

Climate-induced habitat suitability intensifies fishing-induced life-history variation of a migratory long-lived fish

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Abstract

Intense fishing pressure and climate change are major threats to coastal fisheries. *Larimichthys crocea* (large yellow croaker) is a long-lived fish, which performs seasonal migrations from its spawning and nursery grounds along the coast of the East China Sea (ECS) to overwintering grounds offshore. This study used length-based analysis and habitat suitability index (HSI) model to evaluate current life-history parameters and overwintering habitat suitability of *L. crocea*, respectively. We compared both life-history parameters and overwintering HSI between recent (2019) and historical (between 1971 to 1982) to analyze the fishing pressure and climate change effects on the overall population and overwintering phase of *L. crocea*. In the context of overfishing, the length-based analysis indicated serious overfishing of *L. crocea*, characterized by reduced catch yield, size truncation, constrained distribution, and advanced maturation in the ECS, namely recruitment bottleneck. In the context of climate change, the overwintering HSI modeling results indicated that climate change has led to decreased sea surface temperature during *L. crocea* overwintering phase over the last half-century, which in turn led to area decrease and an offshore-oriented shifting of optimal overwintering habitat. The fishing-caused size truncation may constrain the migratory ability and distribution of *L. crocea*, subsequently led to the mismatch of the optimal overwintering habitat against climate change background, namely habitat bottleneck. Hence, while heavily fishing was the major cause of *L. crocea* fishery collapse, climate-induced overwintering habitat suitability may have intensified the fishery collapse of *L. crocea* population. It is important for management to take both overfishing and climate change issues into consideration when developing stock enhancement activities and policy regulations, particularly for migratory long-lived fish that share a similar life history to *L. crocea*. Combined with China's current restocking and stock enhancement initiatives, we propose recommendations for future restocking of *L. crocea* in China.

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Abstract

Intense fishing pressure and climate change are major threats to coastal fisheries. *Larimichthys crocea* (large yellow croaker) is a long-lived fish, which performs seasonal migrations from its spawning and nursery grounds along the coast of the East China Sea (ECS) to overwintering grounds offshore. This study used length-based analysis and habitat suitability index (HSI) model to evaluate current life-history parameters and overwintering habitat suitability of *L. crocea*, respectively. We compared both life-history parameters and overwintering HSI between recent (2019) and historical (between 1971 to 1982) to analyze the fishing pressure and climate change effects on the overall population and overwintering phase of *L. crocea*. In the context of overfishing, the length-based analysis indicated serious overfishing of *L. crocea*, characterized by reduced catch yield, size truncation, constrained distribution, and advanced maturation in the ECS, namely recruitment bottleneck. In the context of climate change, the overwintering HSI modeling results indicated that climate change has led to decreased sea surface temperature during *L. crocea* overwintering phase over the last half-century, which in turn led to area decrease and an offshore-oriented shifting of optimal overwintering habitat of *L. crocea*. The fishing-caused size truncation may have constrained the migratory ability and distribution of *L. crocea* subsequently led to the mismatch of the optimal overwintering habitat against climate change background, namely habitat bottleneck. Hence, while heavily fishing was the major cause of *L. crocea* fishery collapse, climate-induced overwintering habitat suitability may have intensified the fishery collapse of *L. crocea* population. It is important for management to take both overfishing and climate change issues into consideration when developing stock enhancement activities and policy regulations, particularly for migratory long-lived fish that share a similar life history to *L. crocea*. Combined with China's current restocking and stock enhancement initiatives, we propose recommendations for future restocking of *L. crocea* in China.

Key words: *Larimichthys crocea*, overfishing, climate change, length-based analysis, HSI model, East China Sea.

INTRODUCTION

Globally, heavily fishing activities and climate change are rapidly reducing the abundance of many marine organisms and increasing the likelihood of species extinction (Hoegh-Guldberg and Bruno 2010, Cinner et al. 2012, Burgess et al. 2013, Payne et al. 2016). For instances, intensive fishing and climate change had caused overfishing and declined catches in Canada, Iceland, and China (Pauly et al. 2011, Du et al. 2014, Liang and Pauly 2017). In addition, 'fishing-induced life-history variation' at population level, together with 'fishing down the marine food web' and/or 'trophic cascade' at ecosystem level have been observed and demonstrated in variety contexts through theoretical and empirical evidence (Essington et al. 2006, Gascuel et al. 2014, Kuparinen et al. 2016, Szuwalski et al. 2017). Previous studies showed that fishing pressures and climate change can affect the (i) the life-history strategy of individuals, via impacts on physiology, morphology and behavior (Ba et al. 2016, Olafsdottir et al. 2016); (ii) the population dynamics, via changes to key population processes throughout an organism's life-history and habitat suitability (Perry et al. 2005). Hence, bottlenecks of any life-history stage (e.g. spawning, hatching, larval survival, recruitment settlement, growth, and death), and habitat suitability can cause overfishing of exploited species. In this context, recruitment bottleneck and habitat bottleneck are probably the most widely known bottlenecks (Almany and Webster 2006, Caddy 2011). Correspondingly, the potential cause of overfishing is mismanagement because of a poor understanding of recruitment bottleneck and habitat bottleneck that constrain the productivity of the overall population.

Fishing alters the size structure throughout remove large fish due to the size-selective of gears. Heavily fishing can diminish the ability of fish to reproduce (recruitment overfishing) and/or constrain the overall recruitment ability before they can fully realize their growth potential (growth overfishing) (Diekert 2012) via size truncation effect (STE) (Berkeley et al. 2004, Ottersen et al. 2006, Froese et al. 2008, Langangen et al. 2019). This effect states that population shifts with decreasing body sizes and advancing maturation characteristic of the life-history changes induced by fishing (Berkeley et al. 2004, Anderson et al. 2008, Bell et al. 2015). Hence, fishing for juveniles (before reaching first maturity) and mega-spawner can weaken the

reproductive potential of a fish stock, called ‘recruitment bottleneck’ (Doherty et al. 2004). Such bottlenecks are visible in respective long-term time series and are a common cause of collapse in intense fished stocks, for example in Western cod, Pacific rockfish and North Sea ground fish (Harvey et al. 2006, Poulsen et al. 2007, Froese et al. 2008).

The impacts of overfishing do not occur in isolation, but against a background of existing climate change-caused environmental conditions shift (Graham et al. 2011, Johnson et al. 2011). In general, species’ distribution patterns are relative with both life-history strategies (Anderson et al. 2013) and physiology tolerance on environmental variables, such as sea surface temperature (SST), chlorophyll-a concentration (Chl-a), sea surface salinity (SSS), currents et al. (Guan et al. 2013, Yu and Chen 2018). Environmental shift can selectively affect the habitat suitability of target species (Farrell et al. 2008). Lower habitat suitability of any life-history stage can lead to species-specific ‘habitat bottleneck’ and latter can have large consequences for climate-induced fishery phenomena, for examples, Norwegian herring, Maine cod and Mid-Atlantic Bight winter flounder (Bell et al. 2015, Pershing et al. 2015).

Heavily fishing activities and environmental conditions shift can have combined effects on fishery collapse, especially for long-lived species (Rose 2004, Hsieh et al. 2009). Specifically, some studies suggested that long-lived species are expected to have slower demographic response to climate change (Berteaux et al. 2004, Wilson et al. 2010). Additionally, fishing-caused STE can exacerbate long-lived fish degradation via diminishing ‘bet-hedging’ capacity, including the ability of migrate and avoid poor areas, having flexibility in spawning times and locations, and production of high-quality offspring that survive in a broader suite of environmental conditions, for adapting to rapid climate change (Bell et al. 2015). However, there is no relevant examples exist that demonstrate the STE and the climate-induced effects on long-lived migratory fish in the most heavily fishing (and minimally managed) marine ecosystem in the world: the East China Sea (ECS). To fill the knowledge gaps, we require a species that (i) under intensive fishing pressure; (ii) has specific habitat requirements; (iii) the habitat of which is affected by rapid climate-induced habitat suitability variation; (iv) can be reliably counted by a long-term field survey.

In the following, we provide an appropriate example by discussing changes in specific population dynamic of an overexploited, long-lived, migratory fish in the ECS, the large yellow croaker (*Larimichthys crocea*). The collapse of *L. crocea* represents an interesting example to explore both heavily fishing and climate change on overall population: (i) *L. crocea* ranked top among the four major marine economical fishes in China in last century (Zhang et al. 2010) but encountered collapse since the 1980s. The latest International Union for Conservation of Nature (IUCN) Red List of Threatened Species labelled *L. crocea* as ‘critically endangered (CR)’ (Liu et al. 2020); (ii) *L. crocea* is a long-lived species with maximum age 21 years in 1960s (Zhang et al. 2017). Accompanied by population collapse, the *L. crocea* population in the ECS is characterized by decreased maximum age and body size, and advanced maturation (Ye et al. 2012). (iii) *L. crocea* is a migratory fish which conduct climatic migrations and gametic migrations between offshore water and coastal water during autumn-winter and spring-summer respectively (Fig. 1A).

2. MATERIALS AND METHODS

In this study, we only considered *L. crocea* in the mid-southern ECS (120°E to 126°E, 25degN to 29degN) that have available data over long-term series. Also, we evaluated only overwintering distribution patterns and overwintering habitat suitability because they are strongly linked to the physiology fitness and survival rate during the juvenile and adult stages and corresponding climatic migration phase of *L. crocea*.

2.1 Fishery data

To investigate how *L. crocea* population declines in the ECS in the last five decades, we analyzed two data sets on *L. crocea* in the ECS.

First, we used information from official commercial landing and hatchery release data. Catch data of *L. crocea* were collected from the *China Fishery Statistical Yearbook*. Annual catches during the year 1950 – 2019 in the ECS were calculated by adding the catch landing in the Jiangsu, Shanghai, Zhejiang and Fujian

province. Hatchery release data in the ECS were obtained from Ningde Oceanic and Fishery Bureau by adding the number of official *L. crocea* hatchery release data in the Zhejiang and Fujian province.

Second, to investigate how geographical distribution of *L. crocea* shifts in the ECS, we analyzed a second data set includes both commercial fishery and scientific cruise data in the *L. crocea* 's overwintering ground (Fig. 1B). Historical overwintering catches information (1970 – 1982) of *L. crocea* was obtained from the East China Sea Fisheries Research Institute. The data set contains location and date, as well as the amount (in tons) of annual winter total catch (with 0.5deg spatial resolution). Overwintering catch information and life-history parameters (including length and maturation) for *L. crocea* were obtained from scientific cruise data in the period 2018 – 2019 through a bottom trawl survey in the mid-southern ECS.

2.2 Environmental data

Three environmental factors were collected for *L. crocea* overwintering habitat suitability modelling: depth (m), sea surface temperature (°C) and sea surface salinity. The Bathymetry data (30 arc-second spatial resolution) was obtained from Gridded Bathymetry Chart of the Oceans (GEBCO) (https://www.gebco.net/data_and_products/gridded_bathymetry_data/, accessed on September 2020) to represent depth. Historical monthly SST and SSS data (0.5deg spatial resolution) between 1971 and 2001 was acquired from the Simple Ocean Data Assimilation (SODA) reanalysis dataset (Carton and Giese 2008) (from the Climate Data Library: <http://iridl.ldeo.columbia.edu/>, accessed on September 2020). Monthly SST data (4 km spatial resolution) between 2002 and 2019 was downloaded from the Moderate Resolution Imaging Spectroradiometer (MODIS) on board the satellite Aqua platform provided by the Ocean Biology Processing Group at NASA Goddard Space Flight Center (<https://oceandata.sci.gsfc.nasa.gov/MODIS-Aqua/Mapped/>, accessed on September 2020). To investigate the environmental data from when fishing occurred, environmental data were resampled by the mean value of each month to 0.5deg spatial resolution, then matched with the fisheries data.

2.3 Life-history parameters of *L. crocea* in the ECS

To understand the life-history parameters of *L. crocea* in the study area, we analyzed the length-based data with electronic length frequency analysis (ELEFAN) using the TropfishR package (Mildenberger et al. 2017). Size-frequency of the commercial fishing catch during 1970 – 1982 are not available but we gather the life-history information from published literature (Yu and Lin 1980, Xu et al. 1984a, b, Liu and de Mitcheson 2008, Ye et al. 2012) consisted with the study period and study area. We evaluated *L. crocea* life-history parameters during 2018 – 2019 using body length data collected by otter trawl cruises, seasonally from November 2018 to November 2019 (e.g. November 18th, 2018; January 20th, 2019; April 18th, 2019; July 17th, 2019; September 28th, 2019; November 18th, 2019). we selected a total of 2074 *L. crocea* individuals between 2018 to 2019: the length and weight of the collected *L. crocea* individuals were measured (n=853), length-weight relationship was estimated based on the equation $w = aL^b$. The length frequency was calculated for each season for Electronic Length Frequency Analysis (ELEFAN) in TropfishR package.

We fit the von Bertalanffy growth function (VBGF) through the length frequency and life-history data to estimate life parameters (e.g. maximum length, weight at length, length at maturity (L_{mat}) and VBGF parameters including von Bertalanffy growth constant (K) and asymptotic length (L_{inf}), age at zero length (t_0) and et al.) (Pauly and David 1981, Brey and Pauly 1986, Sparre and Venema 1998) and estimated mortality parameters (e.g. total mortality (Z), natural mortality (M) and fishing mortality (F)) (See details in Supporting Information). Specifically, the VBGF and mortality parameters were estimated following four approaches, including: (i) K-Scan for the estimation of K for a fixed value of L_{inf} (ELEFAN K.S.); (ii) ELEFAN Response Surface Analysis (ELEFAN R.S.A.); (iii) ELEFAN with simulated annealing (ELEFAN S.A.); (iv) ELEFAN with a genetic algorithm (ELEFAN G.A.). Among above four workflows, ELEFAN R.S.A, ELEFAN S.A and ELEFAN G.A. allow the simultaneous estimation of K and L_{inf} (Taylor and Mildenberger 2017), while a advantage of ELEFAN S.A. and ELEFAN G.A. is the possibility to estimate all parameters of the seasonalized VBGF simultaneous (Scrucca 2013, Xiang et al. 2013). Therefore, we estimated life-history

parameters using the 60 scenarios with different bin of length (bin=10 and bin=20), move average (MA) value (MA=5, MA=7, MA=9, MA=11) and four different workflows (ELEFAN K.S., ELEFAN R.S.A., ELEFAN S.A., ELEFAN G.A.) following Mildenberger et al. (2017).

For model validation and selection, we used all-subsets model selection based on the fraction of the estimated sum of peaks (R_n) following Gayanilo et al.(1997). Additionally, other ratios of life-history parameters, such as M/K and F/M , were calculated with the estimated parameters. Moreover, Caddy et al. (1998) pointed out that the trophic level of a certain fish would be changing with size. Hence, we used size and trophic levels relationship to estimate the size truncation effect on overall population trophic level between 1980s and recent study (Supporting information).

2.4 *L. crocea* overwintering distribution patterns and overwintering habitat suitability in the ECS

L. crocea is overall habitat specialist during overwintering phase, previous studies have shown that *L. crocea* has strong depth, temperature, and salinity preferences, while pH, dissolved oxygen, light intensity, sound, water velocity and other factors may affect its distribution pattern, survival and growth in different life-history stages (Liu 2013, Wang et al. 2016, 2017). Unfortunately, detailed data on seasonal environmental data was limited between 1971 and 1982. Hence, only depth, SST and SSS data were available as model inputs to determine suitable habitats for *L. crocea*. We used HSI model, which is a kind of well-known SDMs (Species Distribution Models) to predict overwintering habitat suitability of *L. crocea* in the ECS. In our HSI model, we used standardized abundance, HSI, as response variable, and three environmental variables with strongest correlation and the best data availability, depth, SST and SSS, as predictor. Firstly, we constructed both fitting-based (Lee et al. 2019, Hua et al. 2020, Yu et al. 2020) and regression-based (Chang et al. 2019, Jin et al. 2020) suitability index (SI) models to describe the relationship between each environmental variable and *L. crocea* abundance (Supporting information). Then, we combined two types of SI models into HSI models, respectively. For each type of SI model, we used two empirical HSI models: the arithmetic mean model and the geometric mean model (Supporting information Fig. S1), under different environmental variable combinations (Lee et al. 2019).

For model validation and selection, we used catch data (abundance) from 1971 to 1980 and corresponding environmental data as training data set, catch data from 1981 to 1982 and corresponding environmental data as testing dataset. We assumed a positive linear relationship between predicted HSI values and *L. crocea* abundance and the evaluated the goodness-of-fit of the above relationship for each HSI model based on R^2 and the Akaike Information Criterion (AIC) value (Chang et al. 2013). Fitting-based arithmetic mean model with two variables (e.g. depth and SST) yielded the maximum R^2 and the minimum AIC value (Supporting information), thus was selected as the final HSI model. Correspondingly, fitting based SI model was selected as the final SI model. Finally, we retrained the SI model (See parameters and statistical test results in Supporting information) and the HSI model using catch data (abundance) from 1971 to 1982 and corresponding environmental data.

We drew SI curves using the retrained final SI models. We then computed winter (December, January, and February next year) mean SST and used them to predict yearly winter mean HSI distribution between 1971 and 2019 with the retrained final HSI model, then calculated decadal winter mean HSI of the 1970s (1971 – 1980), 1980s (1981 – 1990), 1990s (1991 – 2000), 2000s (2001 – 2010) and 2010s (2011 – 2019). Regions with HSI value > 0.7 , $0.7 > \text{HSI value} > 0.3$, and HSI value < 0.3 were regarded as optimal, common, and poor habitat, respectively. We computed the area of different habitat types in each year and analyzed if there are significant difference in area between decades using Person One-way ANOVA and Scheffe test.

3. RESULTS

3.1 Catch, hatchery release and life-history parameters of *L. crocea* in the mid-southern ECS

Based on the reported landing information, the overall production of *L. crocea* in the ECS has been continuously decline since 1970s. The variation of landing data indicated that the recent annual catch is now less

than 4400 tons, which have declined by $> 90\%$, compared with peak yields of the 1970s (Fig. 2A). Meanwhile, several long-term and large-scale restocking programs have been conducted since the 1990s. Millions of *L. crocea* have been released in the coastal areas of Fujian and Zhejiang provinces by government (Fig. 2B).

The life parameters results show that since 1980s, using length-based data, we fit a series of ELEFAN models and most the workflows were within feasible ranges for data limited measurement (Hordyk et al. 2015). The best model (ELEFAN S.A. with $\text{bin}=10$, $\text{MA}=11$, see details in Supporting information Table S3) exhibited serious overfished status of *L. crocea* stock in the ECS (Table 1, Fig. 3C). The most recent assessment found that (i) the average body length was 130.4 mm, with the body length of the predominant group being 145 – 155 mm (Fig. 3A), while the average body weight was 34.5 g, with the dominant group weight being 10 – 50 g; (ii) the growth curve (Fig. 3C) and maturation proportion (Fig. 3B) shows that juvenile *L. crocea* and the recruitment population have been the main catch targets, which the age of first capture and age of probability 95% of capture is the only 0.37 year and 0.49 year respectively (Fig. 3D); (iii) the exploitation rate (E) of stock is now as high as 0.84, which reveals serious overfished of *L. crocea* stock. Our results consist with previous studies that identified species as being smaller, younger, and maturing faster in ECS due to the overfishing and STE: Firstly, both size truncation and age truncation have occurred in *L. crocea* population alongside with decrease of L (555.4 mm in 1980s vs. 434 mm in 2018 – 2019), trophic level ($[?]TL=0.15$), maximum age (8 years in 1980s vs. 6 years in 2019), and predominant body length (144 – 155mm). Also, the increase in body growth rate from the 1980s to the current study ($K : 0.36$ vs. 0.43 , respectively) is consistent with advanced and smaller size at maturity ($L_{mat} : 350 - 400$ mm vs. $L_{mat} : 200 - 205$ mm, respectively) (Table 1). Still, the fishing mortality (F) and exploitation rate ($E = F/Z$) was predicted to be 1.57 and 0.84, respectively, which are continuously increasing compared with the 1980s (Table 1).

3.2 Overwintering habitat suitability of *L. crocea* in the ECS

We used both fitting-based and regression-based methods to construct SI models of each environmental variable and employed both the arithmetic mean model and the geometric mean model under different environmental variable combinations to calculate HSI values. Fitting-based arithmetic mean model with two variables (e.g. depth and SST) yielded the maximum R^2 and the minimum AIC value (Supporting information), thus was selected as the final HSI model. The statistical analysis of fitting-based SI models (Supporting information) shows they were all significant ($P < 0.05$). As shown by the SI curves (Supporting information, Fig. S1), the optimal range for depth, SST and SSS during winter in our study area was 36 – 72 m, 18.2 – 20.5 and 33.89 – 34.27, respectively.

The recent five decades' cooling trend in winter is remarkable, the reduced average SST ($-0.028/\text{year}$, $R^2=0.31$, $P<0.05$) between 1982 and 2019 in the mid-southern ECS in winter (Fig. 4). Consisted with the cooling trend of SST, the results of HSI models show the mean habitat suitability of the 1970s (1971 – 1980), 1980s (1981 – 1990), 1990s (1991 – 2000), 2000s (2001 – 2010) and 2010s (2011 – 2019) shifting in our study area. Fig. 5A shows that there was no significant change ($P > 0.05$) in the common and optimal habitat area from the 1970s to the 1990s. However, the percentage of optimal habitat decreased significantly ($P < 0.05$) from 13%, 12% and 13% in 1970s, 1980s and 1990s to 4% and 5% in 2000s and 2010s. Fig. 5B shows that the spatial distribution of habitat suitability also changed: optimal area has moved toward a southeast direction, with suitable habitats became offshore-oriented.

4. DISCUSSION

4.1 Fishing-induced life-history variation

Overall, this study provides evidence of serious fishing-induced life-history variation in *L. crocea* population and represent a glimpse of fishery collapse. The observed life-history parameters show that body size of *L. crocea* have on average, decreased during the last five decades (table 1), whereas we would expect an overall decrease of body size if the heavily fishing was the dominated driver of body size changes and STE. China's marine resources have suffered serious overfishing issues, characterized by the progressive depletion of economic stocks (Cao et al. 2017). Specifically, indiscriminate fishing ($\sim 50\%$ trawl with 54 mm mesh size)

in China can cause both age or size truncation of target populations, leading to increasing instability and vulnerability of the population dynamic (Kirby 2004, Gaichas et al. 2014, Kuparinen et al. 2016). Hence, the extremely high fishing mortality and exploitation rate have caused systematic decline in landing catch. Previous studies in the 1970s and 1980s revealed that the main catch of *L. crocea* consisted of two or three years old (400 – 800g) individuals (Yu and Lin 1980), while 95% of catches in this study were individuals aged zero or one years old. Another major finding was that ~70% of potential catch area have disappeared (Supporting information Fig. S2), with the highest disappearance rate in offshore areas (122degE – 125degE), which follows the life-history variation of *L. crocea* during the last five decades.

Previous studies have identified continuous fishing pressures and subsequent fishing-induced life-history variation is likely to have negative effects on overall population structure and their distribution patterns in several ways. First, continuous fishing pressure can erode fish biomass by substantially decreasing the proportion of large, old individuals. Still, STE-caused decline in maturity size and increase in mortality, may reduce reproductive output or the size of the breeding population (Johnston and Temple 2002, Morita et al. 2005, McMahan et al. 2020), and subsequent cause irreversible changes such as recruitment bottleneck, even extinction, to some populations, such as the collapse of Eastern blue groper, gemfish and blue-eye trevalla populations, following intense commercial fishing in Australia (Last et al. 2011). Second, a decrease in the population size can also reduce variation (causing inbreeding and genetic abnormalities) and, therefore, restrict the potential for adaption (Langangen et al. 2019). Thirdly, fishing-induced life-history variation may constrain species distribution because the migratory ability of a species is strongly dependent on dispersal characteristics, such as morphological traits, like body-size (Hsieh et al. 2009). Consequently, constriction of geographic distribution, associated with a decline in body size, may reduce the ability to respond to climatic stress, by limiting movement (Reusch et al. 2005).

4.2 Climate-induced overwintering habitat degradation may intensify the effect of overfishing

The best model (next best model: [?]AIC=2, for other models, Supporting information Table S2) to explain catch patterns under unexploited status over time included SST and depth. The result of SI suggested that the optimal overwintering temperature range (18.2 – 20.5) and depth (36 – 72m) of *L. crocea* mirror previous lab-based observation of optimal growth temperature (17– 24) and empirical observation of optimal overwintering depth (50 – 60 m) (Xu and Chen 2011, Liu 2013). It is worth noting that SST in the mid-southern ECS have decreased by an average of 1 between the 1980s and 2010s with annual decrease SST rate – 0.028/year (Fig. 4). HSI variation results in the last five decades suggests that cooling trend of SST in the ECS has significantly reduced the proportion of optimal and common overwintering habitats for *L. crocea* (Fig. 5B).

Consequently, in response to the SST decrease in winter, migratory species, like *L. crocea* are expected to respond in two ways as follows. Generally, marine organisms respond to climate change through shifts in distribution (Guisan and Thuiller 2005). For instances, in the North Sea, both exploited and un-exploited fish species have shifted to higher latitudes and deeper water between 1977 and 2001, in response to rising sea temperatures (Perry et al. 2005); in the Eastern Tropical Pacific, demersal species were projected to move into shallow water by the mid-21st century, in response to high greenhouse gas emissions (Representative Concentration Pathways, RCP8.5) and strong migration (RCP2.6) scenarios (Clarke et al. 2020). Alternatively, it is also commonly observed that species stay in poor habitat against climate change but suffered climate-induced life-history variation. Particularly, it occurs when marine fishes are living in temperature outside their physiology optima: this results in reduced aerobic scope, which negatively affects their growth and reproduction (Pearson and Dawson 2003, Portner and Knust 2007, Toresen et al. 2019). Hence, species like *L. crocea* must either migrate to remain within suitable habitat or suffer the consequences (Bell et al. 2015).

Interesting, *L. crocea* overwintering distribution pattern did not shift alongside a decrease in winter SST, which is a good indicator that temperature per se did not explain the overall shift of *L. crocea* distribution. Such absence of a clear systematic impact of temperature may be due to the life-history parameters degradation, which could constrain the hedging capacity against climate change (Thorson et al. 2017). It is

not uncommon that that heavily exploited species that do not ‘fill’ their suitable habitat against climate change background. For example, STE-caused a change in the length-age structure is the main driver of inter-annual shifts in summer flounder distribution, while temperature had little influence on the change in distribution (Bell et al. 2015). More broadly, the ‘match/mismatch hypotheses’ may explain the combined effects of heavily fishing and climate change on decrease of overall population (Cushing 1990, Edwards and Richardson 2004). Based on our study, we suggest that fishing-induced life-history variation leading to the ‘mismatch’ of *L. crocea* optimal overwintering habitat. Firstly, our study demonstrated that *L. crocea* have both life-history degradation and size truncation compared with 1980s, with significantly smaller body size and advanced maturation (Fig. 2B). This truncation in overall size-structure can significantly affect swimming ability, such as reducing the sustained swimming time and average swimming speed, namely size dependent, consequently reducing the distribution range of *L. crocea* (Jorgensen et al. 2008, Opdal and Jorgensen 2015, 2016). Ultimately, given the climate-induced changes in overwintering habitat suitability that occurs in the mid-southern ECS, the fishing-induced life-history population variation that constrains dispersal capability could pose a significant ‘mismatch’ of optimal overwintering habitat to *L. crocea*-like migratory species (Fig. 6). Such applicability of ‘mismatch hypotheses’ to the specific long-lived migratory fish exposed to fishing and climate change had rarely been demonstrated.

4.3 Management implication

In China, approximately 50% of China’s fish stocks have been overexploited or collapsed (Cao et al. 2017). In response to fishery collapse, the Chinese government has introduced comprehensive management tools, including input controls (restriction on fishing net mesh-size, fishing vessel numbers and horsepower, and seasonal closure policies) and, more recently, output controls, MPAs and co-management approaches (Shen and Heino 2014, Su et al. 2020). Our approach can provide insight in anticipation of stock enhancement and management that may facilitate conservation and re-stocking. While our results highlight that, as well as the previously described ‘lack of timely, effective or sufficient management, combined with heavy fishing pressure, particularly at spawning and overwintering grounds were major factors responsible for croaker stock declines’ (Liu and de Mitcheson 2008), climate change-induced overwintering habitat is another potential reason for the stock depletion. This is highly worrying because long-lived migratory fish like *L. crocea* decline even faster where both heavily fishing and climate-induced habitat suitability synergies (Farber et al. 2018).

The severe situation has led to an urgent need to re-evaluate fishery management and calls for a species-specific or life-history-based approach to stock enhancement (Young et al. 2006, Lotze et al. 2011, Pinsky et al. 2018, Dubik et al. 2019). First, regarding the fishing-caused size truncation effects, the deficiencies in china’s input control allow fishers to conduct indiscriminate intense fishing on large individuals of long-lived species after seasonal closure, and consequently alter the dynamics of the harvested species and the ecosystem. Hence, if capture fishery activities are not fully regulated in a scientific and deliberate way, restocking of long-lived migratory fish will be difficult. Here, we suggest establishing stricter input controls on fishery, including reducing the fishing capacity and efforts, eliminating unregistered/illegal fishing vessels, increasing the minimum mesh-size standard and adopting output controls, especially for single-species total allowable catch (TAC) or/and ecosystem TAC of *L. crocea*-like species. Secondly, regarding the climate-induced overwintering habitat, we recommend designing seasonal special reserve zones and more targeted regulations in crucial *L. crocea* habitats, which should be managed like MPAs. Ultimately, our application of HSI model illuminates the mechanisms of fishing-induced life-history variation and climate change-caused ‘mismatch’ impacts on long-lived migratory species (Wilson et al. 2008). Also, fishery managers often deploy hatchery release to address the recruitment bottleneck of species’ restocking (Myers et al. 2004, Taylor et al. 2017, Kitada 2018). Because *L. crocea*’s suitable overwintering habitats have shifted towards offshore areas, to tackle both recruitment and habitat bottleneck, we recommend that stakeholders choose larger juveniles, even mega-spawner for hatchery release to keep pace with the shifting of suitable habitats caused by climate change.

ILLUSTRATIONS AND TABLES

Figure 1. (A) Life-history migration patterns of *Larimichthys crocea* in the ECS; (B) The fishing area (gray

area) during winter 1971–1982 and the survey stations (crosses) in the winter of 2018 for *L. crocea* in the mid-southern East China Sea.

Figure 2. (A) Annual catch (1956–2019, 1000 tons) of *L. crocea* in Jiangsu, Shanghai, Zhejiang, and Fujian provinces, China; (B) Total catch (1956–2019, 1000 tons) and the number of hatchery release of *L. crocea* at coastal Zhejiang and Fujian provinces (main catch and stock enhancement provinces in China).

Figure 3. The Graphical fit of current life-history parameters and grow curves of *L. crocea* through length-frequency data with Electronic Length Frequency Analysis (ELEFAN) of bin=10mm, moving average (MA)=11 scenario. (A) Histogram of length-frequency distribution (bin=10mm); (B) Histogram of maturation of *L. crocea*; (C) Growth curve of *L. crocea* with ELEFAN S.A. (bin=10mm, MA=11) scenario; (D) Graphical fit of catch probability of bin=10mm, MA=11 scenario, t_{50} represent the relative age of first capture.

Figure 4. Annual winter season sea surface temperature (SST) anomalies (grey triangles) from 1970 to 2019. Showing long-term SST decline from 1970 to 2019 (blue solid line) and from 1982 to 2019 (red dashed line).

Figure 5. Decadal variations of (A) spatial distribution of predicted habitat suitability and (B) area percentage of optimal, common, and poor habitat since the 1970s. The areas with habitat suitability index (HSI) value > 0.7 , $0.7 > \text{HSI value} > 0.3$, and $\text{HSI value} < 0.3$ were regarded as optimal, common, and poor habitat, respectively.

Figure 6. Spatial distribution of (A) mean winter total catch of *L. crocea*, overlaid with the predicted HSI map in 1971–1982 and (B) biomass of *L. crocea* overlaid with the predicted HSI map in 2018.

Table 1. Current life-history parameters fitted with ELEFAN S.A. of bin=10mm, MA=11 scenario and historical life-history parameters of *L. crocea*.

Parameter	Description	Current (2019)
Life-history		
a, b	Coefficients of allometric length-weight relationship	2.60×10^{-6} (mm, g) 3.26
L_{mean}	Mean body length	130.4mm
L_{inf}	Asymptotic length	434mm
L_{mat}	Size of maturity	200–210mm
K	Growth coefficient	0.43
M	Natural mortality	0.30
F	Fishing mortality	1.57
Z	Total mortality	1.87
E	Exploitation rate	0.84
t_0	Age of length zero	-0.06year
t_{50}	Age of first catch	0.37 year
t_{95}	Age of probability 95% of capture	0.49 year
Goodness of fit		
R_n	The score value of true parameter can be calculate by model	0.61

Data Accessibility:

-Catch data, distribution data and hatchery release data: Dryad doi:10.5061/dryad.08kpr538

-Sampling locations and fish life history parameters data: Dryad doi:10.5061/dryad.08kpr538

-Climate data, bathymetry data and input files: Dryad doi:10.5061/dryad.08kpr538

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