



Effects of climate change and fishing on the Pearl River Estuary ecosystem and fisheries

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Abstract Climate change poses a challenge to the management of marine ecosystems and fisheries. Estuarine ecosystems in particular are exposed to a broad range of environmental changes caused by the effects of climate change both on land and in the ocean, and such ecosystems have also had a long history of human disturbance from over-exploitation and habitat changes. In this study, we examine the effects of climate change and fishing on the Pearl River Estuary (PRE) ecosystem using Ecopath with Ecosim. Our results show that changes in net primary production and ocean warming are the dominant climatic factors impacting biomass and fisheries productivity in the PRE. Additionally, physiological changes of fishes and invertebrates that are induced by climate change were projected to be modified by trophic interactions. Overall, our study suggests that the combined effects of climate change and fishing will reduce the potential fisheries catches in the PRE. Reducing fishing efforts can reduce the impacts of climate change on selected

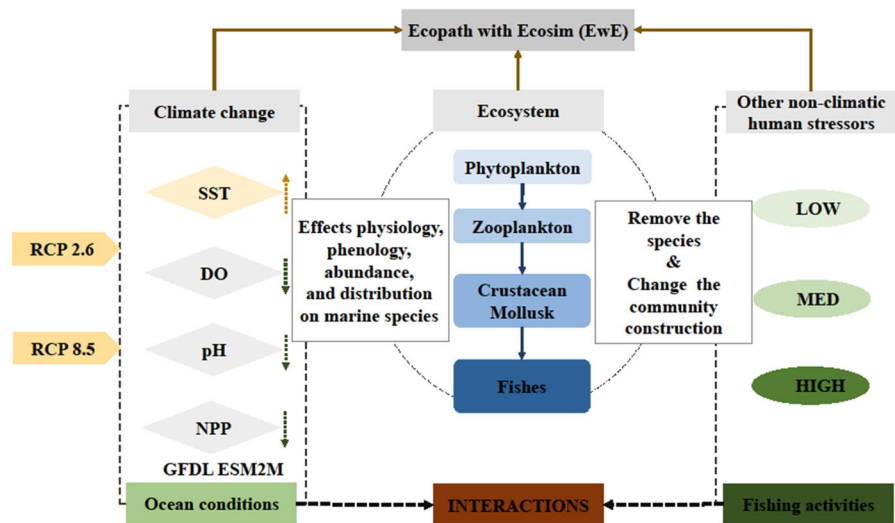
functional groups; however, some prey fishes are expected to experience higher predation mortality and consequently decreases in biomass under low fishing intensity scenarios. Thus, our study highlights the non-linearity of the responses of estuarine ecosystems when climate change interacts with other human stressors.

Graphic abstract In this study, the whole-ecosystem model (Ecopath with Ecosim) is used to examine the effects of climate change and fishing on a highly developed estuarine ecosystem (Pearl River Estuary, PRE) in the subtropical western Pacific. The oceans variables are extracted from the global earth system model (GFDL ESM2M), including changes in sea surface temperature (SST), hydrogen ion concentration (pH), dissolved oxygen (DO) concentration and net primary production (NPP) under the two scenarios RCP2.6 and RCP8.5. We developed a EwE model of the PRE ecosystem and simulated the effects of changing ocean conditions under alternative climate change scenarios as well as three fishing scenarios on the biodiversity and fisheries productivity of the PRE.

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Keywords Climate change · Ocean warming · Ocean acidification · Net primary production · Fishing effort · Ecosim · Pearl river estuary ecosystem

Introduction

The global ocean has become warmer, less oxygenated and more acidic with increases in anthropogenic emissions of carbon dioxide and other greenhouse gases since the industrial revolution (Gattuso et al. 2015). These changes in ocean conditions affect the nutrient conditions and productivity of marine ecosystems (Doney et al. 2012). Marine species are responding to these changes in environmental conditions through changes in physiology (Pörtner and Farrell 2008), phenology (Edwards and Richardson 2004), abundance and distribution (Cheung et al. 2013). Consequently, the community composition and structure of marine ecosystems are affected by these biological responses (Brown et al. 2010; Cheung et al. 2015).

Other non-climatic human stressors may interact with biological responses to climate change, potentially attenuating or exacerbating the impacts of

climate change on marine ecosystems (Engelhard et al. 2014). Such interactions are particularly important in coastal marine areas where diverse and intensive human activities take place (Jackson et al. 2001). For example, overfishing can lead to the truncation of size structure, increase in dominance of species with short lifespans, and degradation of genetic variabilities that may consequently increase the sensitivity or reduce the adaptive capacity of marine species and ecosystems to climate change impacts (Perry et al. 2010; Pörtner et al. 2014; Cheung et al. 2018). The combined impacts of climate change and other non-climatic human stressors are expected to alter the availability of fisheries resources and the livelihoods of coastal-dependent communities (Savo et al. 2017). Therefore, it is important to consider the interactions between non-climatic human stressors, such as fishing and climate change, when assessing the impacts of climate on marine ecosystems and exploring the potential human interventions that may help reduce these impacts (Perry et al. 2010).

The Pearl River Estuary (PRE) is located at latitudes 21°N–23°N and longitudes 112°30′E–115°30′E (Fig. 1). The Pearl River discharges into the northern South China Sea, which is the second largest river in terms of flow rates in China (Wang et al. 2015). The PRE is a traditional fishing ground and an important nursery ground for numerous fish species as well as the rare *Sousa chinensis* (Qiu et al. 2008). In recent years, human activities have led to the deterioration of the environmental and ecological

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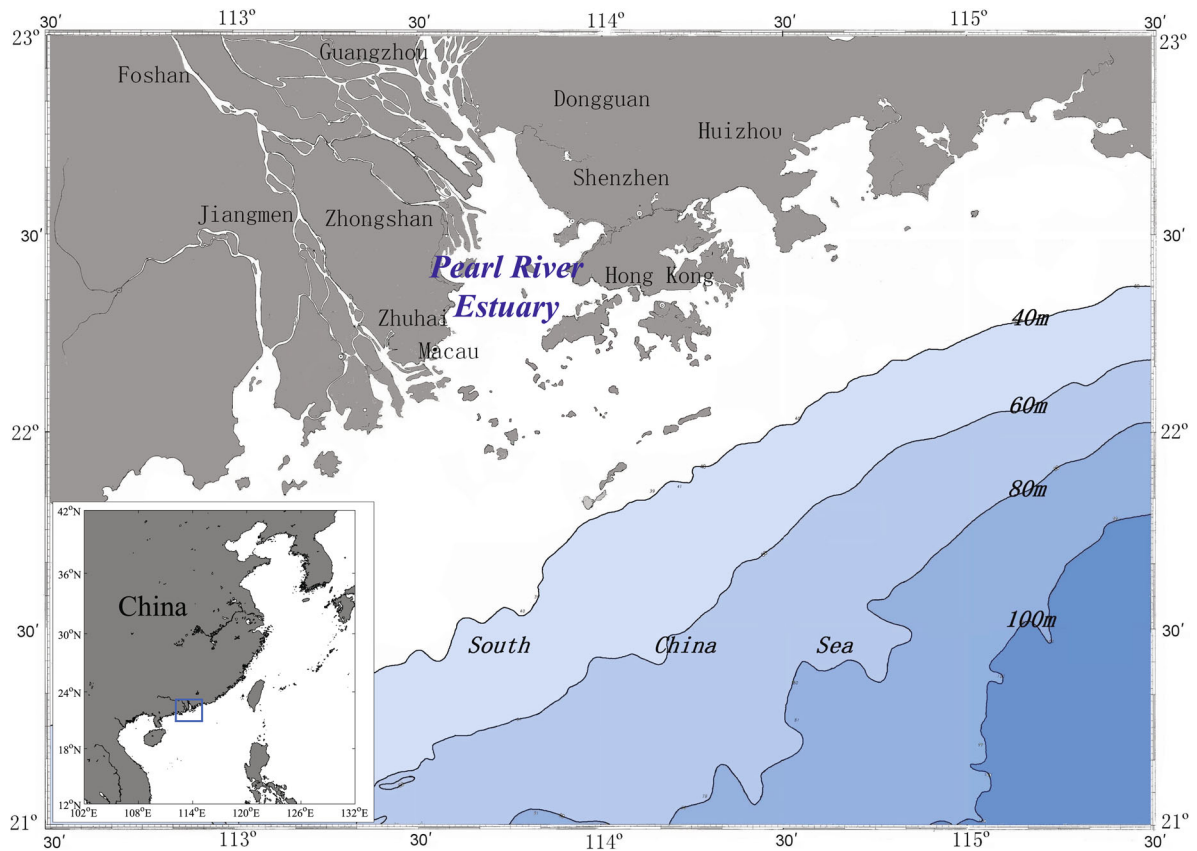


Fig. 1 Coverage of the EwE model in the PRE

conditions of the PRE ecosystem (Ke et al. 2007). High fishing intensity in the PRE is the primary human disturbance, particularly since 1978, because of the large increase in the number of fishing boats and the improvement of fishing technology associated with the economic reform of China (Jia et al. 2005). Fishing has led to extensive changes in the community structure of fishes and decreases in the abundance of high trophic level exploited marine species and the level of maturity of the ecosystem (Duan et al. 2009b; Wang et al. 2015). Given that the PRE has been heavily exploited for decades and evidence of over-exploitation of fisheries resources has been demonstrated, it is important to explore the interactions between climatic and non-climatic human stressors in the PRE ecosystem as a typical coastal system in China.

Whole-ecosystem models integrate the interactions and responses of different levels of biological organization as well as multiple human stressors on marine ecosystems (Koenigstein et al. 2016). Generally, the

interactions and responses are embodied in physiological and ecological processes. Whole-ecosystem models are able to quantify the integration of physiological and ecological processes (Koenigstein et al. 2016) and predict possible shifts in organization and the ecosystem. Specifically, whole-ecosystem models that are based on trophodynamic principles represent the energy flow across trophic groups in the ecosystem (Gascuel et al. 2012), through which the effects of changing environmental conditions on physiological and ecological processes can be represented (Koenigstein et al. 2016).

In this study, we applied the widely used whole-ecosystem trophodynamic model, Ecopath with Ecosim (EwE, version 6.5) to examine the interactions between climatic stressors (warming, ocean acidification, deoxygenation and changes in net primary production) and a non-climatic stressor (fishing) in a highly developed estuarine ecosystem (PRE) in the subtropical western Pacific. We developed an EwE

model of the PRE ecosystem and simulated the effects of changing ocean conditions under alternative climate change scenarios as well as three fishing scenarios on the biodiversity and fisheries productivity of the PRE. We then used the modelling results to generate hypotheses of potential ecological changes that were used to develop empirical studies to examine the responses of the PRE ecosystems to climate change and fishing and inform the development of ecosystem-based management policies.

Materials and methods

Ecopath with Ecosim model

The EwE model combines ecosystem trophic mass balance analysis (Ecopath) and time-dynamic model (Ecosim) to explore the temporal dynamics of a food web under fishing and environmental disturbances (Christensen and Walters 2004). There are two equations that are the basic dynamic principles for the simulation of biomass changes of ecosystem functional groups (Walters et al. 2000), Eq. (1) for primary production and Eq. (2) for consumers:

$$\frac{dB_i}{dt} = \gamma B_i \left(\frac{P}{B} \right)_i EE_i - \sum_{j=1}^n f(B_i, B_j) - M_i B_i \quad (1)$$

$$\frac{dB_i}{dt} = \gamma g_i \sum_{j=1}^n f(B_j, B_i) - \sum_{j=1}^n f(B_i, B_j) + I_i - (M_i + F_i + e_i) B_i \quad (2)$$

where B_i and B_j are the biomasses of prey(i) and predator (j), respectively, P is the production rate, EE_i is the ecotrophic efficiency, $f()$ is a functional relationship used to predict consumption rates, M_i is the natural mortality, F_i is the fishing mortality, I_i is the immigration rate, e_i is the emigration rate, g_i is the growth efficiency, and γ is the scalar we used to describe the climate change factors as represented by the forcing functions (Ainsworth et al. 2011).

An Ecopath model was developed to represent a hypothesis of the structure of the PRE ecosystem in the 2000s (hereafter called the 2000s Ecopath model). The basic parameter values for the 2000s Ecopath model were based on a 1998 PRE Ecopath model (Wang et al.

2016), an Ecopath model of the Hong Kong marine ecosystem (Buchary et al. 2002; Pitcher et al. 2002), an Ecopath model of the Northern South China Sea (Cheung 2007) and fisheries and environmental survey data for the PRE. The Ecopath model was composed of 38 functional groups with six fishing fleets. The parameter values for the 2000s Ecopath model and their estimation are documented in the Supplemental Materials (Supplemental Table S1).

Simulating climate change effects in Ecosim

We simulated the effects of changes in temperature, dissolved oxygen (DO) concentration, pH and primary production on the PRE using Ecosim. The impacts of changing ocean variables on species included effects on the growth, survival and distribution of marine organisms. Changes in these biological rates and characteristics are related to the ecophysiological responses of the marine organisms to changing ocean conditions (Pörtner et al. 2014). The EwE model can represent these different biological rates and characteristics through modelling changes in the production rate of each functional group as established in previous modelling studies (Ainsworth et al. 2011; Alava et al. 2018). This approach adopted the algorithm that had been applied by Ainsworth et al. (2011) to simulate the impacts of climate change on the Northeast Pacific marine ecosystem. However, we applied the biological representativeness of the algorithm by changing the prey vulnerability value. If the values of the forcing function time series were greater than 1, then the biomass production would increase by increasing consumption and more successful predation, and vice versa.

We evaluated the impacts of climate change on the fisheries and ecosystem in the PRE under two contrasting carbon dioxide emission scenarios: Representative Concentration Pathway (RCP) 2.6 and 8.5, which represent low (strong mitigation) and high (business-as-usual) emission scenarios, respectively (Moss et al. 2008; Gattuso et al. 2015). The annual average sea surface temperature (SST), hydrogen ion concentration, DO and net primary production (NPP) in the PRE during the period of 1991–2060 were extracted from the outputs of the NOAA's Geophysical Fluid Dynamics Laboratory Earth System Model (GFDL ESM2M) (<https://www.gfdl.noaa.gov/earth-system-model/>). The annual variations of each

variable relative to the mean values from 1991 to 2010 were calculated.

Temperature

In the EwE model, the forcing functions associated with temperature change were adopted to represent the responses of functional groups to temperature change, and they were based on the interannual variabilities relative to the current temperature and the species' temperature preferences and tolerance limits. Species' preferred temperatures in the PRE were calculated based on the dataset of Cheung et al. (2013). Briefly, Cheung et al. (2013) overlaid the predicted species relative abundance of each exploited marine fish and invertebrate species with sea water temperature to predict the mean temperature preferences and the variability. For simplification, we calculated the temperature preference functions by assuming a normal distribution of the predicted mean temperature preference and its standard deviation. Based on this function, we calculated normalized preference indices for different environmental temperatures. We assumed that temperature above or below the preferred temperature would reduce the biomass and productivity of the species depending on the forcing function of each functional group. A time-series of projected SST was estimated by adding the change in SST obtained from the GFDL ESM2M (under RCP2.6 and RCP8.5) to the average SST from 1991 to 2010 obtained from the Hadley Centre Global Sea Surface Temperature survey data. The indices of the temperature preferences of species ($n = 14$) in 14 fish functional groups from 2000 to 2060 under the two emission scenarios were forecasted.

Acidification

Sensitivities to ocean acidification vary among taxonomic groups (Kroeker et al. 2010). Sensitivity is generally shown to be the highest for molluscs, followed by crustaceans and fishes (Melzner et al. 2009; Kroeker et al. 2013). The analysis in Kroeker et al. (2013) revealed that molluscs and echinoderms were the two most vulnerable taxonomic groups and acidification had a significant negative effect on the survival, calcification, growth and development of species belong to these groups. In contrast, more mobile crustaceans and fishes were less sensitive to

acidification (Kroeker et al. 2013). Therefore, we focused on the potential effects of ocean acidification on molluscs and echinoderms in this study.

The effects of ocean acidification on molluscs and echinoderms were represented in the model by a set of forcing functions that drove changes in biomass productivity of the mollusc and echinoderm functional groups in relation to the projected ocean hydrogen ion concentration ($[H^+]$). We hypothesized that the biomass productivity of species would decrease with an increase in $[H^+]$. The sensitivity of biomass productivity to $[H^+]$ was based on the effect sizes of ocean acidification on the growth and survival of molluscs, and the growth and development of echinoderms, and these effect sizes were from the meta-analysis of Kroeker et al (2013) with the conditions of pH decreasing 0.5 units. Current (average 1991–2010) and future changes in $[H^+]$ under RCP2.6 and RCP8.5 were projected from the GFDL ESM2M.

Oxygen

Species have different sensitivities to changes in DO (Townhill et al. 2017). We adopted the approach used by Ainsworth et al. (2011) to define the functional groups' sensitivities to change in DO, and it is based on the median lethal oxygen concentration and the median sub-lethal concentration of the marine organisms across the global review by Vaquer-Sunyer and Duarte (2008). The sensitivities of ecosystem functional groups to DO were classified as small-, medium-, or large-scale impacts based on the assumption made by Ainsworth et al. (2011) for Northeast Pacific marine ecosystems, specifically from the 'moderate scenario' of Ainsworth et al. (2011), with -7% , -22% and -37% of the baseline productivity for small-, medium-, and large-scale impacting species (Table 1), respectively. These values were used to quantify the forcing functions with the change in DO.

We assumed that the DO changes would affect the production rate of the consumer functional groups (except for air-breathing organisms). The sensitivity of the functional groups to DO would affect the projections of the production rate of each functional group through changes in their vulnerability to their predators in the EwE model. For instance, when DO decreased, some fishes would respond by moving to the near-surface waters or shallower areas to avoid hypoxic waters, which would increase their

Table 1 Susceptibility to changes in DO applied to forcing functions

Taxa	Direction of effect	Effect size
Zooplankton	Negative	Large
Jellyfish	Negative	Small
Polychaetes	Negative	Large
Molluscs	Negative	Median
Echinoderms	Negative	Median
Benthic crustaceans	Negative	Large
Other zoobenthos	Negative	Large
Shrimps	Negative	Median
Crabs	Negative	Large
Cephalopods	Negative	Small
Fish species	Negative	Large
Sharks	Negative	Large

vulnerability to predators (Wu 2002). The consequence of these processes could decrease the biomass or abundance of these species. The forcing function representing the effects of oxygen assumes a direct proportional relationship between changes in DO and the production of consumer functional groups. The changes in DO were projected based on the outputs of the GFDL ESM2M under RCP2.6 and RCP8.5 from 1990 to 2060.

Net primary production

NPP is the fundamental element of the food web (Hunt and McKinnell 2006). In the PRE ecosystem, primary production supplies more than half of the energy flow to consumers (Duan 2009). We assumed that changes in phytoplankton production were proportional to the changes in NPP in the PRE as projected by the GFDL ESM2M under RCP2.6 and RCP8.5 (Fig. 2d). Thus, the model reflected the mean trends as well as the interannual variability of primary production under climate change scenarios. Previous studies suggested that the sensitivity of the PRE ecosystems to benthic primary production might be low because of their low estimated ecotrophic efficiency (EE), which is approximately 1–2% (Cheung 2007; Duan et al. 2009a); thus, we did not account for the effects of climate change on benthic producers.

Combined impacts of climate change

The interactions of multiple stressors on an ecosystem may have synergistic, antagonistic or additive effects (Darling and Cote 2008). In our study, the responses of multiple CO₂-related changes in ocean variables were combined by incorporating the forcing functions for temperature, acidification, oxygen and primary production simultaneously in Ecosim for each functional group.

Climate change and fishing interaction impact scenarios

To investigate the potential interactions between fishing and climate change in the PRE, we developed three (low, medium and high) fishing scenarios to combine with the two climate scenarios. The low, medium and high fishing scenarios were represented by multiplying 80%, 100% and 120% of the current (2000s) fishing mortality rates estimated from the baseline Ecopath model.

Sensitivity analyses of individual climate factors

We examined the sensitivity of the ecosystem in the PRE to each climatic factor. The sensitivity indices of the functional groups to the different climate factors were calculated based on the ratio between the change in biomass relative to the baseline scenario (without the climate change model in 2050) of each group and the change in the ocean variable of concern. If the values are less than or equal to 1, the functional groups have low sensitivity to the influencing factor, and vice versa:

$$Index_{ij} = \frac{|\Delta Biomass_{ij}/SD_B|}{|\Delta F_i/SD_i|} \quad (3)$$

where i is the individual ocean variable (SST, H⁺ concentration, DO and NPP), j is the functional group, $\Delta Biomass_{ij}$ is the biomass change relative to the base model of group j in the impact of influence factor i , SD_B is the standard deviation of the biomass of functional group j , ΔF_i is the change in the value of ocean variable i , and SD_i is the standard deviation of the ocean variable from 2041 to 2060.

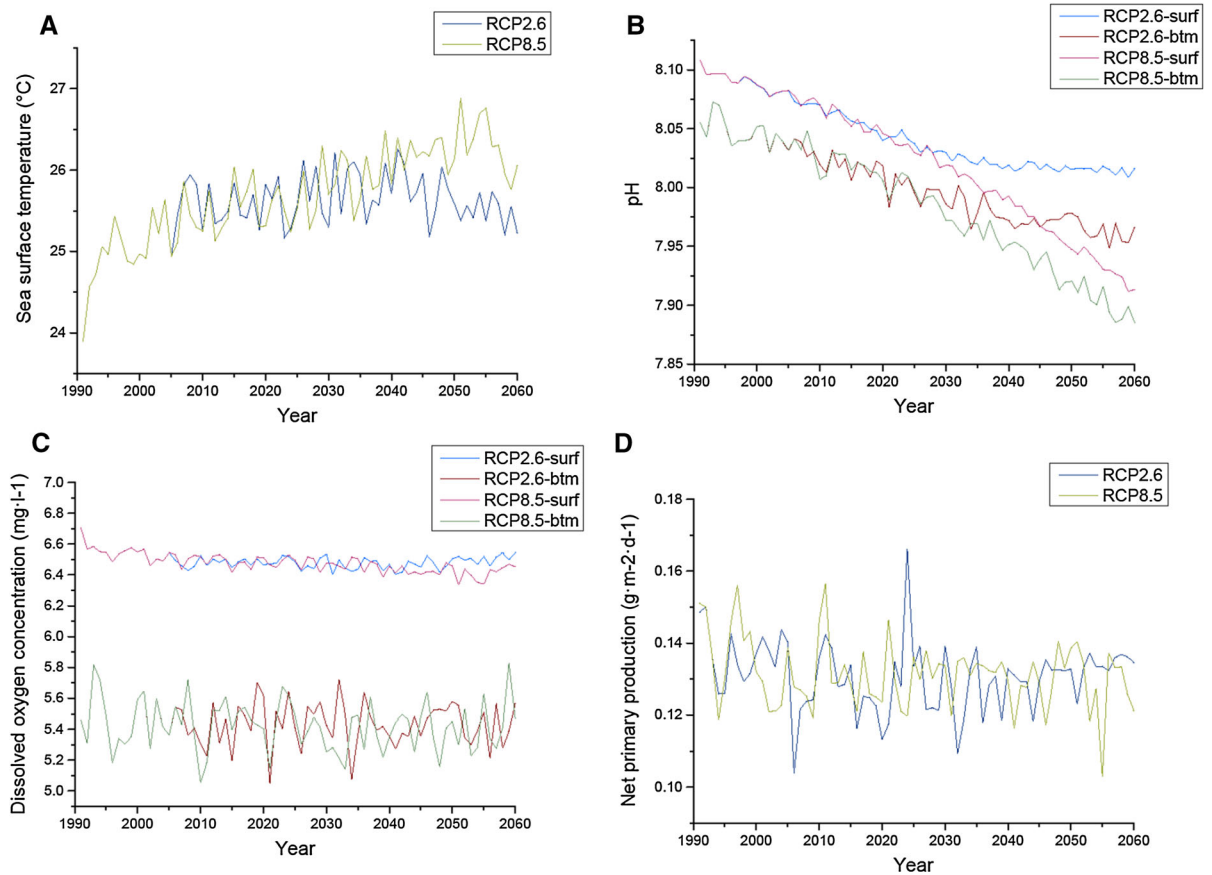


Fig. 2 Ocean variables from 1991 to 2060 in the PRE (results of GFDL ESM2M with RCP2.6 and RCP8.5)

Sensitivity analyses of vulnerability formulations

In this study, time series of biomass or relative biomass data were not available to estimate the parameters for the PRE Ecosim model, particularly for the ‘vulnerability settings’ that would determine the form of the functional response of the predator–prey interactions (Koenigstein et al. 2016). Vulnerability settings could represent the risk-sensitive foraging or predation behaviours of the predator–prey interactions of the ecosystem (Ahrens et al. 2012). We assumed vulnerability settings of 2, 3.5 and 5 for all predator–prey interactions in the model, and they represented ‘bottom-up’, ‘mixed bottom-up and top-down’ and ‘top-down’ controlled ecosystems, respectively. We then discussed how different assumptions on the predator–prey interactions would affect the functional groups’ ecological responses to climate change. Thus, our simulation results should be viewed as scenarios for the plausible climate change impacts

to the PRE ecosystem rather than as an accurate forecast of ecosystem change in the climate change scenarios.

Calculating ecological indicators

We evaluated the changes in the status of the PRE ecosystem by calculating a range of biodiversity and trophodynamic indicators. These indicators include landings and biomass of functional groups, trophic level of catch (TLC), trophic level of community (TLcom), Shannon index and Kempton’s Q index. To evaluate the impacts of climate change and fishing on fisheries, ecosystem communities and biodiversity, we calculated the relative changes of each indicator under alternative climate change and fishing scenarios relative to the baseline scenario. Specifically, TLC and TLcom were calculated by Equations S1 and S2 (in the Supplemental Materials). The Shannon index, which indicates the change in biomass evenness for all

functional groups to climate change and fishing, was calculated by Equation S3 (in the Supplemental Materials).

A variant of the initial Kempton's Q index (in the Supplemental Materials Equation S4) that included two modifications was calculated to measure the biomass diversity. The first modification was that the EwE model used the inter-quartile slope of the cumulative abundance to evaluate the biomass diversity of an ecosystem; and the second modification was to calculate Kempton's Q index using only the groups (trophic level, TL > 3) in which the number of the included groups should be more than 10; otherwise, it was based on the calculations for all living groups (Christensen et al. 2005). Therefore, Kempton's Q index in the EwE model was expected to track the effects of climate change and fishing on the changes in the biomass and diversity of the high trophic level species (specifically fished species). However, Kempton's Q index cannot reflect the richness of the overall biodiversity because of the lack of a filter to discriminate functional group depletions or extirpations in the ecosystem (Ainsworth and Pitcher 2006).

Results

Changes in ocean variables

Ocean variables were projected to change to different extents between RCP2.6 and RCP8.5 (Fig. 2) in the PRE in the twenty-first century (1991–2060). SST was projected to increase by approximately 0.47 °C under RCP2.6 and 1.19 °C under RCP8.5, while pH was projected to decrease more than 0.1 units under RCP8.5 in both surface and bottom layers. The annual average DO rarely dropped to < 5 mg l⁻¹ for both RCP2.6 and RCP8.5. The NPP of the phytoplankton was projected to fluctuate inter-annually with a slight decreasing mean trend for both RCP2.6 and RCP8.5.

Projected changes in fisheries catches

The model projected a decrease in fishery catches from 2000 to 2060 under both RCP2.6 and RCP8.5 in all fishing scenarios, except for RCP2.6 under the low fishing intensity scenario (Fig. 3). The total fisheries catches in the PRE were projected to decrease by 1.6% (0.1–6.9%) and 3.8% (0.2–10.6%) by the 2050s

(average of 2041–2060) relative to the baseline scenario under RCP2.6 and RCP8.5, respectively, across the four ocean variables (Fig. 3a). With ocean acidification and changes in DO implemented separately in the model (i.e., changing only one ocean variable while keeping the others constant), the total catches in the PRE were projected to decrease by less than 1.4%. Changes in NPP and ocean warming were projected to reduce the total catches by 4.5% (1.6–7.1%) and 5.1% (2.0–10.6%), respectively, across the vulnerability settings tested in this study. When changes in all variables were incorporated into the simulation simultaneously, the total catches values were approximately 93.7% and 85.7% of the baseline scenario under RCP2.6 and RCP8.5, respectively (Fig. 3b).

Fishing was projected to be a major factor for determining future catches, with lower fishing intensity reducing the sensitivity of fisheries catches to climate change (Fig. 3b). The average across climate change scenarios of the projected fisheries catches by the 2050s relative to the baseline scenario were approximately 101.1%, 89.7% and 76.6% under the low, medium and high fishing intensities, respectively. The shifts in catches between RCP2.6 and RCP8.5 showed significant differences. A greater decrease in fisheries catches occurred under RCP8.5 than RCP2.6 except for the low fishing intensity, for which the catches were projected to increase (5.3%) under RCP 2.6. The decrease of catches was projected to be exacerbated by the higher fishing intensity. Our results suggested that there would be more serious impacts on fisheries catches in the PRE under higher emission climatic scenarios or higher fishing intensities.

Projected changes in biomass

The biomass of the functional groups was affected by individual climatic factors to different degrees, and ocean warming was the only factor that was projected to lead to an increase in the total biomass of non-primary producer species (Fig. 4). The projected ocean warming led to a 1.7% increase in the total biomass of non-primary producer species under RCP2.6 and RCP8.5 between 2000 and 2050 across all vulnerability settings. The increase in the biomass of non-primary producer species was driven by the projected increase in low trophic species, such as benthic crustaceans and other zoobenthos. However,

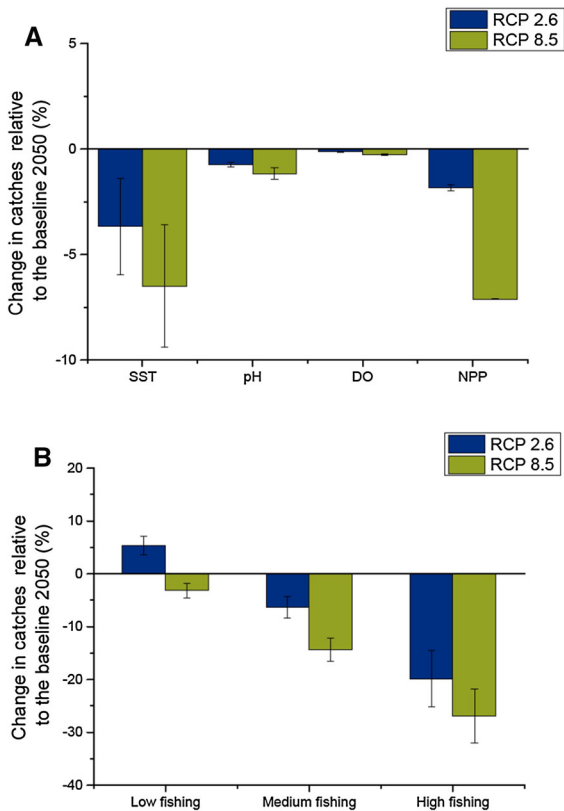


Fig. 3 Changes in fisheries catches relative to the baseline (2050) under individual climatic drivers (a) and the combination of climate change scenarios (RCP2.6 and RCP8.5) with three fishing scenarios (low, medium and high) (b). Climatic drivers: ocean warming (SST), acidification (pH), dissolved oxygen (DO) concentration and change in net primary production (NPP). The error bars indicate the range of outputs observed by the three different trophic interactions (low, median and high vulnerability) of ecosystem status

the biomass of most functional groups that were exploited by the fisheries was projected to decrease under both RCP2.6 and RCP8.5 (Supplemental Figure S2). Specifically, the biomass of crabs, *Trachurus japonicus* and *Psenopsis anomala* was projected to decrease by 80.4% (36.5–100%), 92.1% (66.2–100%) and 93.4% (62.6–100%) respectively, across RCPs and vulnerability settings. A few exploited functional groups were projected to increase, such as benthopelagic fish and nemipterids, which increased by 140.6% (10.9–424.9%) and 179.7% (56.6–398.6%) respectively, during the same period. The responses of functional groups to ocean warming were partly a result of changes in trophic interactions. For instance, our model projected an increase in biomass (85.8%) of

priacanthids, which consequently increased the predation mortality of *Decapterus maruadsi*, thereby resulting in a decrease in biomass (34.1%).

For the other ocean variables, NPP was projected to strongly affect the biomass of functional groups in the PRE, while changes in DO and ocean acidification did not show strong effects on the ecosystem biomass (Fig. 4a). The total biomass of the non-primary producer species was forecasted to decrease by approximately 1.9% (1.7–2.1%) and 6.0% (5.9–6.1%) under RCP2.6 and RCP8.5, respectively, with the change in NPP across vulnerability settings. Particularly, under RCP8.5, the biomass of almost all the groups was projected to decrease as a result of the decrease in NPP (Supplemental Figure S2).

The combined effects of ocean warming, acidification and changes in DO and NPP were projected to reduce the total biomass of non-primary producer species, with significant differences observed in the

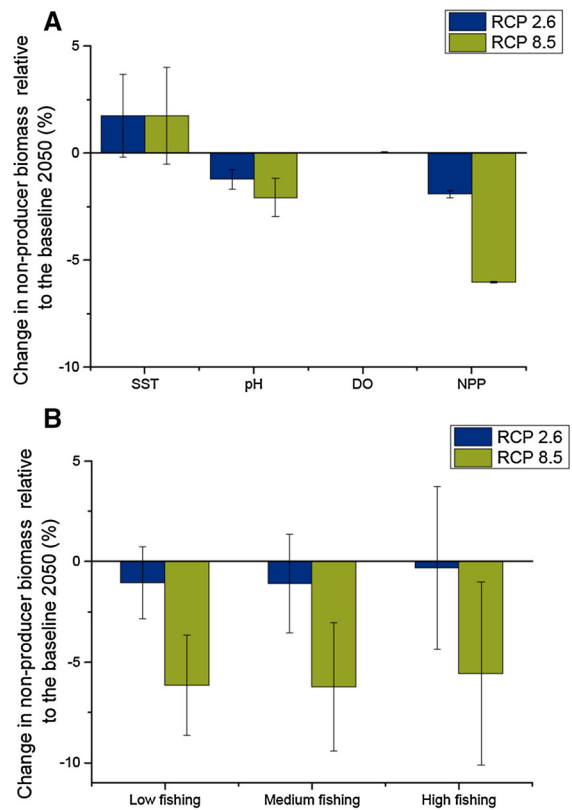


Fig. 4 Non-producer biomass change relative to the baseline (2050) under individual climatic drivers (a) and the combination of climate change scenarios (RCP2.6 and RCP8.5) with three fishing scenarios (low, medium and high) (b)

projected trends between RCP2.6 and RCP8.5 by the 2050s relative to the 2000s (average decreases of 0.8% and 6.0%, respectively, across the three fishing settings) (Fig. 4b). Different fishing intensities did not affect the impacts of climate change on the total biomass of non-primary producer species. However, the biomass of most of the exploited groups was projected to be substantially higher under the low fishing scenario relative to the high fishing scenario, for both RCP2.6 and RCP8.5 (Supplemental Table S2).

Impacts on the food web structure

The model projected that climate change (RCP2.6 and RCP8.5) would have only small impacts on the mean trophic level of the ecosystem (TLcom) and fisheries catch (TLC) in the PRE (Fig. 5a, b). Either individual or multiple ocean variables do not cause shifts of more than 1% in the TLcom and TLC in either RCP2.6 or RCP8.5 across all fishing settings.

Climate change was predicted to impact the Shannon index slightly, which indicated the biomass evenness of the ecosystem. When the changes of each ocean variable were implemented separately in the model, this index was projected to shift to small extents with the impacts of ocean warming, acidification, changes in the DO and NPP (Fig. 5c). When the changes of all the ocean variables were implemented simultaneously, the projected Shannon index by the 2050s reduced to a greater extent under RCP8.5 (5.2%) than RCP2.6 (1.6%) across all fishing scenarios (Fig. 5d).

However, Kempton's Q index showed a different pattern of changes compared to the Shannon index. Kempton's Q index was projected to shift slightly with individual changes of DO, NPP and ocean acidification, whereas the index was projected to decrease largely under the impact of ocean warming, which would be attributed to greater increases or decreases in the biomass of fish species under the impacts of ocean warming. When the changes of all the ocean variables were taken into account simultaneously, Kempton's Q index was projected to decrease by approximately 31.7% and 42.6% for the low and medium fishing effort scenarios, respectively, across climatic scenarios. Notably, under the high fishing scenarios, Kempton's Q index was projected to increase, for the possible reason that the high fishing effort reduced the

biomass of most of the species with high biomass across the high trophic level, then increased the evenness of ecosystem ($TL > 3$).

Sensitivities to changing ocean variables

Overall, the functional groups of the PRE ecosystem were projected to be most sensitive to ocean warming, followed by the changes in NPP and DO (measured by the changes in biomass per normalized unit change in each ocean variable) (Fig. 6). Acidification was the weakest sensitive factor. The sensitivity to the change in DO was small, when coupled with the lower inter-annually variability of DO in the simulation period, would be the reason for the small change in biomass of the functional groups under both emission scenarios (Supplemental Figure S2). Some functional groups were more sensitive to the NPP change, including the high trophic level species, such as shark, seabirds and marine mammal. About one half of the fish species were predicted to be sensitive to ocean warming. It was possibly due to the large ecophysiological responses of fish species to ocean warming.

Discussion

Our results provided insights into the potential impacts of climate change and fishing on the PRE ecosystem and fishery. First, marine species in the region were predicted to be most strongly impacted by ocean warming, and the PRE ecosystem and fishery resources could be highly threatened by the change in NPP under the high emission scenario in the next few decades. Second, the species were predicted to be directly and indirectly affected by climate change, and the trophic interaction in the ecosystem would change the physiological responses of specific species to climate change. Third, climate change and fishing interact non-linearly changing ecosystem communities with a result of the high fishing intensity scenario exacerbating the effects of climate change.

The large impacts of ocean warming projected for the next few decades were a result of the larger exposure to warming and the sensitivity of functional groups to temperature. Particularly, the model was largely driven by the forcing functions under the impacts of ocean warming, which were defined by their distribution change depending on the ocean

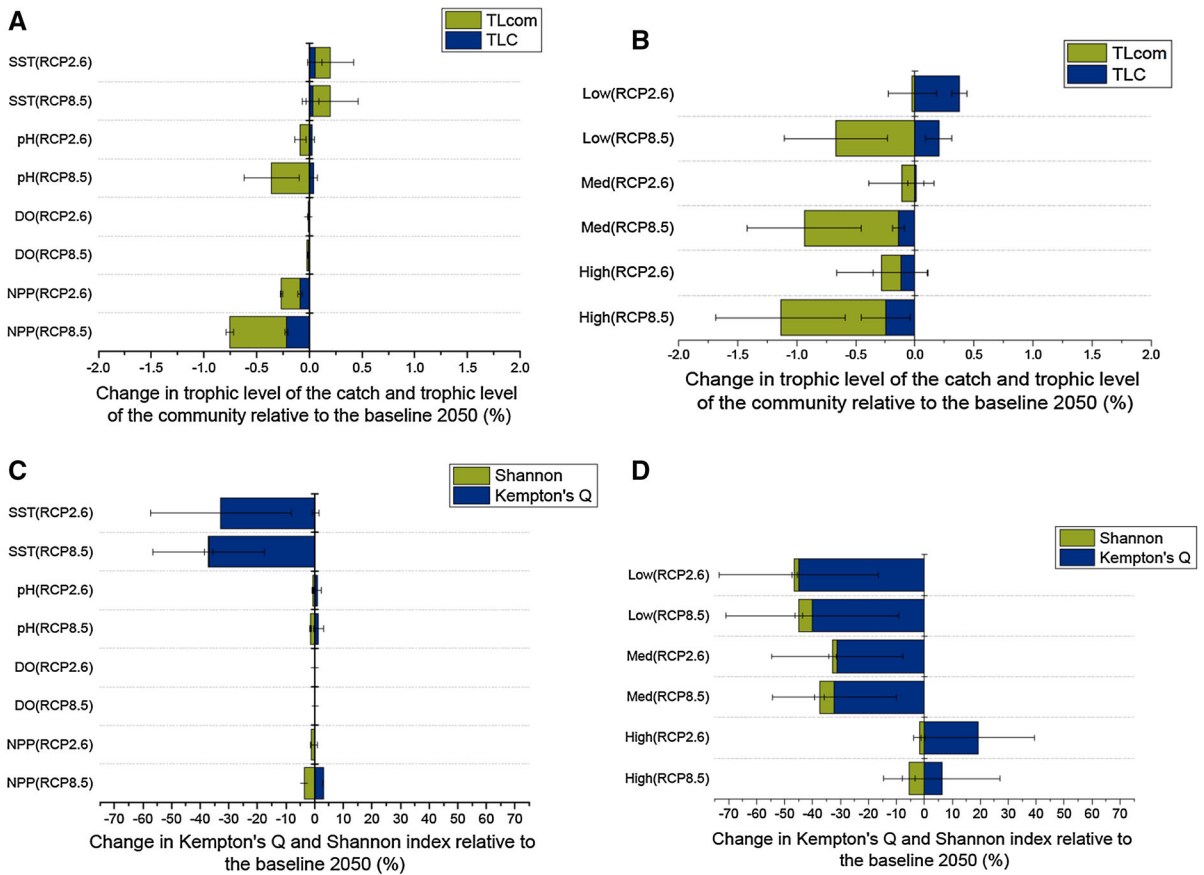


Fig. 5 Ecosystem response relative to the baseline (2050) under individual climatic drivers and the combination of climate change (RCP2.6 and RCP8.5) with three fishing scenarios (low,

medium and high). **a, b** Mean trophic level of the catch and mean trophic level of the ecosystem; and **c, d** Kempton's Q and Shannon index

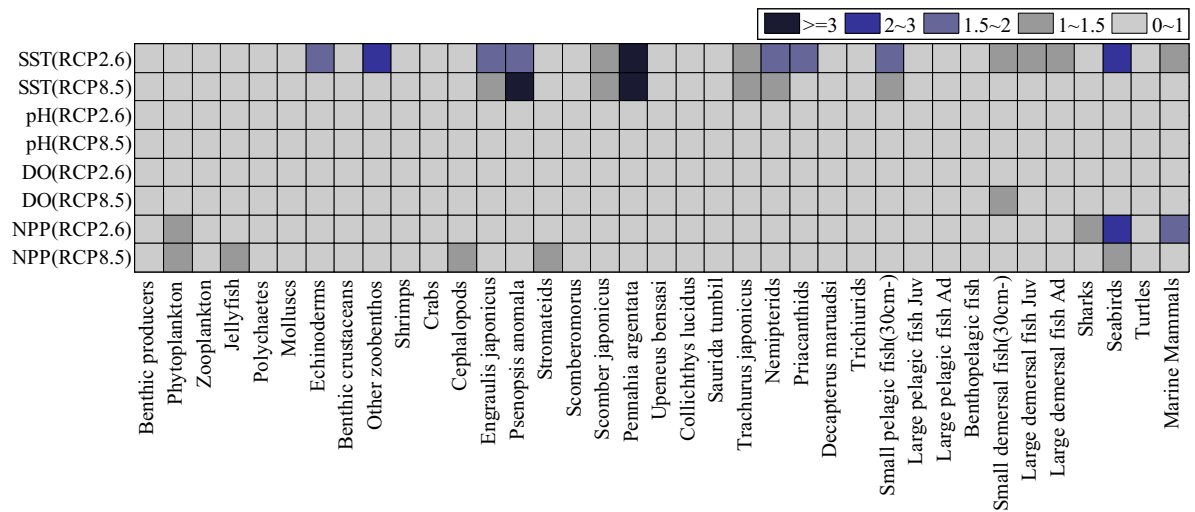


Fig. 6 Sensitivities of the functional groups to individual climatic stressors under high and low emission scenarios

temperature shift in the study area. The large impacts of ocean warming on the PRE ecosystem corroborated the expectations from theories and empirical findings. The change in ocean water temperature could result in a shift of the geographical distribution of species, which could profoundly impact fisheries and alter communities (Perry et al. 2005; Cheung et al. 2013; Roberts et al. 2017). Cheung et al. (2016) predicted that ocean warming could reduce the potential landings by more than 3 million metric tons per degree Celsius increase, with ocean warming being the main contributing factor.

The catch and biomass would largely reduce with decreases in NPP in the PRE under RCP8.5. Our model results revealed that the indirect effects of changes in NPP would affect high trophic level species. However, the change in primary production throughout the global ocean under the impact of climate change is still uncertain (Cheung et al. 2011). A study by Brown et al. (2010) indicated that primary production would increase under a plausible climate change scenario, which would benefit fish resource stocks around Australia. However, Cheung et al. (2011) indicated that the catch potential may reduce by approximately 10% due to the impacts of changes in the phytoplankton community structure caused by climate change in the Northeast Atlantic. The change in NPP is another major variable that reduces the catch and biomass in the PRE, and it outweighed the effects of changes in acidification and DO.

Although our model did not project a severe impact of change in DO on the fisheries and ecosystem in the PRE, it should still be considered a crucial factor in this area. Worldwide, the oxygen content is expected to decrease in the long term under climate change (Schmidtko et al. 2017), and oxygen depletion was highlighted to be one of the major threats to fisheries and marine ecosystems. The Earth system model has high uncertainty in projecting the changes in oxygen in coastal and estuarine areas, where the model poorly resolves the key processes driving changes in biogeochemistry (Asch et al. 2016). In fact, the hypoxia is common in the PRE during summer caused by increasing anthropogenic pollutant inputs. Deoxygenation in coastal waters around the world has been shown to impact the animal populations by changing their distributions and abundances (Breitbart et al. 2018).

Reducing fishing efforts can mitigate the effects of climate change for most groups of fished species. However, some species have the potential to experience higher predation mortality, which causes decreases in their biomass in the low fishing scenario. Many previous studies also found that fishing activities could exacerbate the impacts of climate change and potentially reduce the resilience of populations to environmental perturbations (Brander 2007; Kirby et al. 2009). Fishing changes the community and functions of an ecosystem by removing the larger and older species, resulting in age-truncated or juvenescent populations in an ecosystem (McOwen et al. 2015), which would make the ecosystem more sensitive to climate change. Particularly in the PRE, fishing had a large effect on the proportion of species and the ecosystem community structure (Duan 2009). The proportions of large-sized and high-value demersal species decreased, but the proportions of small-sized and low-value pelagic fish increased (Duan et al. 2009b), which increased the risk of climate change impacts to the ecosystem.

In our study, the possible responses of species to climate impacts may be opposite in different ecosystem states because of the different level of top-down controls and competition between groups in ecological processes (Brown et al. 2010). Ecological processes can modify the physiological responses of a species to climate change by impacting the energy flow and material circulation of a food web (Cornwall and Eddy 2015). According to the changes in the biomasses of functional groups in the PRE, the ecological processes could change at different intensities based on the trophic interactions of the ecosystem, and most species under the higher vulnerability scenarios were more sensitive to climate change. These findings revealed that strong interactions between prey and predator were expected to shift the impacts of climate change to various degrees. Hence, quantifying the strength of the trophic interactions that affect the responses of species to climate change is necessary to understand the ecological processes of an ecosystem, which can improve the prediction capability of the model.

The uncertainties of the projections are associated with the limits of the data and an incomplete understanding of the physiological responses of some functional groups to the changing ocean variables and their interactions with fishing. Such uncertainties can be reduced by improving our understanding on the

organism-level physiological response of estuarine species to climate change (Ainsworth et al. 2011). Moreover, interactions with other non-fishing human stressors are not included in the model. For example, the pollutant inputs have been causing seasonal hypoxia in the PRE, accompanying with the population increasing and the economic developing in the coastal area (Zhang and Li 2010). Pollution-induced hypoxia can be intensified by climatic stressors, e.g., ocean warming can reduce the solubility and transfer of oxygen in the water column (Schmidtko et al. 2017), and the decrease of DO can also weaken the thermal tolerance of species (Portner and Knust 2007). Moreover, this study used outputs from global Earth system models that do not represent coastal and estuarine physical and chemical processes well (Stock et al. 2011). Future studies could build on this analysis by using outputs from finer-scale regional oceanographic models for the PRE region, which were not available at the time of this study. Notwithstanding these uncertainties, the EwE model helps understand the impacts of climate change at the ecosystem level and could provide useful information to support ecosystem management in the PRE ecosystem, where prior knowledge on this topic is limited. This study also provides a framework for similar assessments for other estuarine ecosystems.

Conclusions

Using the EwE model, we simulated the effects of multiple climate stressors, including ocean warming, ocean acidification, deoxygenation and changes in NPP on the structure and functions of the PRE ecosystem under different fishing scenarios. We identified three reliable trends of the ecosystem and fisheries under the impacts of climate change and fishing. (1) Regarding the effects of individual ocean variables, changes in NPP and ocean warming had important implications for biomass and catches in the PRE. (2) Climate change was predicted to be a potential threat to the fisheries and ecosystem in the PRE, especially under RCP8.5, and reducing fishing efforts could moderate the impacts in climate change on the total catches and some fished species of the ecosystem. (3) The individual species' responses to climate change and fishing were not uniform and exhibited non-linearity in different stressors, and those

processes were affected by the trophic interactions. By the use of trophodynamic modelling, we generated a hypothesis on the potential ecological changes in order to develop an empirical study for examining the responses of the PRE ecosystem to climate change and fishing and promote the development of fishery resource management and policies.

The impacts of climate change on the ecosystems, human societies and economies that rely on fishery resources are interactional processes. Understanding the relationships of these objectives under the impacts of climate change is important for designing policies to manage or restore ecosystems. In particular, the estuary ecosystem is vulnerable to human stresses; for instance, mariculture provides dual functions for the ecosystem. Hence, we expect to discuss the trade-off relationships among ecological, economic and social objectives under climate change and the risk of climate change to the safety of food exposed to heavy metal pollution in the water in the PRE in our next two articles. These two studies will be based on the results of the ecosystem in this work.

Supplemental material

We provide the details of the basic parameters of the 2000s Ecopath model used in this work, the forcing functions of the functional groups for ocean variables of climate change, and the computations of the ecosystem indices and other results of the model simulation in the following supplemental material.

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