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Potential poleward distribution shift of dolphinfish (*Coryphaena hippurus*) along the southern California Current System

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Abstract The dolphinfish (*Coryphaena hippurus* Linnaeus, 1758) is an epipelagic top-predator that is globally distributed in tropical and subtropical waters. In the Eastern Tropical and Subtropical Pacific, this fish represents a target species for commercial and recreational fisheries. Climate change is affecting biodiversity, and a poleward expansion was suggested for dolphinfish due to its affinity for warm waters. Considering that hypothesis, the objective of this research is to model the historical distribution of dolphinfish within the northern limit of its distribution in the Eastern Tropical Pacific and to evaluate the potential distribution shift along the North American temperate coast due to environmental changes under climate change scenarios. According to the Ecological Niche Model, a poleward shift in dolphinfish distribution is expected during this century as a consequence of gradual northern displacement of the sea surface temperature isotherm along the North American coast.

Keywords Climate change · Sportfishing · Dorado · Ocean warming · Highly migratory species

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Introduction

Climate change is affecting biodiversity and causing additional pressure on already overused, degraded, and fragmented ecosystems (Parmesan and Yohe 2003; Root et al. 2003). The vulnerability of fish and invertebrates to warming depends on their physiology and thermal sensitivity (Bernardo and Spotila 2006; Huey et al. 2012). Over the last 40 years, oceans have warmed at average rates of > 0.1 °C per decade in the upper 75 m (IPCC 2013), and this situation has induced poleward shifts in geographic distribution of many marine species as well as changes in migration patterns and timing of seasonal activities, such as reproduction (Beaugrand et al. 2009; Salvadeo et al. 2010; Péron et al. 2012; Poloczanska et al. 2013). Moreover, all climate scenarios agree that the oceans will heat up even more in the future, with estimates of average increases for the end of the century between 0.6 and 2 °C in the shallowest 100 m of the water column; this warming is expected to be greater in tropical and subtropical regions (Collins et al. 2013).

The dolphinfish (*Coryphaena hippurus* Linnaeus, 1758) is an epipelagic top-predator that is globally distributed in tropical and subtropical waters (Díaz-Jaimes et al. 2010). This species has a fast-growth rate; it can reach 1.5 m in length and 30 kg in weight and become sexually mature at sizes over 50 cm fork length (Madrid and Beltrán-Pimienta 2001; Zúñiga-Flores et al. 2008; Alejo-Plata et al. 2011). The dolphinfish is an opportunistic feeder with a wide trophic spectrum that includes small and medium size pelagic species (Aguilar-Palomino et al. 1998; Tripp-Valdez et al. 2010; Teffer et al. 2015). In the Eastern Pacific, this species represents a target for commercial and small-scale fisheries in Ecuador, Peru and Central America, where fishermen take advantage of its schooling behavior under floating objects to catch it (Alejo-Plata et al. 2014). In contrast, in Mexico, the stock is reserved by law for recreational fishing within 60 nautical miles (96 km) from the coast (DOF 1995).

In the temperate and subtropical waters of the southern California Current System and in the Gulf of California, the water temperature showed a warming trend during the past century (Lluch-Belda et al. 2009). As this trend is likely to be maintained, poleward expansion of tropical fish species is expected, and this phenomenon is already in process according to some authors (Salvadeo et al. 2010; González-Cuéllar et al. 2013; Booth et al. 2018; Fernández-Rivera Melo et al. 2015). As Norton (1999) proposed, dolphinfish may present a geographic range extension to the north due to its affinity for warm water. Considering that hypothesis, the objective of this study was to determine the distribution of dolphinfish in the north section of the Eastern Tropical Pacific and evaluate, through ecological niche models, the possible distribution shifts along the North American temperate coast caused by temperature changes predicted by different global warming scenarios. We discuss the ecological and fisheries management implications of this event in the region.

Methods

Study area

In this study, we restricted the analysis along the tropical-temperate transitional area of the eastern Pacific because we wanted to evaluate potential dolphinfish changes in the northern limit of its historical distribution, an area where the species is an important resource for sport fishing activity. Northwest Mexico is part of a highly dynamic transition zone, where the California Current System (cool), the Eastern Pacific warm pool (warm) and water from the Gulf of California (temperate) converge, causing great seasonal variability in temperature and ocean productivity (Lluch-Cota et al. 2017). In addition, that region is characterized by other oceanographic processes of biological importance, such as wind-driven coastal upwelling, ocean gyres and thermal fronts (Santamaría-del-Angel et al. 1994; Lluch-Belda et al. 2000; Navarro-Olache et al. 2004; Etnoyer et al. 2004; Kurczyn et al. 2012). These oceanic features generate adequate habitat conditions for larval development and recruitment of many species of commercial importance; they are also feeding grounds for pelagic top predators (Hewitt 1981; Lluch-Belda et al. 2003a; Etnoyer et al. 2006; Yen et al. 2006). In addition to the seasonal changes, other natural processes affect productivity and temperature in multiannual time scales, including the El Niño Southern Oscillation (ENSO). ENSO is the dominant mode of climate variability at interannual timescales in this region (Lluch-Cota et al. 2001; Wang and Fiedler 2006; Lluch-Cota et al. 2010; Salvadeo et al. 2013), in particular because the warm phase of ENSO causes the collapse of primary productivity along the region and affects the biological richness and latitudinal distribution of marine fauna (Benson et al. 2002; Lluch-Belda et al. 2003b, 2005; Salvadeo et al. 2011, 2015).

Dolphinfish occurrence and environmental data

Since *Coryphaena hippurus* is a pantropical species, we gathered georeferenced records all around the world and in all seasons from Global Biodiversity Information Facility (GBIF.org 2018). To reduce misleading records, we excluded data obtained before 1970 and eliminated inconsistent occurrences (for example, records obtained on land or misidentification records corresponding to dolphins). In addition, once a record existed for a given 9-km spatial unit along the study region, we eliminated the remaining ones to reduce spatial autocorrelation (Boria et al. 2014; Prieto-Torres and Pinilla-Buitrago 2017); such distance was selected to retain the spatial resolution of satellite data used for spatial modeling. The final database was composed of a total of 12,517 occurrence records (Fig. 1).

The marine environmental data used for modeling were obtained from the Bio-ORACLE v2.0 webpage, which offers a wide set of 18 variables in a spatial resolution of 9 km (e.g., temperature, salinity, current

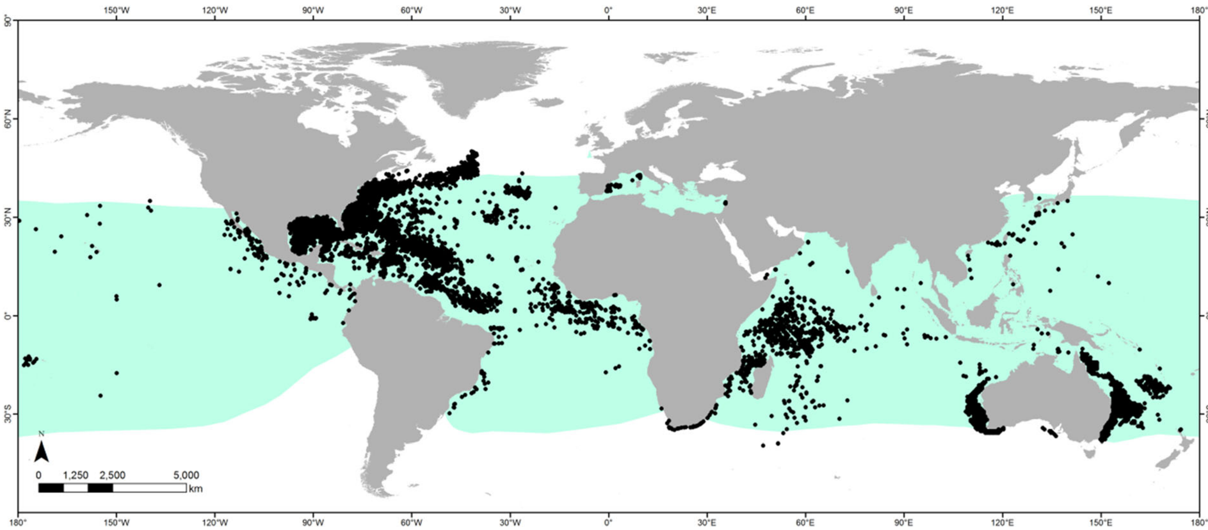

Fig. 1 *Coryphaena hippurus* geographic records used in modeling process, each black dot corresponds to a record. The distribution area according to IUCN is shown in turquoise

velocity, nitrates, chlorophyll, primary productivity etc.; see details of the whole set in Assis et al. 2018) including maximum, long term maximum, minimum, long term minimum, mean and range values (a total of 88 layers). From the complete set of these variables we selected the maximum, minimum, range and mean values, then, to avoid collinearity between variables, we removed those with higher Pearson correlation coefficients (> 0.8). Subsequently, we evaluated the contribution percentage of the remaining non-correlated variables according to a Jackknife analysis in model calibration stage, such variables were: mean calcite, light diffuse attenuation coefficient, mean nitrates, pH, mean phosphates, mean primary productivity, minimum primary productivity, mean salinity, mean silicates, mean temperature and range of temperature. Finally, we selected the variables with the higher contribution to the model and with major biological relevance according to others works (Zuñiga-Flores et al. 2008; Martínez-Rincón et al. 2009; Farrell et al. 2014; Kitchens and Rooker 2014; Brodie et al. 2015, 2017; Marín-Enríquez et al. 2017; Marín-Enríquez and Muhlia-Melo 2018): the annual mean and range of sea surface temperature (both in C°), primary productivity (g/m^3/day) and annual mean salinity (practical salinity units).

Historic ecological niche model (ENM)

We used the maximum entropy routine (Maxent 3.3.3 k) to build the historic dolphinfish ENM (Phillips et al. 2006). Maxent is a machine learning algorithm that estimates the potential distribution of a species based on its environmental requirements. Maxent has a strong theoretical basis (Soberón and Nakamura 2009) and is particularly efficient at predicting the presence of species in areas with poor sampling efforts or that are difficult to access, and it has become a useful tool to prioritize localities for conservation and evaluate the potential impacts of climate change in natural communities (Freeman et al. 2013).

We performed the historic ENM using the four non-correlated environmental variables described above. We used 10 model replicates with random occurrences seeded into each one. We used 10,000 random points for background characterization, and we allocated 20% of occurrence data to model evaluation and 80% to build the ENM. We turned off the clamping and extrapolation options. All remaining program parameters were used by default. To evaluate performance, we used partial Receiver Operating Characteristic (ROC) from the Niche toolbox portal (Peterson et al. 2008; Osorio-Olvera et al. 2018), and we tested if our ENM was better compared to a random model with a statistical significance value. To identify the presence/absence of dolphinfish from Maxent output, we averaged the three replicates with the best performance (with the higher partial ROC value and the lower omission rate), and then we applied a fifth percentile training presence threshold. This threshold minimizes the omission error because it rejects the 5% of presence records with the lowest suitability value, which has been demonstrated to better identify the distribution area of species (Escalante et al. 2013).

ENM for future conditions

To evaluate future dolphinfish distributions under climate change scenarios, we made projections based on the expected surface temperature data under RCP 2.6, RCP 4.5, RCP 6.0 and RCP 8.5 scenarios for the decades 2040–2050 (hereafter 2050) and 2090–2100 (hereafter 2100). A RCP (Representative Concentration Pathway) is a greenhouse gas concentration trajectory adopted by the IPCC in 2014 (IPCC 2013), where the emissions peak could be approximately 2020 (RCP 2.6), 2040 (RCP 4.5), 2080 (RCP 6) and to the end of this century (RCP 8.5). These data were taken from BIO-ORACLE (Assis et al. 2018).

We projected the future potential distribution on the study area, from Mexican Tropical Pacific to the Northern California ecoregions (Spalding et al. 2007) since we are interested in evaluating a potential northward distribution shift (Fig. 2A). We used the same set of oceanographic variables, as well as the Maxent configuration applied for historic ENM, and applied the fifth percentile commission threshold rule to determine future presence. However, as primary productivity projected data are not available, we assumed no change in this variable; thus, we used the same layer of primary productivity used in the historic ENM.

Potential distribution shift

We calculated the area (in square kilometers) that ENM predicted to encompass the historic and future presence of dolphinfish in the southern California Current System; from direct observation of the maps of current and potential species occurrences, we explored a potential poleward expansion of the environmental conditions that were suitable for *C. hippurus* in this region. In addition to the direct comparison of future and current distribution maps, we calculated the position of the niche centroid for each climate change scenario since this is an estimation of the most suitable conditions for the species. From these results, we visually compared the latitude of the historic and projected suitability centroid (Ortega-Andrade et al. 2015).

Results

Historic ENM

The three best replicates in ENM showed good performance according to partial ROC (average value 1.86 ± 0.002) and were also significantly different when compared to a random model ($p < 0.001$), confirming that

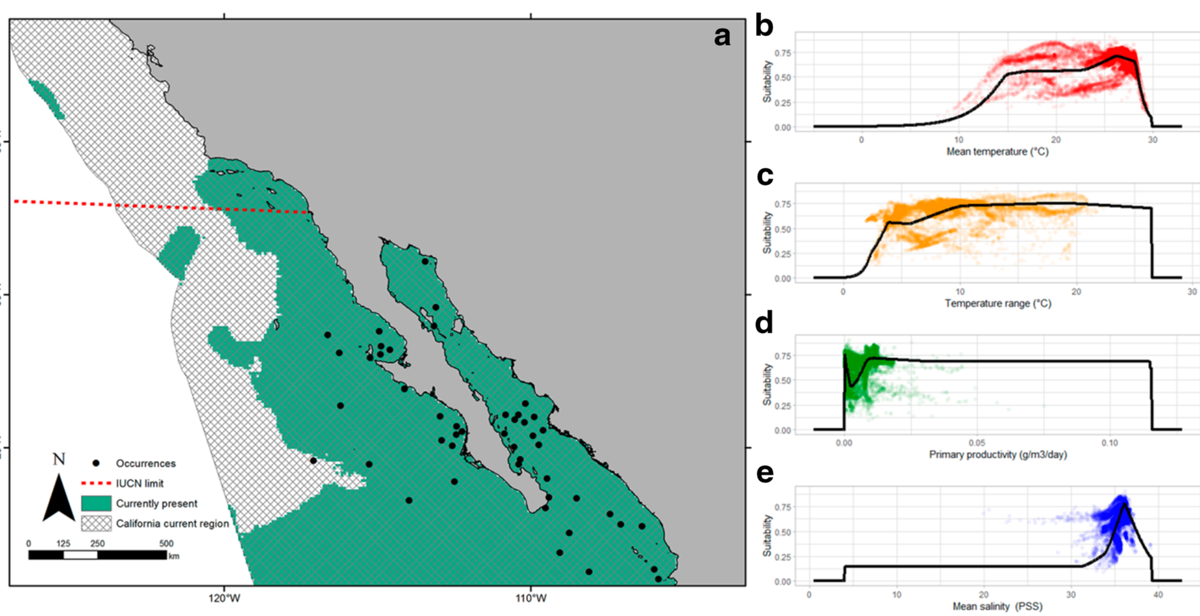

Fig. 2 In panel A we show Dolphinfish distribution area predicted by ENM for historic conditions in California Current System and Gulf of California (grid grey area) which correspond to the study area. The black dots are *Coryphaena hippurus* occurrences. We also show panels B-E the response curves of dolphinfish to environmental variables according to Maxent; points in these panels correspond to occurrences

our approach has strong statistical support to describe the ecological niche of the species.

According to the ENM, dolphinfish are present along the California Current System from the southern Gulf of California to the United States (34° N), covering an area of ~1,203,755 km^2 (Fig. 2a). Considering the four variables used for the simulation, the most important ones related to the distribution of dolphinfish were SST annual mean, with 85.7% of contribution, followed by mean SST annual range (9.7%), annual mean salinity (4.0%), and mean primary productivity (0.6%), with a high suitability habitat between 15 and 28 °C of annual mean SST (Fig. 2b), SST ranges higher than 3 °C and lower than 21 °C (Fig. 2c), low primary productivity (Fig. 2d), and salinity ~35 psu (Fig. 2e).

Projected ENM under climate change scenarios

According to the IPCC climate scenarios applied, the projected warming along the study area showed a latitudinal displacement of the mean SST isotherms towards the north (Fig. 3). On average, in the southern California Current region, the projections depicted a temperature rise between 1.44 and 2.03 °C over the historic SST average.

Analyzing the response of dolphinfish to these changes, we predict a poleward habitat expansion for the species along the California Current (Fig. 4). In general, we found that the dolphinfish habitat suitability area will increase in the future (Table 1). Last, the analysis of variation on suitability according to latitude revealed that the centroid moves northward (Table 1; Fig. 5). This means that *C. hippurus* will likely find better conditions for its presence in the north section of the subtropical eastern Pacific as temperatures rise.

Discussion

The historic ENM of the species in the study region includes the southern California coast (USA), the west coast of Baja California Peninsula and the Gulf of California in Mexico (Fig. 2a), with a centroid around 24.91 degrees of latitude (Table 1; Fig. 5), which corresponds to the southern Gulf of Ulloa in the west coast of Baja California Peninsula, a region important for the oceanic migratory corridor of the species (Marín-Enríquez et al. 2017; Marín-Enríquez and Muhlia-Melo 2018), and with the central part and mouth of the Gulf of California, an area with high catches during warm months of the year (Zúñiga-Flores et al. 2008). The historic EMN for dolphinfish (Fig. 2) showed that the annual mean and annual range of SST and the primary productivity are important factors in habitats occupied by dolphinfish in the Northeast Pacific; this finding is consistent with observations of other authors regarding the relevance of ocean productivity and SST to determine dolphinfish distribution and movements in the Eastern Tropical Pacific (Zúñiga-Flores et al. 2008; Martínez-Rincón et al. 2009; Marín-Enríquez et al. 2017; Marín-Enríquez and Muhlia-Melo 2018).

The relationship between habitat suitability and mean annual SST showed a peak preference of the species for temperatures between 24 and 28 °C (Fig. 2b), a fact that has been confirmed repeatedly in the region (Martínez-Rincón et al. 2009; Marín-Enríquez et al. 2017; Marín-Enríquez and Muhlia-Melo 2018) and in other regions, such as the east coast of the USA (Farrell et al. 2014) and eastern Australia (Brodie et al. 2015, 2017). In addition, the SST range showed high habitat suitability between 10 and 25 °C (Fig. 2c); this SST range is indicative of areas with high seasonal thermal amplitude due to seasonal upwelling

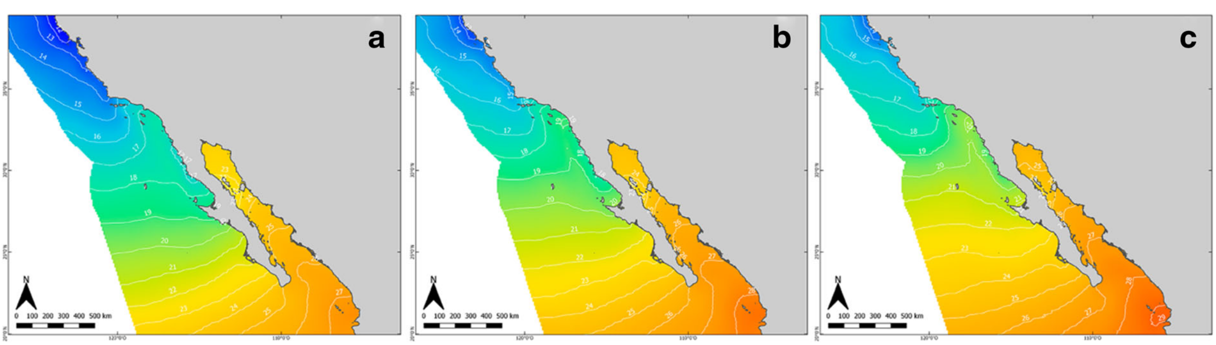

Fig. 3 Annual mean of sea surface temperature (°C): Historic (2003–2015) (**A**), and projection for the year 2050 (**B**) and 2100 (**C**) under the RCP 4.5 scenario

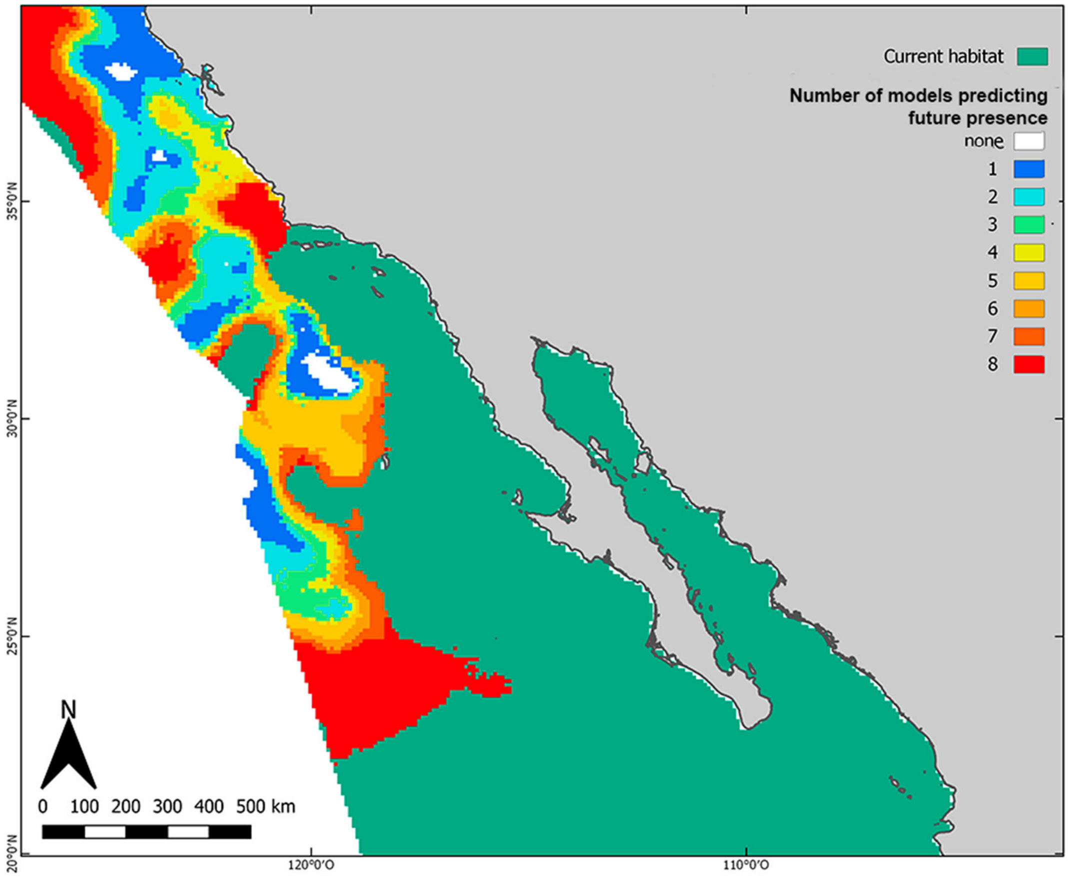

Fig. 4 Historic distribution of dolphinfish calculated by ENM (green area), and the predicted habitat extension under different climate change scenarios. The different colors indicate the number of scenarios predicting future environmental suitability in the region

activity, such as the Gulf of California and the southern part of the California Current System (Lluch-Cota et al. 2007; Turrent and Zaitsev 2014). This result highlights the importance of these ecosystems for the species: they stand out for their well-marked seasonality and high biological productivity (Lluch-Belda et al. 2000) and are part of its migratory corridor (Marín-Enríquez et al. 2017). With respect to primary productivity, the ENM presents a habitat suitability peak at low concentrations (Fig. 2d). In general, the presence of this species is associated with low surface chlorophyll concentrations (Farrell et al. 2014; Marín-Enríquez and Muhlia-Melo 2018); this is due to the temporal lag between the productive upwelling season and the presence of the species in the study region (Marín-Enríquez and Muhlia-Melo 2018). On the other hand, habitat suitability related to salinity showed a peak in areas with 34–38 psu (Fig. 2e), this salinity range include the range of the Gulf of California and the Southern region of the California Current System (Berón-Vera and Ripa 2002; Schneider et al. 2005).

Studies on marine fish indicates that the effects of ocean acidification and temperature on the growth, development and swimming ability on the early planktonic life stages are species-specific, so the potential effects cannot be generalized and the elevated temperature seems to have the greater impact (Bignami et al. 2017; Cominassi et al. 2019; Downie et al. 2020). For dolphinfish, the scientific literature contradicts itself since one study conclude that egg incubation under acidified conditions had a negative impact on larvae metabolism and swimming behavior (Pimentel et al. 2014); while in other study the authors concluded that the lack of effect provides an optimistic indication that this large tropical species may not be overly susceptible to ocean acidification (Bignami et al. 2014). The reproductive season for dolphinfish in the study area occurs

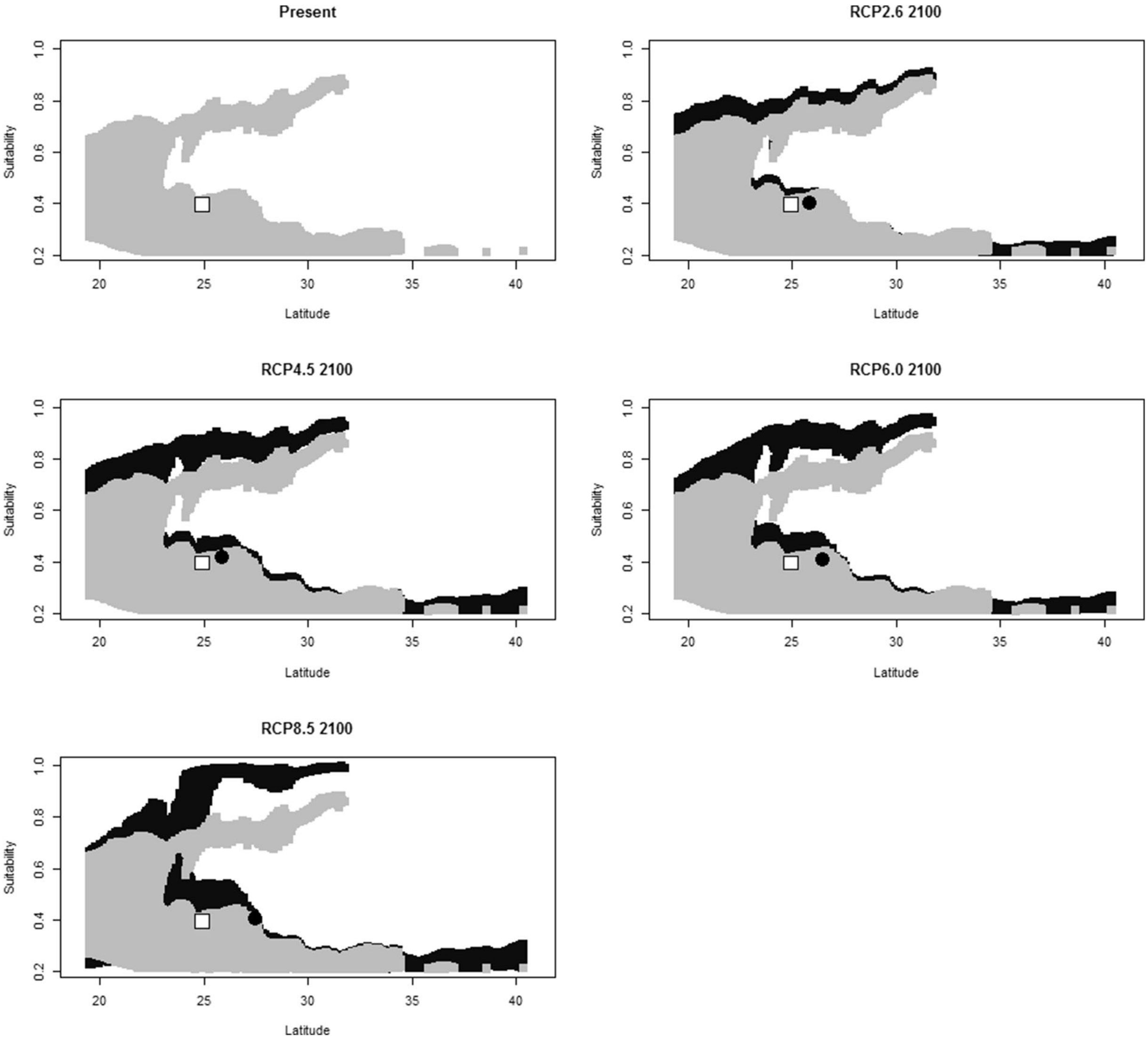

Fig. 5 Environmental suitability estimated in ENM by latitude for the historic state and the different climate change scenarios for 2100. Grey and black areas represent current and future conditions respectively. The niche centroid for historic (white square) and future (black point) conditions of dolphinfish are also shown

mainly during the second half of the year, in the warm months of summer-autumn (Zúñiga-Flores et al. 2011); for that reason it would be expected that the increase in temperature stimulates the reproduction of this species throughout its new distribution range.

With regard to the potential distribution shift of dolphinfish under different global warming scenarios during the present century, the predictive ENM shows that this pelagic predator may find suitable conditions farther north (~ 300 km), crossing the United States-Mexico border and reaching the San Francisco bay area (Fig. 4). The potential northward shift in dolphinfish distribution presented here was initially suggested by Norton (1999) as a result of poleward habitat extension determined by the increased catch of dolphinfish of commercial and recreational fishing vessels during warm years. The habitat extension coincides with the displacement of subtropical species to the north forced by anomalous warm conditions in the California Current; these warming events are related locally to changes in upwelling and onshore transport and remotely to coastal-trapped long wave transmission from the equatorial ocean related to ENSO (California Department of Fish and Game 1986; McLain

Table 1 Suitable habitat area predicted for *C. hippurus* in the California current zone, the latitude of the suitability habitat centroid is located according to ENM for each scenario, and the difference relative to the historic suitable habitat area

Scenario	Area (km^2)	Increased area relative to the historic (%)	Latitude centroid	Latitudinal difference relative to the historic
Historic	1,203,755	-	24.91	-
RCP 2.6 2050	1,527,438	10.9	26.20	1.29
RCP 4.5 2050	1,595,201	15.7	26.85	1.94
RCP 6.0 2050	1,424,501	5.9	25.88	0.97
RCP 8.5 2050	1,553,883	18	26.51	1.6
RCP 2.6 2100	1,363,075	7.5	25.80	0.89
RCP 4.5 2100	1,415,384	12.3	25.88	0.97
RCP 6.0 2100	1,559,315	17.9	26.45	1.54
RCP 8.5 2100	1,660,571	38	27.49	2.58

et al. 1985; Stull et al. 1987; Norton 1999; Lluch-Belda et al. 2005).

If this poleward shift occurs in the dolphinfish distribution, the species may become more abundant in the California Current Ecosystem in future decades, especially during the summer-fall period. The successful colonization of that ecosystem by the species depends on environmental conditions as well as on biological context, in particular the presence of adequate prey. Thus, during the displacement to the north, dolphinfish populations could take advantage of the high productivity of the upwelling ecosystem and the presence of potential prey, such as pelagic red crabs, mesopelagic squid and small pelagic fish (Aguilar-Palomino et al. 1998; Olson and Galván-Magaña 2002; Tripp-Valdez et al. 2010, 2015).

The arrival of dolphinfish to temperate regions in the west coast of North America may cause a severe trophic overlapping and the consequent competition with other top predators, such as tunas, sharks, cetaceans and even sea turtles, all of which feed on the same or similar prey (Etnoyer et al. 2004, 2006; Boustany et al. 2010; Block et al. 2011; Schaefer et al. 2011; Teffer et al. 2015). Nevertheless, it is also possible that some of those subtropical and temperate top predators will present a similar distribution shift to the north under future climate changes (Hazen et al. 2013), as reported for dolphin species in the region (Salvadeo et al. 2010), cancelling or minimizing any competitive interactions. These potential trophic interactions due to geographical overlapping are relevant for ecosystem-based management of pelagic fisheries, especially in the context of shifting fish populations in response to climate change. However, given its rapid growth and wide trophic spectrum, the dolphinfish can be characterized as a resilient resource capable of withstanding high rates of capture and adapting to environmental changes (Alejo-Plata et al. 2014).

The livelihoods of many communities on the western coast of Baja California Peninsula depend mostly on artisanal fisheries, an activity considered highly vulnerable to global warming. In these circumstances, the diversification of activities is an important adaptation measure that must be implemented to reduce their vulnerability (Morzaria-Luna et al. 2014; Lluch-Cota et al. 2017). Considering that the dolphinfish is reserved for sport fishing in Mexico, the poleward distribution shift of the species could be used to promote sport fishing in the northern communities as a way to diversify their productive activities, to decrease their vulnerability and to raise their resilience to climate change effects. However, the potential poleward shift also benefits recreational fishing in California (USA), which could compete as a destination with the fishing sites along the Baja California Peninsula. Furthermore, dolphinfish occur in the California recreational catch primarily during warm water years, mostly in the Southern California Bight, and they are occasionally taken by the high-seas longline fishery landing in California (FMP-HMS 2018). This could add conflicts between commercial and recreational fisheries on both sides of the border, making the management of this high migratory species complex.

It is important to remark that ENM have some methodological constraints that need to be considered in the interpretation of results (Jarnevichet al. 2015). Aspects such as the species record data quality, the biological relevance of the environmental variables, the modeling algorithm, and the modeling assumptions may impact on the results. Because of that, it is important to minimize the possible constraints of ENM by taking conscious precautions of all these aspects (Feng et al. 2019). Despite that, ENM are a useful tool (Warren 2012; Melo-Merino et al. 2020) that may improve our capacity to respond to climate change, but that implicates a continuous process of model calibration and validation.

In conclusion, a poleward shift in dolphinfish distribution is expected during this century (Figs. 4 and 5) due to warming of the southern California Current Ecosystem region as a consequence of gradual northern displacement of the sea surface temperature isotherm along the North American coast (Fig. 3).

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