

Future distribution patterns of cuttlefishes under climate change

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Abstract

While most coastal communities are expected to have been negatively impacted by climate change, cephalopods have thrived with shifting ocean conditions. However, whilst benefitting from the same physiological flexibility that characterized cephalopods, cuttlefish remain bounded to specific locations by their particularly low vagility. To test the beneficial effects of climate change on cuttlefish, Species Distribution Models were applied on nine species of genus *Sepia* to assess distribution on present and different representative concentration pathway (RCP) scenarios (2.6, 4.5, 6.0, and 8.5; CMIP5) for the years 2050 and 2100. We show that projections of future cuttlefish distribution decrease relative to present model predictions. Harshes hit species, *Sepia braggi*, was observed to decline as much as 30.77% (from present 55.26% to 24.48% at RCP 8.5 in 2100), to *Sepia officinalis* with low maximum decrease of 1.64% (from present 59.62% to 57.98% at RCP 8.5 in 2100). Increases in habitat suitability occurred mostly at higher latitudes, while habitat decrease was predicted for the tropical regions and lower latitudinal limits of species distribution. Cuttlefish will not benefit from future changes in climate, as their habitats will decrease in suitability. If suitability of habitat translates into cuttlefish abundance, many coastal fishing communities in the global south will be affected by the future decreases in these fishing resources. Additionally, as potential “sea canaries” for coastal ecosystems, we may see many species and habitats from these systems affected by climate change, namely in tropical regions.

Introduction

Coastal systems are currently the marine ecosystems most affected by anthropogenic pressures (Halpern et al., 2008), due to their close proximity to urban centers (Hinrichsen 1996). These areas are valuable to humans, as they are highly productive (Nixon et al., 1986; Carr et al., 2006), maintaining high biodiversity levels (Kaiser et al. 2005) and serving as nursing grounds for fisheries species, thus promoting the proliferation of heavy fishing efforts (Hinrichsen 1996; Chassot et al., 2010; Stock et al., 2017). Also, waste resulting from human activities (e.g., agricultural, industrial and sewage waste) can lead to impacts such as eutrophication (Smith et al. 1999; Paerl and Otten 2013) and the associated high mortality rates in wildlife communities (Burkholder et al. 1992; Penela-Arenaz et al. 2009). Furthermore, anthropogenic climate change is poised to affect these areas through changes in temperature, local currents, chemistry, bathymetry, and geomorphology, which, in turn, are likely to impact biological communities (Harley et al. 2006; Cinner et al. 2012; Ranasinghe 2016).

Coastal benthic communities are under added high risk due to climate change (IPCC 2022). The shallow depths at which these communities live in are under increased risk of stratification, as warming is expected to reduce vertical mixing (Hallet et al. 2018). These, in turn, translate into greater exposure to ocean warming (OW), oxygen loss, and ocean acidification over coastal regions (Sampaio et al. 2021; IPCC 2022). Furthermore, shifts in precipitation regime, greater runoff and water input into these systems is expected in the future, with implications for the levels of salinity and primary productivity (Bindoff et al. 2019). Shell bearing benthic and demersal coastal species, having limited mobility to find new suitable habitat to escape, could be particularly affected by these combined phenomena. Currently, the distribution of coastal species has been either observed (Lu and Lee, 2014; Pang et al. 2018) or projected (Boavida-Portugal et al., 2018; 2022; Borges et al., 2022) to shift poleward or into deeper waters (Perry et al. 2005) under climate change. Additionally, coastal communities are expected to face local extinctions (Albouy et al., 2013) along with structural and functional changes at the ecosystem-scale (Osland et al., 2013).

Cephalopods (i.e., squid, octopuses, and cuttlefish) are considered climate change indicator species (Jackson and Domeier, 2003). These molluscs are characterized by their life strategy of “live fast, die young” (Boyle & Rodhouse, 2005), that allows them to adapt quickly to new thermal environments (Rodhouse 2013). They are also important sources of food and play an increasingly important role on both artisanal and commercial fishing (Caddy and Rodhouse, 1998; Jereb & Roper, 2005). Furthermore, cephalopods are important trophic mid-points on the food-web, between low trophic levels (Rodhouse and Nigmatullin, 1996) and top predators (Klages 1996; Clarke, 1996; Croxal & Prince, 1996). Therefore, they meet most of the attributes for being good ecological indicators (Fulton et al., 2005): i) short life cycles and fast growth rates; ii) targeted by fisheries; and iii) keystone species (Rosas-Luis et al., 2008); with populations sensitive to environmental changes. Within the cephalopods, cuttlefish (family Sepiidae) are particularly dependent of the coastal systems. Demersal animals, they carry a developed internal calcareous shell for fluctuation (cuttlebone). The composition and structure of the cuttlebone, which implodes over a certain depth (between 300 and 600 meters; Ward and Von Boletzky, 1984; Jereb & Roper, 2005), limits the ability of this group to seek refuge across the vertical plane. Furthermore, their population dispersal is horizontally limited, as their eggs are fixed into benthic structures (Jereb & Roper, 2005; Xavier et al., 2016). Lastly, their eggs and early developmental stages are vulnerable to the effects of climate change, namely with cuttlebone development being affected by OA (Dorey et al., 2013; Sigwart et al., 2016; Otjacques et al., 2020) and OW leading to higher respiration rates, protein damage, membrane fluidity and organ malfunction, lower survival rates and to decreases in average body mass (Lacoue-Labarthe et al., 2009; Rosa et al., 2013; Sigwart et al., 2016). Hence, if cuttlefish closely follow the quality trend of the coastal systems with climate change, their populations can potentially decrease in the near-future (Harley et al. 2006). In fact, while overall coastal and oceanic cephalopod populations have increased over the last sixty years worldwide (Doubleday et al. 2016), both due to decrease in competition and predation from commercial fish species and to cephalopod's ability to adapt to changing environments (Andre et al. 2010), populations of certain cuttlefish species have been in decline (Pang et al. 2018).

Species distribution models (SDMs), which allow for the estimation of species habitat suitability, have been used to predict and project distribution of cephalopods, (Schickele et al., 2021; Boavida-Portugal et al., 2022; Borges et al., 2022). If the presence of a species in a given location means that the area gathers good environmental conditions for the species to survive (Kearney and Porter, 2009; Pearson, 2007), we can collect the

environmental data from the areas where the species was present to predict the species' broader distribution and apply it in a broader region (e.g., project the invasive potential of species; Borges et al., 2021; Sung et al. 2018; Barbet-Massin et al., 2018) or timeline (e.g., project the potential impact of future climate change scenarios; Araújo & Rahbek, 2006; Melo-Merino et al., 2020; Borges et al., 2021) and provide values of suitability of habitats across this new environments. Hence, if the ongoing cephalopod populational increase is due to climate change, SDM projections with future scenarios of worsening climate change should show an ocean with increased of habitat suitability for cephalopods. This should be especially evident in coastal ecosystems that are more exposed to these changes. In these areas, cuttlefish are the cephalopods more dependent on the environmental conditions, as they are limited in depth to the coastal area (due to their cuttlebone implosion depth), have a benthopelagic lifestyle and their eggs (fixed into the sessile structure) do not get parental care to compensate for conditions in harsher years.

If cephalopods are benefiting from climate change, cuttlefish, as benthopelagic coastal representatives of this group should benefit as well, especially as the environment they occupy will be so severely and rapidly affected. To test this hypothesis, we used data collected from online repositories and SDM framework to forecast the potential future distribution of nine commercial cuttlefish under different climate change representative concentration pathway (RCP) scenarios (numbered according to the radiative forcing [W/m²; Moss et al., 2008] projections; RCP 2.6, 4.5, 6.0 and 8.5) and timeframes (present, year 2050 and 2100). With the overall habitat suitabilities from these forecasts, we can check if coastal cephalopods will benefit from worse climate change scenarios and expand their habitat range into a wider latitudinal amplitude.

Materials And Methods

Data collection

We collected geolocated data on species occurrence from the Global Biodiversity Information Facility (GBIF; GBIF 2022) and the Ocean Biodiversity Information System (OBIS; OBIS 2022). From the FAO catalogue for cuttlefish (Jereb and Roper, 2005) we selected species that had fisheries, which provided a total of 28 species of the genus *Sepia* (Table 1). On the online repositories, we used the search term 'Sepia' to limit our search to the genus, and with the downloaded occurrences (GBIF 2022, OBIS 2022) we limited to the 28 previously mentioned species programmatically. Of the observations obtained for our species, only nine species were selected for modelling that presented more than 50 occurrences (Table 1). To curate our occurrence dataset for points in wrong locations (i.e.: located on land, wrong ocean basin, outside of distribution range; Jereb and Roper, 2005; for the locations of the point dataset, See Online Resource 1), by manually curating it in QGIS (QGIS.org, 2022). Lastly, a species-level thinning step (rarefaction) was implemented by randomly picking occurrences distanced 20 km or more from each other, as this reduces spatial sampling biases (Radosavljević and Anderson 2014; Elith et al., 2011). The distance selected (20 km) for this last step, was the one that made our models present-day predictions resemble best the literature (Jereb and Roper, 2005). In total, 15695 observation points were retrieved from the repositories for the nine species (Table 1). Of these, 2463 were removed due to errors in location. From the 13232 curated locations, only 3407 were used after rarefaction (Table 1).

We selected temperature, salinity, current velocity, depth and chlorophyll for the environmental variables for modelling. These were retrieved from the Bio-Oracle project (Tyberghein et al. 2012; Assis et al. 2017). The values for these layers correspond to the measurements performed at the average seabed depth (except for chlorophyll, where values were retrieved for the sea surface), with a resolution of 0.00833(3) degrees (latitude and longitude; projection = "+proj=longlat +datum=WGS84 +no_defs"). For each environmental variable, 3 raster layers were collected, one for the longterm mean, another for maximum and the last for minimum values. These were retrieved for both the present-day, as well as all future climate scenarios (years 2050 and 2100; RCP 2.6, 4.5, 6.0 and 8.5; CMIP5). To assess the collinearity between the environmental variables, we used Pearson's method (*r*). We removed variables with a collinearity > 0.7 (Naimi and Araújo., 2016) to decrease potential biases in inference statistics of the models (Dormann et al. 2013). After this step, only the mean values were kept for most environmental samples, with minimum chlorophyll also maintained.

Species distribution models

To build our species distribution models, we made use of the MaxEnt algorithm (Phillips & Dudík 2008). A total of five model runs were done using all data (presence points plus 1 000 [randomly selected] background points) for each species, where the data was randomly partitioned and shuffled between calibration (75%) and validation (25%) datasets at each run. Subsequently, we used True Skill Statistic (TSS; Allouche et al. 2006) to assess the performance of each model. Models with a TSS lower than 0.7 were discarded. We calculated the weighted median of the remaining models to produce the ensemble (Araújo & New 2007) by weighting each of the model runs forecasts with the square difference of its TSS score with 0.5. The ensemble model TSS as well as for environmental variable contribution to the model used the same computation. The previous step was performed for each of the nine climate scenarios and for each species, producing 81 Habitat suitability forecasts (9 species x 9 scenarios [present + 2100*four RCPs + 2050*four RCPs]). These forecasts were restricted to the distribution range of each species, both the latitudinal and longitudinal ranges, ocean basins, and depth range (Jereb and Roper, 2005). The ensemble forecasts were outputted as raster layers.

The average habitat suitability of each species was calculated by weighting each grid point on the rasters with its corresponding area and dividing the sum of all values with the sum of the whole species range area. To assess latitudinal change, we calculated the difference between the row

mean habitat suitability of each future scenario and the mean of the “present-day” scenario at the same latitude. Furthermore, main contributing environmental variables were retrieved. We used R (R Core Team, 2021) to run all analysis, with resource to the packages *dismo* (Hijmans et al. 2017) and *sdm* (Naimi and Araújo. 2016). Maps were built using Qgis (QGIS.org, 2022).

Results

The TSS value for the ensemble models ranged from 94.75% (*S. bertheloti*) to 99.60% (*S. braggi*). Overall, *Sepia* showed decreases in future habitat suitability (Figure 1 and 2; all other scenarios can be seen on the Online Resource 2; distribution of habitat suitability for all scenarios and species on the Online Resource 3), with losses of habitat focused mainly on lower latitudes (Figure 3).

Overall habitat suitability trends

For 2100, HS declines increase with RCP severity for all targeted species (Figure 1A-I). For 2050, an overall decline in mean habitat suitability (mHS) over time was projected across all emission scenarios for most cuttlefish species (Figure 2 & Table 3). The only exception was *S. braggi*, which represented the only species with a projected increase of mHS (1.65% increase; RCP 2.6, year 2050; Table 3). The species with the highest differences in mHS between present and future scenarios was *S. braggi* (i.e., biggest decrease: 30.77%; RCP 8.5, year 2100; Table 3), and *S. officinalis* presented the lowest differences between present mHS and future scenarios (biggest decrease: 1.64%; RCP 8.5, year 2100; Table 3).

The overall trends in mHS varied between species and RCP scenarios under consideration. The mHS values from the projections for different RCP for the year 2100 deviated more from the predicted present values than the same values for 2050 (Figure 2). The mHS for the 2050 RCPs' are very similar to each other, with the exception of *S. apama* (Figure 2A), *S. bertheloti* (Figure 2C), *S. braggi* (Figure 2D) and *S. pharaonis* (Figure 2I) and do not show a value order related to RCP. However, mHS for the 2100 RCPs' are lower than the mHS for the predictions for the present, with lower values according to the severity of RCP (i.e.: 2.6>4.5>6.0>8.5) (Figure 2).

Detailed habitat suitability trends

Australian coast

Similar projections were observed for *S. apama* (mHS: 46.31%; TSS: 98.14%) and *S. braggi* (mHS: 55.26%; TSS: 99.60%), namely showcasing a marked decline in habitat suitability (HS) near the northern limits of their distribution. Moreover, a decline in HS was also observed on the Bass strait and the coast of Southern Australia (Figure 1A, D), corresponding to negative peaks in habitat suitability at 32.5°S (all RCPs), 36°S (all RCPs except 2.6) and 40°S (all RCPs) (Figure 3A, D), as well as north of 30°S for *S. apama*. Increases of HS (of half the amplitude of the negative peaks) appear on the southern coast of Tasmania, south of 42°S (all RCPs) (Figure 1A, D and 3A, D). Furthermore, in 2050 RCPs' mHS for these species followed a different pattern than in 2100 (which had lower values with severity of RCP), where RCP 4.5 had lower values than 6.0 (or even lower than 8.5 for *S. braggi*).

Indo-Pacific

Within the Indo-Pacific coasts, the projected HS for *S. latimanus* (mHS: 53.06%; TSS: 95.28%) and *S. pharaonis* (mHS: 53.18%; TSS: 95.09%) was observed to decrease in all future scenarios. For *S. latimanus*, we observed a decrease in future HS on the coast of Oman, West Coast of Australia, Andaman Sea, Gulf of Thailand and the Delta of the Ganges, between the latitudes 20°S and 20°N (Figure 1F and 3F). On the other hand, we observed HS increases on the Yellow sea, North of the South China Sea and on the south coast of Japan (North of 30°N; Figure 1F and 3F), on the Coast of Tasmania, and on the Coral Sea (South of 25°S; Figure 1F and 3F). Between 30°N and 20°S, future HS values decreased by less than 10% relative to present predictions irrespective of RCP and year with exception of RCP 8.5 in the year 2100, with a difference of ~20% at 10°N, and ~10% between 15°S and 20°S (Figure 3F). North of 30°N and south of 25°S, HS values for the future projections increased with latitude, time and RCP severity (Figure 3F). For *S. pharaonis*, projected decreases of HS were observed between latitudes 30°N and 20°N (Southern coast of Oman and Persian Gulf; Figure 1I and 3I), between the latitudes 20°N and the equator (Andaman Sea, Gulf of Thailand, Ganges Delta and the West coast of India; Figure 1I and 3I) and south of equator/10°S (Western coast of Australia, Sea of Timor and Sea of Arafura; Figure 1I and 3I). For 2100, HS declines increase with RCP severity (Figure 1I; Figure 3I), peaking around the 25°S (up to ~50% HS decline), the 10°S (~ -40% HS), the equator (~ -30% HS) and 25°N (~ -30% HS; Figure 3I). On the other hand, for 2050, and specifically between the equator and 30°N, RCP6.0 resulted in the lowest HS decline (~ -5% HS) while RCP2.6 resulted in the highest (~ -25% HS), being closely followed by RCP8.5 (~ -25% HS; Figure 3I), with HS declines still increasing with RCP severity for the remaining latitudinal range. This same pattern found between the equator and 30°N for the year 2050 RCPs is also observed for the mHS (Figure 2I). Increases in HS were observed north of 30°N (Yellow Sea, north of the South China Sea and Southern coast of Japan; Figure 1I and 3I), with this trend being exacerbated over time and with RCP severity (Figure 3I).

African Coast

The HS for *S. australis* (mHS: 41.98%; TSS: 96.00%) and *S. bertheloti* (mHS: 54.86%; TSS: 94.75%) mostly decreased throughout their distribution around the African coast. *S. australis* experienced a decrease throughout its latitudinal range in HS, except for an increase between 5°S and 10°S in 2050 (mouth of the Congo River for RCPs 6.0 and 8.5, at the south coast of the Horn of Africa for RCP 2.6; Figure 1B and 3B) where it experiences a 40% increase peak (RCP 6.0; Figure 3B). Largest decreases were observed on all future scenarios between the equator and 5°S (-40%; from the Horn of Africa to Zanzibar Island; Figure 1B and 3B), between 10°S and 15°S (-30%; mouth of the Congo River; Figure 1B and 3B) and around 10°N (-30%; Horn of Africa; Figure 1B and 3B). Only for the RCP 8.5 in 2100 projection, a couple of additional large decreases were observed between 17°S and 20°S (-40%; Benguela coast; Figure 1B and 3B) and between 20°S and 30°S (-20%; Namibia and South Africa coasts; Figure 1B and 3B). For *S. bertheloti*, we observed a decrease in HS throughout its range in habitat suitability, except between 20°N and 25°N (<5% decrease in all RCPs and years; Western Sahara coast; Figure 1C and 3C), north of 25°N both in 2050 (~ 10% increase; RCP 8.5 and 6.0) and 2100 (~ 20% increase; RCPs 2.6 and 4.5), and finally around 10°N (~ 10% increase; Coast of Guinea; 2050 RCP 4.5, 6.0 and 8.5; 2100 RCP 8.5) (Figure 3B). Between 5°N and 20°N, strongest decreases in 2050 were observed on the RCP 2.6 projection (and RCP 6.0 showed the weakest decreases, to punctual increases) and in the year 2100 it changes to the RCPs 6.0 and 8.5. This same pattern is also observed for the mHS (Figure 2B), where RCP 6.0 presented the highest (and RCP 2.6 the lowest) values for the year 2050. South of 5°N, lower values are exacerbated over time and with RCP severity (Figure 3B). Within the latitudes close to the equator (+/-5°), low differences (<5%) were observed between habitat suitability on future projections.

Eastern Atlantic

On the eastern Atlantic coast, increases in HS were observed for *S. elegans* (mHS: 55.43%; TSS: 96.09%), *S. officinalis* (mHS: 59.62%; TSS: 97.05%) and *S. orbignyana* (MHS: 46.80%; TSS: 98.06%) north of 50°N (around the northern portion of the North sea and the coast of Iceland, with losses observed the south North Sea and south of Ireland; Figure 1E, G, H and 3E, G, H) and south of 20°S (South Africa coast) (Figure 1E,G,H and 3E,G,H). Both *S. elegans* and *S. orbignyana* showed a positive HS spike at 15°S on the southern half of the Angolan coast (Figure 1E, H and 3E, H), with *S. orbignyana* further spiking around the equator (Figure 3H). Decreases are observed for *S. officinalis* south of 45°N for RCP 8.5 and south of 35°N for all other scenarios (Figure 3G), with HS values between 20°N and 30°N (Western Sahara coast; Figure 1G and 3G) remaining similar to those found in the present (difference<5%). In fact, the highest differences between present and future scenarios for *S. officinalis* are observed south the 20°N (Mauritanian coast) and north of the 30°N (Mediterranean African coast) for this species (Figure 1G and 3G). Decreases between the present and future scenarios for *S. elegans* and *S. orbignyana* varied wildly between 20°N and 20°S, but were closer to zero with lower RCP scenarios, and with scenarios from 2050 *versus* 2100. However, these differences became more consensual between RCP scenarios north of 30°N, with decreases up to 50°N (Mediterranean and continental shelf south of Ireland and west of Brittany) in the year 2050, and up to 60°N in the year 2100 (expansion of decrease from the continental shelf south of Ireland to northern latitudes) (Figure 1E, H and 3E, H).

Environmental Variable contribution

The environmental variable that most contributed to the distribution models here presented was median seabed temperature (Table 2; from *S. officinalis* 98.22 % to *S. bertheloti* 70.10%). Only *S. bertheloti* (70.10 %), *S. australis* (71.04 %), and *S. latimanus* (79.56 %) had contributions from temperature below 90 % (Table 2). Second highest contributing variable was depth, the exceptions being *S. braggi* (mean chlorophyll), and *S. australis* (chlorophyll minimum) and *S. bertheloti* (mean chlorophyll) (Table 2).

Discussion

Overall, the results obtained in the present study suggest a decrease in habitat suitability for the *Sepia* genus, with slightly differential responses between the different species analyzed. However, the distribution of the loss in habitat suitability is not uniform, being most evident at lower latitudes, while some gains are projected on the higher latitudes (that do not compensate enough for the losses).

Despite the high resemblance of the ensemble models' projections for the present-day scenario, with the current descriptions of the distributions of the targeted cuttlefish species (Jereb and Roper, 2005), limitations inherent to species distribution models (SDM) and the data used may explain divergences between the habitat suitability values projected and to be observed over incoming decades. First, the absence of trophic interactions or prey biomass as variable predictors can lead to instances of overprediction in habitat suitability, as prey availability and the existence of predators and competitors can limit the distribution of cuttlefish. Second, given that dissolved oxygen and pH projections are not available at a global scale for the future scenarios analyzed, these were not integrated in the present analysis, limiting its predictive power as both these abiotic variables are important for these animals. Specifically, dissolved oxygen acts as a limiting factor in the distribution of many cuttlefish species (Augustyn et al., 1995; Melzner et al., 2004) while lower pH conditions leads to hyper-calcification of the cuttlebone (Dorey et al., 2013; Sigwart et al., 2016; Oti Jacques et al., 2020) and thus, impacts the vertical distribution of these animals. Third, many observations of these animals were made post-mortem, using their sepions. Floating to the surface after the death and decomposition of the organism, these structures can end up hundreds of kilometers from their original location (Reid 2016), distorting their real distribution. With a large portion of data points retrieved from GBIF resulting from citizen science (iNaturalist 2022), where many of these observations are made along the seashore (GBIF 2022), such method of detection is likely frequent.

Fourth, for many species targeted in this study, occurrence data available online were either low in extent (less than 200 occurrence points; *S. bertheloti*, *S. latimanus* and *S. braggi*), or skewed to waters of countries with extensive resources for surveys (particularly European, South African and Australian coastlines), with other parts of the ranges of these species have either very few or no observations (*S. australis*, *S. pharaonis*, *S. latimanus*, *S. bertheloti*, *S. orbignyana* and *S. elegans*). Finally, due to the difficulty in distinguishing some of the more closely related cuttlefish species, many occurrence points may have been misattributed to a different species, especially in areas where two confounding species overlap their distributions (e.g.: *Sepia officinalis* vs. *S. hierreda* vs. *S. bertheloti* vs. *S. elegans* vs. *S. australis* vs. *S. orbignyana*, *S. pharaonis* vs *S. ramani*; Jereb and Roper., 2005). This is especially relevant for the eastern Atlantic cuttlefish, as this may have contributed to the underprediction of the models for these species on the western African coast.

Sepia apama is the largest cuttlefish in the ocean, and occurs in the southern shores of Australia, being separated into 2 lineages, one eastern and one southeastern around the Bass strait, due to historical vicariance (Kassahn et al. 2003). One of the five populations on the southern lineage forms a unique and only spawning ground known for cuttlefish, with thousands of individuals, located at the north end of the Spencer gulf (Hall and Hanlon, 2002; Hall and Fowler, 2003; Kassahn et al. 2003). According to our findings, this spawning ground is projected to exhibit a considerable decrease in habitat suitability starting in 2050 and getting worse in 2100 (for all RCPs except 2.6; worse for each higher RCP), which may lead to declines in population recruitment, at least for the Spencer gulf population, which is in line with population trends previously observed (Prowse et al. 2015). If the eastern population uses the Bass strait as a breeding ground, the entire species may be at a higher risk than the models here suggest, as these 2 locations (i.e., Spencer gulf and Bass strait) are projected to undergo the greater habitat suitability loss for the species. However, if the spawning ground at Spencer gulf is unique to the animals living in the region, and not to the entire species, we may see a future shift southward towards the coastline of Tasmania, together with the isolation of the westernmost groups of animals on the South-west of Australia (this last effect appearing in 2100 for scenarios higher than 2.6). Finally, our modelling for this species predicted what previous studies have suggested: that temperature represents a primary contributor for habitat suitability, as it affects egg and juvenile development (Hall and Fowler, 2003). Around the same region, the habitat of *Sepia braggi* is projected to undergo a considerable decrease in suitability, relative to all the other species (except for RCP 2.6 in 2050; worse for each higher RCP in the year 2100). This species has a very limited depth range (30 to 86 m; Roper and Jereb 2005) in the south coast of Australia, limiting their ability to migrate to new habitat. In this context, this species is particularly sensitive to the projected environmental change, especially temperature, as it explained more than 90% of the distribution in our models. The only two options for escape from rising temperatures is either to move down the (very limited) continental shelf or further south around the Tasmanian coast. This species will be facing the largest declines in the set of cuttlefish targeted by this study and be reduced to two separated regions of Australia as early as 2050 (southwestern tip and the Tasmanian coast) regardless of future climate change scenario (except for RCP 2.6 in 2050).

Sepia latimanus and, particularly, *Sepia pharaonis* represent the main commercial cuttlefish species in the Indo-Pacific. The *S. latimanus* inhabits shallow tropical waters (no deeper than 30 m), relying on coral reefs and mangrove areas (Jereb and Roper 2005) for shelter and egg laying grounds. Both these ecosystems are projected to experience distribution shifts in the future climate change scenarios (Record et al., 2013; Kornder et al., 2018) which may affect recruitment success and survival of the early stages of this species. Furthermore, with temperature being the most contributing factor for the models of this species (~80%), followed by depth (~11%) and salinity (~6%), future increases in coastal water temperatures and precipitation (and terrestrial runoff) will impact the survivability of this species in enclosed and calm seas. More specifically, in the Indonesian archipelago, Andaman Sea and the gulf of Thailand, starting in 2050 (all RCPs) and becoming worse with RCP severity by 2100 (with signs of recovery with RCP 2.6). *S. pharaonis* does not differ much from the previous species in terms of trends in our projections, as it is projected that will be losing suitable habitat in the Indonesian archipelago, Andaman Sea and the gulf of Thailand as well, starting in 2050 (all RCPs) and becoming worse with RCP severity by 2100 (with signs of recovery with RCP 2.6). However, as it can inhabit deeper (up to 100 m) and colder (spawning takes place between 18°C and 24°C) waters (Jereb and Roper 2005), this may explain the difference between main contributing environmental variables to the distribution between the 2 co-occurring species (*S. pharaonis* temperatures contributes more than 90%). Also, as the most contributing factor is the seabed temperature, greater losses in habitat suitability in 2050 for RCP 2.6 compared to RCP 6.0 can be explained by average higher (seabed) temperatures on RCP 2.6 and average lower (seabed) temperatures in RCP 6.0. This is especially relevant between the equator and 30°N, where the species has a greater distribution. Additionally, we should consider that *S. pharaonis* is in fact a group of 5 cryptic species (Anderson et al., 2007; 2011). If the projections that start in RCPs 2.6 and 8.5 at 2050 and worsen by 2100 (for RCPs greater than 2.6) are to materialize, the cryptic species from western Indian Ocean, northeastern Australia and Persian Gulf/Arabian Sea ('Iranian') could be endangered by the loss of habitat suitability.

Off the sub-Saharan coast of Africa, *Sepia australis* and *Sepia bertheloti* represent the main stocks of cuttlefish. According to our models for *S. australis*, this species seems to be unlikely to inhabit the coasts of eastern Africa north of the equator, as it has been described previously (Gulf of Aden and Red Sea; Jereb and Roper 2005). Also, this species is currently caught mostly in waters with temperatures between 9° (Roeleveld et al., 1993) and 11°C (Augustyn et al., 1995) and the main contributing environmental variable for the distribution was temperature (~70%; followed by minimum chlorophyll a at ~20%), which further supports the absence in the areas previously described. Even if it is present there, projections from our models suggest that the habitat suitability of this species will shift southward, with loss of suitability in the north and off-shore (Agulhas and Namibian; Lipinsky et al., 1992; Roeleveld et al., 1993) banks of South Africa by the year 2100, habitats which are likely to represent spawning grounds for the species (Jereb and Roper 2005), and increase slightly in the south-eastern coast of Africa. A similar pattern for *S. bertheloti* is indicated by our models, where however, due to the narrowness of the continental shelf and hence, suitable bathymetry for *S. bertheloti* is limited,

which may explain the high variance of values observed in our observations. Even so, according to our projections, if RCP 8.5 is to be observed, the distribution of the later species could become restricted to the Mauritanian coast by the year 2100, with the Guinea gulf and southward populations declining or even eradicated.

The European common cuttlefish (*S. officinalis*) is by far the most well studied species of the genus (Jereb and Roper 2005; Guerra 2006). Their cuttlebone implodes at depths greater than 150 m (Ward and Boletzky, 1984) and temperature limits of the species are known to be between 10°C to 30°C, with animals entering a lethargic stage below 10°C (Richard, 1971; Bettencourt, 2000) and above 30°C, due to oxygen limitation (Melzner et al. 2006; 2007). Fittingly, the main environmental contributions for this species distribution models were seabed temperature (>98%) and depth (~2%). Additionally, salinity being a minor contributor (<0.1%) fits with the fact that, in comparison to other cephalopods, this species is less sensitive to salinity, being able survive in coastal lagoons and estuaries with salinities as low as 18 ± 2 (Boletzky, 1983; Guerra and Castro, 1988). Projections for the next 300 years suggest that this species may move into the arctic and colonize the American continent (Xavier et al. 2016) - a first for the sepiids. Our results partially support the previous findings, as all our projections point towards an increase of habitat suitability of the northern regions, which can potentially be used by this species as steppingstones into the Arctic basin and American continent. Indeed, our models for this species entail the lowest habitat suitability decrease across the whole group of target species, seemingly benefitting from future ocean changes. By 2100, the losses in the south and gains in the north increase with RCP severity. However, this same trend is not clear by 2050, which can be explained by the variance and error of the modelling being greater than the differences between RCPs environmental values up to this year. Also, we should consider that this species, along with *S. elegans* and *S. orbignyana*, presented the lowest changes in habitat suitability, further contributing to the odd results projected for the middle of the century.

Suggested species for the subgenus *Rhombosepion*, *Sepia elegans* and *Sepia orbignyana* (Pérez-Losada et al., 1996; Sanjuan et al., 1996; Khromov et al., 1998), are distributed throughout the eastern Atlantic Ocean, from the North Sea to South Africa. They are small sized cuttlefish with slender cuttlebones with closely packed septa and modified sutures (Ward 1991), that allow them to reach greater depths than most other cuttlefish (~450 m). Hence, along with *S. officinalis*, they represent one of the species with the lowest levels of habitat suitability decrease for futures scenarios, having greater environmental flexibility and being able to occupy many habitats throughout their latitudinal range and are not so restrained as other species by their cuttlebone to depth limitations. However, the fact that both *S. elegans* and *S. orbignyana* are more stenohaline and stenothermal than *S. officinalis* may explain the difference observed between these species (Jereb et al., 2015). Despite this, our results showed a similar contribution from temperature for the 3 species (>95%) with slightly different contributions from salinity (*S. officinalis*=0.05% vs. *S. elegans*=0.43% and *S. orbignyana*=0.68%). Both Rhombosepids seem to be on a downward trend on the Mediterranean Sea, especially *S. orbignyana* in 2100, where they represent the most abundant cephalopod species (Jereb et al., 2015). However, a poleward shift in habitat suitability is to be expected, with the colonization of the northern parts of the English and Irish islands and *S. elegans* even venturing to Iceland. As such, much like with *S. officinalis*, this pattern may lead in the future to the colonization of the Arctic and American continent (Xavier et al. 2016) at the expense of a loss of habitat at lower latitudes, namely in the Mediterranean and North Sea. Further, for the same reasons noted for *S. officinalis*, this northern shift in habitat suitability is exacerbated under higher RCPs by year 2100 but not by 2050. The high variance observed in the latitudinal trends of our models for both *S. elegans* and *S. orbignyana* can be attributed, in part, to the narrowness of the continental shelf across their African range (as previously mentioned for *S. bertheloti*). As there are very few pixels for these areas (narrow shelf), changes in a few pixels can easily be translated into big variations in the latitudinal trends observed.

The trends exhibited in the present study suggest a potential loss of cephalopod diversity at lower latitudes, which are currently the areas with the highest diversity (Rosa et al., 2019). Additionally, if cuttlefish are neritic 'canaries in the coalmine', as are other cephalopods for the broader ocean (Jackson and Domeier, 2003), loss of habitat suitability may also occur for other organisms in the near-tropical regions, thus suggesting a poleward shift of many coastal communities. Also, since cuttlefish are demersal predators, their presence in new areas will put them in contact with new prey and competitors. Due to their buoyance adaptation, they are less energetically expensive with depth than fish (Webber et al., 2000) and hence, they can easily become aggressive predators of new shallow water trophic webs, where predators undergo daily vertical migrations (Guerra 2006), competitively displacing other species from their trophic role and/or suppressing prey populations. Additionally, they are prey for many marine top predators (Guerra 2006; Jereb and Roper 2005). Hatchlings and juveniles can be targeted by benthic and demersal fish, while adults are targeted mostly by marine mammals (Guerra 2006; Jereb and Roper 2005). If habitat suitability is translated into abundance, predators that rely on these species may also be forced to migrate or face a populational decline (Arkhipin et al., 2015).

In many of the areas where these species are located, they are reliable marine resources and important sources of income, with most of the areas affected by habitat suitability declines located around the tropics and on the southern side of the Mediterranean Sea. If habitat suitability is translated into abundance, with these species often sustaining artisanal and industrial fisheries throughout their distribution, a considerable source of income and food security may be under threat (Jereb and Roper 2005). In fact, many of the fishing grounds of these species will be affected by habitat suitability decreases: *S. australis* in the banks around south Africa; *S. bertheloti* throughout the African coast; *S. elegans* and *S. orbignyana* in the Mediterranean, where it often represents the most abundant cephalopod fisheries species; *S. pharaonis* on the gulf of Thailand, Persian Sea and Indonesian archipelago, where it locally is the dominant cephalopod species fishery; *S. latimanus* in the Indonesian archipelago and South China sea (Jereb and Roper 2005). This may lead to hardship to local fishing communities, especially those in the global south.

Declarations

Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Author Contributions

MFG and RR conceptualized the study; MFG was responsible for data gathering and curation; MFG conducted the SDM analysis and post-analysis processing; MFG wrote the original draft of the manuscript; MFG, CPS, FOB, and RR reviewed and edited the manuscript.

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Data Availability

The datasets generated during and/or analysed during the current study are available in the Zenodo repository, at <https://doi.org/10.5281/zenodo.7595276>

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Tables

Table 1. Species presence points retrieved for the analysis. Raw stands for presence points collected from the repositories; Curated is the number of points that were attributed to correct locations; rarefied is the number of points used for the analysis after picking only the points 20 kms far apart.

| Species | Raw | Curated | Rarefied |
|----------------------------|-------|---------|----------|
| <i>Sepia aculeata</i> | 49 | | |
| <i>Sepia andreana</i> | 24 | | |
| <i>Sepia apama</i> | 1440 | 1057 | 213 |
| <i>Sepia australis</i> | 3834 | 3749 | 606 |
| <i>Sepia bertheloti</i> | 87 | 87 | 72 |
| <i>Sepia braggi</i> | 152 | 126 | 83 |
| <i>Sepia brevimana</i> | 8 | | |
| <i>Sepia elegans</i> | 1089 | 1058 | 488 |
| <i>Sepia esculenta</i> | 32 | | |
| <i>Sepia hierredda</i> | 5 | | |
| <i>Sepia kobiensis</i> | 50 | | |
| <i>Sepia latimanus</i> | 298 | 278 | 141 |
| <i>Sepia longipes</i> | 0 | | |
| <i>Sepia lorigera</i> | 0 | | |
| <i>Sepia lycidas</i> | 1 | | |
| <i>Sepia madokai</i> | 0 | | |
| <i>Sepia officinalis</i> | 7376 | 5551 | 1202 |
| <i>Sepia orbignyana</i> | 954 | 900 | 358 |
| <i>Sepia pharaonis</i> | 465 | 426 | 244 |
| <i>Sepia prabahari</i> | 1 | | |
| <i>Sepia prashadi</i> | 20 | | |
| <i>Sepia ramani</i> | 1 | | |
| <i>Sepia recurvirostra</i> | 17 | | |
| <i>Sepia stellifera</i> | 4 | | |
| <i>Sepia trygonina</i> | 10 | | |
| <i>Sepia vietnamica</i> | 1 | | |
| <i>Sepia vossi</i> | 0 | | |
| <i>Sepia zanzibarica</i> | 5 | | |
| Total | 15923 | 13232 | 3407 |

Table 2. Species SDMs' TSS and environmental variable contribution (%) to the model.

| Species | Contributions | | | | | | |
|--------------------------|---------------|-------------|----------|--------|---------|------------|-----------|
| | TSS | Temperature | Salinity | Depth | Current | mean Chl a | min Chl a |
| <i>Sepia apama</i> | 98.14% | 95.82% | 1.67% | 2.02% | 0.12% | 0.37% | 0.00% |
| <i>Sepia australis</i> | 96.00% | 71.04% | 0.03% | 2.98% | 0.14% | 5.38% | 20.43% |
| <i>Sepia bertheloti</i> | 94.75% | 70.10% | 1.17% | 2.57% | 1.01% | 24.70% | 0.44% |
| <i>Sepia braggi</i> | 99.60% | 90.67% | 0.40% | 1.23% | 0.00% | 7.71% | 0.00% |
| <i>Sepia elegans</i> | 96.09% | 96.10% | 0.43% | 3.29% | 0.11% | 0.06% | 0.02% |
| <i>Sepia latimanus</i> | 95.28% | 79.56% | 6.18% | 11.32% | 0.33% | 1.40% | 1.20% |
| <i>Sepia officinalis</i> | 97.05% | 98.22% | 0.05% | 1.73% | 0.00% | 0.00% | 0.00% |
| <i>Sepia orbignyana</i> | 98.06% | 97.85% | 0.68% | 0.92% | 0.15% | 0.27% | 0.13% |
| <i>Sepia pharaonis</i> | 95.09% | 90.10% | 1.97% | 6.34% | 0.00% | 0.82% | 0.77% |

Table 3. Species mean habitat suitability (%) under different climate change scenarios.

| Species | 2050 | | | | | 2100 | | | |
|--------------------------|---------|--------|--------|--------|--------|--------|--------|--------|--------|
| | Present | RCP8.5 | RCP6.0 | RCP4.5 | RCP2.6 | RCP8.5 | RCP6.0 | RCP4.5 | RCP2.6 |
| <i>Sepia apama</i> | 46.31% | 39.49% | 41.69% | 40.77% | 43.97% | 29.56% | 35.03% | 37.99% | 42.23% |
| <i>Sepia australis</i> | 41.98% | 37.67% | 39.22% | 37.78% | 38.59% | 29.95% | 36.71% | 36.94% | 37.56% |
| <i>Sepia bertheloti</i> | 54.86% | 42.86% | 50.35% | 42.37% | 41.02% | 34.14% | 32.66% | 35.12% | 41.45% |
| <i>Sepia braggi</i> | 55.26% | 44.29% | 49.38% | 43.77% | 56.90% | 24.48% | 32.73% | 38.42% | 51.67% |
| <i>Sepia elegans</i> | 55.43% | 52.95% | 53.62% | 53.68% | 53.14% | 48.16% | 50.33% | 51.61% | 52.69% |
| <i>Sepia latimanus</i> | 53.06% | 49.22% | 50.38% | 50.13% | 49.71% | 46.45% | 48.15% | 49.80% | 50.96% |
| <i>Sepia officinalis</i> | 59.62% | 59.46% | 59.28% | 59.48% | 59.48% | 57.98% | 59.20% | 59.28% | 59.51% |
| <i>Sepia orbignyana</i> | 46.80% | 45.21% | 45.43% | 45.51% | 44.71% | 43.62% | 43.41% | 43.76% | 43.91% |
| <i>Sepia pharaonis</i> | 53.18% | 46.33% | 49.78% | 48.44% | 46.76% | 41.86% | 43.36% | 46.84% | 50.70% |

Figures

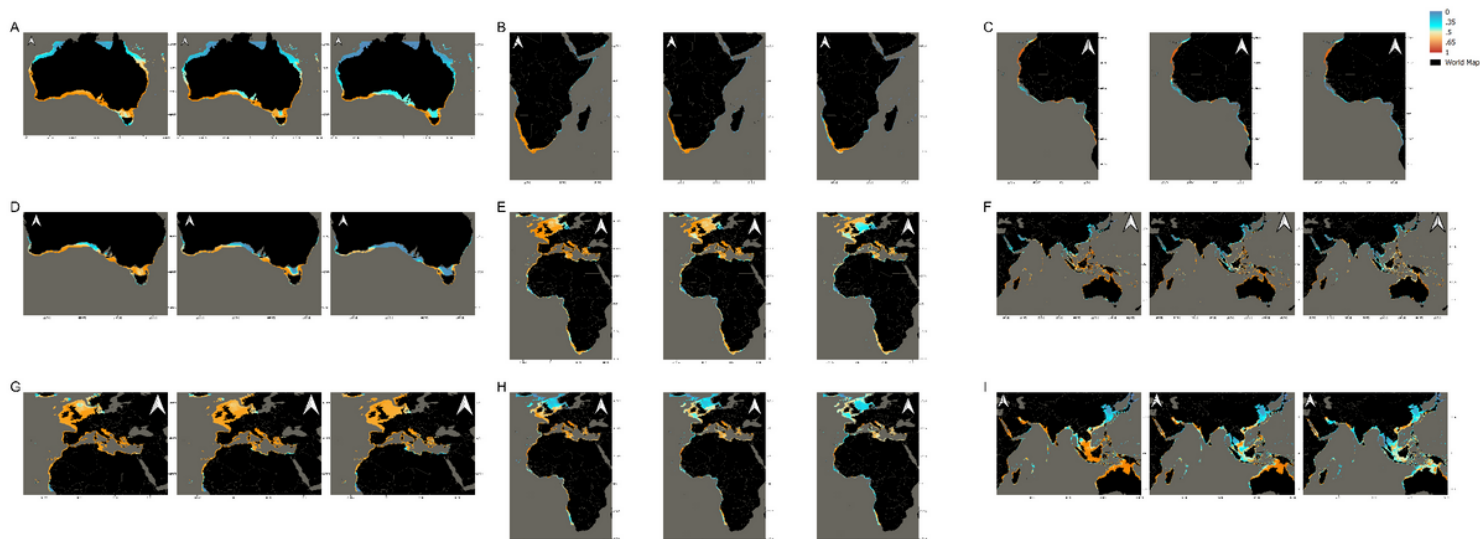


Figure 1

Map of the Distribution of nine *Sepia* species at the present, year 2050 RCP 8.5 and year 2100 RCP 8.5. Map source QGIS. A) *S. apama*; B) *S. australis*; C) *S. bertheloti*; D) *S. braggi*; E) *S. elegans*; F) *S. latimanus*; G) *S. officinalis*; H) *S. orbignyana*; I) *S. pharaonic*

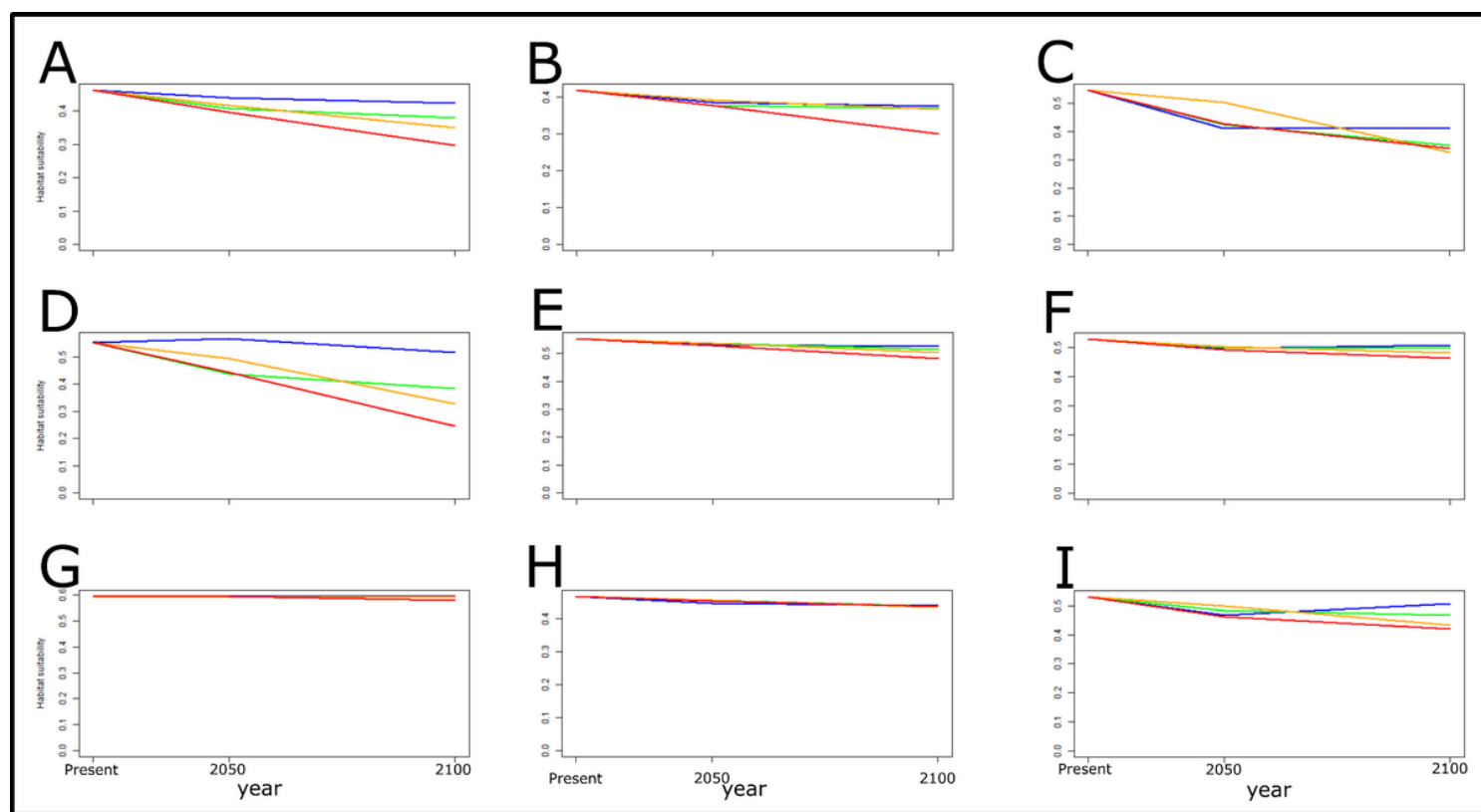


Figure 2

Mean habitat suitability of nine *Sepia* species on their current distribution, at the present, and future scenarios (years 2050 and 2100). RCP scenarios are represented by blue (RCP 2.6), green (RCP 4.5), orange (RCP 6.0) and red (RCP 8.5). A) *S. apama*; B) *S. australis*; C) *S. bertheloti*; D) *S. braggi*; E) *S. elegans*; F) *S. latimanus*; G) *S. officinalis*; H) *S. orbignyana*; I) *S. pharaonis*

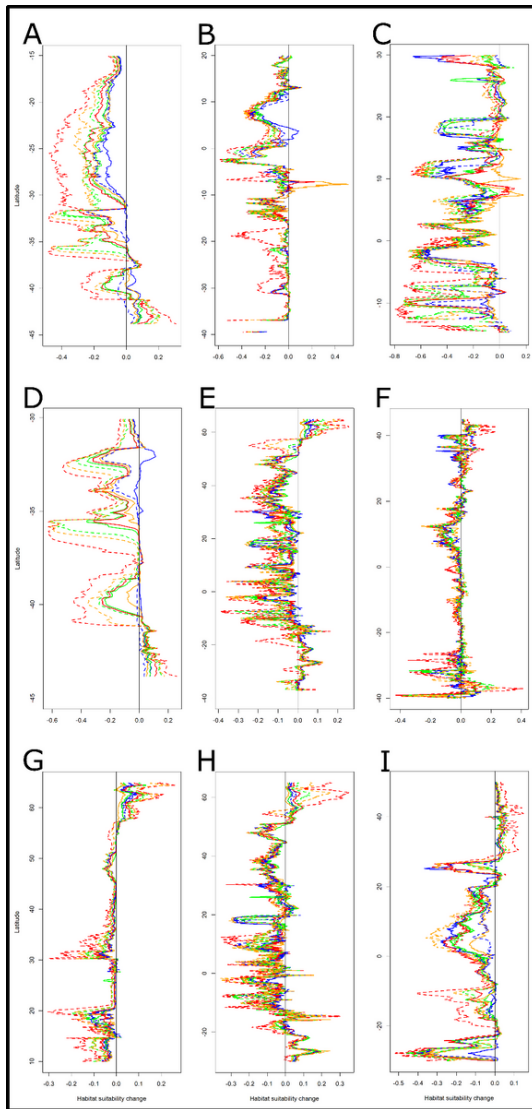


Figure 3

Habitat suitability average shift at each latitude for nine *Sepia* species. Lines for the different years are represented with continuous lines (2050) and dotted lines (2100). RCP scenarios are represented by blue (RCP 2.6), green (RCP 4.5), orange (RCP 6.0) and red (RCP 8.5). A) *S. apama*; B) *S. australis*; C) *S. bertheloti*; D) *S. braggi*; E) *S. elegans*; F) *S. latimanus*; G) *S. officinalis*; H) *S. orbignyana*; I) *S. pharaonis*

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