



Potential geographic shifts in the coral reef ecosystem under climate change

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ABSTRACT

The coral reefs are the most diverse marine ecosystem in the world. Considering its contribution as a natural resource for humanity and global biodiversity, it is critical to understand its response to climatic change. To date, no global predictions have been made about potential ecosystem changes in relation to its inhabiting species. Predicting changes in species' climatic suitability under increasing temperature and comparing them among species would be the first step in understanding the geographic and taxonomic coherence and discrepancies that may occur within the ecosystem. Using 57 species-specific global climate suitability models (of corals, molluscs, fish, crustaceans, and polychaetes) under present and future climate scenarios (RCP 4.5 and 8.5), we compared the potential coherence and differences and their cumulative impact on the ecosystem in warm, cold, shallow, and deep waters.

Under the climatic scenarios, nearly 90% of 30 warm-water species were predicted to lose their suitability in the parts of the Indo-west Pacific, the Coast of Northern Australia, the South China Sea, the Caribbean Sea, and the Gulf of Mexico, resulting in the overall southward shift in their distributions. In contrast, a mixed response occurred in 27 cold-water species, with most northern temperate/boreal ones increasing their suitability in the Arctic Ocean and the Arctic species declining overall. We noticed that irrespective of their taxonomic group, the species with wider distribution ranges (thermal and geographic) had larger predicted gains in their suitability than their stenothermal counterparts, suggesting an increase of generalist species and a decline of specialist (endemic) species of the ecosystem under a warming climate.

Our coherent projections of species' climatic suitability in warm and cold habitats of the tropics, temperate, boreal, and the Arctic, represent significant taxonomic groups of the ecosystem. This might indicate mass extinction risk (local– in the tropics and northern temperate regions, and overall– in the Arctic) in native habitats and a high species turnover across the ecosystem under a warming climate. This may also destabilise predator–prey dynamics in the ecosystem, especially if foraging specialists dominate coral food webs and adversely affect the associated countries. Our global projections highlight the regions of species' potential loss and gain; stakeholders could use the information to protect biodiversity and maintain human well-being.

1. Introduction

The coral reef ecosystem hosts a wide diversity of known marine species (Gibson et al., 2011; Bridge et al., 2013) and supports several important ecosystem services, such as food resources and recreational activities that contribute to the economies of numerous associated

countries (Bridge et al., 2013; Barbier, 2017; Hoegh-Guldberg et al., 2017; O'Mahoney et al., 2017). For instance, the estimated asset value of coral reefs was nearly \$1 trillion and the livelihood of 500 million people (Hoegh-Guldberg et al., 2017). Given its importance to the well-being of humanity, it is essential to maintain its healthy functioning.

Global temperature has increased by 1 °C over pre-industrial times

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and is rising by 0.2 °C per decade (Allen et al., 2018). To provide a clear picture of global warming in the future (2050 and 2100), the International Panel on Climate Change (IPCC) has proposed seven emissions scenarios with representative concentration pathways (RCPs) for greenhouse gas emissions and mitigation effects (IPCC, 2014). Temperature plays a vital role in species physiology, such as maximum growth and fecundity within an optimal tolerance range, and determines their spatial distribution (Pörtner, 2021). It is thus of utmost importance to understand their geographic response to climate change. Given species' geographic locations and environmental information, the ecological niche modeling approach such as MaxEnt, random forest, and generalised additive modeling (Phillips et al., 2006; Melo-Merino et al., 2020; Valavi et al., 2022), have been widely used as powerful tools for predicting current and future species distributions. The most commonly used climatic RCP scenarios, such as minimum 2.6, moderate 4.5, and extreme 8.5 carbon emissions (IPCC, 2014), are generally used to predict the future climatic suitability of species across space (Elith et al., 2011; Saeedi et al., 2017; Freeman et al., 2013; Bargain et al., 2017; Kinlan et al., 2020; Pittman and Brown., 2011; Cobos and Osorio-Olvera., 2019; Cobos et al., 2019; Simões et al., 2021).

Coral reefs are considered one of the most important and fastest-responding indicators of climate change, as they bleach and perish during marine heat waves (Roberts and Cairns., 2014; Hughes et al., 2018; Guan et al., 2020; Guo et al., 2020; Anthony et al., 2020; Chen, 2021). Nearly half of the UNESCO World Heritage coral reef sites experienced heat stress leading to coral bleaching on average twice per decade between 1985 and 2013 (Heron et al., 2017; Sully et al., 2019). The reefs have been estimated to lose 70–90% globally at 1.5 °C and more at 2 °C global warming (Meredith et al., 2019; Chen, 2021). Any change in coral reefs can adversely affect their inhabitants (Hoegh-Guldberg et al., 2017). For example, under thermal stress, warm-water corals reduce their mucus secretion, which is an important food component for many other marine species (Baker et al., 2008; Wild et al., 2011). Such impacts can disrupt ecosystem functioning and lead to overall shifts in the distribution of the taxa of concern, and adversely affect the economies of associated countries (Cooley et al., 2022). In cold waters, climate change-induced ocean acidification may weaken coral reef skeletons by altering calcification rates and reducing growth rates, in addition to increasing bioerosion, thus leading to the decline of coral-reef habitats (Büscher et al., 2017; Morato et al., 2020a, 2020b).

It is unclear whether coral-associated/inhabitant (dependent or independent) species will exhibit similar distributional changes as corals or whether they will diverge under climate change. There is limited information on how the species-specific response of corals and their inhabitants would affect the distribution of the ecosystem as a whole under warmer temperatures (Munday et al., 2013; Hoegh-Guldberg et al., 2017; Torda et al., 2017). To date, no global predictions have been made about potential ecosystem changes in relation to the species living within it. Predicting and comparing the climatic suitability of species under current and future RCP scenarios would be the first step in understanding the geographic and taxonomic coherence and discrepancies that may arise within the ecosystem. Given the general shift in species range to higher latitudes, where species follow their thermal niche as global warming progresses (Chaudhary et al., 2021; Molinos et al., 2016; Poloczanska et al., 2013), we hypothesise that all ecosystem inhabitants would respond coherently by following the same direction of their climatic suitability distribution under warmer temperatures.

Here, we examined potential coherence and discrepancy in species responses to climate change and their cumulative ecosystem impacts in warm, cold, shallow, and deep waters and in taxonomic groups with broad and narrow distributions from the tropics to the Arctic Ocean (AO). We used 57 species from five major groups (corals, crustaceans, fishes, molluscs, and polychaetes) representing the ecosystem and predicted their climatic suitability under current and future RCP scenarios (Table S1). The predictions were then compared to determine geographic and taxonomic coherence among the species as an indicator

of ecosystem response to climate change. We then calculated the change in the number of species per unit area in each future climatic scenario. The coherent regions of potential loss and gain in species richness indicated geographic shifts in the ecosystem in the future. We further provided fine-scale global predictions of expected climatic suitability loss and gain of the species that stakeholders can use to identify regions where species are losing climatic refugia, which can help better develop habitat conservation and protection strategies for commercially and ecologically important species (Morato et al., 2020a, 2020b).

2. Materials and methods

2.1. Data collection, compilation, and cleaning

2.1.1. Species selection

We used the species list of corals based on the data from previous publications (i.e., Brandt and Malyutina, 2015; Malyutina et al., 2018; Saeedi et al., 2019; Saeedi et al., 2020; Saeedi and Brandt, 2020; Brandt et al., 2020), predominantly in the North-West Pacific (NWP) and the adjacent AO to select 15 coral species occurring in the tropics, subtropics, and the AO (Table S2). Then, we classified the species as cold- and warm-water species based on their climate zone distribution available at SeaLifeBase (Palomares and Pauly, 2022) (<https://www.sealifebase.ca/>) (Table S2) and mapped their global occurrences using the QGIS version 3.14 (2020). We selected 42 species belonging to different taxa: crustaceans (10), fish (11), molluscs (13), and polychaetes (8) based on their co-occurrences (in the same vicinity- overlaying distribution records) and/or their association/co-habitation with corals species (Table S1). We have a combination of both co-occurred non-coral reef-associated and coral reef-associated species. The list of species was then cross-checked with the World Register of Marine Species (WoRMS) (<https://www.marinespecies.org>) to identify any discrepancies (such as taxon status and habitat) in taxonomic information. All species with at least one benthic life stage were considered as benthic (Chaudhary et al., 2021), and all the warm-water species were shallow-water species due to their coastal occurrences (<200 m of the shelf); while all cold-water species predominantly occurring in the cold waters of the NWP and the Atlantic Ocean adjacent to the AO (Figure S1). Thus, we had a list of 30 warm-water and 27 cold-water species for data analysis (Table S1). Their global occurrences (timeline 1920–2020) were extracted from the Ocean Biodiversity Information System (OBIS; <https://obis.org/>) via R package “robis” (Provoost and Bosch, 2019) on 20th September 2020, and Global Biodiversity Information Facility (GBIF; <https://www.gbif.org/>) via “rgbif” (Chamberlain and Boettiger, 2017), on 1st October 2020. The duplicate occurrence records (based on latitude and longitude) from the two datasets and records occurring outside their respective species' native range were deleted, following the standard procedure of Saeedi et al. (2019). We assembled a quality-controlled dataset of 147,043 distribution records belonged to 57 marine species, each having at least 30 occurrences (Table S2, Figure S1).

2.1.2. Environmental data

We used mean- sea bottom temperature (°C) (SBT), salinity (PSS), and current velocity (m^{-1}) as relevant environmental predictors of benthic species distributions (Couce et al., 2012; Morato et al., 2020a, 2020b; Pearman et al., 2020; Gonzalez-Mirelis et al., 2021; Simões et al., 2021). These variables were selected at five arcminutes (ca. 0.083°, ~9.2 km at the equator) spatial resolution from Bio-ORACLE version 2.1 (<https://www.bio-oracle.org/>; Assis et al., 2018, Tyberghein et al., 2012), for the present, and future (2050 and 2100) based on the two representative concentration pathway emission scenarios (RCP), 4.5 and 8.5 (Moss et al., 2008). The values of environmental layers in the present scenario are monthly averaged from the year 2000 to 2014. The future layers are based on the climate change projections from different Atmospheric Ocean General Circulation Models (AOGCM) (Assis et al., 2018). The maximum depth layer was downloaded from the General

Bathymetric Chart of the Oceans (GEBCO; <https://www.gebco.net/>).

2.2. Data preparation

We rarefied the records using spatial thinning to match the spatial resolution (ca. 0.083° , ~ 9.2 km at the equator) of the environmental variables. We used the thinned occurrences to calibrate and create habitat suitability models for each species (Table S2); in total, they were 21,026. We then divided the occurrences into two subsets; 75% were used for ecological niche model training, and 25% for testing and evaluating the model's accuracy (Table S2) following Simões et al., 2021. These processes were performed in the packages “spThin” (Aiello-Lammens et al., 2015), “raster” (Hijmans et al., 2015) and “rgdal” (Bivand et al., 2015) in R 3.6.3 (R Core Team, 2020).

2.3. Ecological niche modeling

The maximum entropy approach (MaxEnt) is an advanced machine-learning method for climatic suitability modeling and requires presence-only data (Phillips et al., 2006). When associated model calibrations and uncertainties are taken care of, it has been reported to be advantageous and best-performing in terms of predictability over conventional methods such as additive modeling and random forest (Valavi et al., 2022). We used MaxEnt (Phillips et al., 2006) to predict species' ecological niche ranges. The uncertainty analysis of the predictions was performed with the help of the “kuenm” package (Cobos et al., 2019) in R 3.6.3 (R Core Team, 2020).

Calibration areas included a buffer of two decimal degrees from the occurrences of each species (Barve et al., 2011) to cover the general maximum dispersal distance of species of multiple taxa, including their larval stages (Green et al., 2015; Markey et al., 2016; Álvarez-Noriega et al., 2020), and was limited to the adjacent areas of sampling (Peterson et al., 2014). Thus, 63 candidate models were created from the combination of nine regularisation multipliers (0.1–1.0 at intervals of 0.2, 2–5 at 1) and seven feature classes representing linear, quadratic, and product combinations. These candidate models were then evaluated to select the best model and its parameters based on statistical significance (partial ROC), prediction ability (omission rates with a threshold of 5% (Anderson et al., 2003), and model complexity (Akaike information criteria; Warren and Seifert, 2011) (Phillips, 2005). We used the selected parameters from the best model to create continuous global climatic suitability projections (based on the median of ten replicates by bootstrap, logistic outputs in the calibration area) under the present and future RCP scenarios, which allowed extrapolation and clamping (Simões et al., 2021). To identify climatically suitable areas, we used a threshold of 5% to convert the continuous suitability to binary projections. The threshold was chosen considering the fair quality of the data and was constant for all the studied species for the simplicity of the methods. Moreover, the species are located in the same vicinity, and they share similar habitats and dispersal in their respective cold, and warm waters, except the ones that are more widespread. In the final models, depth had the highest permutation importance, followed by temperature, salinity and current velocity (Figure S9, S10).

We further conducted Mobility-oriented parity (MOP) analysis to assess the extrapolation risk in the final binary projections (Owens et al., 2013). The study measured similarity (as a continuous similarity index from 0 to 1) between the closest 3% (to ensure the robustness of the model) of the environmental conditions of the calibration area and each environmental condition of the projected area, highlighting the geographic regions with minimum similarity closer to 0, representing these regions of high extrapolation (Owens et al., 2013). We converted the continuous MOP similarity into binary values (>0 as 1), where values = 0 were considered as strict extrapolation (i.e., with no resemblance). We then excluded the regions of strict extrapolation from the final binary projections of their respective species and named them reduced binary projections.

To estimate the potential change in climatic suitability, we compared the regions and area (km^2) of the suitability between the present and future scenarios. In future, the differences occurred when there was either a loss of suitability in the regions of present suitability or a gain in new locations (Cobos et al., 2019). These predicted loss and gain regions were plotted on the world map for visual interpretation. We then overlaid the regions of differences of all species to highlight the common regions of loss and gain in their respective RCP scenarios. Further, the area (km^2) of the difference per species at a scale of $\sim 0.083^\circ \times \sim 0.083^\circ$ grids in each RCP scenario was quantified using the R package “raster” (Hijmans et al., 2015).

To highlight the common regions of the differences, representing the overall shift in the coral reef ecosystem under climate change, we overlaid the regions of predicted differences that occurred in all the species' climatic suitability in each year and RCP scenario. To understand if there is any coherence in the areas of predicted loss (native locations—within the extent of present geographical occurrences) and gain between the species and taxa, we quantified areas (km^2) of the predicted difference per species at a scale of $\sim 0.083^\circ \times \sim 0.083^\circ$ grids using the R package “raster” (Hijmans et al., 2015) in each RCP scenario. We then compared the difference between species and groups in their respective warm- and cold-water.

To further assess the spatial change in the future species' climatic suitability within their feasible dispersal distance, i.e., 200 km discussed above (Álvarez-Noriega et al., 2020), we calculated the geographic centroid of the reduced binary suitability area. We then computed centroid shift (km) as a difference between the future and present centroid of climatic suitability using the “raster” (Hijmans et al., 2015) and “ellipsenm” (Cobos and Osorio-Olvera., 2019) package in R. The negative difference between the centroid latitudes indicated a southward shift, and the centroid longitudes marked a westward shift. In contrast, the positive difference showed a northward and eastward shift.

3. Results

3.1. Regions of predicted loss and gain in climatic suitability under climate change

3.1.1. Warm-water

We predicted a loss in climatic suitability of 90% of all 30 species of all five groups- (corals, crustaceans, fish, molluscs, and polychaetes) (predominantly occurring in latitude 30°N – 30°S) (Table S1) in the parts of the South China Sea, the Indo-West Pacific, the Caribbean Sea, the Gulf of Mexico, and the North coast of Australia under both RCP 4.5 and 8.5 (Fig. 1). Moreover, the loss area was higher under RCP 8.5 than under RCP 4.5 in their respective years (Figs. 1 & 2a, 3a). The potential suitability gain occurred on the northern coast of the Sea of Okhotsk for all the species; Figure S2, (note that the increase in the AO and the Southern Ocean is beyond the general dispersal limit of the species (Table S1) and had a high extrapolation risk based on the MOP analysis (Figure S3); was thus excluded from the area analysis.

3.1.2. Cold-water

The cold-water species, having current distribution in the Arctic/boreal and northern temperate regions (Table S1), were projected to lose their climatic suitability in the parts of southern coastal areas of the Norwegian Sea, Barents Sea, Bering Sea, North-Western Passages, Hudson Bay, American coast of North Atlantic, and the Mediterranean Sea under both RCP 4.5 and 8.5 scenarios (Fig. 1). The number of species that were predicted to lose their suitability increased from 9 to 13, from the year 2050 to 2100, respectively, under RCP 4.5 and 8.5 (Fig. 1- latitude $> 30^\circ\text{N}$ & 30°S). We further predicted a northward increase in the climatic suitability of almost all of the 27 species, in the parts of AO (the Kara Sea, Laptev Sea, East Siberian Sea, Chuckchi Sea, East Barents Sea, Baffin Bay, North Hudson Bay, North Bering Sea), from 2050 to 2100 (RCP 4.5 & RCP 8.5) (Fig. 4), with high certainty (Figure S4). For

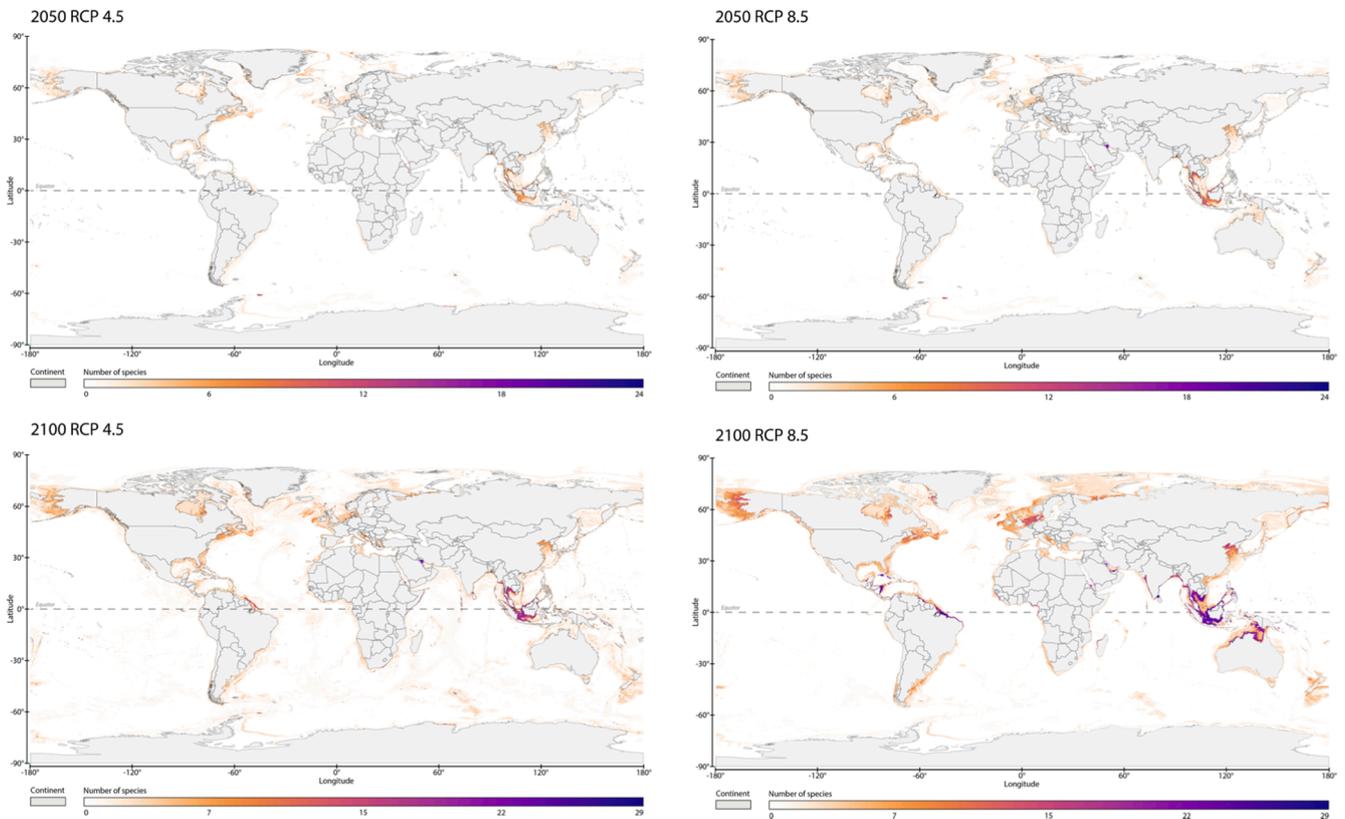


Fig. 1. The maps show the regions of collective loss in the habitat availability of the cold ($n = 27$) and warm-water species ($n = 30$) in the years 2050 and 2100 under both RCP 4.5 and 8.5 scenarios (red colour indicating the maximum loss). The number of models (each model is the future unavailability per species) represents the total number of species that lost their availability in the future ranging from 0 (lowest) to 29 (highest).

each species, the predicted change was maximum under RCP 8.5 2100 (Figs. 1, 4).

3.2. Discrepancy within warm-water species' response to climate change

A coherent response was predicted for 90% of the 30 warm-water species for each RCP scenario, with a greater decline than gain in climatic suitability (Fig. 2a, 3a). The area of predicted loss was comparable among all the groups in their respective climatic scenarios (Fig. 2a, 3). On average, the area of loss per group ranged from 0.2 (RCP 4.5) to 1 million km^2 (RCP 8.5) in 2050 and from 1.2 (RCP 4.5) to 3 million km^2 (RCP 8.5) in 2100 (Fig. 2a, Table S3). In comparison to the loss, we predicted a much lower (<0.25 million km^2) mean predicted gain in suitability in new locations under RCP 4.5 (2050), RCP 8.5 (2050 and 2100) (Fig. 2b, Table S3, S4). Exceptionally, under RCP 4.5 (2100), the predicted area of gain of all 30 species was the highest among all the scenarios (Table S4); fish showed the largest mean area of gain (1.2 million km^2) with higher variability than the other four groups (<0.25 million km^2) (Fig. 2, Table S4). The species of fish *Acanthurus nigrofocus* (Forsskål, 1775), *Balistapus undulatus* (Park, 1797), and *Ctenochetus striatus* (Quoy & Gaimard, 1825) were predicted to gain larger area than lost (Fig. 3a). Moreover, the magnitude of projected centroid shift in fish was the highest (mean 300 km) among all the groups in RCP 4.5, 2100, while it remained comparable among the groups in other scenarios (Figure S5).

At both group and species levels, the magnitude of the predicted area of loss and centroid shift was higher under RCP 8.5 than under RCP 4.5 in their respective years; and in 2100 than in 2050 under their separate scenarios (Figs. 2, 3, S5, Table S3 & S5). The model outputs predicted an increase in the number of species (from 2050 to 2100) with centroid shift > 100 km (median), from 6 to 30 and 9 to 27 under RCP 4.5 and 8.5, respectively (Fig. 3b). The highest shift was predicted under RCP

8.5 (2100) and was accompanied by a larger predicted area of loss than gain (Fig. 3). The species with the highest shift (>500 km) were crustacean *Ciliopagurus strigatus* (Herbst, 1804), *Stenopus hispidus* (Olivier, 1811), fish *C. striatus*, *A. nigrofocus*, *B. undulatus*, molluscs *Tridacna crocea* (Röding, 1798), *Drupa ricinus* (Linnaeus, 1758), and polychaetes *Eurythoe complanata* (Pallas, 1766), *Spirobranchus giganteus* (Pallas, 1766) (Fig. 3b, Table S5). Almost all species showed a southward (east and west) centroid shift (Figure S6).

3.3. Discrepancy within cold-water species' response to climate change

Under climate change, the predicted average loss in the climatic suitability varied (0.2 to 4 million km^2) among all the 27 species (Fig. 5a, Table S6). Across all five groups, we found high variability in species suitability area of loss and gain in their respective RCP scenarios (Fig. 5a, b). Irrespective of their group, almost 13 species were predicted to gain a larger area than loss and vice-versa in the rest (Fig. 6a, Table S6 & S7). Higher loss than gain occurred in all corals (except *Epizoanthus papillosum* Johnston, 1842) and crustaceans (except *Pagurus pubescens* Krøyer, 1838), and all polychaetes gained overall (except *Laonice cirrata* (M. Sars, 1851)) (Fig. 6a). The species of fish and molluscs showed a mixed response, with some predicted to lose more than gain and vice-versa (Fig. 6a).

The Arctic species were predicted to decline in their overall suitability; they were fish *Liparis tunicatus* Reinhardt, 1836, *Triglops pingelii* Reinhardt, 1837, crustacea *Acanthostepheia malmgreni* (Goës, 1866), *Sabinea septemcarinata* (Sabine, 1824). While the rest of the boreal species of fish (Table S1) having current distribution in the AO were predicted to increase their overall suitability further in the AO (Figs. 4 & 6a), resulting in a northward centroid shift (Figure S7, Table S8). Generally, the species which predicted to increase their overall habitat suitability (Fig. 6), have wide distribution ranges in the Boreal and the

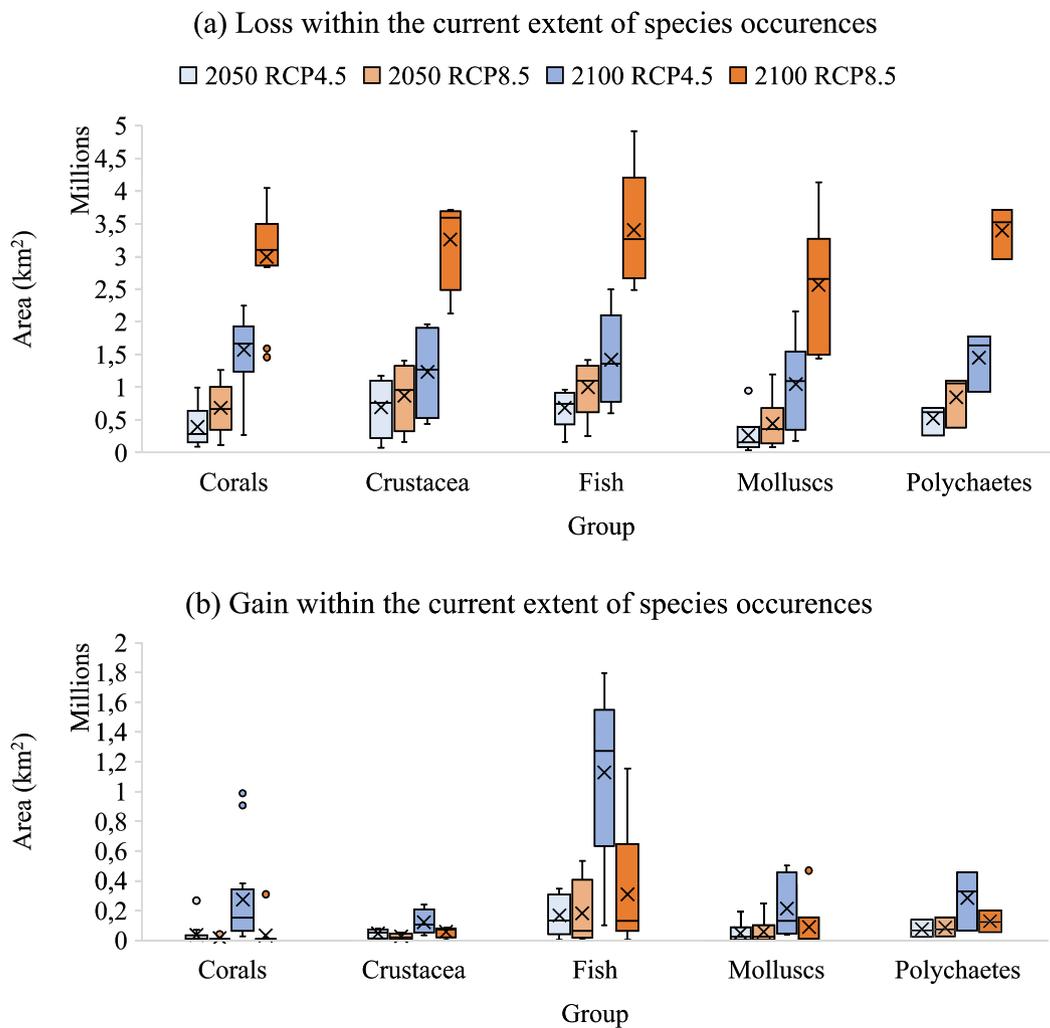


Fig. 2. Box plots showing the taxa-wise distribution of the predicted area (km²) (y-axis) of (a) loss; and (b) gain (x-axis) in the climatic suitability of warm-water species ($n = 30$) under the RCP scenarios 4.5 (blue) and 8.5 (orange) in the future [2050 (lighter shade) and 2100 (darker shade)]. Each box plot represents the mean (cross), median (horizontal line in the box), the ends (lower and upper quartiles) of the predicted (a) loss, and (b) gain in the species of each group. The dots outside of the plots are outliers. The area is calculated based on the geographical extent of the species' present distribution.

North Atlantic and Pacific Oceans (Table S1).

Species-wise, the maximum centroid shift was predicted under RCP 8.5 2100, attributed to their overall suitability loss or gain, respectively (Fig. 6 & Table S8). The shift of > 250 km was predicted in coral (*P. arborea*), crustaceans *S.septemcarinata* (Sabine, 1824), *P.pubescens* Krøyer, 1838, *Diastylis goodsiri* (Bell, 1855), fish *Gymnocanthus tricuspis* (Reinhardt, 1830), molluscs *Yoldiella lucida* (Lovén, 1846), *Parathyasira equalis* (Verrill & Bush, 1898), and polychaetes *Chone dumeri* Malmgren, 1867, *Chaetozone setosa* Malmgren, 1867 (Fig. 6b). While group-wise, we predicted a high variability in the shift, which remained comparable in their respective RCP scenarios (Figure S8).

4. Discussion

Although coral reef loss due to climate change has been predicted and previously reported (Meredith et al., 2019; Chen, 2021), a comprehensive overview of the overall response of the coral reef ecosystem is still unclear, especially when the response of corals and their inhabitants coincide. In this study, we examined the coherence and discrepancy between global species distributions of five significant taxonomic groups of the coral ecosystems and identified the regions of potential loss and gain in species richness under climate change. We

used the correlative MaxEnt approach to predict the climatic suitability of 30 warm- and 27 cold-water species for present and future (2050 and 2100) under RCP 4.5 and 8.5 (Moss et al., 2008). Depth had the highest permutation importance, followed by SBT (Figure S9, S10); as the depth remains the same in all climatic scenarios, an increase in SBT declines the habitat suitability for the species in the regions of predicted loss. Our results are consistent with the review of Hoegh-Guldberg et al. (2017); suggesting an intense loss not only of corals but also of their inhabitants, followed by local and general mass extinctions in the regions with uncontrolled temperature rise.

4.1. Regions of predicted loss and gain in climatic suitability under climate change

4.1.1. Warm-water species

Under climate change, we predicted loss in the climatic suitability of 90% of the 30 warm-water species in today's tropical biodiversity hotspots, such as the Indo-West Pacific, the coast of northern Australia, the South China Sea, the Caribbean Sea, and the Gulf of Mexico. These regions gained extreme temperatures under the climatic scenarios and had highly extrapolated suitability with MOP index = 0 (Figure S3), becoming potentially unsuitable for the species to inhabit. Furthermore,

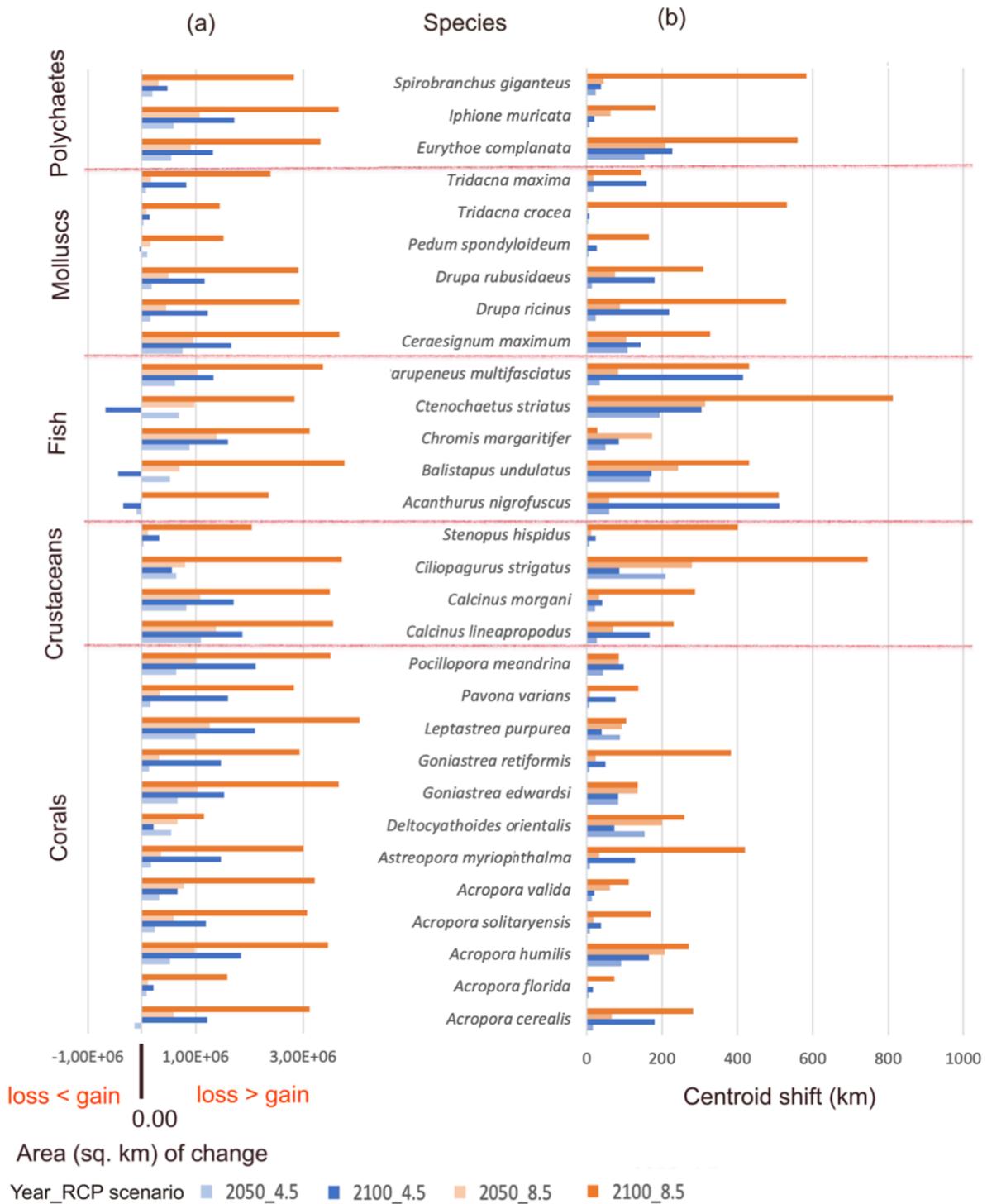


Fig. 3. Change (difference between) in the overall (a) area of predicted loss and gain; and (b) centroid, in the climatic suitability of the warm-water species (y-axis), under the RCP scenarios 4.5 and 8.5 for the years 2050 and 2100.

the expected gain in more north and adjacent longitudes was comparatively small, resulting in an overall southward shift. The species would still occur in their current subtropical locations but could become extinct in the above-mentioned parts of the tropics under extreme temperatures. A similar loss from a mass extinction of tropical corals during excessive temperature increases occurred nearly 125,000 years ago (Kiessling et al., 2012; Quattrini et al., 2020). All warm-water species studied here are stenothermal, meaning they live in a long-term stable and narrow temperature range and are restricted to migrating to newer environments. They may be at a high risk of mortality under climate change

(Pörtner, 2002; Pörtner and Peck, 2010; Deutsch et al., 2015; Yasuhara and Danovaro, 2016), which would lead to a contraction of the entire warm and shallow water ecosystem.

4.1.2. Cold water species

For cold-water species, nearly 52% of the 27 species could lose their climatic suitability in the southernmost parts of the Norwegian Sea, western Barents Sea, Bering Sea, Northwest Passage, Hudson Bay, U.S. North Atlantic Coast, and the Mediterranean Sea. However, they may all find new habitats further into the AO, particularly in the Kara Sea,

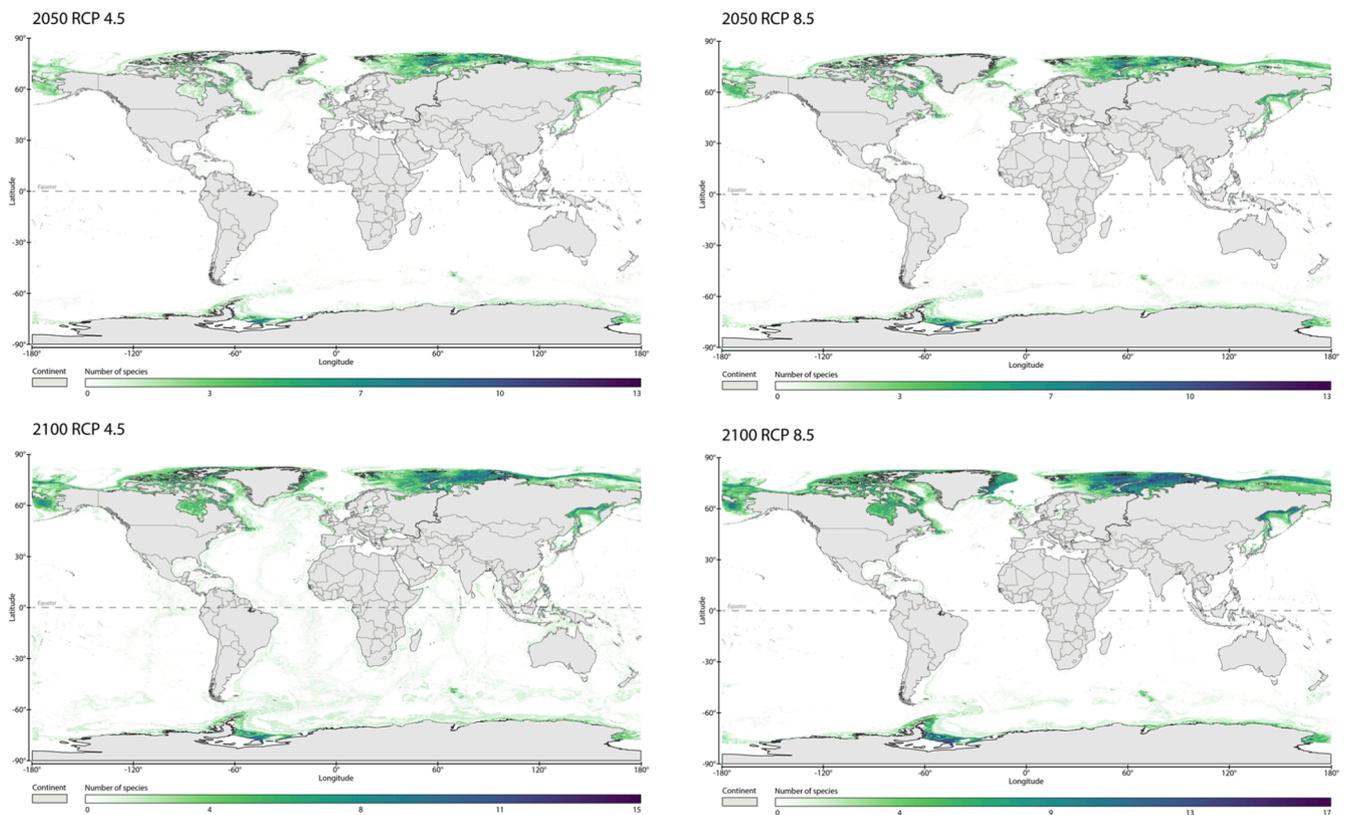


Fig. 4. The maps show the regions and number of cold-water species [ranging from 0 lowest to 13 highest] that are predicted to gain climatic suitability under both RCP 4.5 ad 8.5 scenarios in 2050 and 2100.

Laptev Sea, East Siberian Sea, Chukchi Sea, and the eastern Barents Sea, resulting in a general shift northward. Such a shift suggests that these species may be following their thermal niche northward to escape warmer temperatures under climate change (Poloczanska et al., 2013; Sully et al., 2019; Burt et al., 2020; Wang et al., 2020; Magel et al., 2020; Tang, 2020; Simões et al., 2021).

Despite facing the most severe climate warming since the 1970 s (Chaudhary et al., 2021), the mid-latitudinal regions facing southward retraction and northward expansion of species habitats are also receiving species from further south (Chaudhary et al., 2021; Frainer et al., 2017; Solan et al., 2020). Therefore, they may not suffer from a lack of species richness but are likely to experience higher species turnover under climate change. In addition, the expected collective displacement of species indicates their local extinction in their original habitats and the potential to become invasive in AOs during climate change. Thus, species displacement may severely interfere with the critical function of the cold-water ecosystem. How the ecosystem will adapt to the new species needs further investigation.

The projected ecosystem changes, which include both ecologically and economically important species (Table S1), would negatively impact associated tropical countries in the Asia, Indo-Pacific, and Mexico regions due to species loss. In contrast, the expected increase in species turnover could benefit northern countries, which may receive new species from the south. Still, it would also pose an unprecedented threat from potentially invasive species that could reduce endemic seafood resources for local indigenous communities (Cooley et al., 2022). However, the timeframe in which these benefits would occur and how the ecosystem would function under species exchange remains to be investigated.

4.2. Discrepancy within warm-water species' response to climate change

In addition to the general coherent response (higher projected loss

than gain in climatic suitability), we exceptionally predicted a larger range of projected gain than loss under RCP 4.5 in 2100 for three fish species and one coral species; furthermore, the gain (for all species) was much higher than under other scenarios. This may be because RCP 4.5 is a mitigation scenario that envisions stabilization/decrease in anthropogenic GHG emissions (Thomson et al., 2011), which may create larger suitable new habitats for species, even if associated with a higher loss than gain in 2050. In contrast, under the worst-case scenario - RCP 8.5 - most species could suffer a major loss, with minimal new habitat gains and significant shifts in climatic suitability associated with higher loss than gain. This is due to the uncontrolled increase in CO₂ emissions under RCP 8.5, leading to unprecedented climatic situations with extremely warm temperatures. This scenario is reported to be the most realistic scenario for the period up to mid-century under current and stated policies (Schwalm et al., 2020). Therefore, the projections under RCP 8.5 should not be underestimated, showing the maximum change in species suitability and indicating the highest number of local extinctions. Such possibilities were also highlighted in empirical data from the Lizard Island reef system, where 28 of 284 species were never recorded after 2011 (Richards et al., 2021). We anticipate that most native coral reef ecosystem species will become extinct in tropical areas facing extreme warming.

Our predictions of the largest gain in new habitats for fish and high variability in their centroid shift indicate that they may have a higher chance of survival by avoiding warm temperatures via migration under climate change (RCP 4.5 2100). The highly mobile organisms under climate change predicted the fastest range expansion and retraction rate (Poloczanska et al., 2013). In contrast, we predicted relatively larger losses accompanied by minimal gains in the habitat of sessile species (which are dependent only on the planktonic stage for migration), suggesting their higher vulnerability and mortality rates under climate change (Wittmann and Pörtner, 2013). Such variable responses of species indicate a higher survival success rate for some over others which

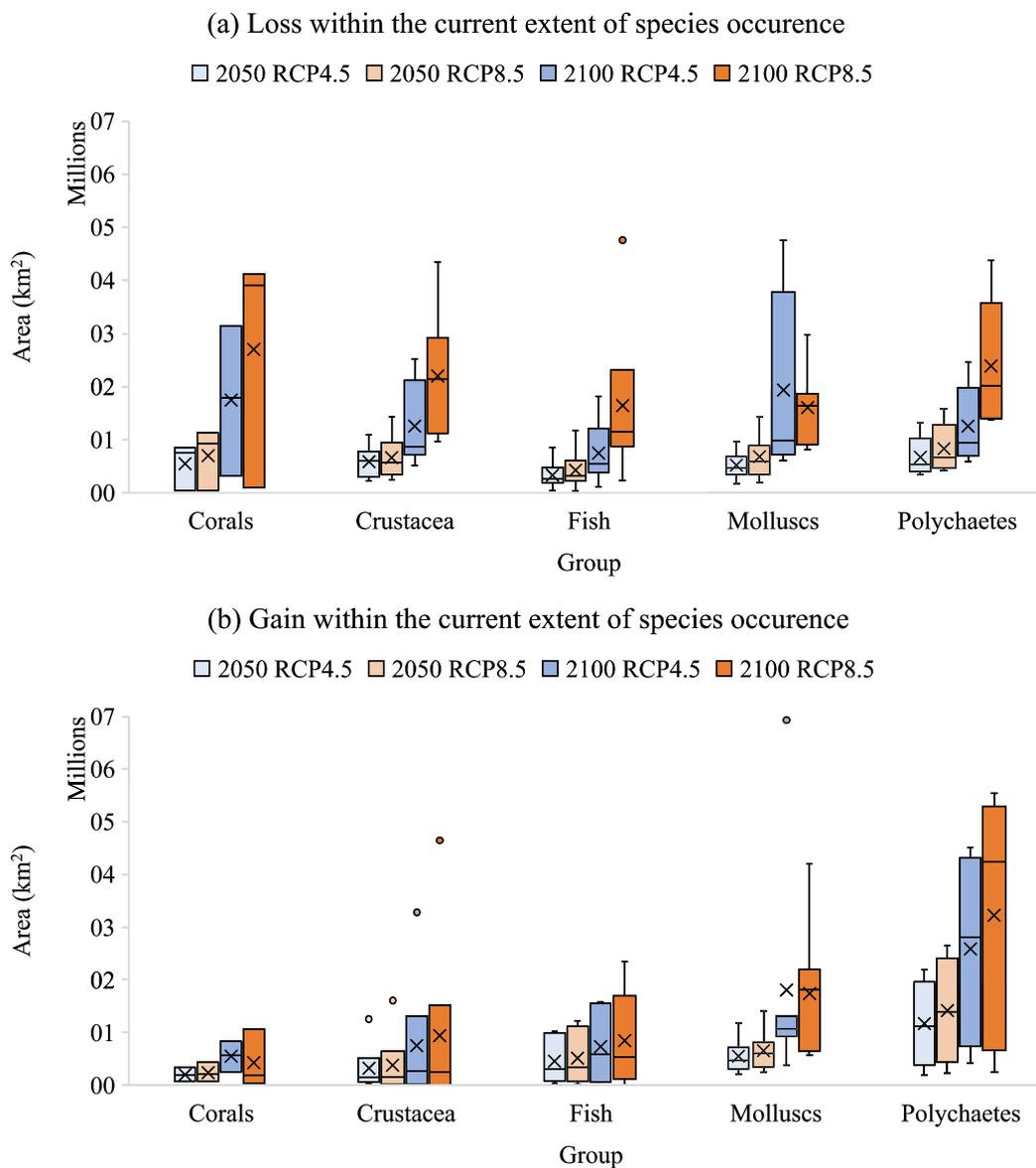


Fig. 5. Box plots showing the taxa-wise distribution of the predicted area (km²) (y-axis) of (a) loss; and (b) gain (x-axis) in the climatic suitability of cold-water species ($n = 27$) under the RCP scenarios 4.5 (blue) and 8.5 (orange) in the future [2050 (lighter shade) and 2100 (darker shade)]. Each box plot represents the mean (cross), median (horizontal line in the box), the ends (lower and upper quartiles) of the predicted (a) loss, and (b) gain in the species of each group. The dots outside of the plots are outliers. The area is calculated based on the geographical extent of the species' present distribution.

may result in the predominance of some species while subduction of others (MacNeil et al., 2019; Romero-Torres et al., 2020; Vercelloni et al., 2020; Tkachenko et al., 2020). Vercelloni et al. (2020) reported the replacement of 71% of hard coral communities with soft corals and algae in the Great Barrier Reef under the highest number of coral bleaching events. Also, the mortality rate among Polynesian corals varied under extreme temperatures post-2016 (Hédouin et al., 2020), and the Eastern Pacific corals were reported to be resilient to thermal stress (Romero-Torres et al., 2020). Such discrepancies suggest the replacement of native and less-tolerant species (via loss in their faunal abundance) and richness with more tolerant and invasive ones resulting in irreversible changes in the ecosystem (Bellwood et al., 2004; McCauley et al., 2015; Williams and Graham, 2019; Graham et al., 2020; Stuart-Smith et al., 2018; Richards et al., 2021). Graham et al. (2020) have already reported a subsequent replacement of higher trophic level fish to lower trophic level herbivore fish, even after the reef restoration in marine reserves of Seychelles that faced coral bleaching events.

Most of the coral species and their inhabitants studied here co-exist

in the same habitat and have ecological associations (both positive and negative) with each other (Table S1), which play an essential role in ecosystem functioning. For example, reef-forming corals provide shelter to the inhabitants, like fish. And in return, the inhabitant fishes such as *A. nigrofuscus* prevent algal growth on the reefs (Marshall and Mumby, 2012), and *B. undulatus* prevents the proliferation of sea urchins on the reefs by preying on them. Any imbalance in the population of these species in the ecosystem would affect the ecosystem's productivity. The loss of coral cover and their native species and the increase in generalist species may not just interfere with ecosystem functioning (Graham et al., 2020) but also negatively impact the endemism and uniqueness of the region (Reddin et al., 2022).

4.3. Discrepancy within cold-water species' response to climate change

Our model outputs predicted species-specific responses to climate change, with nearly 50% of the cold-water species increasing their overall suitability and the rest decreasing. We did not find a clear trend

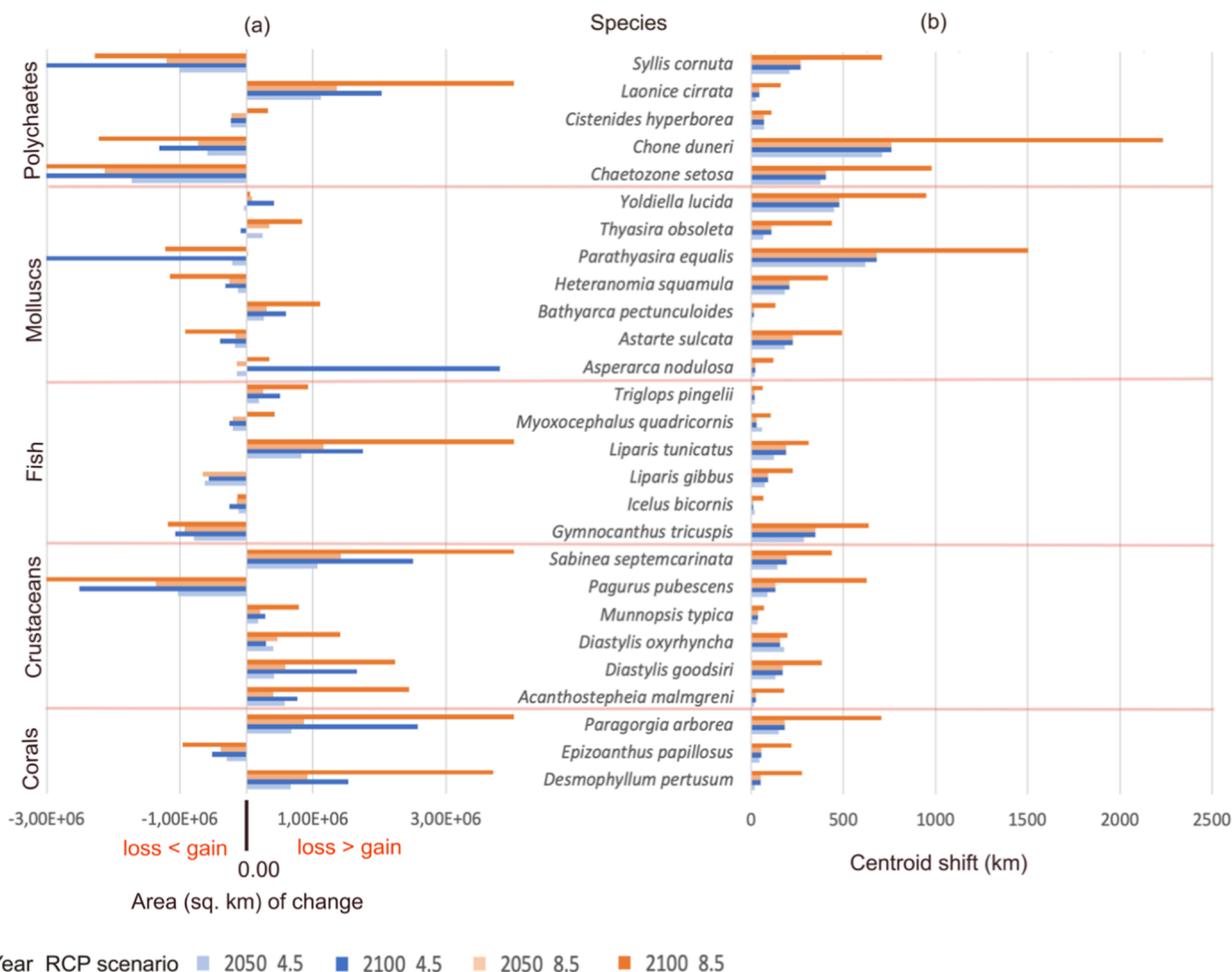


Fig. 6. Change (difference between) in the (a) area of predicted loss and gain; and (b) centroid, in the climatic suitability of the cold-water species (y-axis) under climate change, under the RCP scenarios 4.5 and 8.5 for the years 2050 and 2100.

within or between groups. However, molluscs, polychaetes, and corals, which are widespread in the Atlantic and Pacific oceans, gained more suitability than Arctic species (fish and crustaceans)- which continued to increase or generally decreased in the AO. Drewnik et al. (2017) also predicted species-specific responses in molluscs and crustaceans of Hornsund fjord; they found that species with a wide thermal range also have a more extensive range of climatic suitability that could expand and further restrict their distribution to the innermost cold basins of the fjord in warmer times. This suggests a higher survival chance of widely distributed eurythermal species via migration under climate change than their stenothermal counterparts (Clarke and Pörtner, 2010; Deutsch et al., 2015; Pörtner, 2021; Bostock et al., 2015; Ross et al., 2020; Morato et al., 2020a, 2020b; Matos et al., 2021). The expansion of North Atlantic species into the newly melted regions of the AO and marginalisation of the Arctic species has already been predicted and reported to alter the ecosystem functioning of the AO (Frainer et al., 2017; Johannesen et al., 2017a, 2017b; Aune et al., 2018; Solan et al., 2020; Kortsch et al., 2015; Frainer et al., 2021).

We predicted an increase in the overall suitability of boreal North-Pacific and -Atlantic fish species in the AO, while the Arctic species such as all crustaceans (except *P.pubescens*), coral *Paragorgia arborea* (Linnaeus, 1758), and fish (*L.tunicatus*, *T.pingelii*) may suffer overall decline. Our results resonated with the predictions of Morato et al. (2020a, 2020b), who also suggested habitat extirpation of cold-water corals such as *D.pertusum* and octocoral *P.arborea*, and northward shift in the habitat of deep-sea fishes, under climate change. Arctic species are more specialised in their benthivores diet and narrow thermal range

(Waga et al., 2020), making them highly vulnerable to climate change (Frainer et al., 2021). Whereas boreal species such as Atlantic cod and tusk, in addition to their broader thermal range, have generalist diets, slower growth rates, greater mobility, and longer lifespans, which increase their chances of survival in the warming the AO (Wiedmann et al., 2014). The expansion of generalist boreal species and their increasing abundance in the AO lead to an increased risk of predation and competition with native Arctic species (Fossheim et al., 2015; Kortsch et al., 2015). Emblemsvåg et al. (2022) have recently reported an overall decline in the functional diversity in the East of Greenland since 2005, characterized by an increase in boreal mobile species (primarily fish) and a decline in native benthos. Thus, Arctic species may be at risk not only of extinction due to warmer temperatures but also of unprecedented threats from potentially invasive boreal species that could also reduce the endemism of the AO. Most importantly, a deep understanding of the complex interrelationships among ecosystem species is needed to understand how expected species fluctuations affect ecosystem functioning (Montano, 2020). There is a need for further research incorporating observational effects of ecological relationships to predict the cascading effects of climate change on the ecosystem.

4.4. Future directions

The model outputs here were based only on mean seafloor temperature, depth, salinity and current velocity. Depth and temperature are reported as the most important factors for the climatic suitability of benthic species (Cheung et al., 2010; Poloczanska et al., 2013; Pearman

et al., 2020; Gonzalez-Mirelis et al., 2021; Simões et al., 2021). They do not consider life stage vulnerability, larval dispersal potential, the effects of water currents as environmental factors, biological linkages between species, and specific predator–prey interactions. Considering these complex interactions can improve estimates of species survival and potential dispersal under climate change (Pörtner, 2021). In addition, under the combined impacts of climate change (including oxygen depletion and increasing acidification) and human influence, increased loss of coral reef biodiversity and associated taxa is expected in the future (Doney et al., 2012; Hoegh-Guldberg et al., 2017; Perry et al., 2018; Spalding and Brown, 2015; Carpenter et al., 2008; Pinsky et al., 2019; Ross et al., 2020; McManus et al., 2020; Pörtner, 2021).

5. Conclusion

Our predictions of native habitat suitability loss of 50–90% in 57 representative species of the coral reef ecosystem indicate a potential mass extinction of marine species (locally - in the tropics and northern temperate regions, and overall - in the AO) under climate warming. In addition, the increase in the suitability of boreal species in the AO suggests an increase in species fluctuation in the AO that could alter its ecosystem functioning and pose a high extinction risk to endemic Arctic fauna. Such responses may destabilise predator–prey dynamics in the ecosystem, primarily if coral food webs are dominated by predators (Pozas-Schacre et al., 2021), making the ecosystem more vulnerable to climate change. Species which were predicted to survive climate warming with lower losses and higher gains, in general have a more extensive thermal, geographic, and dietary range compared to narrow-range species. Therefore, these species have a higher survival rate and potential to become invasive in new locations and are expected to increase in generalist species and decrease in endemic species, resulting in an overall decrease in endemism in the ecosystem. This would impact populations that depend on ecosystem services for their livelihood worldwide. In particular, we highlight regions where ecosystems as a whole are being lost (especially tropical and temperate biodiversity hotspots) or could gain (AO). This information can be used in planning adaptation and mitigation measures to address the impacts of climate change and in establishing marine protected areas in these regions to sustain human well-being.

Declaration of Competing Interest

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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.pocan.2023.103001>.

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