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Anthropogenic footprints are invading global habitats of Indo-Pacific humpback dolphins

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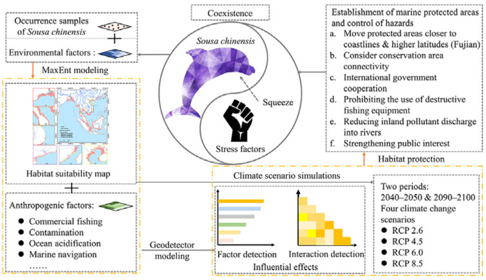
HIGHLIGHTS

- Superior-suitability IPHD habitats are mainly in southern China.
- Human activities have seriously impacted current habitats.
- Some habitats in China will be lost under the analyzed climate change scenarios.
- MPAs need to be established closer to coastlines and connected.

GRAPHICAL ABSTRACT



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ABSTRACT

As ecologically fragile areas, coastal zones are affected by both anthropogenic activities and climate change. However, the impacts of these factors on large nearshore mammals, such as Indo-Pacific humpback dolphins (IPHDs, *Sousa chinensis*), are poorly understood. Here, modeling revealed that the suitable habitats of IPHDs are affected mainly by the sea surface temperature (SST), and the habitat suitability decreases as the distance to the nearest coastline increases. In addition, anthropogenic activities involving demersal fishing, contamination and shipping have narrowed IPHD habitats and reduced the habitat suitability. We found that climate change will further narrow suitable habitats located farther than 7 km from coastlines and trigger habitat losses in the eastern Taiwan Strait by 2090–2100 under the Representative Concentration Pathway (RCP) 8.5 scenario. The projected decreases in habitat suitability and area emphasize the urgency of establishing connected marine protected areas (MPAs) while considering climate change, intergovernmental cooperation, and public involvement.

1. Introduction

As the borders between oceans and continents, coastal zones pool nutrients from both land and sea, thus providing food and habitats for coastal marine life and allowing rich biodiversity to form (Costanza et al., 1997). With the increasing demands for marine spaces and resources, development in coastal areas is intensifying (Halpern et al., 2015; Nyström et al., 2019). Coastal zones contain most cities, with over 2.6 billion people; these areas experience accelerated urbanization and land use transitions, severe pollution and ecosystem destruction (Sale et al., 2014; Wang et al., 2017; Ross et al., 2010). Moreover, densely populated coastal areas and the frequent exchanges of materials and energy that occur therein make these areas particularly sensitive and vulnerable to the effects of climate change (Lu et al., 2018). Climate change alters ocean environments and marine habitats and threatens associated species, particularly those that are not highly resilient to climate change (Behrenfeld et al., 2006; Cheung et al., 2011; Sumaila et al., 2011; Hazen et al., 2013; Rogers et al., 2019). Coastal pollution combined with climate change may cause habitat degradation and fragmentation, thus exacerbating the vulnerability of coastal zones to climate change (Cheung et al., 2011; Rogers et al., 2019; Rabalais et al., 2009). Habitat losses also increase the survival pressure on species and chal-

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lenge biodiversity in coastal zones (Cheung et al., 2011; Henson et al., 2021; Wang et al., 2017). Anthropogenic activities, climate change and habitat losses therefore all present coastal zones with existential challenges.

The Indo-Pacific humpback dolphin (IPHD), inhabiting shallow waters below 20 meters along open coasts and bays in the Pacific and tropical coastal zones (Ross et al., 2010; Jefferson et al., 2017), is considered to be in danger because of the severe influences of climate change and human activities (Ross et al., 2010; Jutapruet et al., 2015; Fu et al., 2021). In general, coastal marine mammals such as IPHDs have simple habitat requirements and are relatively sensitive to habitat alterations (Rogers et al., 2019; Huang et al., 2012). According to the International Union for the Conservation of Nature (IUCN) Assessment Report, IPHDs in the Taiwan Strait are Critically Endangered; in other regions, this species is Vulnerable, with declining numbers of mature individuals (Ross et al., 2010; Jefferson et al., 2017). Habitat deterioration caused by anthropogenic activities could drive a continuous decline in IPHD populations, and climate change could further exacerbate this trend and thereby seriously threaten the survival of these dolphins, requiring their conservation status to be raised to the “Endangered” level for their protection (Huang et al., 2012).

Previous studies have focused mainly on local areas, such as the Pearl River Estuary (Jefferson, 2000; Wu et al., 2013), Beibu Gulf (Wu et al., 2017a), Fujian (Chen et al., 2020), Taiwan (Ross et al., 2010; Slooten et al., 2013), Hainan Island (Caruso et al., 2020), Malaysia (Kuit et al., 2019), India (Jog et al., 2018), and Thailand (Jutapruet et al., 2015); however, analyses performed at the global perspective are lacking. Moreover, in past studies, the distributions of IPHD populations (Huang et al., 2012; Jutapruet et al., 2015; Jefferson, 2000; Slooten et al., 2013), their habitat conditions (Chen et al., 2020; Kuit et al., 2019; Jog et al., 2018) and the impacts of different factors on this species (Ross et al., 2010; Wu et al., 2013; Caruso et al., 2020; Sun et al., 2017; Fu et al., 2021) were analyzed, thus providing scientific evidence for IPHD population-recovery and habitat-conservation measures (Jefferson et al., 2017; Wang et al., 2017; Chen et al., 2020; Fu et al., 2021). However, studies quantitatively describing the combined effects of multiple human activities on IPHD habitats are limited. Clarifying the effects of multiple human activities and climate change on the habitats of IPHDs can offer important insights for marine and coastal conservation planning and management, such as the establishment of marine protected areas (MPAs).

To illustrate the impacts of human activities and climate change on IPHD habitat suitability, we built a suitability evaluation model based on MaxEnt and GeoDetector using environmental indicators and marine human activity intensity indicators. Thus, we aimed to (1) analyze the current suitability of IPHD habitats, (2) quantify the anthropogenic pressures on current habitats, (3) assess the effects of climate change on the IPHD habitat distribution under four scenarios over the 2040–2050 and 2090–2100 periods, and (4) provide a reference for the conservation of IPHDs and other large coastal mammals.

2. Materials and methods

2.1. Data sources

We selected ocean surface data from the Bio-ORACLE database (https://www.bio-oracle.org/) as environmental indicators (Assis et al., 2018). Global administrative boundary and water data in vector format were obtained from the Resource and Environmental Science and Data Centre of the Chinese Academy of Sciences. We selected product data, including 16 indicators of anthropogenic activities, from a dataset of cumulative human impacts on the world’s oceans constructed by Halpern et al. (2015). Finally, we obtained vector data representing the areas protected for IPHDs from the World Database of Protected Areas (https://www.protectedplanet.net/) and from the officially published documents of Guangdong, Guangxi, Fujian and Hong Kong of China.

2.2. Determination of the habitat scope of IPHDs

In early research, IPHDs were considered small coastal cetaceans with a geographical range spanning along the coastline of South Africa to the western Pacific Ocean (Jefferson, 2000; Jefferson and Rosenbaum, 2014). However, Jefferson et al. (2014) concluded that the dolphin species in western to northern Australia and in the western Indian Ocean were not IPHDs based on a novel taxonomic approach, and this finding was recognized by the Taxonomy Committee of the Society for Marine Mammalogy (Jefferson, 2000; Jefferson and Rosenbaum, 2014). Although this novel taxonomic approach could not identify the dolphins in the Bay of Bengal and eastern Indian waters as IPHDs, the Taxonomy Committee still prefers to consider these regions as IPHD habitats. Thus, we defined the eastern Indian Ocean and Southeast Asian and Chinese waters as the scope of IPHDs (see detail in Fig. A1). Vector data of the IPHD distribution were provided by the IUCN, but these data were too sparse in estuaries to effectively cover the gridded environmental indicators. Thus, we created a 500-m buffer to minimize the errors caused by the differences between these two datasets.

2.3. IPHD occurrence point cleaning

Based on the abovementioned geographical scope of IPHDs, we collected literature from the Web of Science and China National Knowledge Infrastructure (CNKI) databases and obtained IPHD occurrence points with accurate corresponding longitude and latitude information by manually filtering data found in the literature. Moreover, we deleted duplicate occurrences recorded among different studies (please see the Supplementary References for more information). Additionally, we collected occurrence points from the Ocean Biodiversity Information System (OBIS) (OBIS, 2021) and Global Biodiversity Information Facility (GBIF) (GBIF.org, 2021). We employed ArcGIS software to build a database of IPHD occurrence points and projected the data to the World Geodetic System 1984 (WGS84) datum ellipsoid (see detail in Fig. A1). To thin the highly aggregated occurrence points, we generated a 1 km × 1 km grid within the study area and counted the number of occurrence points in each pixel. Then, we assigned a value of one to pixels with numbers greater than or equal to 1 and converted those pixels to point data.

2.4. Climate change scenarios

Representative concentration pathways (RCPs) were proposed by the World Climate Research Programme’s Working Group on Coupled Modelling (WGCM) to reveal the potential climate change conditions under different greenhouse gas emission, aerosol concentration and land use change scenarios (IPCC, 2014). Here, the complex potential future human emissions situations have been reduced to only four representative concentration pathways, namely, the optimal scenario (RCP2.6) in which the global temperature rise is controlled to within 2°C by 2100, an intermediate scenario (RCP4.5) in which a global temperature rise of 2–3 °C is maintained, a poor scenario (RCP6.0) with an emission peak in approximately 2080, and a worst-case scenario (RCP8.5) with a continuous rise in emissions (IPCC, 2014). The Paris Agreement aims to control global warming to 1.5°C by 2100. However, the first section of the latest IPCC Sixth Assessment Report (AR6) states that unless large-scale greenhouse gas reductions are implemented, it will be impossible to maintain the warming level at 1.5°C or even at 2°C. Therefore, the middle and late 21st century are extremely important timeframes for assessing climate change, and we correspondingly selected two periods, 2040–2050 and 2090–2100, to evaluate the impacts of different climate change scenarios on the habitat suitability of IPHDs. Therefore, in this study, we employed future global climate data (predicted under the RCP2.6, RCP4.5, RCP6, and RCP8.5 scenarios) based on three atmosphere-ocean global circulation models (AOGCMs) (the Hadley Centre Global Environment

Model version 2-Earth System (HadGEM2-ES), Community Climate System Model version 4 (CCSM4) and Model for Interdisciplinary Research on Climate version 5 (MIROC5)) from the Coupled Model Intercomparison Project (CMIP) version 5 simulations for the 2040–2050 and 2090–2100 periods (Assis et al., 2018).

2.5. Habitat prediction and evaluation

Species distribution models (SDMs) are effective tools for predicting the potential distributions of species; these models combine species distribution data with remote sensing data to project the ecological positions of species via statistical algorithms (Hernandez et al., 2006). Compared to other models designed for predicting species distributions, MaxEnt can produce better predictions by using only species 'occurrence' data when the species distribution data are incomplete (Hernandez et al., 2006). As a common model for predicting species distributions, MaxEnt can obtain highly accurate predictions even with small sample sizes, assess the suitability of existing habitats, and predict future habitat changes (Chen et al., 2020). In addition, in association with relevant climatic and environmental indicators, MaxEnt can predict species distributions under future climate change scenarios.

Previous studies have shown that the factors affecting the habitat distribution of IPHDs include the distance to the nearest coastline, sea surface temperature (SST), and chlorophyll concentration (Caruso et al., 2020). Because IPHDs inhabit nearshore areas, the distance to the nearest coastline is a good indicator of their various habits, including their feeding habits and habitat use (Wu et al., 2017a). The chlorophyll concentration can influence the distribution of nutrients, which in turn impacts the feeding conditions and habitat distribution of IPHDs (Lin et al., 2020). Most importantly, the SST determines the habitat distribution of IPHDs and can directly reflect the impacts of climate change on this species (Wu et al., 2017a). In contrast, the seawater salinity and pH can indicate the habitat selection and living habits of IPHDs. Thus, we selected the SST, chlorophyll concentration, seawater salinity, distance to the nearest coastline, and pH as potential environmental indicators of the IPHD habitat distribution. However, due to data availability, we used only SST and seawater salinity data to predict future habitat changes while keeping the other environmental indicators constant. Artificially generating finer-resolution data without performing reinterpolation can maintain the characteristics of the original data and maintain consistent resolutions of all gridded indicators (Martin et al., 2014). To maintain consistency in the spatial resolutions of the raster data, we converted all raster data to WGS84 geographic coordinates and maintained a data resolution of 0.009° (approximately 1 km).

Previous studies have shown that highly correlated variables can affect the results of SDMs (Kramer-Schadt et al., 2013). Therefore, we performed a correlation analysis on the five selected environmental indicators. The Pearson correlation coefficients of the indicator pairs were all less than 0.65, indicating weak correlations among the selected indicators and, thus, their independence in the MaxEnt model (see detail in Table A1).

We evaluated the global habitat suitability of IPHDs and predicted their future suitable habitat distribution using the MaxEnt model in two future periods: 2040–2050 and 2090–2100. In the MaxEnt modeling process, the processed environmental indicators and occurrence points had to be converted into the American Standard Code for Information Interchange (ASCII) and comma-separated value (CSV) formats, respectively. MaxEnt modeling was performed by adjusting the relevant parameters, repeating the run 15 times, selecting cross-validation as the run method, and iterating each run for a maximum of 5,000 times. The jackknife test was selected to determine the weight of each environmental indicator, and the output format was logistic. Receiver operating characteristic (ROC) curves were used to assess the reliability of the simulated results; these curves were plotted according to a series of different dichotomous classifications, with the false positive rate and true positive rate set as the horizontal and vertical coordinates, respectively. The area under the curve (AUC), ranging from 0 to 1, can directly measure the accuracy of the model predictions. The AUC value indicates whether the model has an average prediction accuracy (values between 0.7 and 0.8), a good prediction accuracy (between 0.8 and 0.9), or an excellent prediction accuracy (greater than 0.9) (Chen et al., 2020). The result obtained after 15 iterative runs indicated that the mean AUC value was 0.922, indicating high levels of accuracy and confidence in the predicted results (see detail in Fig. A2).

To evaluate the influence of different indicators, we employed three estimation methods in the MaxEnt model, namely, the contribution percentage, permutation importance, and jackknife test. The output raster data, with values ranging from 0 to 1, were used to characterize the habitat suitability alongside the maximum training sensitivity plus specificity method; the mean value was 0.1317 after 15 iterative runs. Then, we reclassified the suitable areas into three categories using the natural breaks method and obtained four suitability classes: unsuitable, marginal-suitability, medium-suitability, and superior-suitability.

2.6. Assessing the impacts of anthropogenic activities on IPHD habitats

We employed the GeoDetector to investigate the impacts of anthropogenic activities on the suitability of different habitats. The GeoDetector combines a set of statistical methods to detect spatial differentiation and reveal the internal driving forces behind that differentiation (Wang and Xu, 2017). Two methods within the GeoDetector, namely, the factor detection and interaction detection methods, were selected herein to illustrate the impacts of anthropogenic activities on IPHD habitats. The factor detection method can reveal how well factor X explains the spatial divergence of attribute Y. This ability is measured using the term q, which can be obtained with the following formula:

$$q = 1 - \frac{1}{N\sigma^2} \sum_{k=1}^{S} N_k \sigma_k^2$$

where S represents the stratification of various factors; N_k and N are the numbers of cells in stratum k and in the whole region, respectively; and σ_k^2 and σ^2 are the variances of the dependent variable in stratum k and the whole region, respectively. The value of q ranges from 0 to 1. A higher q value indicates a stronger explanatory power of factor X with regards to attribute Y. The interaction detector method can recognize the interaction between two factors and identifies five types of interactions (see detail in Table A2).

Supplementary Table A3 lists 16 anthropogenic stressors, including commercial fishing, marine pollution, and shipping (Halpern et al., 2015), that were corrected for our analyses of stress and vulnerability. To better explore the effects of these anthropogenic stressors on the suitability of different habitats, we extracted different habitats with corresponding anthropogenic data separately and then revealed the quantitative relationships between suitability and anthropogenic activities by using the R package GeoDetector. Then, we removed anthropogenic stressors that failed the 99% confidence interval test.

3. Results

3.1. Influence of environmental indicators on habitat suitability

The percent contribution of the SST was highest among the environmental indicators (81.3%), followed by those of the distance to the nearest coastline (13%) and chlorophyll concentration (3.8%); the percent contributions of the pH value and seawater salinity were lowest (Fig. 1). The permutation importance levels of the SST and distance to the nearest coastline were 50.6% and 26.4%, respectively, similar to their percent contributions. Compared to the corresponding percent contributions, the permutation importance levels of the chlorophyll concentration and pH increased to 12.6% and 7.7%, respectively, while that of seawater salinity was lowest among the environmental indicators.

(a)

Variable	Percent contribution	Permutation importance
Sea surface temperature	81.3%	50.6%
The distance to the nearest coastline	13%	26.4%
Chlorophyll	3.8%	12.6%
pH	1%	7.7%
Ocean salinity	0.9%	2.6%

(b)

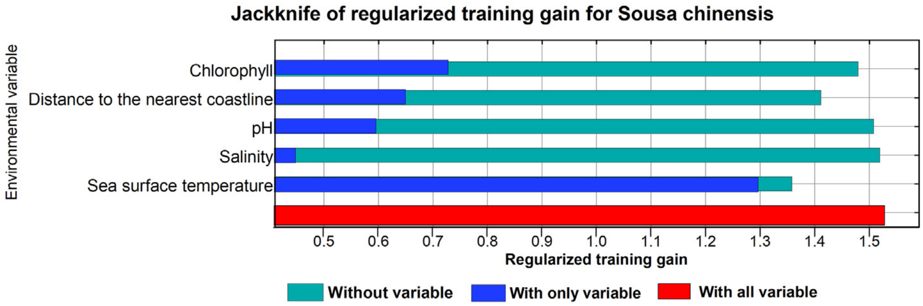

Fig. 1. Evaluation of the impacts of environmental factors on habitat suitability. (a) shows the effects of each environmental factor obtained based on both the percent contribution and permutation importance evaluation methods. (b) shows the jackknife method results.

The jackknife test showed that the SST was the most critical factor affecting habitat suitability, with training gains over 1.2. The chlorophyll concentration was also important, with a separate training score over 0.7, followed by the distance to the nearest coastline, pH and seawater salinity. The abovementioned results led to the conclusion that the SST, chlorophyll concentration, and distance to the nearest coastline were the most important factors affecting habitat suitability, while the pH value and seawater salinity had limited effects.

IPHDs prefer to inhabit areas at the intersection of seawater and freshwater, with suitable pH values ranging from 8.16 to 8.19 (Fig. 2). The suitable chlorophyll concentrations range from 0.13 to 0.84 mg/m^3. The habitat suitability increased when the chlorophyll concentrations increased from 0 to 0.38 mg/m^3. With an increase in the chlorophyll concentration beyond 1.2 mg/m^3, the habitat suitability remained constant. The habitat suitability changed sharply with increasing seawater salinity, and the optimal salinity was less than 30.6‰. The SST results showed fluctuating trends with both rising and falling characteristics, and the suitable range was between 21.9°C and 24.7°C. The results characterizing the distance to the nearest coastline indicated that IPHDs were active in coastal regions, with habitat suitability increasing within 2 km of coastlines. Habitats less than 4 km from the nearest coastline were the most suitable.

3.2. Areal and spatial distributions of IPHD habitat suitability

We found that the unsuitable areas for IPHDs were larger in the Indonesian Sea, Sulu-Sulawesi Sea, and Gulf of Thailand and along the Malaysian coast than in other areas under current climate conditions. Marginal-suitability areas were mainly located near Myanmar and along parts of the Vietnam coast, while medium-suitability areas were concentrated around the eastern coast of Vietnam and the western coast of Hainan. Superior-suitability areas were basically located in the coastal areas of China, including near Guangxi, Guangdong, Fujian, Hainan and Taiwan (Fig. 3).

Among the existing habitats of IPHDs, the total suitable habitat area is 10.003×10^4 km^2, with areas of 4.569×10^4 km^2, 2.364×10^4 km^2 and 3.07×10^4 km^2 representing marginal-, medium- and superior- suitability areas, respectively, with these categories accounting for 45.7%, 23.6% and 30.7% of the total suitable area (Table 1). The South China Sea covers the largest suitable area, spanning 8.749×10^4 km^2 and accounting for 87.5% of the total suitable area. The second largest suitable area is in the East China Sea, with a suitable area of 0.484×10^4 km^2, accounting for 4.8% of the total suitable area. Other regions accounted for less than 10% of the total suitable area, including 3.9% in the Gulf of Thailand and 1.8%, 1.9% and 0.10% in the Sulu-Sulawesi Sea, Bay of Bengal and Indonesian Sea, respectively. Only the South China Sea and East China Sea contained both medium-suitability and superior-suitability areas. Moreover, the areas of medium-suitability and superior-suitability in the South China Sea were both largest among the study areas, at 2.265×10^4 km^2 and 3.050×10^4 km^2, respectively. Therefore, the simulated results show that the South China Sea and the East China Sea are the most suitable regions for the survival and reproduction of IPHDs.

3.3. Relationships between human activities and habitat suitability

By using the GeoDetector method, we derived the effects of human activities on IPHD habitats with three suitability levels (Fig. 4). The q values obtained for some of the stress factors did not pass the 99% confidence interval test; thus, these stress factors were removed. The factor detection results showed that the type of commercial fishing, such as demersal nondestructive high-bycatch fishing (DHBF), demersal nondestructive low-bycatch fishing (DLBF), demersal destructive fishing (DDF) and pelagic low-bycatch fishing (PLBF), was the main factor affecting the marginal-suitability areas, with q-values of 0.114, 0.046, 0.07786 and 0.04407, respectively. In addition to commercial fishing, navigation pollution and commercial shipping activities also had strong impacts on the marginal-suitability areas for IPHDs. The interaction analysis results indicated that the interaction between DHBF and fertilizer pollution had the greatest impact on the marginal-suitability areas, exhibiting a nonlinear enhancement effect (q=0.192). In addition, the interactions of DHBF and DDF with other stress factors were also significant, with q-values basically greater than 0.1. These results demonstrate that commercial fishing is the main factor placing pressure on marginal-suitability areas.

DHBF was the dominant stressor affecting medium-suitability IPHD habitat areas, with a q-value of 0.042, followed by DLBF and DDF, with q-values of 0.036 and 0.029, respectively. Ocean acidification and navigation pollution had comparable effects, with q-values of approximately 0.029. In addition, sea level rise (q=0.014) due to climate change also had a significant impact on the medium-suitability areas. The interactions of DHBF with sea level rise and navigation pollution had the largest effects on the medium-suitability areas, with q-values of 0.109 and 0.106, respectively. Both of these interactions showed nonlinear in-

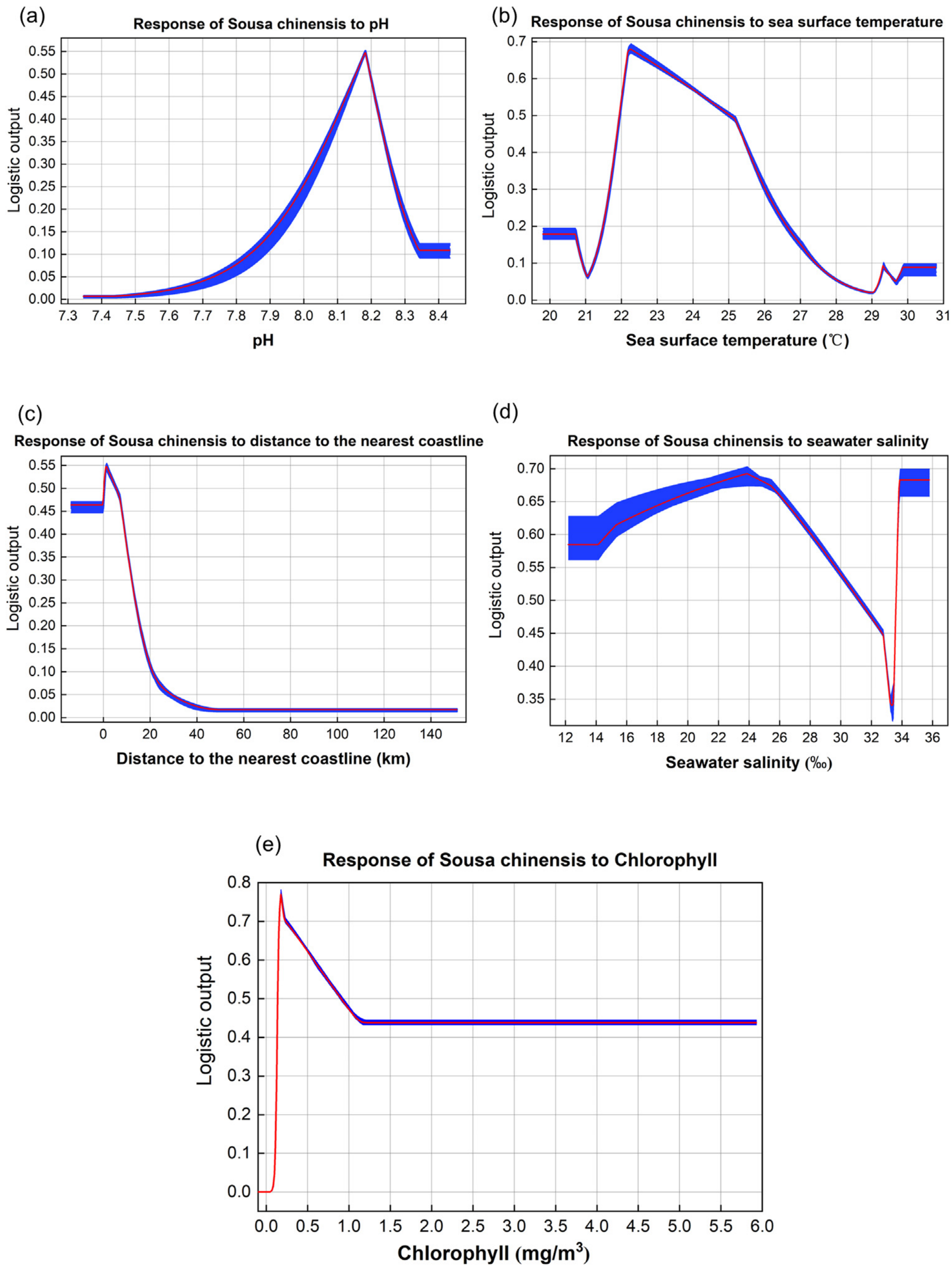

Fig. 2. Response curves representing different environmental indicators: the (a) pH, (b) chlorophyll concentration, (c) seawater salinity, (d) distance to the nearest coastline, and (e) sea surface temperature. All response curves are averages of the results of 15 individual runs; the *x*-axis and *y*-axis represent the environmental indicator and the corresponding logistic output results, respectively.

Table 1

Areas and proportions of areas with different suitability in different ocean ecosystems. “Area” represents the habitat area with a certain level of suitability; “proportion” represents the ratio of the habitat area with a certain level of suitability to the total area of habitats in the corresponding region.

	Unsuitable		Marginal-suitability		Medium-suitability		Superior-suitability	
Ocean ecosystem	Area (× 10^4 km^2)	Proportion	Area (× 10^4 km^2)	Proportion	Area (× 10^4 km^2)	Proportion	Area (× 10^4 km^2)	Proportion
East China Sea	0.988	0.671	0.365	0.248	0.099	0.067	0.020	0.014
Bay of Bengal	27.896	0.993	0.189	0.007	0	0	0	0
South China Sea	28.772	0.767	3.434	0.092	2.265	0.060	3.050	0.081
Sulu-Celebes Sea	3.208	0.947	0.180	0.053	0	0	0	0
Gulf of Thailand	14.451	0.974	0.388	0.026	0	0	0	0
Indonesian Sea	22.125	0.999	0.013	0.001	0	0	0	0

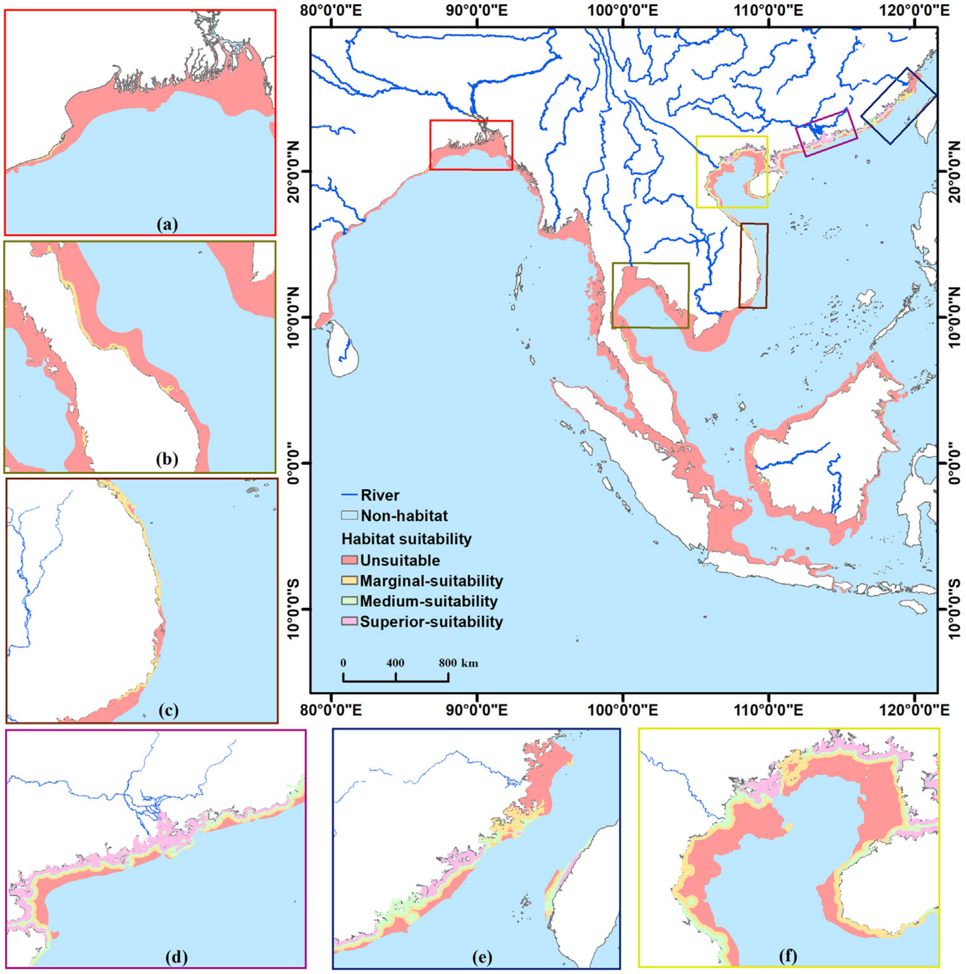

Fig. 3. Spatially explicit habitat suitability results obtained under current climate conditions: the (a) Bay of Bengal; (b) Gulf of Thailand; (c) eastern waters of Vietnam; (d) Guangdong coastal waters, China; (e) Taiwan Strait, China; and (f) Beibu Gulf, China.

creases. Ocean acidification also exhibited significant interactions with both DHBF and DLBF, showing nonlinear increases with q-values of 0.095 and 0.102, respectively. In contrast to the results obtained for marginal-suitability areas, commercial fishing was not the only major influencing factor affecting the medium-suitability areas. The effects of ocean acidification and navigation pollution on these habitats were found to be increasing.

DDF had the greatest effect on the habitats of IPHDs (q=0.085) in the superior-suitability areas, followed by inorganic pollution, DHBF and navigation pollution, with q-values of 0.076, 0.069 and 0.061, respectively. Fertilizer pollution and organic pollution also influenced these habitats, with q-values greater than 0.037. The interactions of inorganic pollution, fertilizer pollution and organic pollution with the commercial fishing factors of DDF, DHBF and DLBF were most significant in these habitats, exhibiting obvious nonlinear enhancement, and the interactions between sea level rise and the commercial fishing factors of DDF and DLBF were very significant. Such evidence shows that the factors influencing superior-suitability habitat areas are highly complex. Not only commercial fishing factors such as DDF, DHBF, and DLBF but also ocean pollution factors such as fertilizer, organic, inorganic and navigation pollution seriously impact these habitats.

4. Discussion

4.1. Impacts of anthropogenic activities on the habitats of IPHDs

The suitable habitats identified under the current climate conditions were located mainly in densely populated estuarine areas that experience frequent human activities, such as the Pearl River Estuary, Beibu Gulf and Xiamen. Therefore, anthropogenic activities have degraded the habitat suitability and thus threatened the survival of IPHDs (Ross et al., 2010; Jefferson et al., 2017). The relationships between human activities and habitat suitability suggest that commercial fishing types such as DDF, DHBF, and DLBF are the dominant factors affecting suitable habitat areas of IPHDs. Commercial fishing involves the use of gillnets and trawls to catch small fishes; these tools not only bycatch IPHDs but also cause harm and even death to these dolphins (Slooten et al., 2013; Lin et al., 2020). Many cases of IPHD deaths due to entanglement in fishing nets have been reported in Hong Kong, Taiwan, Malaysia and other regions (Ross et al., 2010; Slooten et al., 2013; Jefferson et al., 2017). If continued, such bycatch could lead to a decline in the population of IPHDs or even to more serious consequences. Thus, bycatch is considered the most serious human behavior affecting IPHDs (Ross et al., 2010; Read et al., 2006). The interactions between factors such as DDF, DHBF and DLBF were significant, indicating that the impacts of fishing on the habitats of IPHDs have increased in severity. Indeed, the distribution of phytoplankton has resulted in a high abundance of fish located relatively close to coastlines, thus increasing coastal fishing activities and posing a serious threat to the survival of IPHDs (Behrenfeld et al., 2006; Henson et al., 2021). IPHDs can then capture less food due to high human catches and subsequently venture into dangerous areas in search of food, thus increasing the negative impacts of these factors on their survival (Slooten et al., 2013; Lin et al., 2020). Demersal fishing not only leads to the capture of many noneconomic fish but also changes the demersal habitat and thus influences the balance of the entire demersal ecosystem (Thomas et al., 2017).

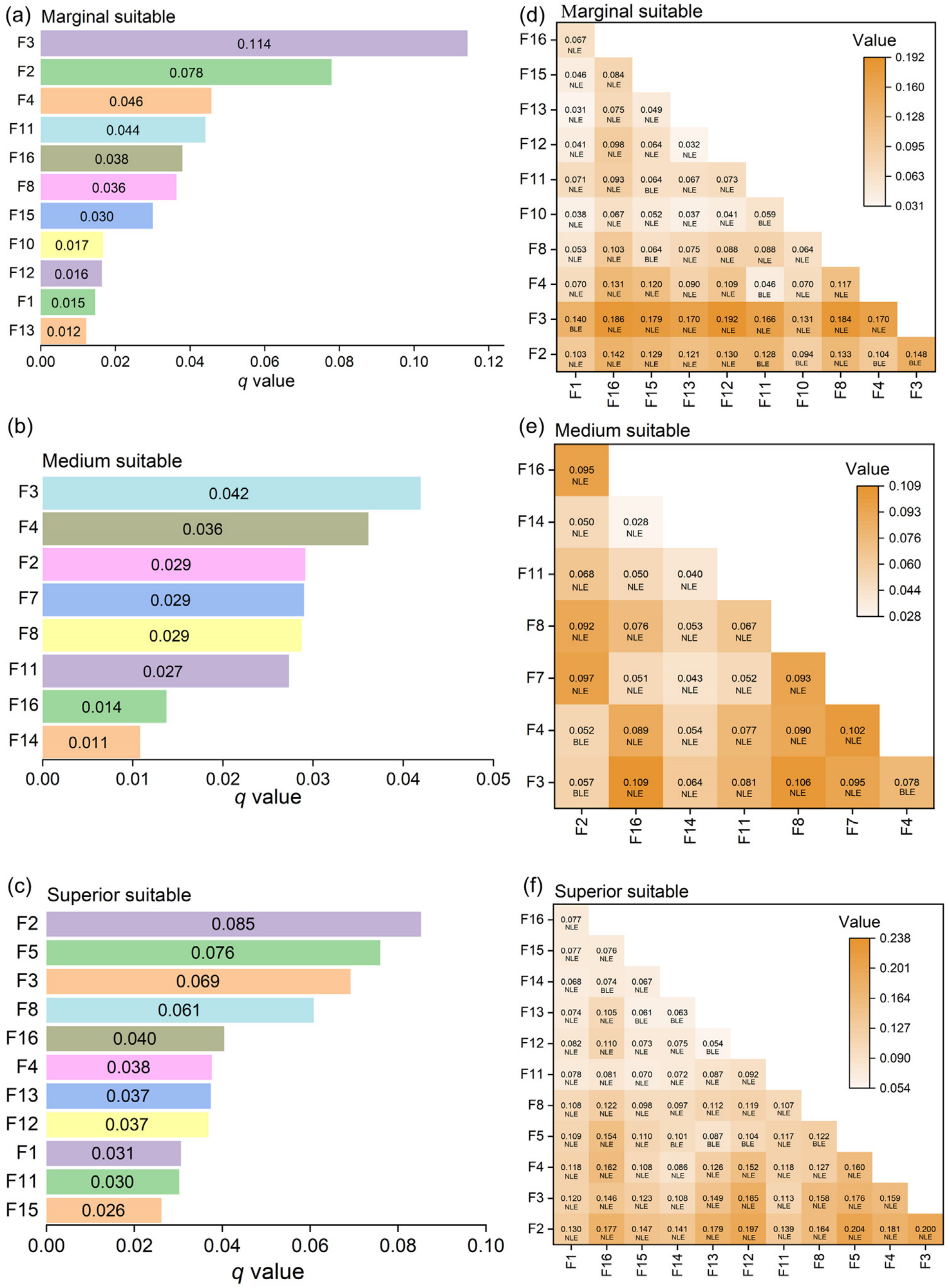

Fig. 4. Influence degrees of anthropogenic stressors on habitat suitability: (a), (b), and (c) show the factor detection results obtained for the marginal-, medium- and superior-suitability areas, respectively, and the results are shown in descending order of *q* values. (d), (e), and (f) show the interaction detection results obtained for the marginal-, medium- and high-suitability areas, respectively; NLE represents a nonlinear enhancement, and BLE represents a bilinear enhancement. A detailed explanation of these results can be found in Supplementary Table A1. The relevant stress factors corresponding to F1–F16 can be found in Supplementary Table A3.

Inorganic and navigation pollution exert strong effects in superior-suitability areas. Such effects put IPHDs under serious threat due to superior-suitability areas being generally located in estuary regions. Previous research has shown that chromium levels in IPHDs inhabiting superior-suitability areas were 9.7 times higher than those in the general population, leading to apoptosis and threatening IPHD survival (Sun et al., 2017). Moreover, their interactions with DDF, DHBF, and DLBF were highly significant. This result further illustrated that demersal fishing is the dominant factor affecting habitat suitability, while pollution could also exacerbate habitat degradation and reduce habitat suitability. We found that the impact of organic pollution on IPHD habitats was similarly critical in superior-suitability areas. Some studies have also demonstrated that high concentrations of persistent organic pollutants (POPs) accumulate in estuaries and can be detected in IPHDs, affecting their development and reproduction (Ross et al., 2010; Wu et al., 2013; Jia et al., 2015). These results are also in line with the findings of our study regarding the impacts of pollution on IPHD habitats with three suitability levels at the global scale. Navigation pollution and commercial shipping activities affected IPHD habitats at all three suitability levels. In fact, shipping generated ocean pollution and noise that affected IPHDs. Additionally, high-speed vessels can strike and kill IPHDs while altering their distributions and movement patterns, and the noise associated with these activities disturbs the normal social interactions of IPHDs by accelerating hearing degradation (Jefferson, 2017; Caruso et al., 2020).

Apart from bycatch, the most severe challenges faced by IPHDs are habitat degradation and loss (Jefferson and Karczmarski, 2001; Huang et al., 2018; Wu et al., 2017b). The simulated medium- and superior- suitability areas for IPHDs are mainly close to coastlines. However, these regions are experiencing significant land use changes, with extensive harbor construction and land reclamation activities resulting in massive core habitat losses (Huang et al., 2018; Wu et al., 2017b). Moreover, actions associated with harbor construction and land reclamation can degrade submerged structures and subsequently al-

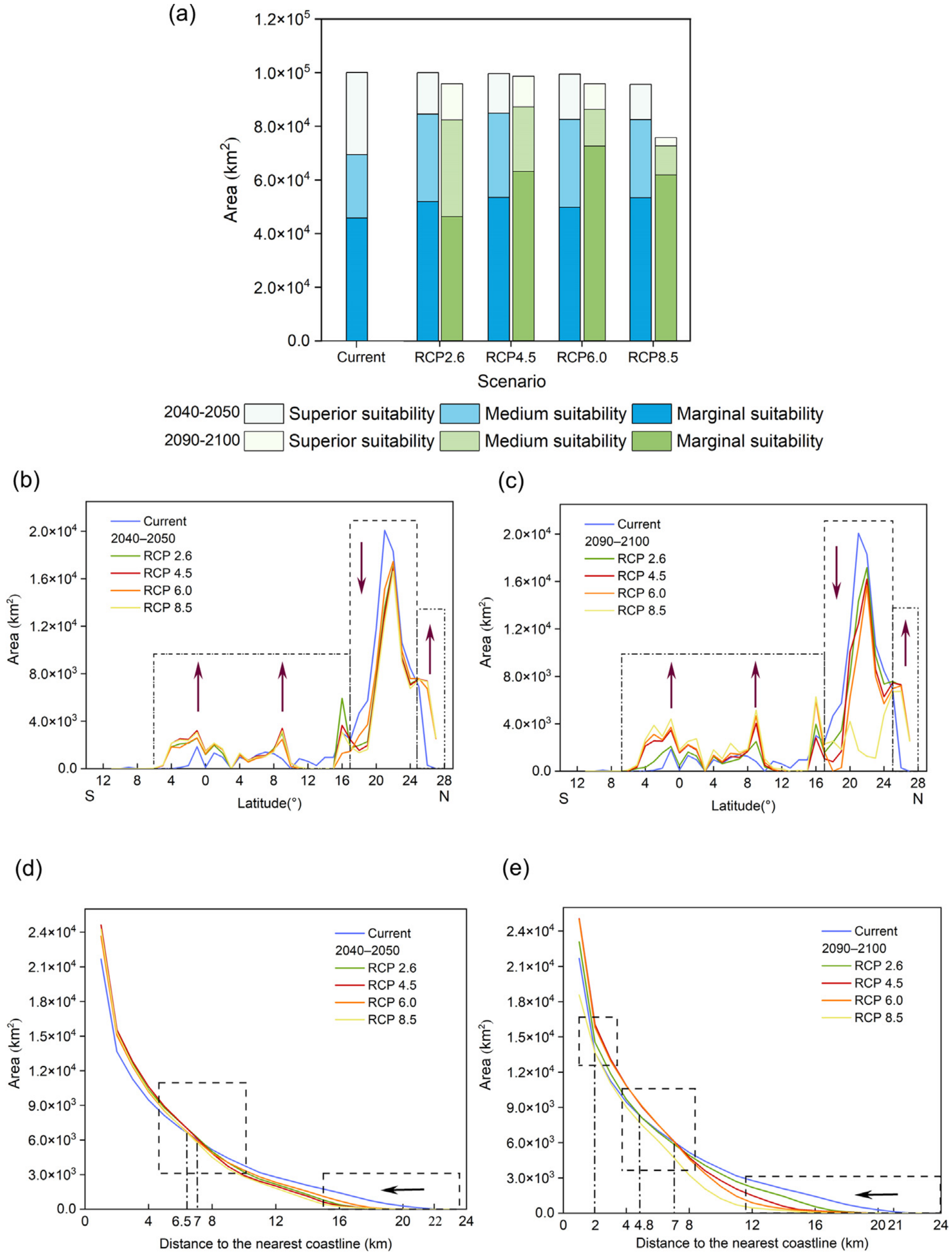

Fig. 5. Variations in the habitat areas of IPHDs under different climate change scenarios: (a) habitat areas with different suitability in different periods and under different climate change scenarios; (b) latitudinal distribution of habitats under different climate change scenarios in the 2040–2050 period; (c) latitudinal distribution of habitats under different climate change scenarios in the 2090–2100 period; (d) distribution of the habitat distances to the nearest coastline under different climate change scenarios in the 2040–2050 period; and (e) distribution of the habitat distances to the nearest coastline under different climate change scenarios in the 2090–2100 period.

ter local sedimentation processes and the chlorophyll distribution, ultimately leading to the degradation of core habitats (Huang et al., 2018; Karczmarski et al., 2017; Wang et al., 2017). The degradation of submerged features and variations in chlorophyll distribution could reduce prey species diversity, thereby increasing foraging pressures on IPHDs (Karczmarski et al., 2017). The massive noise and disturbance generated during piling operations can also alter the movements and distribution patterns of IPHDs (Caruso et al., 2020).

4.2. Impacts of climate change on the habitats of IPHDs

The results described above demonstrate that anthropogenic activities severely reduced the habitat suitability, shrink the habitat area and considerably impact IPHDs. To make matters worse, climate change could aggravate this situation and further threaten the habitat range of this species. Under identical climate change scenarios, the suitable habitat areas decreased from the 2040–2050 period to the 2090–2100 period, with the area of superior-suitability habitats decreasing but the areas of medium- and marginal-suitability habitats increasing (Fig. 5(a)). In the same period, the suitable habitat area showed a continued decrease as the SST increased, with the maximum suitable area obtained under RCP2.6 scenario and the smallest suitable area obtained under RCP8.5 scenario. Although superior-suitability areas increased under the RCP6.0 scenario compared to the other three scenarios in the 2040–2050 period, this area was still smaller than the current area of superior-suitability habitats. The abovementioned situation is obvious in the Pearl River Estuary, Beibu Gulf and coastal areas of Vietnam. Increasingly severe conditions are predicted in the 2090–2100 period. As the SST increases, medium- and superior- suitability areas are expected to decrease sharply under the RCP4.5 and RCP6.0 scenarios, with marginal-suitability areas remaining almost exclusively under the RCP8.5 scenario. This situation will lead to continued decreases in the areas of suitable habitats in the Pearl River Estuary and Beibu Gulf as the SSTs increase, and the suitable habitat areas in the eastern Taiwan Strait are even expected to disappear under the RCP6.0 and RCP8.5 scenarios (Fig. 6). Such evidence indicates that the habi-

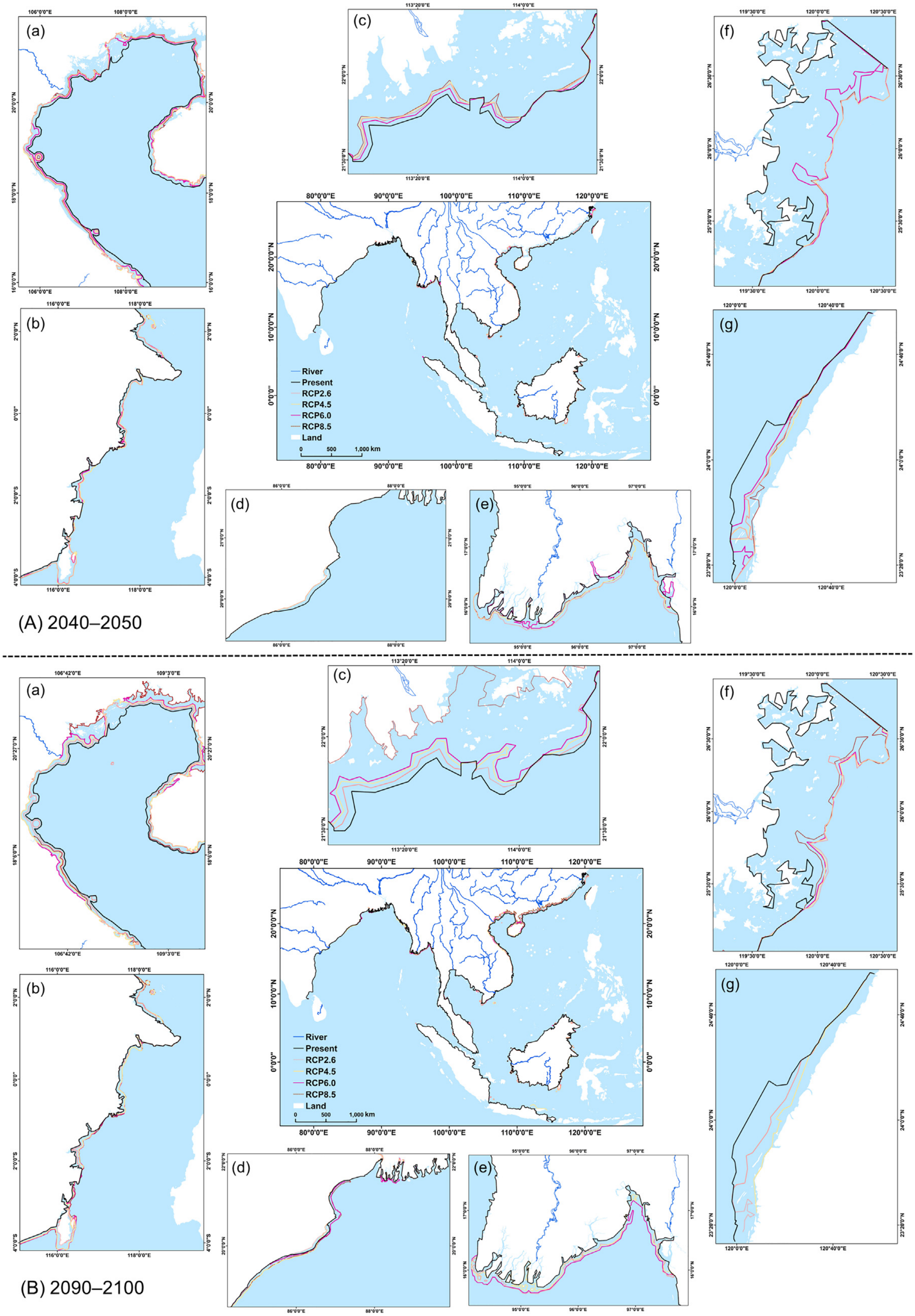

Fig. 6. Changes in suitable habitat areas under different scenarios in two future periods. (A) The 2040–2050 period; the following areas are represented from (a) to (g): (a) the Beibu Gulf; (b) waters of southeastern Kalimantan; (c) Pearl River Estuary; (d) Bay of Bengal; (e) Gulf of Martaban; (f) waters of Fuzhou and Ningde, China; and (g) waters of western Taiwan. (B) The 2090–2100 period; (a)–(g) represent the same areas as those indicated for the 2040–2050 period.

tats of IPHDs will be severely constrained by climate change. Similar findings regarding the effects of climate change on other marine species have also been reported. For instance, climate change reduced the habitats of fishes in New England in the United States (Rogers et al., 2019). Similarly, top predators in the Atlantic Ocean experienced habitat losses and significant changes in their core habitats due to climate change (Henson et al., 2021). In addition, increasing SSTs and temperature sensitivity have forced Arctic narwhals to abandon their traditional habitats (Chambault et al., 2020). In the Southern Ocean, the average seafloor life habitat loss of 12% was also attributed to climate change (Griffiths et al., 2017).

In the 2040–2050 and 2090–2100 periods, suitable habitat areas are projected to increase around the equator and north of 24°N under the four analyzed scenarios but are expected to significantly decrease at approximately 20°N (Fig. 5(b), (c)). In the 2040–2050 period, the suitable areas mainly increased around the equator and north of 24°N under the RCP4.5 and RCP8.5 scenarios and mainly increased near 16°N under the RCP2.6 scenario. In contrast, suitable areas mainly increased around the equator and near 16°N under the RCP8.5 scenario in the 2090–2100 period, while the suitable areas north of 24°N increased under the other three scenarios. The northward habitat shifts observed in response to climate change indicate that rising SSTs will severely shrink the traditional habitat area of IPHDs. Similar situations have been reported in other regions. For instance, increasing SSTs forced the habitats of top predators northward in the Pacific Ocean (Henson et al., 2021). The distribution of Mediterranean cephalopods has been predicted to shift northward and westward, with a gradual reduction in habitat suitability expected due to enhanced climate change (Schickele et al., 2021). We detected an expansion of suitable habitats around the Equator caused by combinations of higher SSTs and lower seawater salinity levels. This finding was consistent with those of studies on increasing phytoplankton abundance around the Equator despite increasing SSTs (Henson et al., 2021), and on the increasing biomass of tuna under climate change scenarios in the equatorial Pacific Ocean (Bell et al., 2021).

The suitable areas predicted under the four scenarios in the 2040–2050 period were larger than those identified under the current scenario within 6.5 km of coastlines, while the opposite trend was observed in regions more than 7 km from coastlines (Fig. 5(d)). The maximum distance to the nearest coastline among the suitable habitat was markedly reduced under the four climate change scenarios. With increasing SSTs, the habitats moved closer to coastlines, and a relatively flat area-distance variation curve was observed under the RCP6.0 scenario; this curve was most dramatic under the RCP8.5 scenario in the 2040–2050 period. Similarly, in the 2090–2100 period, the area-distance variation curves changed smoothly under the RCP2.6 scenario but sharply under the RCP8.5 scenario. The variations in suitable habitat areas with the distance to the nearest coastline were more dramatic in the 2090–2100 period than in the 2040–2050 period, thus forcing IPHDs to inhabit areas closer to coastlines (Fig. 5(e)). Such habitat compression due to climate change would further lead to the overlap of IPHD habitats with areas of high human activity. Estuary areas such as the Pearl River Estuary and those in the Taiwan Strait are the traditional superior-suitability habitats of IPHDs, and these areas are also the region most severely affected by cumulative human activities and are influenced by a combination of factors simultaneously (Halpern et al., 2015). This situation is expected to continue for the foreseeable future as existing human activities intensify and new activities such as marine aquaculture and human settlements commence (Halpern et al., 2019). These lines of evidence all suggest that the habitat variations in IPHDs caused by climate change will lead to more significant impacts of human activities on the habitats used by this species in the foreseeable future.

4.3. Establishment of MPAs and protection of IPHDs

Human activities and future climate change will drastically decrease the habitat area of IPHDs, necessitating urgent protection efforts. Aichi Target 11 stated that marine ecosystems and endangered species should be protected by establishing MPAs (IPBES, 2019). Numerous MPAs have been established in the coastal waters of Southeast China to protect IPHDs (see detail in Fig. A3). However, MPAs lack validity when the definitions of their boundaries, protection measures and effectiveness are not specified (Jefferson et al., 2017). Because MPAs represent critical measures for maintaining marine biodiversity and mitigating the impacts of climate change on species (IPBES, 2019; Lawson et al., 2014), we recommended that anthropogenic footprints and climate change should be fully considered when establishing such areas. We revealed that the MPAs in the Guangdong coastal regions are located far from coastlines, thus leaving superior-suitability habitats nearer the coastlines without appropriate protection. Moreover, the MPAs in these regions would become ineffective under climate change due to declining habitat suitability, while the suitable areas that will emerge in Fujian lack MPAs, thus leaving IPHDs without protection against climate change (Lawson et al., 2014). IPHD habitats are expected to move closer to coastlines and higher latitudes as SSTs increase. Consequently, we propose adapting the existing MPAs in Guangdong and Guangxi to bring their boundaries closer to coastlines as well as designating new MPAs in Fujian for climate change adaptation. Although studies have assessed that the eastern Taiwan Strait is inhabited by a Critically Endangered IPHD subspecies, no protective measures have been established (Ross et al., 2010; Slooten et al., 2013). The habitat suitability in this region has decreased because of climate change; thus, MPA establishment is needed here.

We found that IPHD habitats are spatially connected, and their connectivity should thus be factored in when planning the establishment of MPAs (Bao et al., 2019). MPAs in coastal China remain isolated; hence, linking MPAs to accommodate the habits of IPHDs would be an effective conservation approach. In addition to China, Bangladesh also established an MPA associated with measures such as adjusting fishing patterns to protect IPHDs. In addition, international government cooperation efforts between Bangladesh and India have been established with the aim of developing MPAs in response to the Aichi target of enhancing international cooperation in biodiversity conservation (IPBES, 2019). The only MPA in Beibu Gulf, containing the border waters between China and Vietnam, is unable to provide optimal protection for IPHDs. As a result, cooperation among countries should be sought for the establishment of MPAs in international waters.

Establishing MPAs is only the first step, and minimizing the human disturbance effect on IPHDs is more important. Our findings show that bycatch, land reclamation and marine pollution are the most harmful human behaviors affecting IPHDs, so measures must be taken to mitigate the effects of these activities. Prohibiting the use of destructive fishing equipment could effectively reduce bycatch and largely improve the protection of IPHDs (Slooten et al., 2013). In addition, reducing inland pollutant discharge into rivers and restoring the natural runoff conditions and structures of rivers could alleviate IPHD habitat degradation (Kroon et al., 2016; Bao et al., 2019). In coastal construction activities, it is necessary to focus on the effects of the destruction of seafloor structures and the alteration of net primary productivity on the overall habitat, thus preventing irreversible damage to the IPHD habitats (Bao et al., 2019). Moreover, public awareness about IPHDs and biodiversity conservation should be increased to better protect IPHDs (Jefferson et al., 2017).

4.4. Modeling performance and limitations

The MaxEnt-simulated results obtained when predicting global habitat suitability are in line with the findings reported in some local regions, indicating the outperformance and high prediction accuracy of our modeling results. For instance, our results show that the superior-suitability areas for IPHDs exist in both relatively high- and relatively low-salinity waters. This finding is similar to the results reported by Lin et al. (2022), who suggested that IPHDs can regulate their internal osmotic pressure to adapt to relatively high-salinity habitats (Lin et al., 2022). Our results found a lower degree of influence of salinity on the IPHD habitat suitability along near-coastal regions. However, the habitat suitability decreased rapidly once the salinity exceeded the tolerance threshold of IPHDs far from coastlines, as the salinity level has been confirmed to strongly influence the survival of IPHDs (Jefferson et al., 2017).

Although climate projection data averaged from three global climate models (GCMs) were used for modeling herein to partially reduce the uncertainty of the results, climate data needs to be projected from additional GCMs to minimize the uncertainties. Additionally, we simulated the distribution of habitats corresponding to five environmental factors, and more essential marine biodiversity variables should be considered in future studies, for instance, the distribution of fish stocks, the tidal conditions, and the habitat preferences of IPHDs. However, corresponding data products derived from Earth observations and other approaches are currently scarce, and these data gaps thus need to be filled in the future.

5. Conclusions

With the intensification of human activities and climate change, the vulnerability of coastal zones has become more prominent, and the IPHDs inhabiting such zones are facing increasingly severe challenges. Here, we provide sufficient evidence that the habitats of IPHDs are influenced mainly by the SST, and the habitat suitability decreases as the distance from the coastline increases. However, the superior-suitability habitats are restricted to limited areas near coastlines in eastern China, and these areas have been severely impacted by human activities such as commercial fishing, pollution, and navigation, thus severely reducing the habitat suitability in such regions. Our results further indicate that climate change will further restrict IPHD habitats in the future, shifting these habitats northward and closer to coastlines. As a result, the habitats of IPHDs are expected to overlap strongly with areas of high-intensity human activities, thus further threatening the survival of IPHDs. Existing MPAs established to protect IPHDs face numerous problems and do not provide effective protection. We recommend that existing MPAs should be restructured to be closer to coastlines and that additional protected areas should be created in the Fujian region to ensure better protection.

Declaration of Competing Interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.geosus.2022.12.001.

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