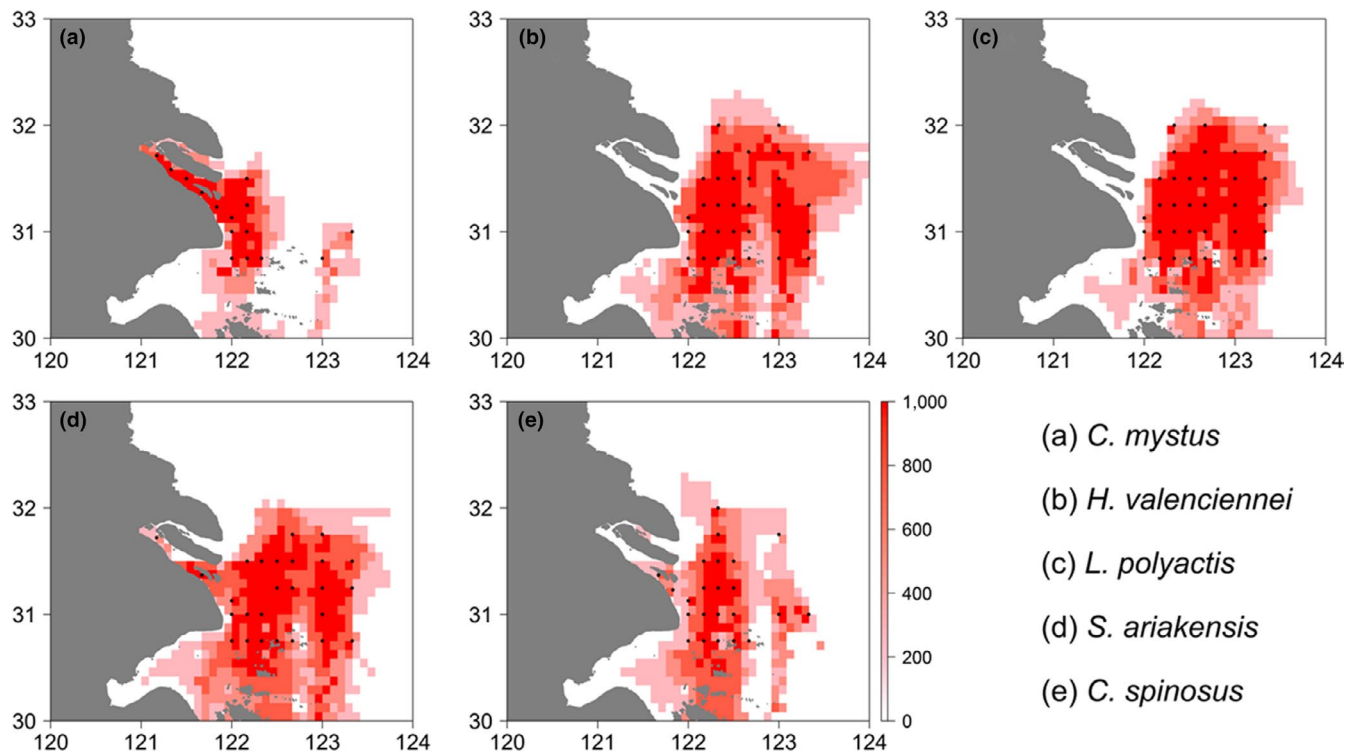


FIGURE 3 Habitat suitability of five ichthyoplankton species under present climate conditions. Black dots represent occurrence records

Species	Period	RCP26	RCP45	RCP60	RCP85
<i>C. mystus</i>	2050s	73.8	72.6	8.3	67.9
	2100s	67.9	106	108.3	60.7
<i>H. valenciennei</i>	2050s	-75.3	-71	-52.3	-92.5
	2100s	-56.6	-96.4	-100	-100
<i>L. polyactis</i>	2050s	-57.5	-53.7	-46.3	-78
	2100s	-48.6	-96.9	-100	-100
<i>S. ariakensis</i>	2050s	-50.4	-51.7	-36.4	-72
	2100s	-41.3	-76.9	-100	-100
<i>C. spinosus</i>	2050s	-78.4	-73.4	-54.7	-89.2
	2100s	-74.1	-92.1	-91.4	-92.8

TABLE 3 Projected range size change (%) of five ichthyoplankton species under future climate scenarios

Note: RCP, Representative Concentration Pathway. 2050s: average of 2040–2050; 2100s: average of 2090–2100.

al., 2009; Vanhatalo et al., 2012). Nevertheless, a large number of studies have stressed out the high uncertainties in SDMs originating from the choice of modelling algorithms (Araújo & New, 2007; Qiao et al., 2015; Thuiller et al., 2019). A multi-model ensemble approach, whereby the predictions of multiple modelling algorithms are synthesized, is typically used to minimize these uncertainties (Araújo & New, 2007; Guisan et al., 2017; Thuiller et al., 2019). In our case, the ensemble SDMs for five ichthyoplankton species exhibited predictive abilities superior to those of single algorithms, and the ensemble of SDM projections of habitat suitability under the present climate was highly consistent with the known distributions of each species.

Despite the potential significance, our modelling approach has at least two limitations. First, we should notice that in addition to environmental variables, other factors including species dispersal capacity are also important in regulating species distributions (Guisan et al., 2017). Ichthyoplankton dispersal is a complex process which can be influenced primarily by passive drift with currents and secondarily by active swimming (Miller & Kendall, 2009); hence, it is difficult to obtain precise estimation of ichthyoplankton dispersal potential. As a result, we assumed no dispersal limitation when estimating ichthyoplankton habitat suitability. We acknowledge that this assumption may lead to overestimation of future shifts (see Boulangeat, Gravel, & Thuiller, 2012; Václavík & Meentemeyer,

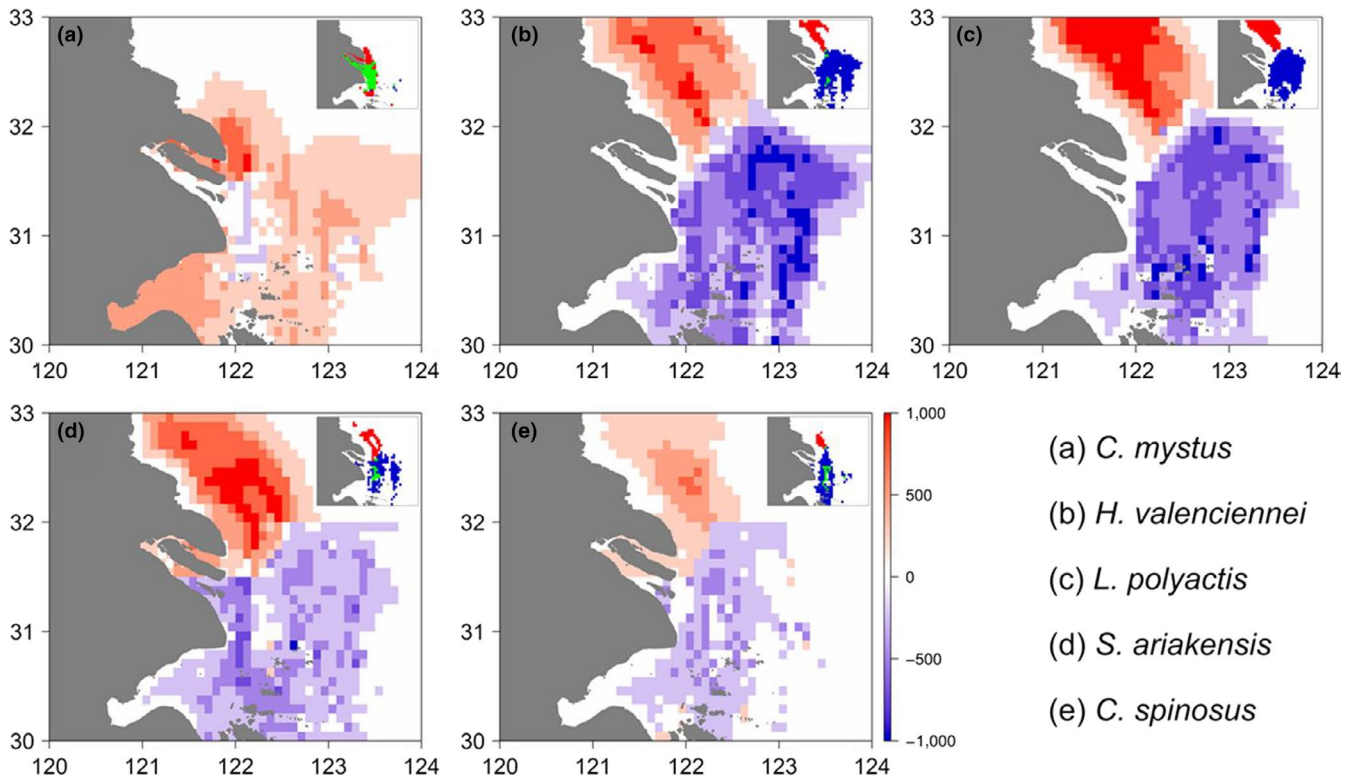


FIGURE 4 Changes in occurrence probability of five ichthyoplankton species in 2050s under RCP45 scenario. Shades of blue indicate areas in which the probability of occurrence will decrease, and vice versa for red areas. Insets on the top right of each graph represent suitable habitats under present-day and future climates. Red areas are projected to be suitable in the future, green areas are projected to be suitable under both present-day and future climates, and blue areas represent present-day suitable habitat that will become unsuitable in the future

2009). Second, long-term ichthyoplankton survey in the Yangtze Estuary yielded relatively small numbers of presence records for the five ichthyoplankton species (between 15 and 34 records), and such a low sample size could affect SDM predictive performances (Hernandez, Graham, Master, & Albert, 2006; Wisz et al., 2008). To improve model accuracy, it would be useful to establish more sampling stations in the Yangtze Estuary.

The five species we studied are common species in the Yangtze Estuary and have great ecological and economic importance. These species, especially *C. mystus* and *L. polyactis*, are important fisheries resources and play an important role in the food web in the Yangtze Estuary. According to previous surveys, ichthyoplankton of the five species are abundant in the Yangtze Estuary (Zhang et al., 2015, 2016, 2019); the early life-history stages of these species represent prey items for a variety of species and are directly related to recruitment success and stock abundance. According to our projections, these five ichthyoplankton species in the Yangtze Estuary are likely to exhibit two different responses to future climate change; a finding that contradicts our initial hypothesis that ichthyoplankton in this region will exclusively respond to climate change by shifting their distribution northward. The projection for *H. valencienni*, *L. polyactis*, *S. ariakensis* and *C. spinosus* provided support for our initial hypothesis. In addition to range contraction and a northward shift, another response pattern—range expansion—was documented in

the present study. Different responses of sympatric species to climate change have been previously demonstrated, both by laboratory experiments (Logan, Huynh, Precious, & Calsbeek, 2013; Ma et al., 2018) and by SDM projections (Van Zuiden, Chen, Stefanoff, Lopez, & Sharma, 2016) and primarily attributed to differences in thermal sensitivity. For instance, Ma et al. (2018) experimentally tested the responses of embryos of two sympatric desert lizards to simulated climate warming and found that climate warming had different impacts on the two species studied. Additionally, Van Zuiden et al. (2016) developed SDMs for three Canadian fish species adapted to warmwater, coolwater and coldwater; their results showed that these distinct thermal preferences led to three different responses to potential climate change (range expansion, northward range shift and range contraction, respectively).

The five ichthyoplankton species considered in the present research have different life-history strategies, which may account for differences in environmental tolerance and consequently explain the different projected impacts of climate change on their distributions. Four of the species, *H. valencienni*, *L. polyactis*, *S. ariakensis* and *C. spinosus*, spend their entire life cycle in marine waters. Conversely, *C. mystus* is an estuarine migratory fish that commonly lives in shallow marine habitats but migrates to brackish estuarine waters in spring as sexually mature individuals (He et al., 2008). Previous studies have proposed that euryhaline species

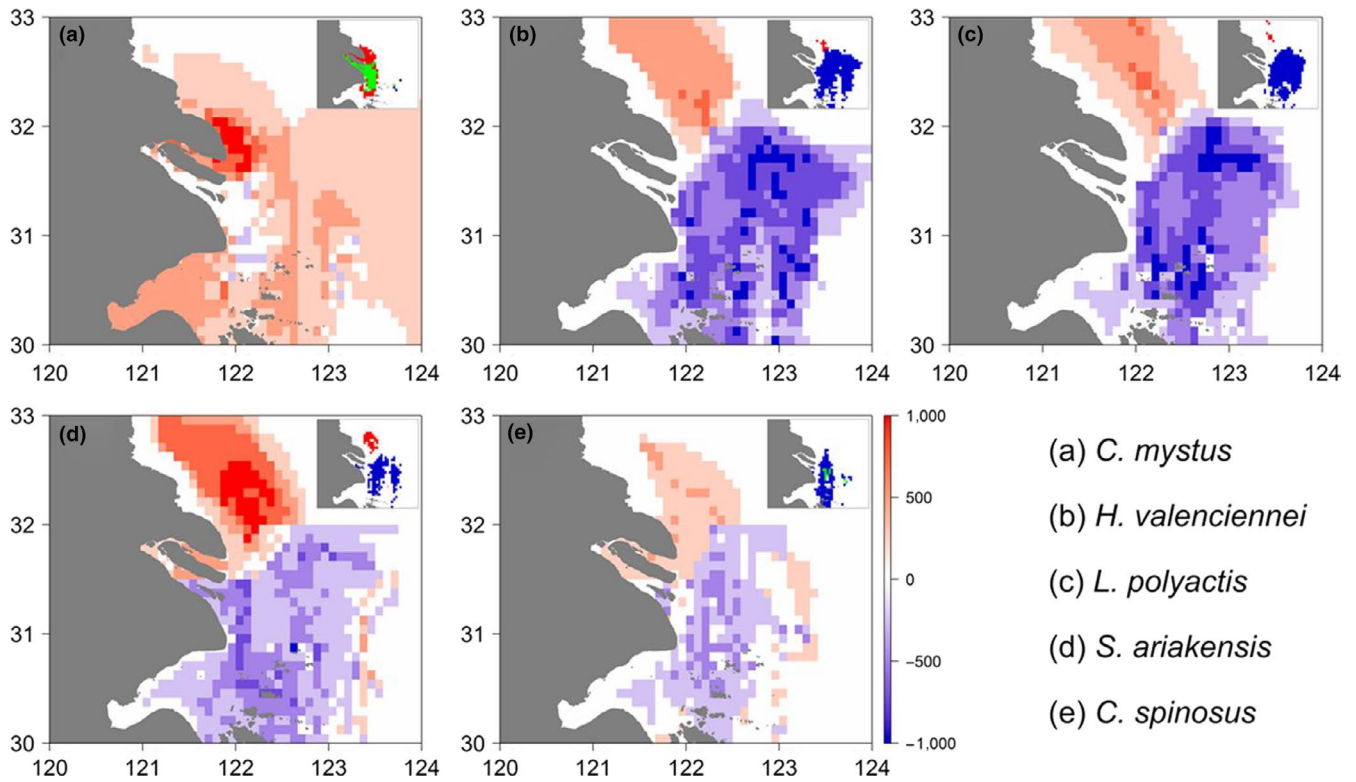


FIGURE 5 Changes in occurrence probability of five ichthyoplankton species in 2100s under RCP45 scenario. Shades of blue indicate areas in which the probability of occurrence will decrease, and vice versa for red areas. Insets on the top right of each graph represent suitable habitats under present-day and future climates. Red areas are projected to be suitable in the future, green areas are projected to be suitable under both present-day and future climates, and blue areas represent present-day suitable habitat that will become unsuitable in the future

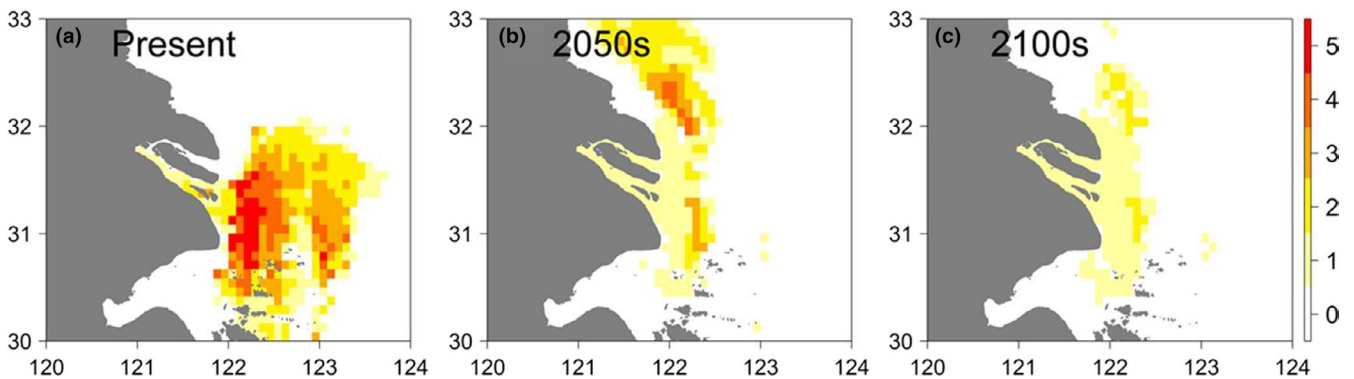


FIGURE 6 The sum of projected presences of the five ichthyoplankton species considered in this study under present conditions and future (RCP45) climate change scenarios. The continuous SDM predictions were converted into binary maps by selecting probability thresholds maximizing the True Skill Statistics (TSS) value (see Guisan et al., 2017; Thuiller et al., 2014). Map scale ranges from 0 (no species is predicted to be present) to 5 (all five species are predicted to be present). (a) present period, (b) RCP45 in 2050s (2040–2050), (c) RCP45 in 2100s (2090–2100)

are generally eurytopic and should be more resistant to environmental stresses than stenohaline marine organisms (Boesch, 1974; Wright, Kennedy, Roosenburg, Castagna, & Mihursky, 1983). Tang, Hu, and Yang (2007) determined 32 complete mitochondrial control region sequences of *Coilia* species to determine the phylogenetic relationships of *Coilia* in China. Their results suggested that *C. mystus* is most basal among the three valid species of *Coilia*

found in China; thus, they presumed that *C. mystus* is the earliest descendant of a *Coilia* ancestor that dispersed from an original “centre” into the north-western Pacific Ocean. Furthermore, they speculated that *C. nasus* and *C. grayii* diverged ecologically from *C. mystus* by adapting to coldwater and warmwater environments. The molecular work would support our SDM projections that the response pattern of *C. mystus* to future climate change is range

expansion. Yet, it would be also useful to investigate physiological variations among different ichthyoplankton species in the Yangtze Estuary to further corroborate this projection.

Projected changes in habitat suitability induced by climate change will likely result in losses and northward shifts of the ichthyoplankton biodiversity in the Yangtze Estuary. This conclusion supports previous studies that found support for changes in species distribution and biodiversity as a result of climate change (Hsieh et al., 2009, 2008; Walsh et al., 2015). In addition to range shifts, changing climates can also affect species abundance (Barrett et al., 2018; Doney et al., 2012; Richardson, 2008). Declines in the abundance of ichthyoplankton have already been observed in the Yangtze Estuary (see Zhang et al., 2015, 2016, 2019). It is important, yet especially challenging, to accurately model species abundance (Oppel et al., 2012; Pearce & Boyce, 2006). We strongly advise that further efforts be made to estimate the impacts of climate change on the abundance of planktonic larvae in this region. It has been revealed that climate change can influence species in a wide variety of ways, such as behavioural changes, range shifts, changes in phenology and alterations in species interactions (Asch, 2015; Doney et al., 2012; Edwards & Richardson, 2004; Vergés et al., 2016; Walsh et al., 2015); hence, future studies should address other possible climate change-driven impacts on ichthyoplankton in the Yangtze Estuary.

Climate change-induced range shifts of marine species have been frequently reported, and many researchers have recommended incorporating such range shifts into the management process (Cheung, Watson, & Pauly, 2013; Link, Nye, & Hare, 2011; Madin et al., 2012). Our study suggests that future climates will likely shift the distribution of ichthyoplankton as well, and future conservation activities should consider this aspect. This study is the first to highlight that species of ichthyoplankton in the Yangtze Estuary are projected to respond differently to future climate change; consequently, there may be no single conservation strategy to protect the total ichthyoplankton resource in this area. Adaptive conservation strategies should take our findings into account. A summer fishing moratorium in the Yangtze Estuary has been imposed by the Chinese government since 1995 for the purpose of protecting the marine fisheries resources. To maximize the benefits of future conservation strategies, further studies, such as annual ichthyoplankton surveys and physiological measurements made in the laboratory, should help to clarify variations in the life-history traits of different species. In addition, species-specific conservation measures, such as species-specific fishing moratoriums (i.e. closure dates and closure areas), should be considered.

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CONFLICT OF INTEREST

The authors declare there are no competing interests.

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DATA AVAILABILITY STATEMENT

All marine predictor variables can be downloaded from the Global Marine Environment Datasets (<http://gmed.auckland.ac.nz>) and the Bio-ORACLE v2.0 data set (<http://www.bio-oracle.org>). Species occurrence records presented in Figure 3 are publicly available in Dryad (<https://doi.org/10.5061/dryad.qv9s4mw9f>).

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BIOSKETCH

Zhixin Zhang is interested in studying impacts of climate change on the distribution of a breadth of species, from commercially important fisheries species, along with species of conservation concern, to invasive species.

Stefano Mammola is an ecologist whose scientific activity focuses primarily on subterranean biology and ecological modelling.

Hui Zhang is a marine biologist interested in marine fisheries diversity and ecology. He relies on multiple methods, such as field survey and molecular markers, to explore the dynamics of marine fish diversity.

Weiwei Xian is an estuarine ecologist, interested in understanding the long-term environmental changes in these peculiar and highly dynamic ecosystems.

Author contributions: H. Z. and W. X. provided data for this study; Z. Z. and H. Z. conceived the idea; Z. Z. performed data analyses and wrote the first draft of the manuscript with constructive comment and suggestions from S. M., H. Z. and W. X.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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