Understanding Ecological Implications of Mesoscale Climatic Impacts on Juvenile White Sharks (*Carcharodon carcharias*) and Southern Sea Otters (*Enhydra lutris nereis*) Along the California Coast

Francesca Stepanov

ABSTRACT

Anthropogenic climate change has expansive effects on ecosystems. A mechanism of change stems from increasing sea surface temperatures (SST) shifting marine organisms' habitat availability. Recent studies have shown increased Juvenile White Shark (*Carcharodon carcharias*) presence further northward along the California coast during marine heatwaves. With SST projections derived from climate models, juvenile *C.carcharias,* that are more susceptible to thermal shifts than their adult counterparts, may have limited thermal suitability in their current habitat range. As a result, juvenile *C.carcharias* may more permanently shift northward along the California coast. Increased presence of juvenile *C.carcharias* directly impacts a keystone species in the Monterey Bay Ecosystem, Southern Sea Otters (*Enhydra lutris nereis*), as they are often mistaken for prey. Studies examining levers that inhibit *E.nereis* population recovery rates point to *C.Carcharias* as a threat. With depleted *E.nereis* populations, Monterey Bay kelp forest ecosystems will suffer. This study aims to model and predict future juvenile *C.carcharias* habitat suitability using electronic tagging data and assess how future habitat availability will coincide with established *E.nereis* populations in California.

KEYWORDS

Carcharodon Carcharias, SPOT and PAT Tagging, *Enhydra lutris nereis* Habitat, Thermal Suitability Model, SST Climatologies

INTRODUCTION

Over the last decade, anthropogenically induced climate change has increased global surface air temperatures (IPCC 2022). According to the IPCC AR6 Report, there has been a 1.1°C average increase in global surface temperature between 2011-2020 relative to a baseline from 1850-1900 (IPCC 2022). This warming has implications on the Earth's oceans. Sea surface temperature (SST), which is the temperature close to the ocean's surface, absorbs heat and serves as an indicator for warming (Huang et al. 2017). In the last three decades, SST has exceeded any temperature recorded before 1880 (Huang et al. 2017). However, SST is not just an indicator for global warming, but presents its own consequences. Fluctuations of SST can have adverse impacts on marine species as habitat ranges are generally governed by thermal ranges based on physiological needs. Current studies analyzing the impact of warming ocean temperature on marine species shifts suggest that many marine species are already migrating poleward (Hastings et al. 2020). Additional studies have investigated future impacts, and those projections suggest that equatorial biodiversity will decrease with increasing ocean temperatures (Poloczanska et al. 2016). Given SST continues to rise, it is imperative that we understand how different marine species will respond to the current trajectory.

Often, perturbations to apex predator habitat ranges can have cascading and widespread consequences on ecosystems (Baum et al. 2009). One predator of interest is the White Shark (*Carcharodon carcharias*) due to increased sightings off the California coast and unresolved migratory patterns (Tanaka et al. 2021). Between the ages of 3 to 4 *C.carcharias* undergo a shift in habitat, diet, and thermal physiology (White et al. 2019). While literature suggests a greater surface area to volume ratio in juveniles can strain their physiological thermoregulation patterns, there is not yet an established explanation for variance between adult and juvenile thermoregulation mechanisms (Tanaka et al. 2021). Although the physiological underpinnings of ontogenetic shifts are not fully understood, there is significant evidence that temperature governs the movement of juvenile *C.carcharias* (Weng et al. 2007). Analysis of juvenile *C.carcharias* movement indicates they occupy narrow thermal ranges, suggesting temperature influences habitat selection (Weng et al. 2007). Generally, juvenile *C.carcharias* along the California coast have not occupied a region above 34° N (Tanaka et al. 2021). Tanaka et al 2021, which this study is an extension of, established an increased presence of juvenile *C.carcharias* above 34° N during the 2014-2016 marine heatwave in coastal California. The novel occurrence of juvenile *C.carcharias* in the Monterey Bay region [36-36.8 °N] suggests climate change may force juvenile *C.carcharias* northward, toward cooler waters. As SST continues to rise, it is important to understand more about how juvenile *C.carcharias* habitat range will change.

Increasing SST may alter juvenile *C.carcharias* habitat range, and as a result indirectly impact other species. Along coastal California, southern sea otters (*Enhydra lutris nereis*) occupy a historically established niche (Johnson et al. 2009). Since the early 20th century, when fur traders exploited *E.nereis* and drove them to near-extinction, *E.nereis* have struggled to regain the entirety of their previous population density due to slow growth rates (Elliott Smith et al. 2020). Recent evidence suggests that *C.carcharias* bites play a pivotal and novel role in slowing *E.nereis* population recovery rates along the California coast, and are the greatest source of *E.nereis* mortality (Moxley et al. 2019). Both *E.nereis* strandings, of injured or deceased otters, and investigation of *C.carcharias* stomach contents, indicate the biting is most likely incidental and nonconsumptive (Moxley et al. 2019). Since *E.nereis* are a keystone species, slowed population growth rates may pose a threat to entire ecosystems along coastal california (Konrad et al. 2022). Aside from transient migratory periods, *E.nereis* and *C.carcharias* have not occupied the same habitat range along the California coast. *E.nereis* are located between 34 and 37°N and only recently have juvenile *C.carcharias* surpassed 34°N (Nicholson et al. 2018). Given the influence of *C.carcharias* over *E.nereis* populations, there must be a more developed understanding of how SST may shift habitat ranges for *C.carcharias*, and how that may coincide with established *E.nereis* habitat.

Species distribution models (SDMs) are a prominent method used to understand how species distributions change over space and time. Tagged marine mammals can serve as a dependable dataset for calibrating SDMs. Weng et al. 2007 used tagging data to visualize juvenile *C.carcharias* movement and hypothesize motives for habitat shifts. Predictive modeling allows us to understand how habitat ranges will fluctuate given changing parameters. These predictions can then be used to determine where different species may overlap or shift. In this study, we use *C.carcharias* tagging data to create a thermal suitability model, which serves as a type of SDM based on the assumption that *C.carcharias* habitat is determined by thermal preference.

This study aims to understand the interactions between increasing SST, juvenile *C.carcharias,* and *E.nereis* along the California coast. Using Tanaka et al 2021 as a foundation, this paper will quantify and visualize both current and future juvenile *C.carcharias* distribution and compare it to *E.nereis* habitat range. First, a model that uses historical SST data will characterize current juvenile *C.carcharias* habitat suitability range along the California coast based on SST. From there, the goal is to understand future *C.carcharias* habitat using downscaled CMIP6 projections under the "business as usual"; SSPS 5-8.5 scenario over the next 30 years (2020-2049). This projected species distribution will be used to interpret how future juvenile *C.carcharias* will overlap with established *E.nereis* habitat along the California coast.

METHODS

Study site and tagging data

The Monterey Bay Aquarium released a dataset for public use in 2020 of tagged *C.Carcharias* using both PAT and SPOT tags (O'Sulliivan et al. 2022). In collaboration with other organizations, this project aimed to understand *C.carcharias* migration and movement along the California coast (O'Sullivan et al. 2022). Tags were deployed along the Southern Bight (SCB) coastline and Vizcaíno Bay in Mexico, which is a known nursing spot for *C.Carcharias* (O'Sullivan et al. 2022). Although the tags were placed on juvenile *C.carcharias* in SCB and Vizcaíno, the *C.carcharias* eventually moved northward and into Monterey. Figure 1 highlights the key deployment and migration sites, including Vizcaíno Bay in Mexico, Point Conception (part of the SCB), and Monterey.

While more *C.carcharias* were tagged, this study uses data that encompasses 14 tagged juvenile *C.carcharias* due to accessibility. Both SPOT and PAT tags only upload data to satellites, such as Argos, when they break above the water and transmit data. Upon transmission the raw data is uploaded and processed. The Monterey Bay Aquarium White Shark tagging dataset provides:

1. date, time and location of tag deployment
2. date, time and location of Argos hits on SPOT tags
3. date, time and location of PAT tag pop-off

4. depth and temperature time series and histograms

Key parameters utilized in this study include temperature and location time series.

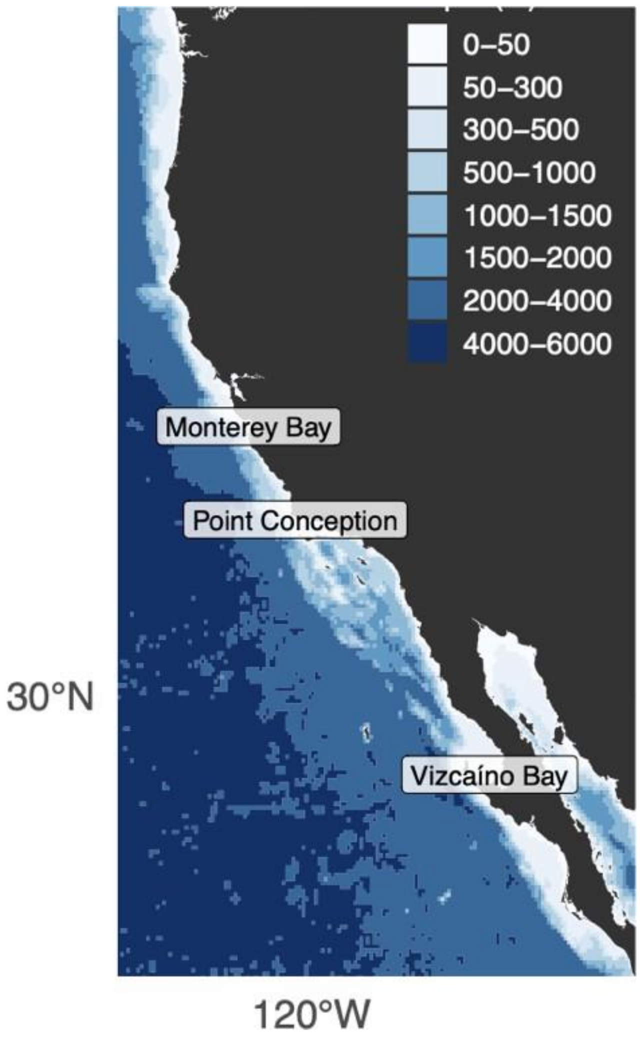


Figure 1. Relevant study sites along the California Coast. Labeled spots include Monterey Bay, Point Conception, and Vizcaíno Bay.

Thermal Suitability Model

A thermal suitability model and future predictions were produced in the R programming environment (R Core Team 2022). In order to understand *C.Carcharias* habitats suitability, we created a thermal suitability model. This model utilized tagging data under the assumption that *C.Carcharias* occupancy of a habitat is based on the temperature in that area. Thus, a thermal suitability model classifies the proportion of occupancy at a given temperature. The thermal suitability model took several different packages in R to build. In order to read a large ecosystem GIS file, I used the readOGR function from the rgdal package (Pebesma and Bivand 2005). The readOGR function enables the software to process a spatial map of data. Since the tagging data and model is spatial, different functions from the raster package are used (Hijmans 2022). For example, the subset function is used to stack different layers from the tagging dataset. Temperatures extrapolated from tagging data were plotted against juvenile *C.carcharias* occurrences at those temperatures using the package ggplot2 (Wickham 2016). Once the thermal suitability model was created, SST temperatures informed the habitat range of juvenile *C.carcharias* using thermal preference.

Modeling current and projected SST data

In order to generate a current and future model of *C.Carcharias* habitat suitability, SST data was combined with the thermal suitability model. The model of *C.Carcharias* habitat from 1984-2014 uses SST data sourced from the NOAA 1/4° Daily Optimum Interpolation Sea Surface Temperature (OISST), which is a complete analysis map of SST data using a variety of data collection methods (Reynolds 2008). This project relies on the OISST dataset from 1982-2019, but specifically uses 1984-2014 data.

Future SST data (2020-2049) will be derived from NOAA's Coupled Model Intercomparison Project 6 (CMIP6). CMIP6 provides a database of ensemble global climate change models used by the IPCC. Within each model, there are projections based on certain warming scenarios. This paper utilized CMIP6 SST data given a SSPS 5-8.5 scenario. SSPS 5-8.5, often referred to as "business as usual", is built on the assumption that global emissions patterns will continue as they do now with minimal policy intervention and large reductions in emissions. Our study uses this scenario as it is most in line with the future as we currently see now.

Similar plotting techniques to the thermal suitability model were employed to create SST climatologies. Since OISST data is stored as a net CDF file, I used the "nc_open" function within the ncdf4 package to open and process the files (Piece 2023). In order to create SST maps along the California coast, functions within the maps package were used (Becker 2022). Within each model, functions from the colorRamps package were used to create density-dependent gradients (Keitt 2022).

***E.nereis* habitat range**

The last piece of this project relies on sufficient *E.nereis* habitat data to understand the established habitat range and areas of highest *E.nereis* density. In order to quantify this, we used *E.Nereis* census data from the U.S. Geographical Survey (USGS) between 1982-2019 (Tinker and Yee 2019). Census excursions occur during the spring on a yearly basis, and *E.nereis* counts are uploaded onto a spatially resolved database.

The original shapefile contained 1985 observations through the 37 years of observations. In order to parse through the *E.nereis* data, we used multiple methods to read the shapefile and then rasterize it using functions from the raster package (Hijmans 2022). Through the iteration process, multiple functions from the sp package were used to rasterize the shapefiles (Pebesmaa et al. 2005). Once the shapefiles were processed and rasterized, we plotted them to visualize density against latitude along the California coast (Becker 2022).

RESULTS

Thermal Suitability Model

The thermal suitability model created using electronic tagging data (Figure 2) shows the frequency of *C.carcharias* occurrence at a given SST. The model was created using frequency of occupancy at given SST from ARGOS satellite data acquired from electronic tags on *C.carcharias*. This model uses color coded density-dependent frequency to depict the highest occupancy in red (Figure 2).

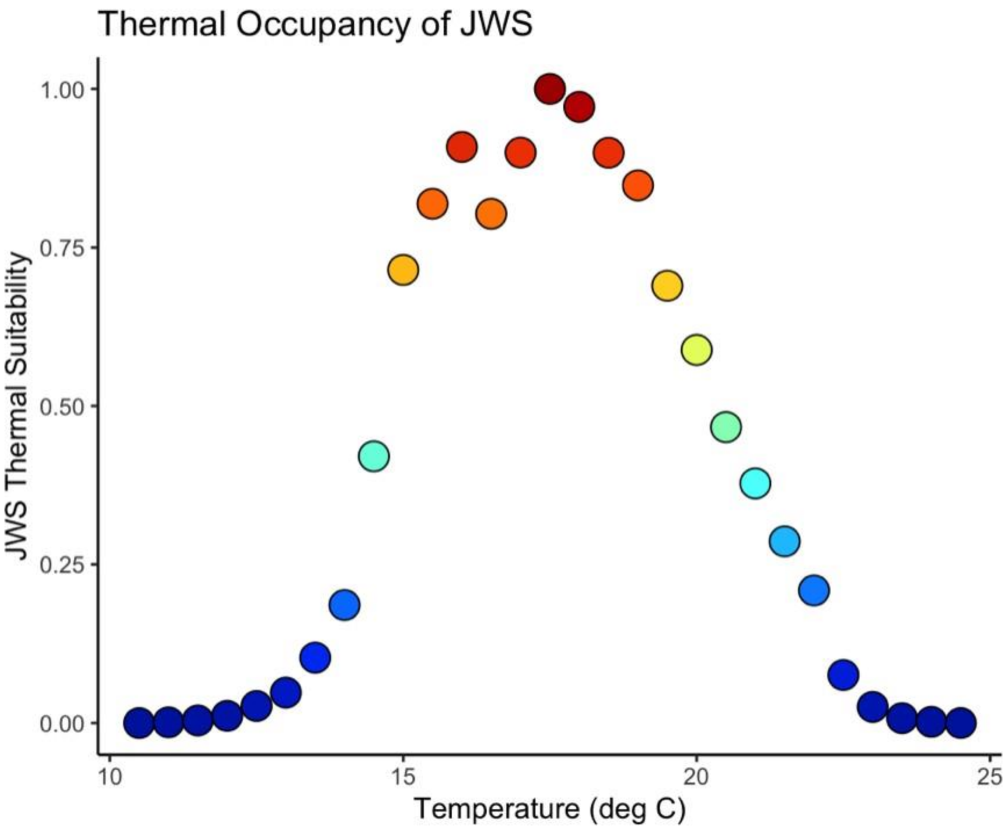
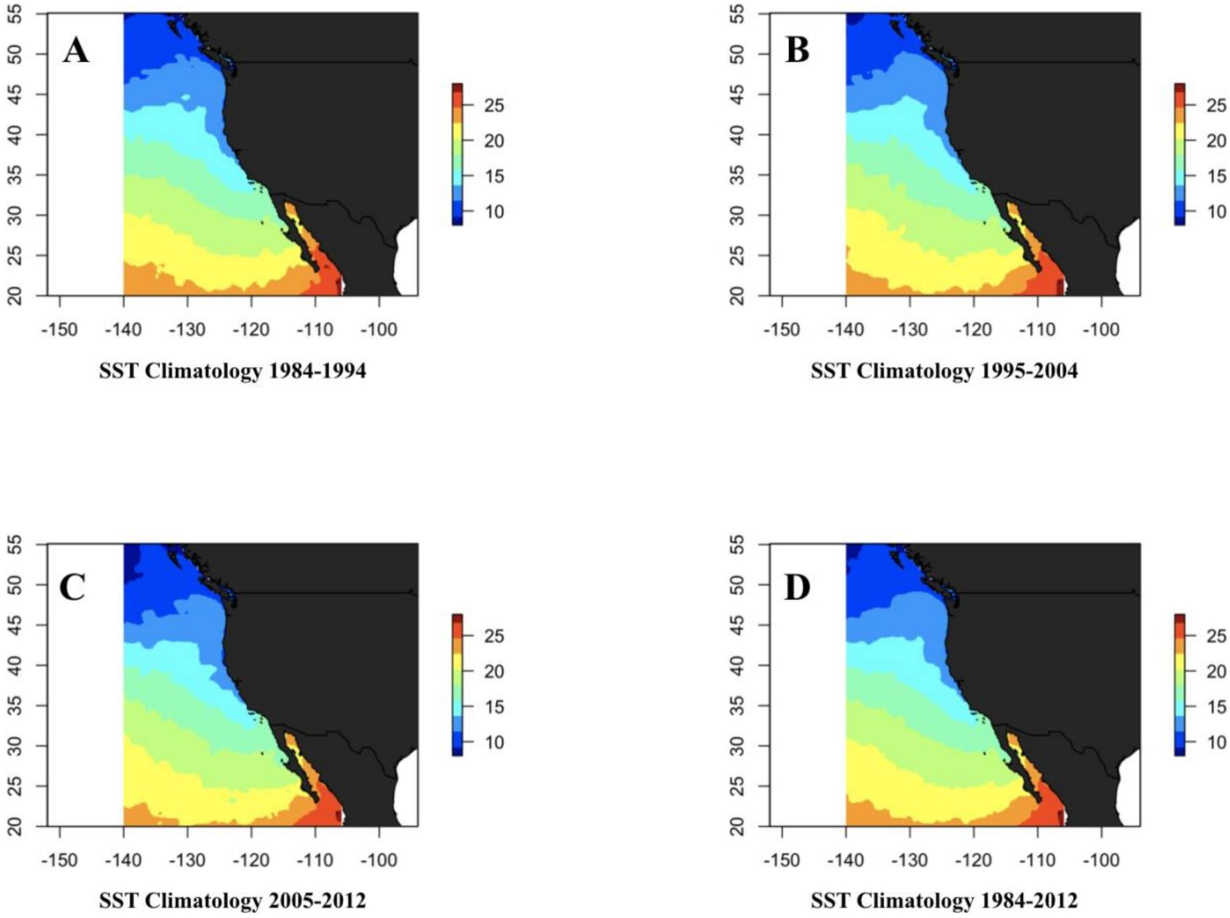


Figure 2. Thermal Occupancy of Juvenile White Shark (JWS). Derived thermal suitability model for JWS using electronic tagging data from PAT and SPOT tags. Highest thermal suitability depicted in red between 16 to 19 °C.

SST Models

Baseline climatologies

Through uploading and parsing through OISST data from NOAA we created 4 different historical (baseline) SST climatologies (Figure 3). In order to create an historical baseline from 1982-2012 we had to overlay all 3 of the time period datasets to create an average. Figure 3A represents the first class of SST data from 1982-1994. Figure 3B represents the next time period of data from 1995-2004. Figure 3C represents the last period of data from 2005-2012. The SST from each of these three periods was then averaged and mapped to create an entire historical baseline from 1982-2012 (Figure 3D). This baseline is used as the reference point for the future anomaly and to model historical juvenile *C. Carcharias* habitat suitability.



SST Climatology 1984-1994

SST Climatology 1995-2004

SST Climatology 2005-2012

SST Climatology 1984-2012

Figure 3. SST Climatology maps using historical NOAA SST data. (A) shows SST data from 1985-1994. (B) shows SST data from 1995-2004. (C) shows SST data from 2005-2012. (D) Represents the SST data averaged from plots A-C to give a comprehensive historical baseline from 1984-2012.

Future and current climatologies

In order to create the future SST projections along the coast of California, we used CMIP6 anomalies for a climate scenario of SSP5-8.5, which is the climate scenario that matches emissions patterns of today. Figure 4 represents the three different maps of importance. The baseline map is adapted from historical (baselie) SST shown in Figure 3D. Projected SST at SSPS 5-8.5 is created using CMIP6 anomalies. Figure 4C depicts the SST anomaly, or deviation from the baseline SST, between 2020-2049 at SSPS 5-8.5 from CMIP6 data. As a result, a future

SST map can be created by essentially overlaying the difference (anomaly) onto the baseline, as the anomaly represents the deviation, which in this case is positive (Figure 4A). In order to classify *C. Caracharias* habitat availability, SST data from Figure 4A and 4B is used in tandem with the thermal suitability model.

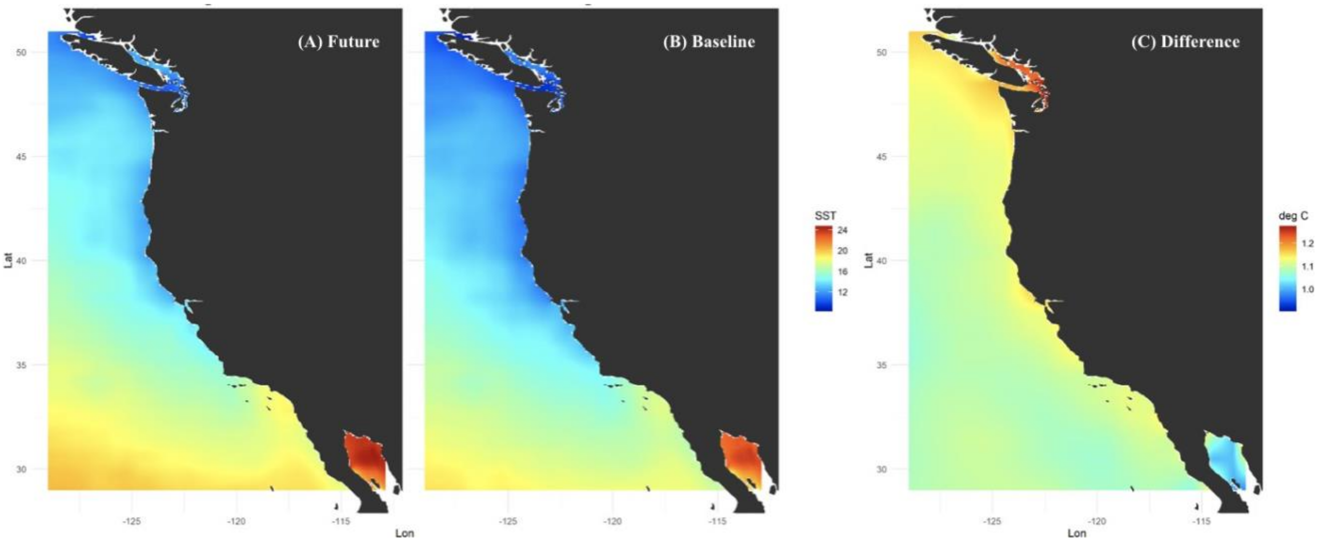


Figure 4. Climatology maps derived from NOAA historical SST data and future SST anomalies at a SSPS-8.5 emissions scenario. (A) Future SST projections using a historical baseline from 1985-2014 and SSPS 5-8.5 anomalies from NASA CMIP6 (C). (B) Historical baseline SST from NOAA SST data between 1985-2014. (C) SST anomaly using a historical baseline of 1985-2014.

C.carcharias habitat suitability

Figure 6 is a visualization of *C.carcharias* range given temperatures. This model combined the thermal suitability produced using electronic tagging data and SST data to develop a map of habitat suitability based on thermal preferences. Based on the thermal distribution outlined, *C.carcharias* will occupy a latitude of 34 to 36 °N more frequently than before.

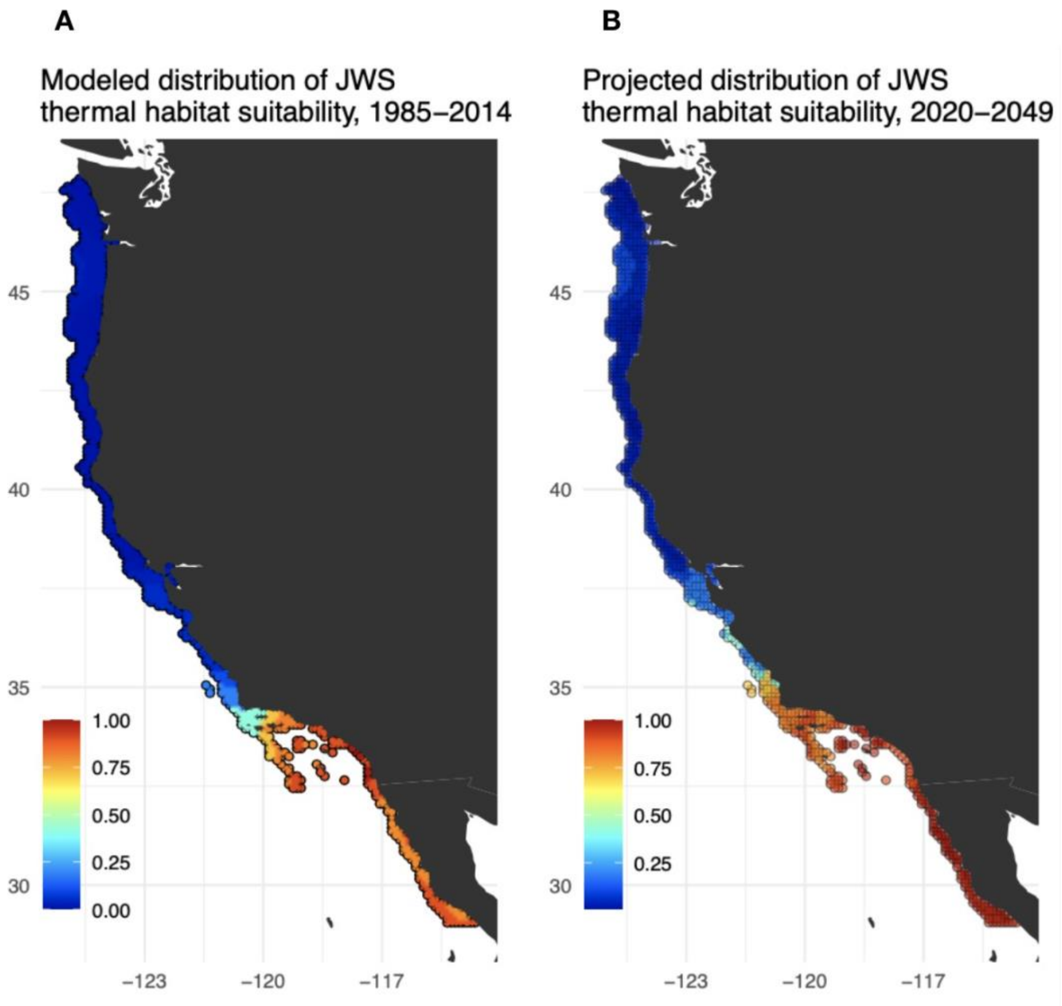


Figure 5. Modeled and Projected JWS Thermal Habitat Suitability. (A) Modeled distribution of JWS using historical (baseline) SST from 1985-2014 and derived thermal suitability. (B) Projected distribution based on derived thermal suitability of JWS and future SST from 2020-2049.

E.nereis habitat and *C.carcharias* thermal availability

E.nereis Habitat

Foundational to this study is the understanding that *E.nereis* populations have occupied an established and constant habitat range. As such, we mapped out the distribution of *E.nereis* populations along the California coast using USGS census data from 1982-2019 (Figure 6). Figure 6A provides a spatial distribution of the population density, with high density represented by red and orange bubbles along the map. Figure 6B resolves density through a bar chart with respect to latitude, outlining high density between 35 to 37 °N.

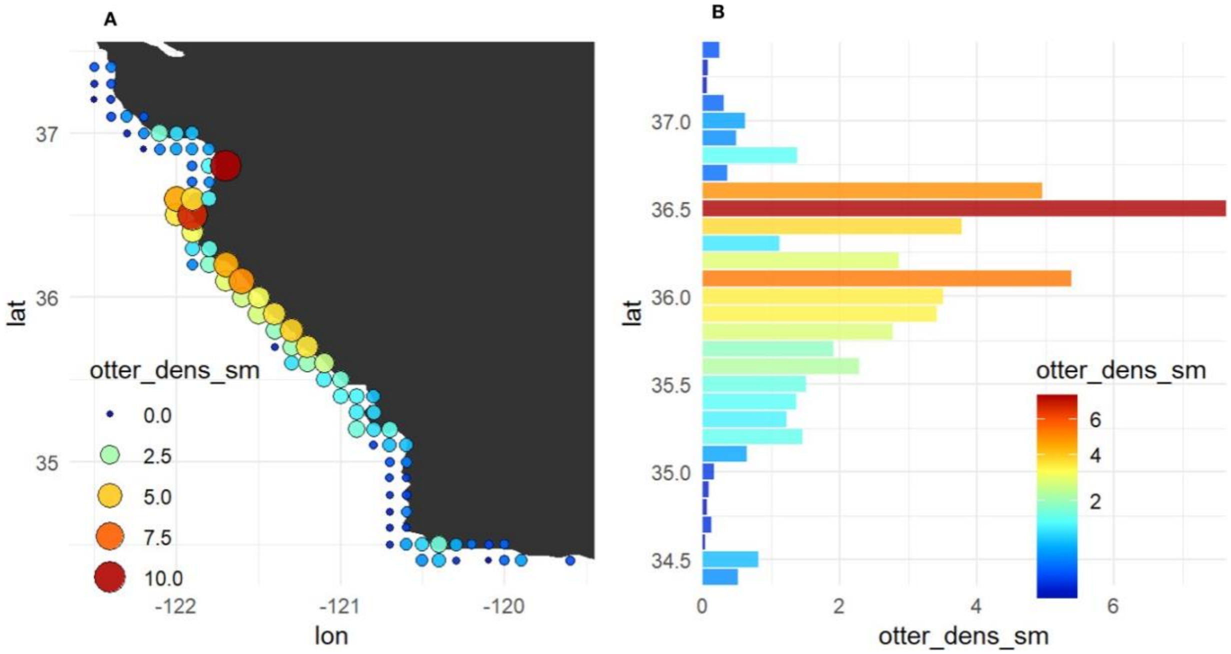


Figure 6. *E.nereis* density along the California Coast using data from the U.S. Geological Survey data from 1985-2019. (A) *E.nereis* density depicted using a bubble plot with largest densities between 36 and 37 °N. (B) Bar chart showing *E.nereis* density by latitude color coded the same as (A).

C.carcharias and E.nereis Habitat Availability

Separately the *C.Carcharias* habitat availability and *E.nereis* density distribution gives us minimal insight into the overlap between the two species. In order to quantify the potential overlap, we created a bar chart to represent the proportion of habitat availability at given latitudes (Figure 7). These are split into the historical (Figure 7A) and projected (Figure 7B) habitat availability. In comparing the two, we find that based on an SSPS 5-.8.5 emissions scenario between 2020-2049 *C. Carcharias* habitat availability will overlap much more with established *E.nereis* populations at latitudes between 34 to 37 °N than in baseline habitat availability between 1982-2014.

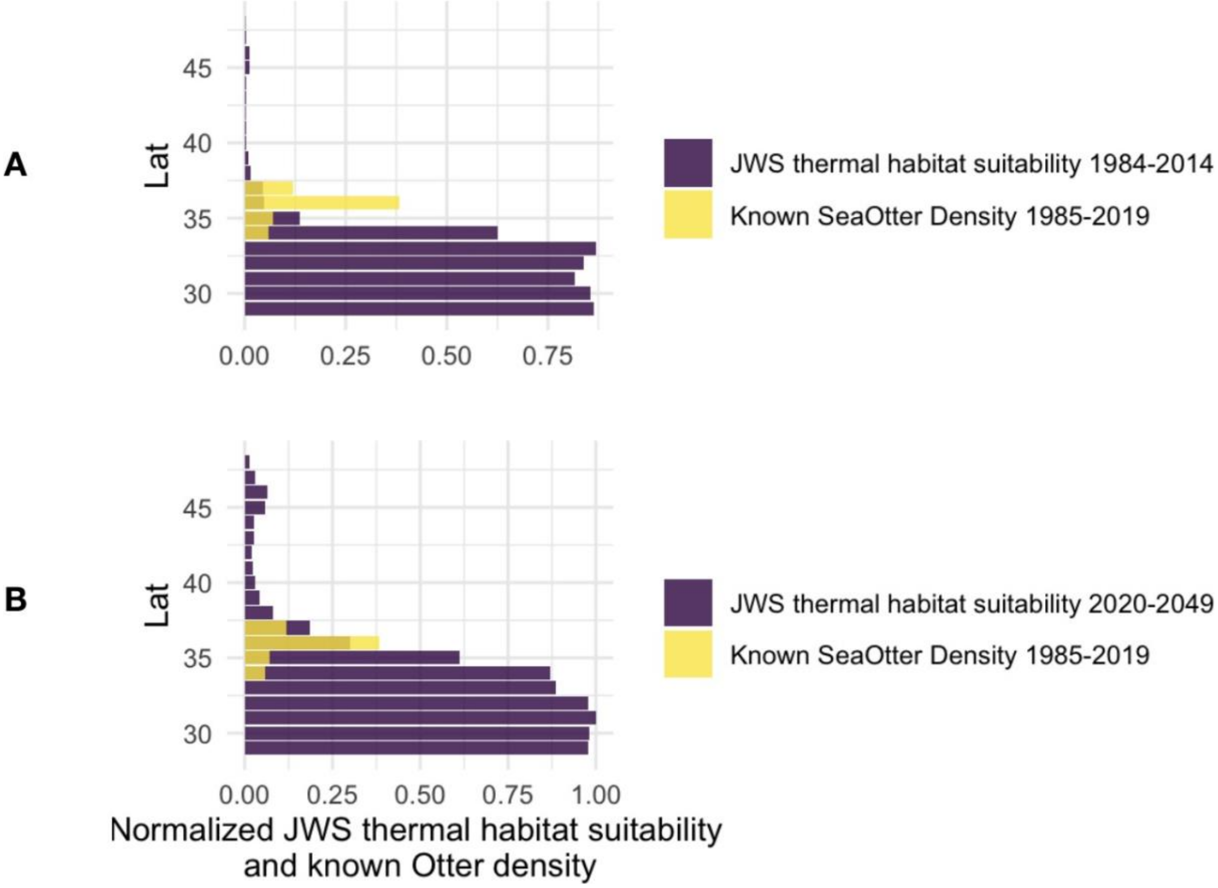


Figure 7. Modeled and Projected Thermal Habitat Suitability and Known Sea Otter (*E.nereis*) Density. (A) Overlap of JWS and Sea Otters calculated by thermal suitability based on historical (baseline) SST from 1985-2014 and known Sea Otter density measured from 1985-2019. (B) Overlap of JWS and Sea Otters calculated by thermal suitability based on future SST projections from 2020-2049 and known Sea Otter density.

DISCUSSION

C.carcharias thermal occupancy

The thermal suitability model created using electronic tagging data depicts thermal preferences for *C.carcharias* (Figure 2). Preferences for certain temperatures align with Tanaka et al 2021 findings, as this thermal suitability model is modeled from Tanaka et al. Conclusions in this study rest on the assumption that *C.carcharias* habitat is determined by *C.carcharias* thermal suitability. As such, we predict that habitat suitability is and will be determined by ocean temperature. This model provides visibility into the temperature at which high *C.carcharias* frequency occurs.

Our model suggests that, assuming a frequency of 75% occupation, *C.carcharias* thermal suitability is highest between temperatures of [15.5- 19°C]. This is consistent with previous data analyzing juvenile *C. Carcharias* thermal suitability (Weng et al. 2007). It is important to note that conclusions on habitat range derived from thermal suitability models rest on both the available electronic tagging data and the translation between thermal suitability and habitat suitability.

C.carcharias **modeled and predicted habitat suitability**

In tandem with the thermal suitability model, our models estimate current and predict future *C.carcharias* habitat suitability along the California Coast. Both of these models are predicated on the thermal suitability model aforementioned. These estimates use historical SST from a baseline of 1985-2014 and predict *C.carcharias* habitat suitability into 2020-2049. The current projections show *C.carcharias* habitat suitability in much lower latitudes than future suitability (Figure 5), where red indicates a higher proportion of *C.carcharias* occupancy from thermal suitability.

In order to paint a comprehensive picture of *C.carcharias* habitat suitability, future directions should include modeling thermal suitability using a wider range of emissions scenarios. This study only included SSPS 5-8.5, under the pretense that this projection forecasts the current trajectory. However, all other emissions scenarios should be outlined as well to account for different pathways the world may take. With a more robust portfolio of thermal occupancy at different climate scenarios, it will be easier to understand the full range of potential impact.

E.nereis **and** ***C.carcharias*** **overlap**

Given modeled *C.carcharias* habitat suitability using historical SST recordings, overlap between *C.carcharias* and *E.nereis* is minimal. However, our models suggest that *C.carcharias* and *E.nereis* habitat suitability will increase at projected emissions scenarios of SSPS 5-8.5. These models are built using dynamic *C.carcharias* habitat suitability ranges contingent on thermal suitability, but static *E.nereis* habitat suitability provided by census data. The models are created this way due to the presumption that *C.carcharias* habitat is predicated by ocean (SST) temperature. However, *E.nereis* have maintained an established niche that does not depend on temperature availability, as their habitat requirements are divergent from those of *C.carcharias* (Nicholson et al. 2018).

At '"business as usual" SST projections, there will be a much larger proportion of *C.carcharias* habitat suitability at the same latitudes as the greatest *E.nereis* population densities. These will occur most prominently at latitudes between 35 to 36 °N. While this may seem futile, increased interactions between the two species at a novel rate could introduce more obstacles for the *E.nereis* population as *C.carcharias* threaten recovery rates (Nicholson et al. 2018). Maintaining *E.nereis* populations in Monterey is critical to ensuring the kelp forest ecosystem remains resilient and continues to flourish (Konrad et al. 2022).

Conclusions

Increasing SST due to anthropogenic emissions will have widespread ramifications on marine ecosystems. As SST continues to rise, projections suggest that *C.carcharias* thermal suitability will continue to move northward along the California coast, presuming modeled thermal suitability windows stay constant. Under the assumption that *C.carcharias* habitat suitability is predicated on thermal suitability, habitat suitability will also shift northward along the California coast. If global anthropogenic emissions continue on our current trajectory, predicted *C.carcharias* habitat will be concentrated further northward along the California coast. Using *E.nereis* census data and comparing modeled and predictive *C.carcharias* habitat, the overlap between *C.carcharias* and vs along the California coast will reach unprecedented levels. *E.nereis* are a keystone species and integral to preserving the integrity of ecosystems in Monterey and beyond. Due to their vital role in Monterey and slowed growth rates, they have been garnering support from both researchers and communities.

While this paper does not assess or quantify the direct impact encroaching *C.carcharias* populations will have on *E.nerei*s in Monterey, amplified interactions between the two species may have adverse and cascading impacts. As such, more research needs to be done to quantitatively investigate how the northward shift of *C.carcharias* along the California coast will affect *E.nereis* populations. Additionally, more habitat suitability models should be generated at more climate scenarios to adequately understand the range of potential outcomes, depending on the future of climate change.

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