



UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
POSGRADO EN CIENCIAS DEL MAR Y LIMNOLOGÍA

**Aplicaciones de la modelación del nicho en el monitoreo de
recursos pesqueros en el contexto del cambio climático:
idoneidad ambiental, distribución y abundancia**

TESIS
(POR ARTÍCULO CIENTÍFICO)

QUE PARA OPTAR POR EL GRADO DE:
DOCTOR EN CIENCIAS

PRESENTA:
LUIS ENRIQUE ÁNGELES GONZÁLEZ

TUTORES PRINCIPALES:
DR. CARLOS ROSAS VÁZQUEZ
FACULTAD DE CIENCIAS

DR. ENRIQUE MARTÍNEZ MEYER
INSTITUTO DE BIOLOGÍA

COMITÉ TUTOR:
DR. CARLOS YÁÑEZ ARENAS
UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

DR. JOSÉ IVÁN VELÁZQUEZ ABUNADER
CENTRO DE INVESTIGACIÓN Y DE ESTUDIOS AVANZADOS DEL IPN

DR. FERNANDO DÍAZ HERRERA
CENTRO DE INVESTIGACIÓN CIENTÍFICA Y DE EDUCACIÓN SUPERIOR DE
ENSENADA

CD. MX., Octubre, 2021



Universidad Nacional
Autónoma de México

Dirección General de Bibliotecas de la UNAM

Biblioteca Central



UNAM – Dirección General de Bibliotecas
Tesis Digitales
Restricciones de uso

DERECHOS RESERVADOS ©
PROHIBIDA SU REPRODUCCIÓN TOTAL O PARCIAL

Todo el material contenido en esta tesis esta protegido por la Ley Federal del Derecho de Autor (LFDA) de los Estados Unidos Mexicanos (México).

El uso de imágenes, fragmentos de videos, y demás material que sea objeto de protección de los derechos de autor, será exclusivamente para fines educativos e informativos y deberá citar la fuente donde la obtuvo mencionando el autor o autores. Cualquier uso distinto como el lucro, reproducción, edición o modificación, será perseguido y sancionado por el respectivo titular de los Derechos de Autor.



Aplicaciones de la modelación del nicho en el monitoreo de recursos pesqueros en el contexto del cambio climático: idoneidad ambiental, distribución y abundancia

**TESIS
(POR ARTÍCULO CIENTÍFICO)**

**QUE PARA OBTENER EL GRADO ACADÉMICO DE:
DOCTOR EN CIENCIAS**

**PRESENTA:
LUIS ENRIQUE ÁNGELES GONZÁLEZ**

**TUTORES PRINCIPALES:
DR. CARLOS ROSAS VÁZQUEZ
FACULTAD DE CIENCIAS**

**DR. ENRIQUE MARTÍNEZ MEYER
INSTITUTO DE BIOLOGÍA**

**COMITÉ TUTOR:
DR. CARLOS YÁÑEZ ARENAS
UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO**

**DR. JOSÉ IVÁN VELÁZQUEZ ABUNADER
CENTRO DE INVESTIGACIÓN Y DE ESTUDIOS AVANZADOS DEL IPN**

**DR. FERNANDO DÍAZ HERRERA
CENTRO DE INVESTIGACIÓN CIENTÍFICA Y DE EDUCACIÓN SUPERIOR DE
ENSENADA**

MÉXICO, CD. MX., Octubre, 2021

AGRADECIMIENTOS

Agradezco al Posgrado de Ciencias del Mar y Limnología por permitirme la oportunidad de realizar mis estudios de doctorado. Adicionalmente, agradezco al Consejo Nacional de Ciencia y Tecnología por el apoyo financiero durante el desarrollo del posgrado (CVU 475262).

Quisiera reconocer particularmente al Dr. Carlos Rosas Vázquez quien ha sido parte de mi formación académica desde la licenciatura ya hace varios años. De igual forma agradezco el apoyo y ánimo ofrecido por el Dr. Enrique Martínez Meyer quien me ha alentado a continuar desarrollando las ideas propuestas en la presente tesis.

Por último, estoy agradecido a los integrantes del jurado de examen de grado; los Dres. Carlos Yáñez Arenas, José Iván Velázquez Abunader y Fernando Díaz Herrera por el tiempo que me han dedicado contestando a mis dudas durante el desarrollo de la presente tesis, de ustedes he aprendido mucho.

Dedicatoria

Dedico esta tesis a mis padres

Resumen

Actualmente, el incremento en las emisiones de CO₂ de origen antropogénico ha generado un cambio climático (CC) que dará lugar a alteraciones en la distribución y abundancia de organismos marinos con disminuciones de capturas predichas en la Península de Yucatán (Golfo de México). La modelación de nichos ecológicos es una disciplina que permite describir los patrones de distribución de las especies caracterizando las condiciones ambientales donde las tasas intrínsecas de crecimiento son positivas. A pesar de su utilidad, sus aplicaciones como herramienta de monitoreo pesquero son escasas. Dada la vulnerabilidad de la región, el presente trabajo evaluó la utilidad de los modelos de nicho como herramientas de monitoreo pesquero y pronosticó las distribuciones y regiones de captura potenciales bajo escenarios de CC para el recurso pulpo (*Octopus americanus*, *O. insularis* y *O. maya*). Para ello, el presente trabajo se apoyó de datos fisiológicos obtenidos de laboratorio (límites térmicos), modelos de nicho correlativos (MC - asociaciones estadísticas entre datos de presencias y capas ambientales) y modelos de nicho mecanísticos (MM - modelos calibrados con datos fisiológicos). Dentro de la presente tesis i) se analizó la correlación entre abundancia y posición en el espacio de nicho mediante elipsoides de volumen mínimo para verificar si la caracterización del nicho sirve como un indicador de las capturas potenciales de *O. maya* provenientes de un muestreo intensivo del año 2012, ii) utilizando una serie de tiempo de 15 años (1993-2008) de capturas de *O. maya* para Campeche y Yucatán, verifiqué si las capturas históricas se encontraba relacionada con la adecuación anual calculada a partir de un MM (basado en alcances metabólicos térmicos) para establecer si los modelos de nicho pueden predecir las tendencias de producción pesquera, iii) mediante datos fisiológicos (sensibilidad térmica) establecí escenarios de CC con las tres especies de pulpo para generar predicciones en cambios en la distribución en el Golfo de México, iv) por último, proyecté un MC (Maxent) y MM para determinar la adecuación, y distribución potencial del *O. maya* en escenarios de CC en el Golfo de México, la proyección de ambos modelos se realizó con el objetivo de reducir la incertidumbre en las predicciones. Los resultados muestran que la caracterización del nicho puede ser utilizado como una herramienta útil para el manejo de recursos pesqueros dado que este describió los patrones espacio-temporales de captura de *O. maya*, particularmente agregaciones estacionales (reclutamiento pesquero) que ocurren en la región occidental de la Península de Yucatán. Además, se encontró una relación significativa entre los MM y las tendencias históricas de captura (1993-2008), mostrando un incremento a corto plazo en los desembarcos de pulpo disponible, sin embargo, si un umbral de tolerancia térmico se supera, es probable que exista una disminución en los volúmenes de captura; un escenario que se estima que sucederá en el futuro. Por último, los datos fisiológicos, los MC y MM señalan reducciones en la adecuación y distribución de *O. maya* y *O. insularis* en escenarios de CC, por lo que si existe una relación entre la abundancia y posición en el espacio de nicho, se prevé que las capturas potenciales en la región disminuyan. Se debe señalar que no fue posible realizar inferencias para *O. americanus* porque los datos provienen de poblaciones adaptadas a regiones templadas (Florianópolis, Brasil). Si las relaciones descritas en el presente trabajo son encontradas para otras especies, el marco de trabajo aquí sería una herramienta útil de monitoreo para recursos pesqueros. Por último, los resultados sugieren que es necesaria la reorganización de la pesquería teniendo en cuenta los posibles cambios de abundancia en un futuro por efecto del cambio climático.

Abstract

Currently, the increase in anthropogenic CO₂ emissions has generated a climate change (CC) that will lead to alterations in the distribution and abundance of marine organisms with predicted decreases in catches in the Yucatan Peninsula (Gulf of Mexico). Ecological niche modeling is a discipline that allows describing the distribution patterns of species by characterizing environmental conditions where intrinsic growth rates are positive. Despite its usefulness, its applications as a fisheries monitoring tool are scarce. Given the vulnerability of the region, the present work evaluated the usefulness of physiological data and niche models as fishing monitoring tools and predicted the distributions and potential catch regions under CC scenarios for the octopus resource (*Octopus americanus*, *O. insularis*, and *O. maya*). For this, I used physiological data obtained from laboratory studies (thermal limits), correlative niche models (CM - statistical associations between occurrence data and environmental layers), and mechanistic niche models (MM - models calibrated with physiological data). Within this dissertation i) the correlation between abundance and position in the niche space was analyzed using minimum volume ellipsoids to verify if the niche characterization serves as an indicator of the potential catches of *O. maya* from an intensive sampling in 2012, ii) using a 15-year time series (1993-2008) of *O. maya* catches for Campeche and Yucatán, I verified if the historical catches were related to the annual fitness calculated from a MM (based on the thermal aerobic scope) to establish if the niche models can predict fishery catches trends, iii) using physiological data (thermal sensitivity) I established the CC scenarios for the three octopus species to generate scenarios that predict changes in distribution in the Gulf of Mexico, iv) finally, I projected CM (Maxent) and MM models to determine the fitness and the potential distribution of *O. maya* in CC scenarios in the Gulf of Mexico, the projection of both type of models (MM and CM) were carried out with the objective of reducing the uncertainty in the predictions. The results show that the characterization of the niche can be used as a useful tool for the management of fishing resources since it described the spatio-temporal patterns of catches of *O. maya*, particularly seasonal aggregations (fishing recruitment) that occur in the western region of the Yucatan Peninsula. In addition, a significant relationship was found between MM and historical catch trends (1993-2008), showing a short-term increase in octopus landing, however, if a thermal tolerance threshold is exceeded, volume catches will likely decrease, a scenario that is expected to happen in the future. Finally, the physiological data, CM and MM indicate reductions in the fitness and distribution of *O. maya* and *O. insularis* in CC scenarios, so assuming that there is a relationship between abundance and position in the niche space, it is expected that potential catches in the region will decrease. It should be noted that it was not possible to make inferences for *O. americanus* because the data come from populations adapted to temperate regions (Florianopolis, Brazil). If the relationships described in the present work are found for other species, the framework here would be a useful monitoring tool for fishery resources. Finally, the results suggest that the reorganization of the fishery is necessary, considering the possible future changes in abundance.

Índice general

Índice general	7
Capítulo uno – Introducción general	8
1.1 Distribución de especies y el nicho.....	9
1.2 Métodos para caracterizar el nicho fundamental.....	12
1.3 Efecto del cambio climático en los recursos pesqueros a nivel mundial	14
1.4. Cambio climático y México.....	16
1.5. Pesca de pulpo en el Golfo de México y plataforma continental de Yucatán	18
1.6 Justificación	21
1.7. Objetivo general.....	22
1.7.1. Objetivos particulares	22
1.8 Referencias.....	23
Capítulo dos - Long term environmental data explain better the abundance of the red octopus (<i>Octopus maya</i>) when testing the niche centroid hypothesis	28
Capítulo tres - Fitness reflects landings trends of the red octopus, <i>Octopus maya</i> (Voss & Solís, 1966), in the Yucatan Peninsula	40
Capítulo cuatro - Exploring the effects of warming seas by using optimal and pejus temperatures of the embryo of three Octopoda species in the Gulf of Mexico.....	56
Capítulo cinco - Climate change effect on <i>Octopus maya</i> (Voss and Solís-Ramírez, 1966) distribution in the Yucatan Peninsula, Gulf of Mexico: A correlative and mechanistic approach	68
Capítulo seis - Discusión y conclusiones	82
6.1 Discusión.....	83
6.2 Conclusiones	90
6.3 Referencias.....	91

Capítulo uno – Introducción general

1.1 Distribución de especies y el nicho

Describir y comprender los patrones de distribución de las especies a diferentes escalas espaciales y temporales ha sido uno de los principales objetivos de la ecología. El modelado de “nichos” –el cual ha tenido un crecimiento exponencial en los últimos 20 años (Guisan et al., 2013)–, ha sido una de las metodologías usadas para inferir las áreas de distribución y redistribución de las especies. Sin embargo, es importante entender bajo qué definición de nicho han operado estos trabajos. A grandes rasgos, el término nicho es comprendido bajo dos grandes enfoques, 1) el efecto de las condiciones ambientales en la distribución de especies, conocido como nicho Grinelliano y; 2) la función que desempeñan las especies en el ecosistema, llamado nicho Eltoniano (variables relacionadas con las interacciones ecológicas y el consumo de recursos) (Soberón, 2007; Soberón y Nakamura, 2009; Peterson et al., 2011).

Hutchinson (1957), definió al nicho como un espacio abstracto de n -dimensiones en donde las variables abióticas (ej. temperatura, salinidad, oxígeno disuelto, entre otros) y bióticas (competencia, depredación, mutualismo, entre otros), constituyen condiciones ideales para el establecimiento de poblaciones y, por ende, las tasas intrínsecas de crecimiento (r) son positivas ($r > 0$) (Hutchinson, 1957; Maguire, 1973; Peterson et al., 2011; Osorio-Olvera et al., 2019, 2020). Esquemáticamente, estas ideas fueron representadas por Soberón y Peterson (2005) mediante el diagrama BAM (por sus siglas en inglés –Biotic, Abiotic y Movements–), la cual representa el efecto conjunto de los factores biótico, abióticos (i.e., el nicho fundamental [NF], definido como el conjunto de condiciones ambientales bajo las cuales la r es positiva) y la capacidad de dispersión determinan la distribución de las especies (geografía ocupada - GO). Por lo tanto, la expansión o disminución en la distribución de las especies dependerá de que existan las condiciones abióticas y bióticas favorables y que las regiones geográficas sean accesibles a la especie (Figura 1). No obstante, el

desarrollo de los modelos de nicho se ha enfocado a la caracterización parcial del NF, específicamente a la parte climática, debido, en parte, a la dificultad de considerar variables bionómicas (interacciones bióticas y dinámicas de recurso-consumidor; Hutchinson, 1978). Por lo tanto, se ha argumentado a favor del concepto de nicho *sensu* "Grinnell" enfocado en variables escenopoéticas (variables no interactivas, ej., temperatura; Hutchinson, 1978), porque, a costa de perder algo de generalidad, este paso conduce a conceptos operativos y sencillos para la determinación de nichos y áreas de distribución (Soberón y Peterson, 2005; Soberón y Nakamura, 2009; Peterson et al., 2011).

Por lo anterior, el objetivo de los modelos de nicho es inferir las condiciones ambientales que se aproximan al NF de las especies (Soberón y Peterson, 2005; Soberón, 2007; Soberón y Nakamura, 2009; Peterson et al., 2011; Soberón et al., 2017). Además, la proyección de estas condiciones al espacio geográfico ofrece información sobre la distribución (Peterson et al., 2011; Soberón et al., 2017) y abundancia potencial de las especies al ser una representación de la adecuación de estas (Martínez-Meyer et al., 2013; Yañez-Arenas et al., 2014; Osorio-Olvera et al., 2019, 2020). En el contexto del cambio climático antropogénico (CC), caracterizar el NF permitiría una descripción en la capacidad que tienen los organismos de responder ante los cambios ambientales (Kearney y Porter, 2004, 2009; Pörtner y Farrell, 2008; Kearney et al., 2010; Pörtner y Peck, 2010; Moyano et al., 2020). Los métodos para caracterizar el NF se discutirá en la siguiente sección.

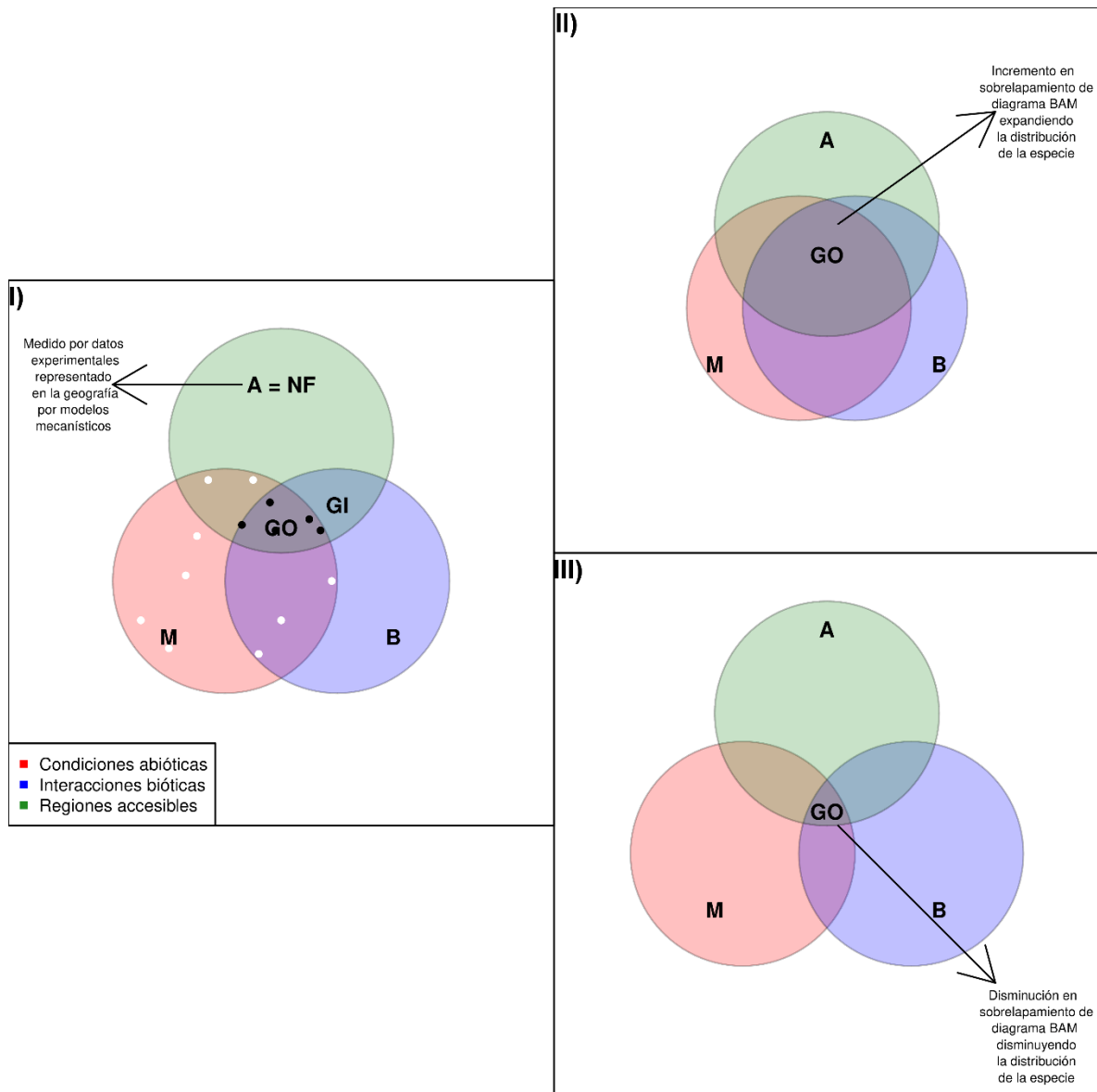


Figura 1. I) Las condiciones abióticas (A), las interacciones bióticas (B) y la capacidad de movilidad (M) permiten que la población de una especie habite una región específica ($B \cap A \cap M = GO$). Los puntos negros representan observaciones de poblaciones fuente ($r > 0$); los puntos blancos son poblaciones sumidero ($r < 0$). Los algoritmos correlativos realizan inferencias a partir de los puntos blancos y negros. Mediciones directas del nicho fundamental ($NF = A$) son realizados por estudios experimentales. La zona GI es una región con condiciones favorables pero que se ha mantenido fuera de las capacidades de dispersión de la especie. Ante escenarios de cambio climático, dos respuestas del diagrama BAM pueden ocurrir: II) incrementa el solapamiento permitiendo una expansión de la GO de las especies (GI se vuelve accesible). III) Por el contrario, si las presiones en el nicho aumentan, el diagrama BAM se desacopla, por lo que la GO de las especies son constreñidas (se debe señalar que usualmente los efectos de B no son considerados en la modelación de nicho dado que el enfoque es el nicho *sensu* Grinnell).

1.2 Métodos para caracterizar el nicho fundamental

En su mayor parte, la caracterización del NF se ha realizado mediante la utilización de modelos de nicho ecológico correlativos (MC). Los MC representan asociaciones estadísticas entre las presencias registradas de una especie y un conjunto de variables ambientales en forma de mapas raster (Martinez-Meyer, 2005; Kearney y Porter, 2009; Guisan et al., 2013; Peterson et al., 2015). La amplia utilización de los MC es producto de la accesibilidad de programas de cómputo y disponibilidad de datos en línea (Martinez-Meyer, 2005; Kearney y Porter, 2009; Peterson et al., 2015).

Aunque accesibles, los MC suelen producir información imprecisa del NF debido a que dependen de la calidad de los datos con que se calibran. Por ejemplo, existe la posibilidad de utilizar poblaciones sumideros (población ubicada en un hábitat inadecuado en el que la tasa de mortalidad supera a la de natalidad, $r < 0$), datos de presencia mal identificadas o que la localidad precisa de su distribución se encuentre sesgada por efecto de factores involuntarios al observador, por ejemplo, sesgos de muestreo (Martinez-Meyer, 2005; Kearney y Porter, 2009; Peterson et al., 2011; Peterson et al., 2015).

Finalmente, es necesario considerar que las presencias no necesariamente reflejan el NF de una especie, ya que la capacidad de movilidad (M) o las interacciones bióticas (B) podrían evitar que las especies maximicen sus capacidades fisiológicas (Soberón y Peterson, 2005; Soberón y Nakamura, 2009; Peterson et al., 2011). En ese sentido, los métodos correlativos estiman por lo general un "nicho" intermedio entre el nicho realizado (condiciones abióticas donde la especie puede sobrevivir limitadas por las interacciones bióticas y el área accesible) y el NF (Jiménez-Valverde et al., 2008; Lobo et al., 2010; Sillero, 2011; Peterson et al., 2011; Soberón et al., 2017).

En contraste, los modelos mecanísticos (MM) están basados en datos fisiológicos obtenidos a partir de experimentos en laboratorio (Figura 2) por lo que tienen la

ventaja de ser mediciones directas del NF (Kearney y Porter, 2004, 2009; Elith et al., 2010; Kearney et al., 2010; Peterson et al., 2015). Este tipo de datos, permiten la identificación de A (NF) sin M y B, los cuales suelen afectar a los MC. Por lo tanto, se ha sugerido que los MM podrían ser más adecuados que los MC para evaluar escenarios de CC dado que el NF determina la respuesta potencial de las especies a estas alteraciones (Kearney y Porter, 2009; Kearney et al., 2010; Peterson et al., 2015; Evans et al., 2015).

No obstante, aunque los MM son de gran utilidad para conocer los límites fisiológicos de una especie y los intervalos donde su desempeño es máximo, los resultados pueden ser difíciles de interpretar debido a que las mediciones usualmente se llevan a cabo en pocas dimensiones ambientales (ej. Unidimensional), ya que la realización de experimentos multifactoriales es excesivamente compleja. Además, la proyección de estas mediciones a distribuciones geográficas potenciales requiere supuestos importantes (B y M), por ejemplo, que las poblaciones medidas podrían estar adaptadas localmente, disminuyendo su capacidad de extrapolación a regiones más allá de donde se obtuvieron los datos (Kearney y Porter, 2009; Evans et al., 2015; Peterson et al., 2015;).

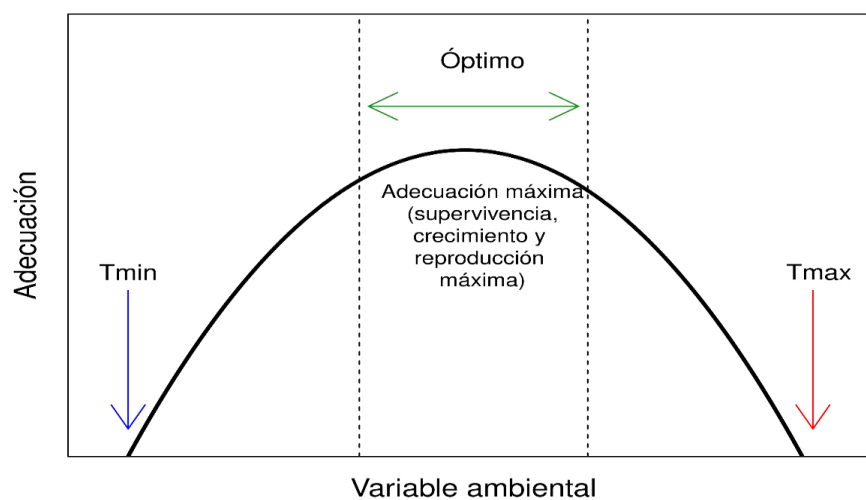


Figura 2. Figura conceptual de tolerancia fisiológica a la temperatura y su efecto en la adecuación. En las condiciones óptimas la adecuación de la especie es máxima, por lo

que su supervivencia, crecimiento y reproducción es favorable ($r > 0$). Conforme se aleja del valor óptimo la adecuación de la especie disminuye. Típicamente se considera que en las zonas de tolerancia mínima (T_{min}) y máxima (T_{max}) solo una existencia pasiva es posible ($r < 0$) (Pörtner y Peck, 2010), por lo que, basado en la condición fisiológica de las especies, estas representarían una población sumidero en un contexto macroecológico (Gutiérrez-Ruelas et al., 2019). Nótese que esta figura representa un nicho unidimensional, pero en realidad el nicho corresponde a muchas dimensiones (n-dimensiones).

Considerando las ventajas y desventajas de los MC y los MM, se ha sugerido la integración de ambos modelos (Hijmans y Graham, 2006; Kearney y Porter, 2009; Kearney et al., 2010; Kumar et al., 2014; Peterson et al., 2015). Una de las ventajas de hacer esta integración es la reducción de la incertidumbre, dado que una comparación de ambos modelos podría dilucidar más claramente las tendencias de distribución, redistribución o abundancia de las especies. En ese sentido, en caso de que ambos métodos coincidan, la utilización conjunta de MC y MM podría servir para la validación de los resultados (Hijmans y Graham, 2006; Kearney y Porter, 2009; Kearney et al., 2010; Kumar et al., 2014; Peterson et al., 2015).

Por el contrario, encontrar diferencias podría dilucidar interesantes hipótesis. Por ejemplo, ¿las diferencias entre lo esperado y lo predicho se encuentran relacionadas a adaptaciones locales? ¿podrían estas diferencias estar relacionadas a variables de accesibilidad (M) o interacciones bióticas (B)? ¿la información biológica disponible es suficientemente robusta como para aplicar MC o MM? Esclarecer estas incógnitas mediante este enfoque integrador puede ofrecer una capacidad considerable de predicción y reflexión para los investigadores, administradores de recursos y formuladores de políticas públicas.

1.3 Efecto del cambio climático en los recursos pesqueros a nivel mundial

El incremento en las emisiones de CO₂ desde inicios del siglo XX ha traído como consecuencia un incremento en la temperatura del océano, aumento en el nivel del mar, la estratificación en la columna de agua, cambio en los patrones de corrientes, surgencias, productividad primaria, reducción de oxígeno y pH (Diaz y Rosenberg, 2008; Solomon et al., 2009; Keeling et al., 2010; Doney et al., 2012; IPCC, 2014). De acuerdo con FAO (2018), se prevé que estas alteraciones ambientales modifiquen la distribución y abundancia de comunidades bióticas marinas, afectando la disponibilidad de los recursos pesqueros. Los impactos del CC han sido ya evidenciados en las alteraciones de las capturas pesqueras a nivel mundial (Simpson et al., 2011; Cheung et al., 2013; Doubleday et al., 2016; Arreguín-Sánchez, 2019).

En relación con esto, Poloczanska et al. (2013) indican que actualmente las tasas de cambio en la distribución y abundancia de organismos marinos son consistentes con los cambios de la temperatura superficial del océano. Estas alteraciones en las capturas representan una seria amenaza por su papel fundamental en la seguridad alimentaria y la generación de ingreso económico para millones de personal a nivel mundial (Sumaila et al., 2011; FAO, 2018).

Tan solo durante el 2017, la pesca a nivel mundial generó un ingreso total de 152 mil millones de dólares en exportaciones. Más de la mitad de ese ingreso provino de países en desarrollo, lo que produjo una derrama económica para ~40 millones de personas (FAO, 2018). Si se considera a toda la cadena de valor, es posible establecer que la pesca mundial benefició indirectamente a más de 200 millones de personas. Además, como resultado de la pesca, las comunidades humanas aseguraron al menos el 20% de su ingesta de proteínas de origen animal y se informa que en algunos países este valor fue tan alto como el 90% (FAO, 2018).

Los modelos que simulan distintos escenarios del CC han señalado que debido a esta condición se espera una tropicalización de los ambientes marinos de altas latitudes. Estos modelos también predicen que el CC puede llegar a contribuir con una

redistribución a gran escala del potencial de captura pesquera global, con un aumento promedio de 30 a 70% en las regiones de latitudes altas y una reducción de captura hasta del 40% en los trópicos (Cheung et al., 2009, 2010). Esa migración ha sido explicada con base en que las especies tropicales se encuentran más cercanos a los límites superiores de sus ventanas térmicas (Pörtner y Farrell, 2008; Pauly y Cheung, 2018; Lam et al., 2020 – Figura 3).

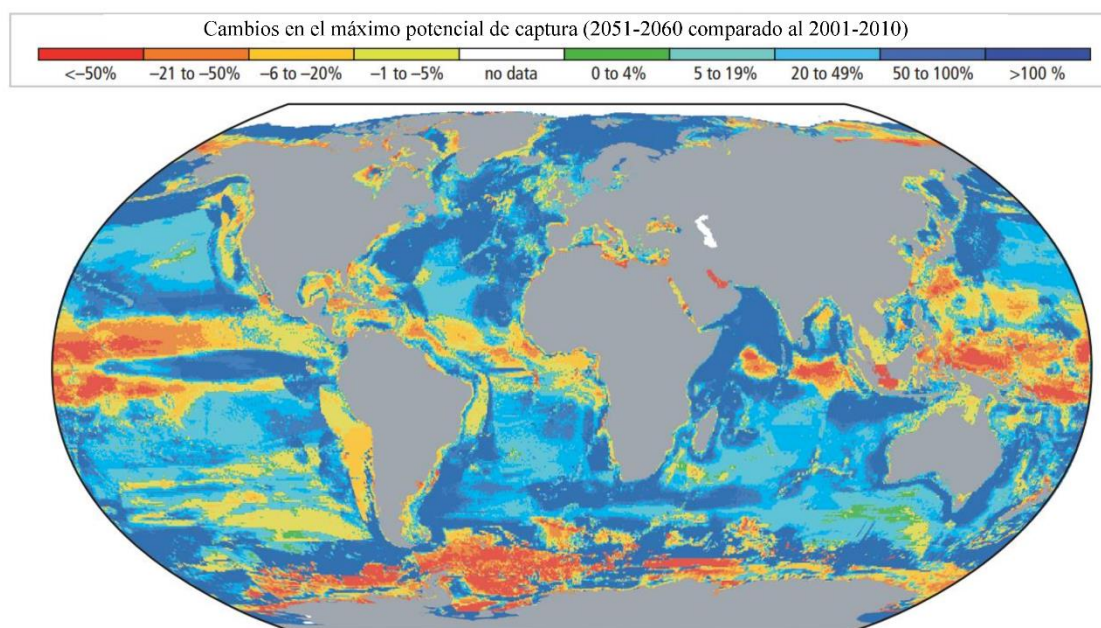


Figura 3. Redistribución global proyectada del potencial de capturas máximas de ~1000 especies de peces e invertebrados de importancia comercial, comparando los promedios obtenidos para las décadas 2001- 2010 y 2051-2060 basadas en un modelo climático de calentamiento de 2°C. Este modelo no considera impactos de la sobreexplotación pesquera o la acidificación del océano. Figura obtenida del IPCC (2014).

1.4. Cambio climático y México

En México, durante el 2018 se reportó un volumen de captura de aproximadamente 2 millones de toneladas de organismos marinos, los cuales representan aproximadamente el 1% del Producto Interno Bruto (PIB). Si bien contribuye poco al PIB del país, esta actividad representa un ingreso para aproximadamente 300,000 pescadores quienes dependen directamente de esta actividad. Además, este sector

genera ~12 millones de empleos indirectamente (CONAPESCA, 2018). En ese sentido, el CC conllevará a alteraciones ecológicas, económicas y sociales a las comunidades pesqueras, a la cadena de procesamiento y valor (empacado y transporte de productos), así como a los consumidores nacionales y mercados de exportación (Cisneros-Montemayor et al., 2013, 2020).

A pesar de los potenciales efectos del CC, cuando se inició este trabajo (2017), eran escasos los estudios que tenían por objetivo evaluar la vulnerabilidad de recursos pesqueros en el Golfo de México y el Caribe mexicano. Martínez-Arroyo et al., (2011) evaluaron el potencial efecto que tendría el CC en los ecosistemas costeros (ej., arrecifes de coral, pastos marinos, lagunas costeras, estuarios) y el impacto que este conllevaría en 16 pesquerías comerciales (Pacífico y Atlántico) que contribuyen con el 70% del volumen y el valor económico de la pesca. Los autores concluyeron que el impacto será negativo para las pesquerías debido a los cambios ambientales en los ecosistemas en que habitan las especies. Adicionalmente, predijeron un efecto sinérgico entre los impactos ya existentes tales como: contaminación, sobreexplotación de especies y destrucción de hábitat, los cuales todos juntos crearán escenarios negativos para las pesquerías evaluadas.

Posteriormente, Cisneros-Mata et al. (2019). realizaron un modelo bioeconómico para 25 stocks pesqueros en el Golfo de California y la costa del Pacífico en el que consideraron la biomasa, la captura y las ganancias económicas bajo políticas de manejo contrastantes con y sin escenarios de CC. Aunque se estipula que el riesgo de sobrepesca es mayor incluso que al del CC, los resultados muestran que de los 25 stocks pesqueros analizados, 24 de ellos sufrirán disminuciones como consecuencia directa del CC. Recientemente un modelo bioclimático generado por Cisneros-Montemayor et al. (2020) para 128 especies marinas predijo una disminución total de 46% ($\pm 9\%$) en la captura potencial de organismos marinos para la costa del Atlántico y del 4% ($\pm 9\%$) para el Pacífico. De acuerdo con ese estudio, los cambios potenciales

de captura más fuertes se producirán en la región del Banco de Campeche y la Península de Yucatán.

1.5. Pesca de pulpo en el Golfo de México y plataforma continental de Yucatán

La pesquería de pulpo es una de las más importantes del país. Se lleva a cabo principalmente en las costas del Banco de Campeche, siendo la primera en cuanto a volumen y la segunda en valor económico para esta región (DOF, 2014; CONAPESCA, 2018). Esta pesquería se encuentra integrada por tres especies: el *Octopus maya*, *O. americanus* y *O. insularis*, cabe señalar que estas dos últimas especies eran consideradas como *O. vulgaris* por la normatividad mexicana (DOF, 2014; 2018).

El pulpo *O. maya* es una especie endémica de la Península de Yucatán, asociada a pastos marinos, fragmentos de coral y oquedades (Voss y Solís-Ramírez, 1966; Zarco-Perelló et al., 2013). Suele pescarse en aguas someras (<30 m) (DOF, 2014) aunque ocasionalmente se encuentra en aguas más profundas (~60 m) (Avendaño et al., 2019). En cambio, *O. americanus* se encuentra distribuida desde Argentina hasta Rhode Island, EU (Avendaño et al., 2020b), siendo abundante entre 50 y 60 m (Avendaño et al., 2020a) de profundidad en donde habitan fondos duros y rocosos principalmente (DOF, 2014). Por último, *O. insularis* se distribuye desde aguas subtropicales del Atlántico sur occidental en la costa brasileña hasta México (Lima et al., 2017; Avendaño et al., 2020b) (Veracruz). Se pesca en bajos o lagunas arrecifales a profundidades de 0 hasta 5 m (DOF, 2014 - Figura 4).

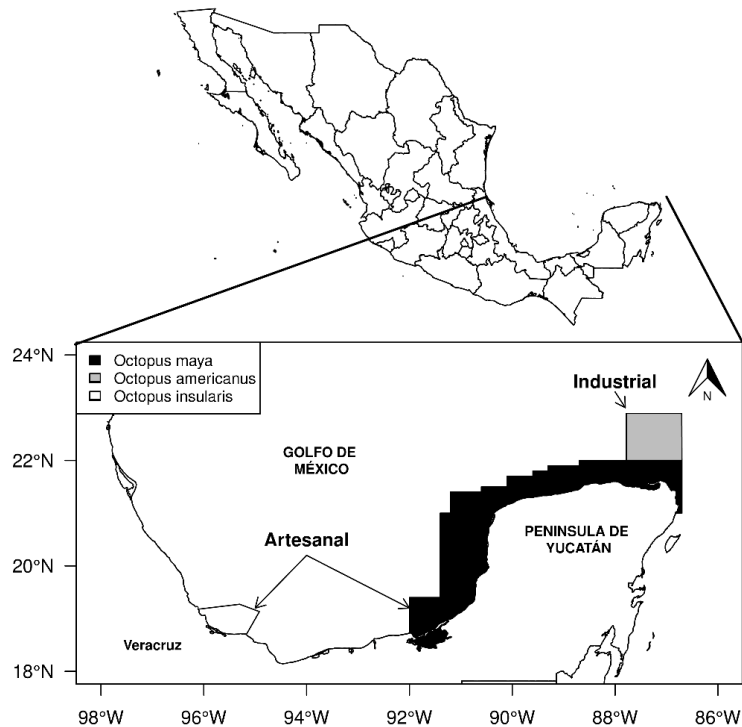


Figura 4. Regiones aproximadas de pesca del pulpo por tipo de flota. La flota artesanal en la Península Yucatán se dedica a la captura del *Octopus maya* y a *O. insularis* en Veracruz. La flota semi-industrial, captura *O. americanus* en el norte de la Península de Yucatán. Figura modificada de Galindo-Cortes et al., (2014).

La pesquería del pulpo se inició en 1950 en Campeche y fue dirigida a la captura principalmente de *O. maya* por parte de la flota ribereña de pequeña escala. Posteriormente, en la década de los 60, la pesquería se extendió hacia los demás puertos de Campeche, alcanzando capturas de ~1300 t en 1965. Durante la década de los 70, Yucatán, Quintana Roo y Veracruz incursionaron en la pesca del pulpo. En 1980 la captura de pulpo parecía que se había estabilizado en 8000 t por año; sin embargo, en el año de 1982 se concesionaron los permisos que permitieron el ingreso de la flota mayor, lo que incrementó las capturas del *O. americanus* en la región de la Península de Yucatán permitiendo la captura de 19000 t anuales de *O. maya* y 6500 t de *O. americanus* durante las últimas dos décadas (Salas et al., 2006; Galindo-Cortez et al., 2014; CONAPESCA, 2018). De acuerdo con los anuarios estadísticos, actualmente las principales zonas de captura corresponden a los estados de

Campeche y Yucatán, con capturas comparativamente bajas en Veracruz y Quintana Roo (CONAPESCA, 2018). En su conjunto estos estados reportan unas capturas de pulpo totales de ~32000 t para el 2018 (CONAPESCA, 2018- Figura 5).

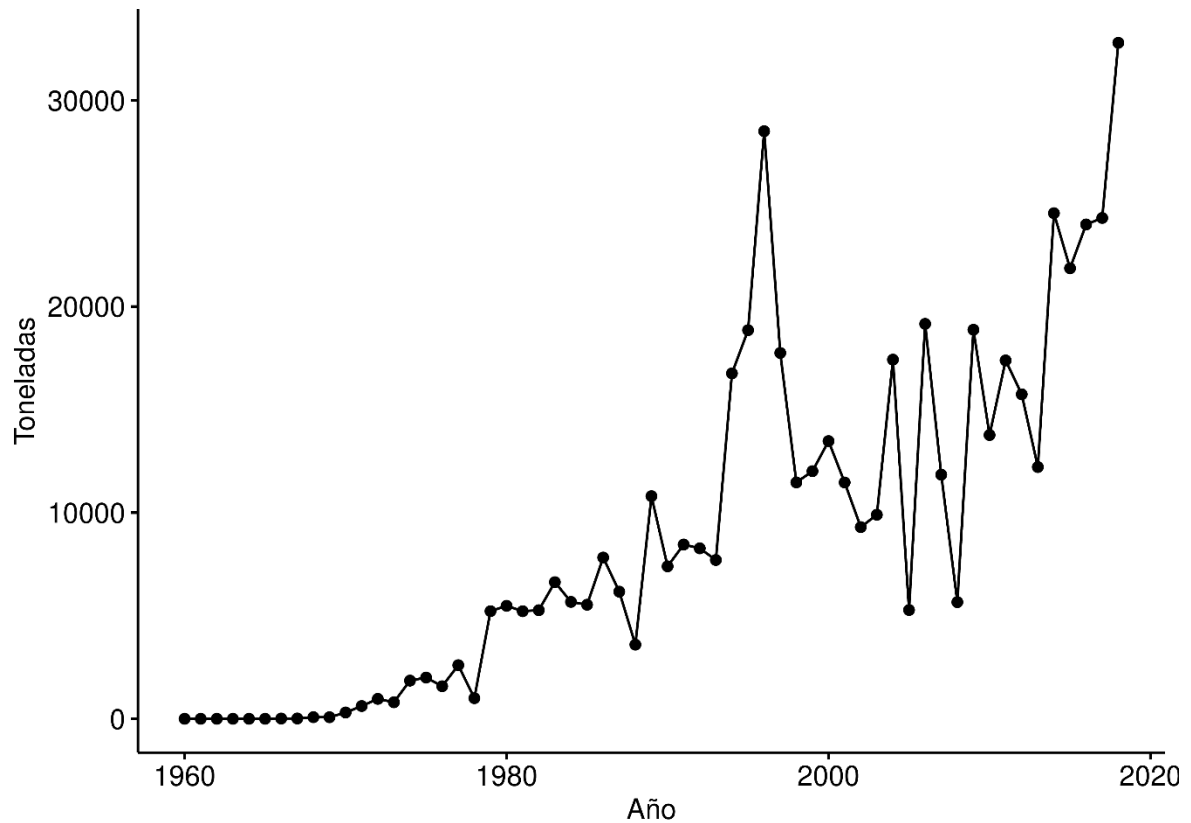


Figura 5. Volúmenes de captura de pulpo durante el periodo de 1966 a 2018.

Con base en los registros oficiales de pesca se han reportado fluctuaciones anuales en las capturas de pulpo (Salas et al., 2006; Galindo-Cortez et al., 2014; Arreguín-Sánchez, 2019) con una tendencia al incremento en las descargas, particularmente del *O. maya* (Arreguín-Sánchez, 2019). Estas oscilaciones han sido asociadas al CC, dado que los aumentos de temperatura han favorecido el crecimiento, lo que además de las importantes disminuciones de los principales depredadores, sugiere un incremento en la supervivencia y el reclutamiento (Arreguín-Sánchez, 2019), contradiciendo la noción de la década de los 80 de que el recurso se encontraba aprovechado al máximo sustentable (Solís-Ramírez y Arreguín-Sánchez, 1984; Arreguín-Sánchez et al., 1987)

1.6 Justificación

En México es necesario generar conocimiento que permita evaluar los potenciales efectos del CC en las pesquerías más importantes en el Golfo de México con el fin de elaborar estrategias de manejo y mitigación ante un ecosistema cambiante. Dado que la teoría del nicho se asocia a la adecuación y por lo tanto a las tasas intrínsecas de crecimiento (r), y las abundancias de las especies, los datos fisiológicos, los MC y MM son herramientas complementarias que permiten dilucidar los efectos potenciales del CC en los recursos pesqueros de la región.

Hoy en día se sabe que la abundancia de los recursos pesqueros está cambiando debido al CC. Por esa razón, es necesario determinar los motivos de estos cambios con el objetivo de pronosticar las oscilaciones en los volúmenes de captura en escenarios futuros sobre las especies de pulpos, las cuales sostienen importantes pesquerías en nuestro país. Es particularmente preocupante la forma en que esta pesquería es abordada por la normatividad oficial mexicana (DOF, 2014) dado que:

- 1) Se asume que el recurso pulpo va a ser beneficiada por el CC.
- 2) Todas las especies, son tratadas como un taxón por el sólo hecho de tener similitudes morfológicas (Lima et al., 2017). En realidad, cada especie tiene un NF diferente que maximiza su tasa intrínseca de crecimiento. Por ejemplo, mediciones directas de las respuestas fisiológicas del *O. maya* (Noyola et al., 2013; Caamal-Monsreal et al., 2016; Juárez et al., 2016; López-Galindo et al., 2019; Pascual et al., 2019) pronostican que el CC será negativo para esta especie.

En ese sentido, existen contradicciones y ausencias de información sobre el impacto del CC.

1.7. Objetivo general

Teniendo en cuenta todo lo anterior, el presente trabajo fue diseñado con el objetivo de desarrollar, integrar y validar datos fisiológicos y modelos de nicho (correlativos y mecanísticos) para evaluar su utilidad como herramientas de monitoreo y pronosticar los potenciales efectos del CC en la distribución de tres especies de octópodos de importancia comercial: *Octopus maya*, *O. insularis* y *O. americanus*, para coadyuvar a los tomadores de decisiones a planificar de la mejor manera estos importantes recursos pesqueros.

1.7.1. Objetivos particulares

- Evaluar si la estructura del nicho (asociada a variables ambientales) representa un indicador del potencial de las capturas de *O. maya* (Capítulo dos).
- Verificar si las tendencias históricas de las capturas anuales del *O. maya* pueden ser asociadas a la adecuación del año correspondiente por un MM, con el fin de establecer si estos modelos son lo suficientemente robustos para predecir las tendencias de producciones pesqueras (Capítulo tres).
- Establecer la relación entre diversos escenarios de CC y la sensibilidad térmica de los embriones de las tres especies de pulpo con el fin de generar escenarios que proyecten los posibles cambios en la distribución de estas especies (Capítulo cuatro).
- Proyectar MC y MM para determinar la distribución potencial y la adecuación de *O. maya* bajo diferentes escenarios de CC (Capítulo cinco).

1.8 Literatura citada

- Arreguín-Sánchez, F. (2019). Climate change and the rise of the octopus fishery in the Campeche Bank, México. *Regional Studies in Marine Science*, 32, 100852. <https://doi.org/10.1016/j.rsma.2019.100852>
- Arreguín-Sánchez, F., Seijo-Gutiérrez, J. ., Fuentes-Castellanos, D., y Solís-Ramírez, M. . (1987). *Estado del conocimiento de los recursos pesqueros de la plataforma continental de Yucatán y región adyacente*.
- Avendaño, O., Hernández-Flores, A., Velázquez-Abunader, I., Fernández-Jardón, C., Cuevas-Jimenez, A., & Guerra, Á. (2020a). Potential biomass and distribution of octopus in the eastern part of the Campeche bank (Yucatán, Mexico). *Scientia Marina*, 84(2), 133–142. <https://doi.org/10.3989/scimar.05007.01A>
- Avendaño, O., Roura, Á., Cedillo-Robles, C. E., González, Á. F., Rodríguez-Canul, R., Velázquez-Abunader, I., y Guerra, Á. (2020b). *Octopus americanus*: a cryptic species of the *O. vulgaris* species complex redescribed from the Caribbean. *Aquatic Ecology*, 54, 909–925. <https://doi.org/10.1007/s10452-020-09778-6>
- Avendaño, O., Velázquez-Abunader, I., Fernández-Jardón, C., Ángeles-González, L. E., Hernández-Flores, A., y Guerra, Á. (2019). Biomass and distribution of the red octopus (*Octopus maya*) in the north-east of the Campeche Bank. *Journal of the Marine Biological Association of the United Kingdom*, 99(6), 1317–1323. <https://doi.org/10.1017/S0025315419000419>
- Caamal-Monsreal, C., Uriarte, I., Farias, A., Díaz, F., Sánchez, A., Re, D., y Rosas, C. (2016). Effects of temperature on embryo development and metabolism of *O. maya*. *Aquaculture*, 451, 156–162. <https://doi.org/10.1016/j.aquaculture.2015.09.011>
- Cheung, W. W. L., Lam, V. W. Y., Sarmiento, J. L., Kearney, K., Watson, R., y Pauly, D. (2009). Projecting global marine biodiversity impacts under climate change scenarios. *Fish and Fisheries*, 10(3), 235–251. <https://doi.org/10.1111/j.1467-2979.2008.00315.x>
- Cheung, W. W. L., Lam, V. W. Y., Sarmiento, J. L., Kearney, K., Watson, R., Zeller, D., y Pauly, D. (2010). Large-scale redistribution of maximum fisheries catch potential in the global ocean under climate change. *Global Change Biology*, 16(1), 24–35. <https://doi.org/10.1111/j.1365-2486.2009.01995.x>
- Cheung, W. W. L., Watson, R., y Pauly, D. (2013). Signature of ocean warming in global fisheries catch. *Nature*, 497(7449), 365–368. <https://doi.org/10.1038/nature12156>
- Cisneros-Mata, M. A., Mangin, T., Bone, J., Rodriguez, L., Smith, S. L., y Gaines, S. D. (2019). Fisheries governance in the face of climate change: Assessment of policy reform implications for Mexican fisheries. *PLoS ONE*, 14(10). <https://doi.org/10.1371/journal.pone.0222317>
- Cisneros-Montemayor, A. M., Abas, M., Palacios-Abrantes, J., y González-Espinosa, P. C. (2020). Análisis espacial de efectos anticipados del cambio climático sobre la pesca en México : Un panorama para la adaptación. *Ciencia Pesquera*, 28, 31–44.
- Cisneros-Montemayor, A. M., Cisneros-Mata, M. A., Harper, S., y Pauly, D. (2013). Extent and implications of IUU catch in Mexico's marine fisheries. *Marine Policy*, 39(1), 283–288. <https://doi.org/10.1016/j.marpol.2012.12.003>

- CONAPESCA. (2018). *Anuario Estadístico de Acuicultura y Pesca 2018*. <https://www.gob.mx/conapesca/documentos/anuario-estadistico-de-acuicultura-y-pesca>
- DOF. (2014). *ACUERDO por el que se da a conocer el Plan de Manejo Pesquero de pulpo (O. maya y O. vulgaris) del Golfo de México y Mar Caribe*. http://dof.gob.mx/nota_detalle_popup.php?codigo=5338727
- DOF. (2018). *Carta Nacional Pesquera*. http://www.dof.gob.mx/nota_detalle.php?codigo=5525712yfecha=11/06/2018yprint=true
- Diaz, R. J., y Rosenberg, R. (2008). Spreading dead zones and consequences for marine ecosystems. *Science*, 321(5891), 926–929. <https://doi.org/10.1126/science.1156401>
- Doney, S. C., Ruckelshaus, M., Emmett Duffy, J., Barry, J. P., Chan, F., English, C. A., Galindo, H. M., Grebmeier, J. M., Hollowed, A. B., Knowlton, N., Polovina, J., Rabalais, N. N., Sydeman, W. J., y Talley, L. D. (2012). Climate Change Impacts on Marine Ecosystems. *Annual Review of Marine Science*, 4(1), 11–37. <https://doi.org/10.1146/annurev-marine-041911-111611>
- Doubleday, Z. A., Prowse, T. A. A., Arkhipkin, A., Pierce, G. J., Semmens, J., Steer, M., Leporati, S. C., Lourenço, S., Quetglas, A., Sauer, W., y Gillanders, B. M. (2016). Global proliferation of cephalopods. *Current Biology*, 26(10), R406–R407. <https://doi.org/10.1016/j.cub.2016.04.002>
- Elith, J., Kearney, M., y Phillips, S. (2010). The art of modelling range-shifting species. *Methods in Ecology and Evolution*, 1(4), 330–342. <https://doi.org/10.1111/j.2041-210X.2010.00036.x>
- Evans, T. G., Diamond, S. E., y Kelly, M. W. (2015). Mechanistic species distribution modelling as a link between physiology and conservation. *Conservation Physiology*, 3(1), 1–16. <https://doi.org/10.1093/conphys/cov056>
- FAO. (2018). *In Brief the State of World Fisheries and Aquaculture*.
- Galindo-Cortez, G., Hernández-Flores, Á., y Santos-Valencia, J. (2014). Pulpo del Golfo de México *Octopus maya* y *Octopus vulgaris*. In L. F. . Beléndez-Moreno, E. Espino-Barr, G. Galindo-Cortez, M. . Gaspar-Dillanes, L. Huidobro-Campos, y E. Morales-Bojórques (Eds.), *Sustentabilidad y Pesca Responsable en México, Evaluación y Manejo* (pp. 177–207). INAPESCA.
- Guisan, A., Tingley, R., Baumgartner, J. B., Naujokaitis-Lewis, I., Sutcliffe, P. R., Tulloch, A. I. T., Regan, T. J., Brotons, L., Mcdonald-Madden, E., Mantyka-Pringle, C., Martin, T. G., Rhodes, J. R., Maggini, R., Setterfield, S. A., Elith, J., Schwartz, M. W., Wintle, B. A., Broennimann, O., Austin, M., Kearney, M.R., Possingham, H.P, y Buckley, Y. M. (2013). Predicting species distributions for conservation decisions. *Ecology Letters*, 16(12), 1424–1435. <https://doi.org/10.1111/ele.12189>
- Gutiérrez-Ruelas, J. S., Jiménez, L., Quiroz-Reyes, A. P., Sotelo-Pedroza, S. C., y Jorge, S. (2019). On Some Problems of Estimating Fundamental Niche from Physiological Data. *BioRxiv*, 716688. <https://doi.org/10.1101/716688>
- Hijmans, R. J., y Graham, C. H. (2006). The ability of climate envelope models to predict the effect of climate change on species distributions. *Global Change Biology*, 12(12), 2272–2281. <https://doi.org/10.1111/j.1365-2486.2006.01256.x>
- Hutchinson, G. E. (1957). Concluding remarks and future work. *Cold Spring Harbor*

Symposia on Quantitative Biology, 22, 415–427. https://doi.org/10.1007/978-3-642-28276-8_6

- Hutchinson, G. E. (1978). *An introduction to population ecology* (Yale Press).
- IPCC. (2014). *Climate Change 2014: Synthesis Report of the IPCC Fifth Assessment Report (AR5)*.
- Jiménez-Valverde, A., Lobo, J. M., y Hortal, J. (2008). Not as good as they seem: The importance of concepts in species distribution modelling. *Diversity and Distributions*, 14(6), 885–890. <https://doi.org/10.1111/j.1472-4642.2008.00496.x>
- Juárez, O. E., Hau, V., Caamal-Monsreal, C., Galindo-Sánchez, C. E., Díaz, F., Re, D., y Rosas, C. (2016). Effect of maternal temperature stress before spawning over the energetic balance of *Octopus maya* juveniles exposed to a gradual temperature change. *Journal of Experimental Marine Biology and Ecology*, 474, 39–45. <https://doi.org/10.1016/j.jembe.2015.10.002>
- Kearney, M., y Porter, W. (2009). Mechanistic niche modelling: Combining physiological and spatial data to predict species' ranges. *Ecology Letters*, 12(4), 334–350. <https://doi.org/10.1111/j.1461-0248.2008.01277.x>
- Kearney, M., y Porter, W. P. (2004). Mapping the Fundamental Niche: Physiology, Climate, and the Distribution of a Nocturnal Lizard. *Ecology*, 85(11), 3119–3131. <http://labs.bio.unc.edu/Buckley/WGdocs/Kearney2004.pdf>
- Kearney, M. R., Wintle, B. A., y Porter, W. P. (2010). Correlative and mechanistic models of species distribution provide congruent forecasts under climate change. *Conservation Letters*, 3(3), 203–213. <https://doi.org/10.1111/j.1755-263X.2010.00097.x>
- Keeling, R. F., Körtzinger, A., y Gruber, N. (2010). Ocean Deoxygenation in a Warming World. *Annual Review of Marine Science*, 2(1), 199–229. <https://doi.org/10.1146/annurev.marine.010908.163855>
- Kumar, S., Neven, L. G., y Yee, W. L. (2014). Evaluating correlative and mechanistic niche models for assessing the risk of pest establishment. *Ecosphere*, 5(7). <https://doi.org/10.1890/ES14-00050.1>
- Lam, V. W. Y., Allison, E. H., Bell, J. D., Blythe, J., Cheung, W. W. L., Frölicher, T. L., Gasalla, M. A., y Sumaila, R. U. (2020). Climate change, tropical fisheries and prospects for sustainable development. *Nature Reviews Earth y Environment*, 1–15. <https://doi.org/10.1038/s43017-020-0071-9>
- Lima, F. D., Berbel-Filho, W. M., Leite, T. S., Rosas, C., y Lima, S. M. Q. (2017). Occurrence of *Octopus insularis* Leite and Haimovici, 2008 in the Tropical Northwestern Atlantic and implications of species misidentification to octopus fisheries management. *Marine Biodiversity*, 47(3), 723–734. <https://doi.org/10.1007/s12526-017-0638-y>
- Lobo, J. M., Jiménez-Valverde, A., y Hortal, J. (2010). The uncertain nature of absences and their importance in species distribution modelling. *Ecography*, 33(1), 103–114. <https://doi.org/10.1111/j.1600-0587.2009.06039.x>
- López-Galindo, L., Galindo-Sánchez, C., Olivares, A., Avila-Poveda, O. H., Díaz, F., Juárez, O. E., Lafarga, F., Pantoja-Pérez, J., Caamal-Monsreal, C., y Rosas, C. (2019). Reproductive performance of *Octopus maya* males conditioned by thermal stress. *Ecological Indicators*, 96, 437–447. <https://doi.org/10.1016/j.ecolind.2018.09.036>

- Maguire, B. J. (1973). Niche Response Structure and the Analytical Potentials of Its Relationship to the Habitat. *The American Naturalist*, 107(954), 213–246. <https://doi.org/10.1086/282827>
- Martínez-Arroyo, A., Manzanilla-Naim, S., y Zavala-Hidalgo, J. (2011). Vulnerability to climate change of marine and coastal fisheries in México. *Atmósfera*, 24(1), 103–123.
- Martinez-Meyer, E. (2005). Climate change and biodiversity: some considerations in forecasting shifts in species' potential distributions. *Biodiversity Informatics*, 2, 42–55. <https://doi.org/10.17161/bi.v2i0.8>
- Martínez-Meyer, E., Díaz-Porras, D., Peterson, A. T., y Yáñez-Arenas, C. (2013). Ecological niche structure and rangewide abundance patterns of species. *Biology Letters*, 9(1). <https://doi.org/10.1098/rsbl.2012.0637>
- Moyano, M., Illing, B., Polte, P., Kotterba, P., Zablotski, Y., Gröhsler, T., Hüdepohl, P., Cooke, S. J., y Peck, M. A. (2020). Linking individual physiological indicators to the productivity of fish populations: A case study of Atlantic herring. *Ecological Indicators*, 113. <https://doi.org/10.1016/j.ecolind.2020.106146>
- Noyola, J., Mascaró, M., Caamal-Monsreal, C., Noreña-Barroso, E., Díaz, F., Re, D., Sánchez, A., y Rosas, C. (2013). Effect of temperature on energetic balance and fatty acid composition of early juveniles of *Octopus maya*. *Journal of Experimental Marine Biology and Ecology*, 445, 156–165. <https://doi.org/10.1016/j.jembe.2013.04.008>
- Osorio-Olvera, L., Soberón, J., y Falconi, M. (2019). On population abundance and niche structure. *Ecography*, 42(8), 1415–1425. <https://doi.org/10.1111/ecog.04442>
- Osorio-Olvera, L., Yañez-Arenas, C., Martínez-Meyer, E., y Peterson, A. T. (2020). Relationships between population densities and niche-centroid distances in North American birds. *Ecology Letters*, 23(3), 555–564. <https://doi.org/10.1111/ele.13453>
- Pascual, C., Mascaró, M., Rodríguez-Canul, R., Gallardo, P., Sánchez, A. A., Rosas, C., y Cruz-López, H. (2019). Sea surface temperature modulates physiological and immunological condition of octopus maya. *Frontiers in Physiology*, 10. <https://doi.org/10.3389/fphys.2019.00739>
- Pauly, D., y Cheung, W. W. L. (2018). Sound physiological knowledge and principles in modeling shrinking of fishes under climate change. *Global Change Biology*, 24(1), e15–e26. <https://doi.org/10.1111/gcb.13831>
- Peterson, A. T., Papeş, M., y Soberón, J. (2015). Mechanistic and correlative models of ecological niches. *European Journal of Ecology*, 1(2), 28–38. <https://doi.org/10.1515/eje-2015-0014>
- Peterson, T. A., Soberón, J., Pearson, R. G., Anderson, R. P., Martínez-Meyer, E., Nakamura, M., y Araújo, M. B. (2011). Ecological niches and geographic distributions. In *Choice Reviews Online*. Princeton University Press.
- Poloczanska, E. S., Brown, C. J., Sydeman, W. J., Kiessling, W., Schoeman, D. S., Moore, P. J., Brander, K., Bruno, J. F., Buckley, L. B., Burrows, M. T., Duarte, C. M., Halpern, B. S., Holding, J., Kappel, C. V., O'Connor, M. I., Pandolfi, J. M., Parmesan, C., Schwing, F., Thompson, S. A., y Richardson, A. J. (2013). Global imprint of climate change on marine life. *Nature Climate Change*, 3, 919–925. <https://doi.org/10.1038/nclimate1958>
- Pörtner, H. O., y Farrell, A. P. (2008). Physiology and Climate Change. *Science*,

322(5902), 690–692. <https://doi.org/10.1126/science.1163156>

- Pörtner, H. O., y Peck, M. A. (2010). Climate change effects on fishes and fisheries: Towards a cause-and-effect understanding. *Journal of Fish Biology*, 77(8), 1745–1779. <https://doi.org/10.1111/j.1095-8649.2010.02783.x>
- Salas, S., Mexicano-Cintora, G., y Cabrera, M. A. (2006). ¿Hacia dónde van las pesquerías en Yucatán? *Tendencias, Retos y Perspectivas*. CINVESTAV.
- Sillero, N. (2011). What does ecological modelling model? A proposed classification of ecological niche models based on their underlying methods. *Ecological Modelling*, 222(8), 1343–1346. <https://doi.org/10.1016/j.ecolmodel.2011.01.018>
- Simpson, S. D., Jennings, S., Johnson, M. P., Blanchard, J. L., Schön, P. J., Sims, D. W., y Genner, M. J. (2011). Continental shelf-wide response of a fish assemblage to rapid warming of the sea. *Current Biology*, 21(18), 1565–1570. <https://doi.org/10.1016/j.cub.2011.08.016>
- Soberón, J. (2007). Grinnellian and Eltonian niches and geographic distribution of species. *Ecology Letters*, 10(12), 1115–1123.
- Soberón, J., y Nakamura, M. (2009). Niches and distributional areas: Concepts, methods, and assumptions. *Analytica Chimica Acta*, 106, 19644–19650. <https://doi.org/10.1073/pnas.0901637106>
- Soberón, J., Osorio-Olvera, L., y Peterson, T. (2017). Diferencias conceptuales entre modelación de nichos y modelación de áreas de distribución. *Revista Mexicana de Biodiversidad*, 88(2), 437–441. <https://doi.org/10.1016/j.rmb.2017.03.011>
- Soberón, J., y Peterson, T. A. (2005). Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodiversity Informatics*, 2, 1–10. <https://doi.org/10.17161/bi.v2i0.4>
- Solís-Ramírez, M., y Arreguín-Sánchez, F. (1984). Analysis of (*Octopus maya*) fishery in the Campeche Bank. *Mem. IX MEXUS Gulf Annual Meeting*, 31–38.
- Solomon, S., Plattner, G.-K., Knutti, R., y Friedlingstein, P. (2009). Irreversible climate change due to carbon dioxide emissions. *Proceedings of the National Academy of Sciences of the United States of America*, 106(6), 1704–1709.
- Sumaila, U. R., Cheung, W. W. L., Lam, V. W. Y., Pauly, D., y Herrick, S. (2011). Climate change impacts on the biophysics and economics of world fisheries. *Nature Climate Change*, 1(9), 449–456. <https://doi.org/10.1038/nclimate1301>
- Voss, G. L., y Solís-Ramírez, M. (1966). *Octopus maya*, a new species from the Bay of Campeche, Mexico. *Bulletin of Marine Science*, 16(3), 615–625.
- Yañez-Arenas, C., Guevara, R., Martínez-Meyer, E., Mandujano, S., y Lobo, J. M. (2014). Predicting species' abundances from occurrence data: Effects of sample size and bias. *Ecological Modelling*, 294, 36–41. <https://doi.org/10.1016/j.ecolmodel.2014.09.014>
- Zarco-Perelló, S., Mascaró, M., Garza-Pérez, R., y Simoes, N. (2013). Topography and coral community of the Sisal Reefs, Campeche Bank, Yucatán, México. *Hidrobiológica*, 23(1), 28–41.

Capítulo dos - Long term environmental data explain better the abundance of the red octopus (*Octopus maya*) when testing the niche centroid hypothesis

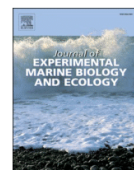
Sometido a:

Journal of Experimental Marine Biology and Ecology

Estado: Aceptado

Contents lists available at [ScienceDirect](https://www.sciencedirect.com)

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Long-term environmental data explain better the abundance of the red octopus (*Octopus maya*) when testing the niche centroid hypothesis

Luis Enrique Ángeles-González^{a,b,c,d}, Enrique Martínez-Meyer^e, Carlos Rosas^{c,d}, Paulina Valeria Guarneros-Narváez^f, Jorge A. López-Rocha^g, Ángel Escamilla-Aké^h, Luis Osorio-Olveraⁱ, Carlos Yáñez-Arenas^{b,*}

^a Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Av. Ciudad Universitaria 3000, 04510, Coyoacán, Ciudad de México, México

^b Laboratorio de Ecología Geográfica, Unidad de Conservación de la Biodiversidad, Parque Científico y Tecnológico de Yucatán, Unidad Académica Sisal, Facultad de Ciencias, Universidad Nacional Autónoma de México, Carretera Sierra Papacal Km 5, Mérida, Yucatán, México

^c Laboratorio Nacional de Resiliencia Costera, Facultad de Ciencias, Universidad Nacional Autónoma de México, 97356, Puerto de Abrigo, Sisal, Yucatán, México

^d Laboratorio de Ecofisiología Aplicada, Unidad Multidisciplinaria de Docencia e Investigación, Facultad de Ciencias, Universidad Nacional Autónoma de México, 97356, Puerto de Abrigo, Sisal, Yucatán, México

^e Instituto de Biología, Universidad Nacional Autónoma de México, Circuito Zona Deportiva Ciudad Universitaria, 04510 Ciudad de México, México

^f Recursos del Mar, Centro de Investigación y de Estudios Avanzados del IPN, Km 6 antigua, Carr. Mérida – Progreso, Loma Bonita, 97310 Mérida, Yucatán, México

^g Laboratorio de Análisis Espacial de Zonas Costeras, Unidad Multidisciplinaria de Docencia e Investigación, Facultad de Ciencias, Universidad Nacional Autónoma de México, 97356, Puerto de Abrigo, Sisal, Yucatán, México

^h Centro para el Desarrollo Educativo, Científico, Tecnológico y Ambiental (CEDECTYA A.C.), Calle 21, 97500 Dzidzantún, Yucatán, México

ⁱ Departamento de Ecología de la Biodiversidad, Instituto de Ecología, Universidad Nacional Autónoma de México, Av. Ciudad Universitaria 3000, 04510, Coyoacán, Ciudad de México, México

ARTICLE INFO

Keywords:

Fundamental niche
Seasonal variation
Distance to niche centroid
Abundance
Octopus maya

ABSTRACT

Correlative ecological niche models have been widely used to infer the organisms' environmental suitability; nevertheless, the relationship between this estimated suitability and their abundance is less clear. The ecological theory proposes that the internal structure of a species niche determines its abundance. Specifically, abundance should decrease from the niche centroid to its margins (i.e., distance to the niche centroid-abundance hypothesis - DNC-abundance), showing a negative relationship. This study tested this hypothesis using a high-quality dataset of catch per unit of effort as a proxy of the abundance of the red octopus (*Octopus maya*) collected during its fishing season in the Yucatan Shelf, Mexico in 2012. Species' niche was estimated with half of the abundance data taken as presence-only records and environmental variables that consisted of temperature and salinity. The remaining data were used to analyze the DNC-abundance. The protocol was repeated using the abundance and environmental data corresponding to each month of the fishing season. The effect of estimating the species niche was also examined using two different environmental datasets: one that matched abundance in a more finely temporal resolution (average values of the corresponding month in 2012 at a resolution of 9 km²) versus another one with a coarser temporal resolution (long-term data: salinity [1955–2006] and temperature [2002–2010] at a resolution of 1 km²). A consistent inverse relationship was found between abundance and distance to the centroid for the most evaluated scenarios, suggesting that niche structure could be informative for fishery monitoring even under climate change scenarios. In addition, contrary to our expectations, relationships were stronger when the coarse temporal resolution variables were used, which suggests that longer temporal environmental conditions may determine population abundance, probably due to seasonal aggregation in the western region of the Yucatan Peninsula.

1. Introduction

Hutchinson originally conceived the niche as a hypercube in a

multivariate environmental space representing an organism's potential tolerance (Hutchinson, 1957). He also suggested an "optimal" region of the niche where conditions for survival are maximized (Holt, 2009).

* Corresponding author.

E-mail address: carlos_yanez@ciencias.unam.mx (C. Yáñez-Arenas).

<https://doi.org/10.1016/j.jembe.2021.151609>

Received 25 January 2021; Received in revised form 14 July 2021; Accepted 15 July 2021

Available online 29 July 2021

0022-0981/© 2021 Elsevier B.V. All rights reserved.

This idea was later adopted and extended by Maguire (1973) describing the niche as an ellipsoid in correspondence with many experimental studies of organism physiology (Biggs and McDermott, 1973; Birch, 1953; Blaszkowski and Moreira, 1986; Haefner, 1969; Hooper et al., 2008; Rothlisberg, 1979). Maguire (1973) stated that different regions of the ellipsoid-like niche structure correspond to different carrying capacities (K) and intrinsic growth rates (r) of populations, and in the center of the ecological niche is where environmental conditions are optimal for populations. In this region, K and r are maximized, potentially allowing populations to achieve higher abundances or densities (Fig. 1).

Brown (1984) admitted the impossibility of considering the influence of environmental variables on population attributes due to the difficulty of obtaining the necessary inputs, which was one significant issue decades ago. Nowadays, environmental data and biological information are widely available because of large scale digitization of data that allows public access to species presence records and environmental information (Soberón and Peterson, 2004). In contrast to the idea that abundance should decrease with the distance to the center of the geographic distribution (geographic-abundance hypothesis Brown, 1984), the highest abundance should occur in the center of the niche, and as populations get farther away from it, abundance decreases (Martínez-Meyer et al., 2013; Yañez-Arenas et al., 2012). This expected negative relationship is usually denominated as the distance to the niche centroid-abundance hypothesis (DNC-abundance), and it is currently a hot topic in the field of ecological niche modeling (Yañez-Arenas et al., 2020).

For instance, Martínez-Meyer et al. (2013) found a consistent negative DNC-abundance relationship across different species of terrestrial vertebrates. This relationship should not be casual since the DNC-abundance represents the species' fundamental niche internal structure. While some studies have provided empirical support to this hypothesis (Escalante and Martínez-Meyer, 2013; Martin et al., 2016; Martínez-Gutiérrez et al., 2018; Osorio-Olvera et al., 2020b; Ureña-Aranda et al., 2015; Yañez-Arenas et al., 2014b), others have found

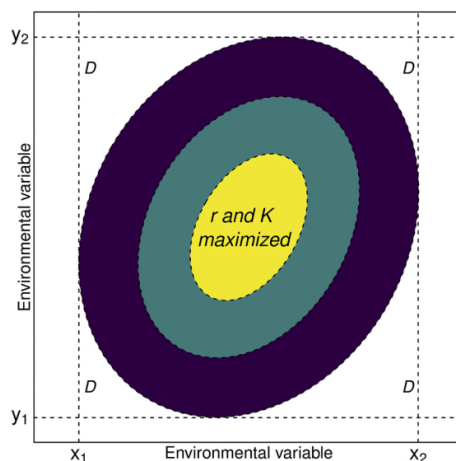


Fig. 1. Representation of the ecological niche and its internal structure *sensu* Maguire (1973). The dashed lines represent the environmental tolerance to variables Y and X. The square made by the dashed lines gives a two-dimensional representation of the niche space where there is no interaction between the variables. The purple curved dashed line illustrates tolerance limits when variables interact. The ellipse center shows the combinations of levels of environmental factors X and Y where r and K are maximum. In D , conditions and beyond species population cannot survive for an ecologically meaningful time (sink populations). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

weak or no support at all (Dallas et al., 2017; Dallas and Santini, 2020; Santini et al., 2019). However, on the one hand, low quality of occurrence data due to sampling bias (Knouft, 2018; Yañez-Arenas et al., 2014a), low pixel resolution (multiple abundance data points falling within a single climate pixel losing environmental information), or inappropriate methodological decisions (e.g., the use of convex hull to represent the niche) (Soberón et al., 2018) can obscure the relationship, even if it exists (Osorio-Olvera et al., 2020b; Osorio-Olvera et al., 2019; Soberón et al., 2018). On the other hand, processes like transitory states, the heterogeneous spatial structure of suitability, Allee effects (Osorio-Olvera et al., 2020b), and unfilled niches due to biotic or dispersal limitations (Soberón and Nakamura, 2009; Soberón and Peterson, 2005; Yañez-Arenas et al., 2020) would break down the expected relationship.

In addition, under the usual modeling approach, the ecological niche is estimated using environmental layers that consist of long-term yearly or monthly averages (defined here as “coarse temporal resolution” - CTR). Although these approaches are helpful, a problem not traditionally considered arises, the environmental conditions do not accurately match occurrence dates. Such procedures could influence niche estimations reducing the DNC-abundance relationship, especially in climates with marked seasonal differences. The proposal in this study is that if the occurrences and environments had a higher temporal match (defined here as “finer temporal resolution” - FTR), the DNC-abundance relationship might increase if compared to the CTR. To our knowledge, no previous work related to DNC-abundance has reviewed the effect of the temporal match between environmental and occurrence data.

Therefore, the objective of this research is to test the viability on the DNC-abundance hypothesis on an endemic holobenthic marine organism of commercial importance in the Yucatan Shelf, Mexico – the red octopus (*Octopus maya* Voss and Solís-Ramírez, 1966). Additionally, a second goal is to compare the FTR and CTR datasets of environmental variables for estimating the species' niche. It is important to highlight that a critical assumption needed to test the DNC-abundance hypothesis is fulfilled in the case of this species. That is, presence and abundance records span most of their entire geographic range (Osorio-Olvera et al., 2020b). Thus, this study anticipates finding a negative correlation between the niche centroid and the red octopus abundance.

Conceivably, if environmental heterogeneity exists in the Yucatan Shelf, the DNC-abundance relationship will be more reliable than if conditions are homogenized since no area should be preferred. If a link can be found between the DNC-abundance hypothesis, understanding the processes that determine the spatio-temporal patterns of the species abundance may increase. In turn, the description of this relationship could help predict the impact of threats, such as climate change, redirecting the predictions to catch potential instead of only suitability values. It would be very important, especially in heat-sensitive species of commercial importance, such as the red octopus (Juárez et al., 2015; Pascual et al., 2019; Sanchez-García et al., 2017).

2. Material and methods

2.1. Study area

The Yucatan Peninsula (YP) is a biogeographical province placed in southeast Mexico that has an extensive continental shelf with a gentle slope (Monreal-Gómez et al., 2004). The region is formed by three Mexican states (Campeche, Yucatán, and Quintana Roo), Belize, and part of Guatemala and divides the Gulf of Mexico from the Caribbean Sea. Generally, in the western region of the YP, the temperature varies from 21 °C in January to 30 °C in September with oscillations up to 4 °C in a summer day (Juárez et al., 2015). However, in the northeastern region, The Yucatan Current generates seasonal upwelling (spring-summer) (Enriquez and Mariño-Tapia, 2014; Monreal-Gómez et al., 2004) that keeps this region colder if compared to the western region (Ángeles-González et al., 2017).

During autumn and winter, the Yucatan Shelf temperature is usually

close to 22.5 °C (Enriquez et al., 2010; Monreal-Gómez et al., 2004). Regarding salinity, studies in the Northern region during summer indicate that salinity values range from 36.25 to 36.75 PSU. However, the process of evaporation or precipitation can provoke quick changes in those values (Enriquez et al., 2013). A haline front forms in the western region due to the discharge of various rivers (Czitrom et al., 1986), with an apparent decrease in salinity in the westernmost region of the YP with values lower than 30 PSU (Phleger and Ayala-Castañares, 1971).

2.2. Species distribution and environmental preferences

The red octopus is a species that can reach mantle lengths of up to 200 mm and weigh as much as 2 kg (Markaida et al., 2016). This species is associated with areas covered by seagrass (*Thalassia testudinum*), coral fragments, and calcite mudstone basins at the seabed bottom (Voss and Solís-Ramírez, 1966; Zarco-Perelló et al., 2013). It is usually fished in shallow waters at depths of <30 m and is endemic to the YP (Diario Oficial de la Federación, 2014). Nevertheless, evidence indicates that this species can be occasionally found in deeper water (~60 m) than in the regions where they are traditionally fished (Avendaño et al., 2019).

Physiological studies about this species have reported that their optimal temperatures change notably during their ontogenetic development, reporting thermal windows from 20 to 26 °C in embryos, 17–33 °C in juveniles, and 21–27 °C in adults (Tremblay et al., 2017). In addition, laboratory studies have been validated in wild populations, e. g. Angeles-Gonzalez et al. (2017) detected a strong seasonality in the YP western region where mature individuals' proportion increase when temperatures are lower. In contrast, adult octopuses are found all year round in the northeastern region due to the relatively stable lower temperatures. Unfortunately, no studies about the salinity preferences of the red octopus have been done. However, successful acclimatization occurs at >32 PSU (Rosas et al., 2014).

2.3. Data collection

Monthly landing samplings of the small-scale fishing fleet were carried out during the fishing season of red octopus (from August to December 2012) in the ports of Sabancuy, Champoton, Seybaplaya, Campeche, Isla Arena, Celestun, Sisal, Progreso, Telchac, Dzilam, San Felipe, El Cuyo, and Holbox in the YP, Mexico (Gamboa-Álvarez et al., 2015) (Fig. 2). The abundance was standardized to catch per unit effort (CPUE), representing the number of octopuses caught per hour of effective fishing (organism per hour). For each month and for a composite database consisting of the whole fishing season (August–December), the abundance databases were randomly partitioned into two-half sets (training and testing) (Supplementary material 1). One group was used to calibrate different models, while the other one was retained with the abundance data to be used in a subsequent analysis (described below). It is important to emphasize that this process was performed for two different environmental datasets: MARSPEC (Sbrocco and Barber, 2013) and the GLORYS12V1 product from the Copernicus Marine Environment Monitoring Service.

The environmental layers from MARSPEC characterize the inter-annual means, extremes, and variances in sea surface salinity (1955–2006) and temperature (2002–2010). Layers were used at a resolution of ~30 arcseconds (~1 km²) for this study. In contrast, GLORYS12V1 provided real-time information on surface temperature and salinity at resolutions of ~5 arcminutes (~9 km²), covering a temporal period that matched the sampling data. Additionally, since the data were monthly-derived environmental layers, a composite layer was also generated by averaging each month's pixel values. MARSPEC bathymetric data of a corresponding resolution was used for both environmental datasets. Environmental variables used for the two datasets are shown in Supplementary material 2. The environmental layers were chosen because of their importance in controlling the fitness of the red octopus (Juárez et al., 2015; Pascual et al., 2019) and other

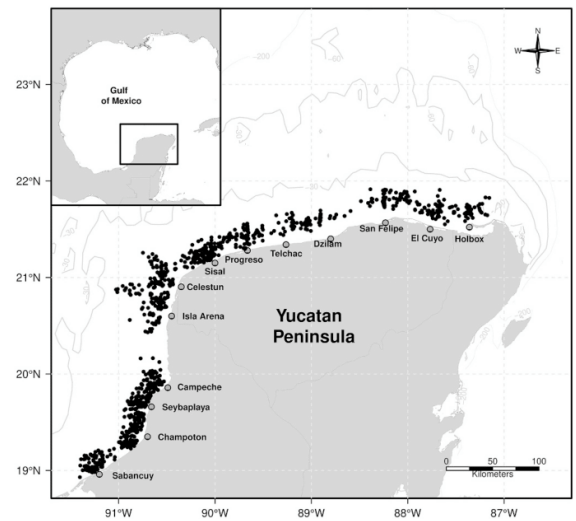


Fig. 2. Study area on the Yucatan Peninsula (YP) continental shelf, showing the ports where the coastal fleet samplings were performed. The dots represent fishing trips where red octopus (*Octopus maya*) were registered (1162) during the sampling periods from August–December 2012 (fishing season). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

marine organisms (Brown et al., 1992; Criales et al., 2011).

2.4. Ecological niche model

The ecological niche of the octopus was modeled using minimum volume ellipsoids (MVE). The MVE is an estimator based on an ellipsoid that includes a determined percentage of n observations (Van Aelst and Rousseeuw, 2009). This process was done with the 'ntbox' library (Osorio-Olvera et al., 2020a) from the programming language R (R Core Team, 2020). This methodology was selected since ellipsoids are a good estimator of species' fundamental niches (Qiao et al., 2016; Soberón et al., 2018). A monthly MVE was fitted using half of the occurrence data (see above) specific for each period and the entire fishing season. Different MVE were fitted, including 90%, 95%, and 99.9% of occurrence records to leave out environmental outliers.

Via this methodology, a total of 1638 and 72 ecological niche models were fitted for the CTR (period averages from MARSPEC) and FTR dataset (monthly averages from GLORYS12V1), respectively, considering two to three dimensions (the number of environmental variables considered to fit MVE) for FTR dataset and two to four dimensions in CTR. Niche models were then projected into geographic space as environmental suitability maps as a representation of the species' fitness (the closer to the niche centroid, the higher suitability). Finally, models were evaluated with the area under the curve ratio of the partial Receiver Operating Characteristic (pROC) technique. Only the models that met statistical significance ($P < 0.05$) were retained.

2.5. DNC-abundance relationship

A Mahalanobis distance to the niche centroid was calculated for each abundance-testing data point (see above) using the Mahalanobis function in base R. For this purpose, the abundance from the test data was overlapped on the suitability maps obtained from the MVE analysis. Later, the relationship between species abundance and Mahalanobis distance was assessed using the Spearman's rank correlation coefficient, a nonparametric measure of rank correlation, selecting the remaining models with the highest negative correlations (Supplementary material

3) following the procedures by Osorio-Olvera et al. (2020b).

Additionally, the relationship with quantile regressions (QR) was also analyzed, estimating standard errors using Kernel's estimate of the sandwich with the package 'quantreg' (Koenker, 2019). The QR can provide a more complete view of causal relationships between ecological processes than classical approaches, such as ordinary least squares, which occurs because conventional methods tend to estimate mean value change rates (Cade and Noon, 2003). However, abundance data usually have high variation levels, creating skew data (Jiménez-Valverde, 2012). In contrast, the QR allows estimating multiple rates of change defined by some specified quantiles (τ), providing a more complete picture of the relationships between variables (Cade and Noon, 2003). Since the hypothesis is to find mainly a relationship between the abundance and the niche centroid in the highest quantiles due to red octopus aggregation near the centroid, multiple high values of τ were tested (75th, 80th, 85th, 90th, 95th and 100th). It is important to point out that although evidence exists that the red octopus may be found in deeper waters than in the regions where the data was recollected (Avendaño et al., 2019; Guarneros-Narváez et al., 2020), a sampling effort proportional to the species local densities can still be useful to test the DNC-abundance relationship (Yañez-Arenas et al., 2014a).

3. Results

3.1. Fishing season data

A total of 76,043 octopuses were collected from ~1162 fishing trips during the fishing season. The months with the highest numbers of total catches and CPUE by fishing trip were obtained in August and September, while the lowest ones were obtained in November and

December (Fig. 3A). The environmental conditions associated with the presence of the red octopus varied between the two temporal resolution datasets of variables (Fig. 3B). For the CTR dataset, individuals are found at temperatures and salinities of 25–27 °C and 36.1–36.5 PSU throughout the year. In the FTR dataset, clear seasonal environmental conditions are found with higher mean temperatures in August and September (~29 °C), decreasing 4° during November and December. In contrast, salinity values are lower from August to October (~36 to 36.3 PSU) than in November and December (~36.3 to 36.5 PSU). Regarding sea depth, red octopuses catch occur at ~10 m, rarely surpassing 30 m.

3.2. Geographic patterns of environmental suitability

In general, niche models showed that the highest suitability tends to occur in the western and northwestern regions of the Yucatan Shelf, from Sabancuy to Dziliam port. In contrast, the northeastern region tends to show lower estimated suitability (Fig. 4 – Supplementary material 4), particularly in November. The highest suitability is restricted to the northwestern region except for the data that included 90%, which predicts suitable conditions along the coast. The maps obtained with the FTR and CTR datasets predict similar trends, although some differences could be observed in ellipses that include 99.9% of species' occurrences (Fig. 4 - Supplementary material 4).

3.3. Niche centroids descriptions

For FTR models, bathymetry and temperature were usually chosen with a stable centroid at shallow waters (7 to 10 m), while temperature diminishes through the year (28–29 °C to 25 °C) and salinity values of 36 PSU when selected (e.g., December). In CTR models, bathymetry and

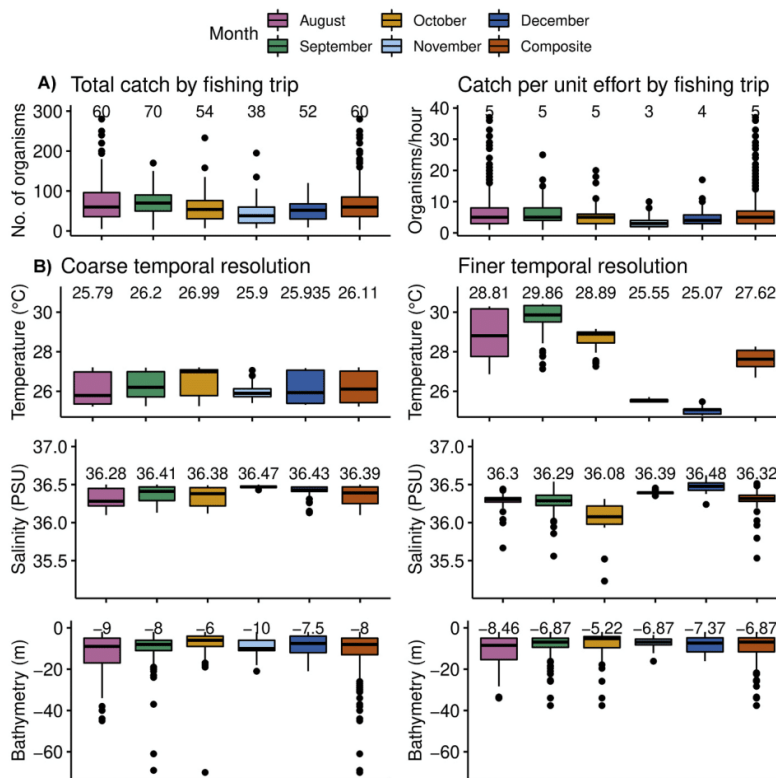


Fig. 3. Total catch and catch per unit effort by fishing trip (a proxy of abundance) are shown at the top of the figure (A). Mean sea surface temperature and salinity where the red octopus (*Octopus maya*) was fished during the 2012 fishing season (August–December). Left column corresponds to values obtained from the coarse temporal resolution, while the right column are values obtained from the finer temporal resolution. Median values are shown in each panel above the box (B). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

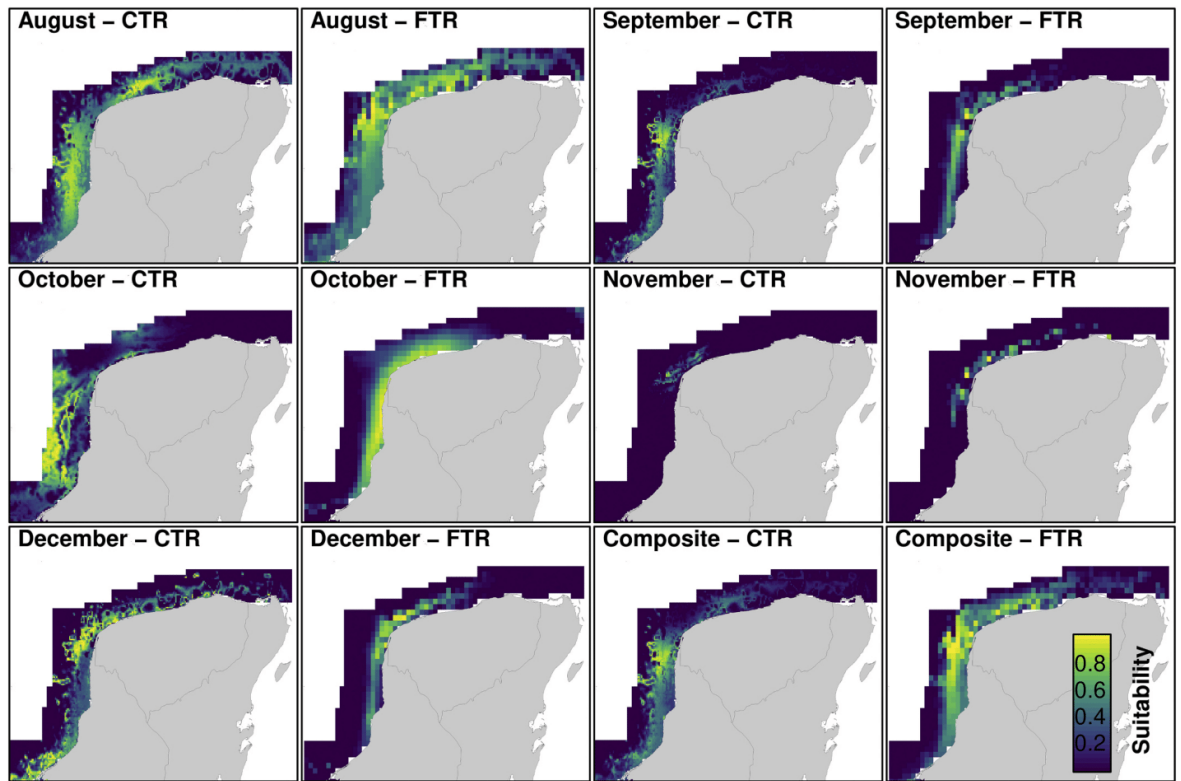


Fig. 4. Niche models as environmental suitability maps obtained through a minimum volume ellipsoid approach that included 95% of red octopus (*Octopus maya*) occurrences for the fishing season (August to December) and a composite scenario for coarse temporal and finer temporal resolution models (CTR and FTR respectively). The closer to the niche centroid the higher suitability. The environmental suitability maps obtained with an inclusion of 90% and 99% of occurrences are presented in the Supplementary material 4. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

environmental variables related to temperature and salinity were usually chosen (range, variance, mean). However, in August, bathymetry and annual salinity were selected (Supplementary material 5).

Table 1

Spearman correlations between the distance to the niche centroid and the catch per unit effort (organism per hour – a proxy of abundance) of the red octopus (*Octopus maya*) for different inclusion percentages of occurrences in ellipsoids.

Time	Training	Testing	Inclusion	Finer temporal resolution		Coarse temporal resolution	
				P value	Rho value	P value	Rho value
August	226	226	90%	0*	-0.39	0*	-0.4
			95%	0*	-0.32	0*	-0.37
			99.9%	0*	-0.34	0*	-0.37
September	156	155	90%	0*	-0.27	0*	-0.34
			95%	0.005*	-0.22	0*	-0.34
			99.9%	0.003*	-0.17	0*	-0.38
October	114	114	90%	0*	-0.39	0*	-0.39
			95%	0*	-0.35	0*	-0.41
			99.9%	0*	-0.38	0*	-0.4
November	43	42	90%	0.3	0.14	0.01	-0.39
			95%	0.3	0.14	0.006*	-0.41
			99.9%	0.3	0.14	0.01*	-0.39
December	43	43	90%	0.1	0.23	0.01*	-0.36
			95%	0.08	0.27	0.01*	-0.36
			99.9%	0.2	0.11	0.01*	-0.36
Fishing Season	581	581	90%	0*	-0.17	0*	-0.35
			95%	0*	-0.14	0*	-0.34
			99.9%	0.001*	-0.13	0*	-0.39

Statistical significance ($P < 0.05$) is shown with an asterisk (*).

3.4. Relationship between the distance to the niche centroid and abundance

Overall, the highest abundance was aggregated near the niche centroid and decreased consistently when moving further away to the niche margins. This pattern was observed for environmental datasets and ellipsoids with different inclusion percentages of occurrences (90%, 95%, 99.9%). Non-significant results ($P > 0.05$) were observed in November and December when using the FTR dataset. Regarding the comparison of the models generated with CTR vs those obtained with the FTR dataset, higher negative correlations were observed in the former one regardless of the percentage of occurrences included in the ellipsoids (Table 1, Fig. 5, Supplementary Material 6).

The relationship between the DNC-abundance tends to be triangular or wedge-shaped, indicating that although higher abundance occurs nearby the centroid, high variability is observed in the data. The QR analyses show a significant relationship between abundance and the distance to the niche centroid of red octopus, particularly at the highest τ values (i.e., 90th, 95th, and 100th). This relationship is more noticeable for August, September, October, and the composite database, particularly for CTR models. In contrast, for November and December (CTR and FTR), non-significant relationships ($P > 0.05$) were found (Table 2 Fig. 6, Supplementary material 7).

4. Discussion

Our results show that generally, the highest abundance tends to be

found near the centroid of the ellipsoid; therefore, as occurrences move further away from the centroid, the potential abundance diminishes, coinciding with what has been reported in other studies (Martínez-Meyer et al., 2013; Osorio-Olvera et al., 2020b; Ureña-Aranda et al., 2015). It is important to point out that the relationships were mainly driven by the right-skewed distribution of the data at low distances of the niche centroid and outliers on the right. They could have been due to ecological processes not being accounted as predictors in the niche estimation (Cade and Noon, 2003), presumably, biotic interactions (Soberón and Nakamura, 2009; Soberón and Peterson, 2005). It is also possible that occurrences far from the niche centroid were due to red octopuses' active migrations searching for suitable conditions or wrongly georeferenced records (Peterson et al., 2011).

When comparing the CTR and FTR environmental datasets, it is important to highlight that the relationship between the niche centroid and abundance is less noticeable in November and December when using the FTR environmental dataset. One possible explanation for a weaker relationship in these months may be that the samples were not large enough to ensure a good niche characterization, which has been previously identified as an important issue that could bias DNC-abundance correlations (Yañez-Arenas et al., 2014a). Even more surprising was that in the CTR dataset, the DNC-abundance relationships were higher than FTR, contradicting the hypothesis in this study that a finer temporal match between the environmental data and the occurrence date would improve correlations. Regardless of those mixed results, insightful conclusions can be achieved since theoretical grounds support our results.

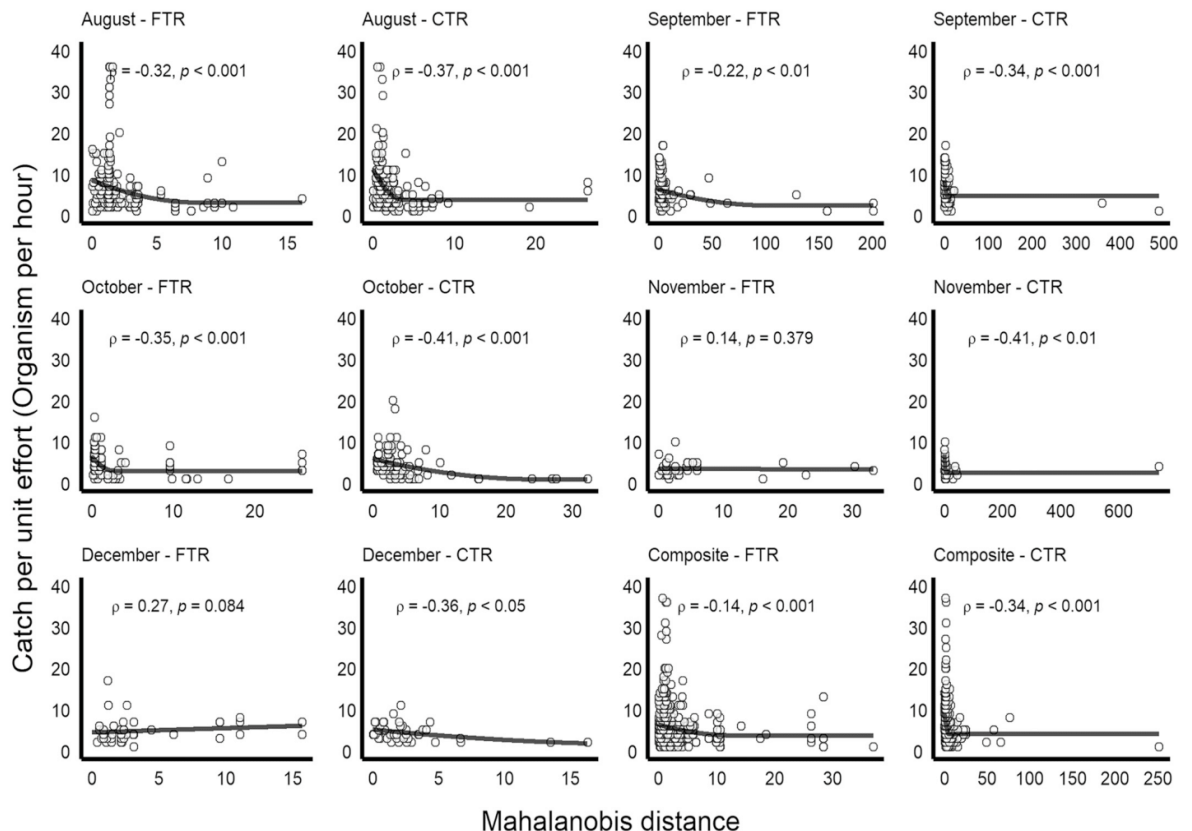


Fig. 5. Correlation plots between the catch per unit effort (organism per hour – a proxy of abundance) and the distance to niche centroid (Mahalanobis distance) of red octopus (*Octopus maya*) for coarse temporal resolution and finer temporal resolution models. Black lines show the trend of the data. These relationships were computed with ellipsoids that included 95% of species' occurrences. Relationships for the models that included 90% and 99% are presented in Supplementary material 6. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Table 2

Quantile regressions between distances to niche centroid and the catch per unit effort (organism per hour – a proxy of abundance) of red octopus (*Octopus maya*) for different quantiles.

	Quantiles	Finer temporal resolution						Coarse temporal resolution					
		Intercept			Slope			Intercept			Slope		
		Value	Standard error	P value	Value	Standard error	P value	Value	Standard error	P value	Value	Standard error	P value
August	75	8.65	0.59	0*	-0.56	0.12	0*	9.23	0.69	0*	-0.37	0.19	0.05
	80	9.88	0.68	0*	-0.68	0.13	0*	10.27	0.72	0*	-0.43	0.19	0.02*
	85	11.06	0.75	0*	-0.8	0.13	0*	11.14	0.68	0*	-0.19	0.098	0.04*
	90	14.88	1.45	0*	-0.67	0.21	0.001*	13.3	0.83	0*	-0.27	0.08	0.002*
	95	18.18	2.08	0*	-0.18	0.21	0*	16.26	1.12	0*	-0.31	0.078	0*
September	100	39.49	0.0001	0*	-2.19	0.00001	0*	36.97	0.00013	0*	-1.09	0	0*
	75	7.12	0.36	0*	-0.02	0.008	0.01*	8.02	0.41	0*	-0.013	0.0045	0.002*
	8	8.06	0.41	0*	-0.025	0.008	0.004*	8.04	0.38	0*	-0.014	0.0041	0*
	85	8.16	0.38	0*	-0.02	0.007	0.001*	9.03	0.42	0*	-0.016	0.0036	0*
	90	11.05	0.7	0*	-0.04	0.08	0*	11.02	0.61	0*	-0.02	0.0033	0*
October	95	13.14	0.63	0*	-0.04	0.0067	0*	13.02	0.72	0*	-0.02	0.003	0*
	100	17.28	0.00009	0*	-0.07	0	0*	17.07	0.0001	0*	-0.03	0	0*
	75	6.04	0.48	0*	-0.1	0.06	0.1	6.35	0.43	0*	-0.19	0.04	0*
	80	7.02	0.52	0*	-0.07	0.06	0.2	7.18	0.48	0*	-0.21	0.04	0*
	85	8.04	0.58	0*	-0.11	0.06	0.06	7.94	0.53	0*	-0.21	0.04	0*
November	90	8.04	0.49	0*	-0.04	0.07	0.5	9.32	0.66	0*	-0.25	0.04	0*
	95	10.04	0.56	0*	-0.11	0.05	0.04*	10.29	0.58	0*	-0.28	0.04	0*
	100	16.12	0.00018	0*	-0.35	0.00001	0*	21.97	0.00015	0*	-0.64	0	0*
	75	4	0.55	0*	0	0.05	1	5.00	0.67	0*	-0.001	0.004	0.7
	80	5	0.63	0*	0	0.06	1	5.00	0.62	0*	-0.001	0.004	0.7
December	85	5	0.57	0*	0	0.058	1	5.00	0.57	0*	-0.001	0.003	0.7
	90	5	0.6	0*	0	0.06	1	6.00	0.71	0*	-0.002	0.005	0.6
	95	7	0.91	0*	-0.09	0.03	0.01*	7.00	0.73	0*	-0.004	0.001	0.005*
	100	10.56	0.00005	0*	-0.21	0	0*	10.01	0.000004	0*	-0.008	0	0*
	75	4.79	0.84	0*	0.23	0.15	0.1	6.14	0.73	0*	-0.25	0.14	0.09
Composite	80	5.79	0.93	0*	0.12	0.14	0.4	7.05	0.79	0*	-0.3	0.15	0.04*
	85	5.93	0.88	0*	0.11	0.14	0.4	7.06	0.72	0*	-0.31	0.14	0.03*
	90	6.73	0.96	0*	0.11	0.16	0.4	7.26	0.76	0*	-0.32	0.16	0.05
	95	11.81	2.91	0*	-0.3	0.24	0.2	8.82	0.84	0*	-0.41	0.07	0*
	100	17.84	0.00007	0*	-0.69	0	0*	12.35	0.00006	0*	-0.63	0	0*
	75	7.17	0.24	0*	-0.14	0.02	0*	7.04	0.23	0*	-0.02	0.007	0*
	80	8.16	0.29	0*	-0.18	0.02	0*	8.02	0.29	0*	-0.02	0.006	0*
	85	9.18	0.36	0*	-0.21	0.02	0*	9.05	0.36	0*	-0.031	0.0057	0*
	90	11.02	0.53	0*	-0.2	0.05	0*	11.05	0.51	0*	-0.03	0.005	0*
	95	13.73	0.84	0*	-0.17	0.12	0.1	13.09	0.59	0*	-0.04	0.0043	0*
100	37.6	0.00009	0*	-0.86	0	0*	37.23	0.00015	0*	-0.14	0	0*	

Statistical significance ($P < 0.05$) is shown with an asterisk (*). The correlations showed here were obtained with ellipsoids that covered 95% of occurrence data. The remaining tables are shown in Supplementary Material 7.

For instance, it seems that the long-term environmental data is the primary source of predictability in the abundance of the red octopus. In this sense, the long environmental data describe well the red octopus abundance probably because of the seasonal “fidelity”, that is, periodic and recurrent aggregations in the western region of the YP (Arreguín-Sánchez et al., 2019; Gamboa-Álvarez et al., 2015). Thus, perhaps the DNC-abundance relationship could be better described from the composite conditions in the western region of the YP during most of the fishing season and not just from what the individuals experienced in a particular month. In this sense, monthly data could be long-term incomplete trends. Indeed, even the composite dataset for FTR and CTR gave good results describing the DNC-abundance relationship (Figs. 5 and 6). In addition, the higher resolution of the pixel in the CTR dataset may have allowed extracting a greater amount of environmental information, increasing the evidence of the DNC-abundance hypothesis (Soberón et al., 2018).

Regarding the octopuses aggregation detected, the results in this study could be related to the Yucatan shelf environmental heterogeneity in temperature and salinity. Indeed, a visual inspection of the temperature and salinity data and abundance allows linking them intuitively (Fig. 7 and Supplementary material 8). Individuals tend to aggregate to suitable conditions in the western region, where temperatures are higher and salinity lower from August to October. As speculated, an increase in food availability could be associated with the discharge of freshwater (which would lower salinity and increase its variability) in the western

region of the YP during the rainy season, creating a pulse in primary productivity (Arreguín-Sánchez and Chávez, 1995) (a predictor not considered in this study). In turn, the red octopus would aggregate nearby this region, searching for food that favors gonadal maturation and reproduction (Arreguín-Sánchez, 2019; Arreguín-Sánchez et al., 2019). This situation would be consistent with the smaller octopuses fished from Sabancuy to Campeche (Gamboa-Álvarez et al., 2015), indicating that younger ones (with preferences up to 30 °C in comparison of adults up to 27 °C – Tremblay et al., 2017) are being over-represented; probably due to suitable temperatures (Angeles-Gonzalez et al., 2017).

Conversely, during November–December, adults are abundant in the Yucatan Shelf which is associated with lower temperatures (Angeles-Gonzalez et al., 2017). However, it was noted that if there is no difference in patch attractiveness due to a homogenization of environmental conditions (Fig. 7, Supplementary Material 8), the DNC-abundance relationship may be challenging to characterize, especially if no environmental data is available to characterize as much of the fundamental niche as possible. This situation probably happened in November, when abundance data was restricted to the northwestern region. Similarly, the use of procedures that reduce the dimensionality, such as the principal component analysis (PCA), usually used to test the DNC-abundance relationship, could make the ecological interpretation of results difficult (e.g. Dallas et al., 2017). Finally, variable selection can vary according to the percentage of occurrences used in the ellipsoid

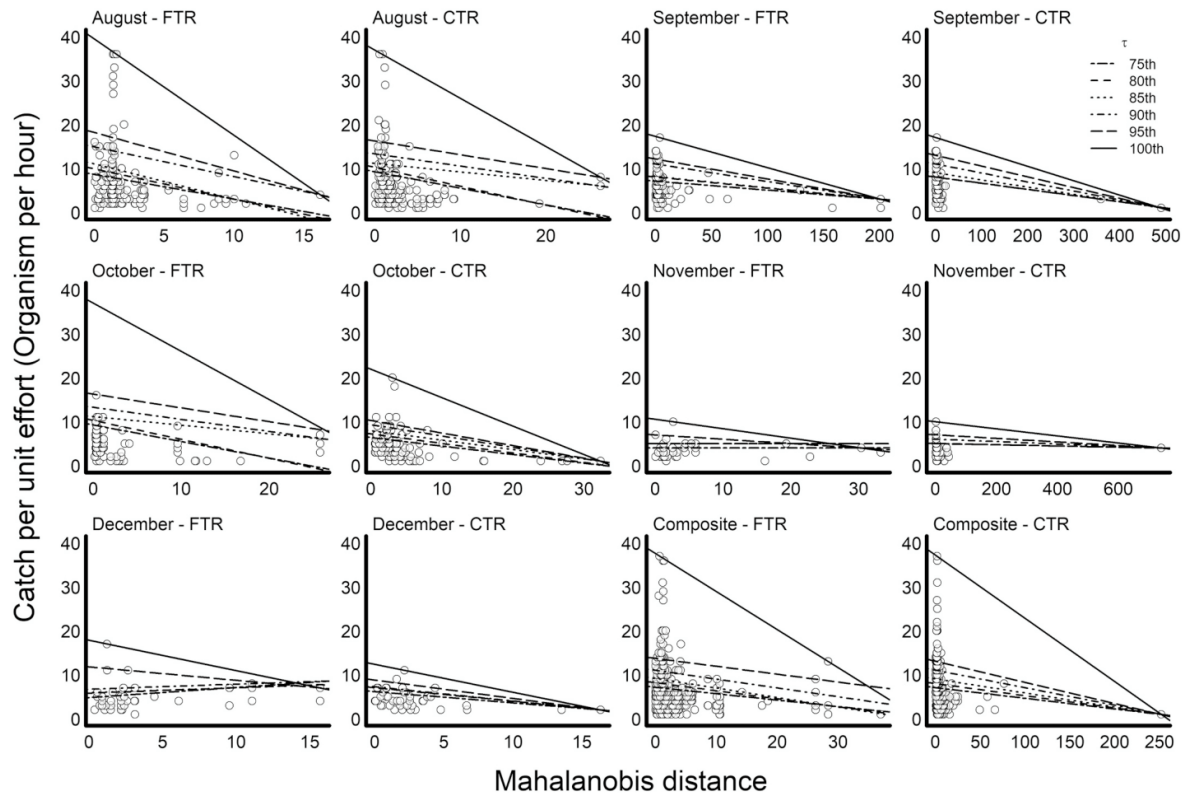


Fig. 6. Relationships between the catch per unit effort (organism per hour – a proxy of abundance) and distances to niche centroids (Mahalanobis distance) obtained from quantile regressions for different quantiles (τ). The relationship showed here was obtained with ellipsoids that covered 95% of occurrence data. Relationships for the models that included 90% and 99.9% are presented in Supplementary material 7.

(Supplementary material 3). One way to solve this problem is to fixate in the model environmental variables relevant to the species. In this sense, researchers should choose environmental variables linked to organism preferences if the intention is resource monitoring since the model selection based on the highest relationship may not always be easily generalized.

Accepting the conjecture that species fitness reaches its maximum value at the center of the n -dimensional fundamental niche and that it decreases with distance to this hypothetical “centroid” some open questions would be (1) What are the dimensions (variables) of the fundamental niche that strongly relate to fitness? (2) Are they the same as the ones selected by statistical criteria? (3) Do they affect fitness equally? It probably depends on the organism, for example, soil pH might not be as important as temperature for a terrestrial mammal as for a mangrove.

Since the ontogenetic shifts in environmental preferences are prevalent in marine organisms (Carr et al., 2003; Robinson et al., 2011) and could influence the DNC-abundance relationship, future empirical works could test this hypothesis according to the development stage. This idea has been proposed theoretically, for instance, Osorio-Olvera et al. (2016) used a mathematical model where the projection matrix depends on a diagonal matrix defined by species suitability by stage. Moreover, Soberón and Peterson (2020) conjecture that niches could show different suitability trajectories during the life cycle. Thus, ideally, the niche for adults and juveniles should be characterized separately and tested to avoid the problems described above, but it was outside the scope of this study although it would link seasonal cycles and abundance with the ontogenetic development under a DNC-abundance framework.

Future works could also consider biotic factors, accessibility, and substrate type since they could influence the abundance and distribution of the red octopus.

Concerning the capacity to predict abundance via the distances to the niche centroid, we would refrain from trying to use it as a tool to accurately predict changes due to the high variability of the data. However, QR seems to be an appropriate tool to test the DNC-abundance relationship. If abundance is considered coming from a network of a complex of environmental, biotic, and dispersal processes (Soberón and Peterson, 2005), an increasing number of factors not measured increase the heterogeneity of the organism response (Cade and Noon, 2003). In this sense, mean value change rates are not useful to predict abundances; but the focus on the highest τ values in QR would be a valuable tool to detect regions with maximum potential catches (Tórres et al., 2012; VanDerWal et al., 2009), particularly if combined with primary productivity since it alters the ecosystem capacity (maximum K), to support fishery catches (Fernandes et al., 2013). Indeed, the potential changes of catches of different marine resources could be followed, which is especially important for the red octopus, a species that has been predicted to migrate to the north in the upwelling zone (Ángeles-González et al., 2017; Ángeles-González et al., 2021) or deeper waters (Ángeles-González et al., 2021) where lower temperatures could favor its reproduction (Ángeles-González et al., 2017). Climate change projections suggest that it could be outcompeted by *O. insularis*, if it invades the region (Ángeles-González et al., 2020; Lima et al., 2020). How other octopuses in the region may respond to climate change is unknown; however, *O. americanus* (previously known as *O. vulgaris* type II - Avendaño et al., 2020), another fishery resource of the Gulf of Mexico, is

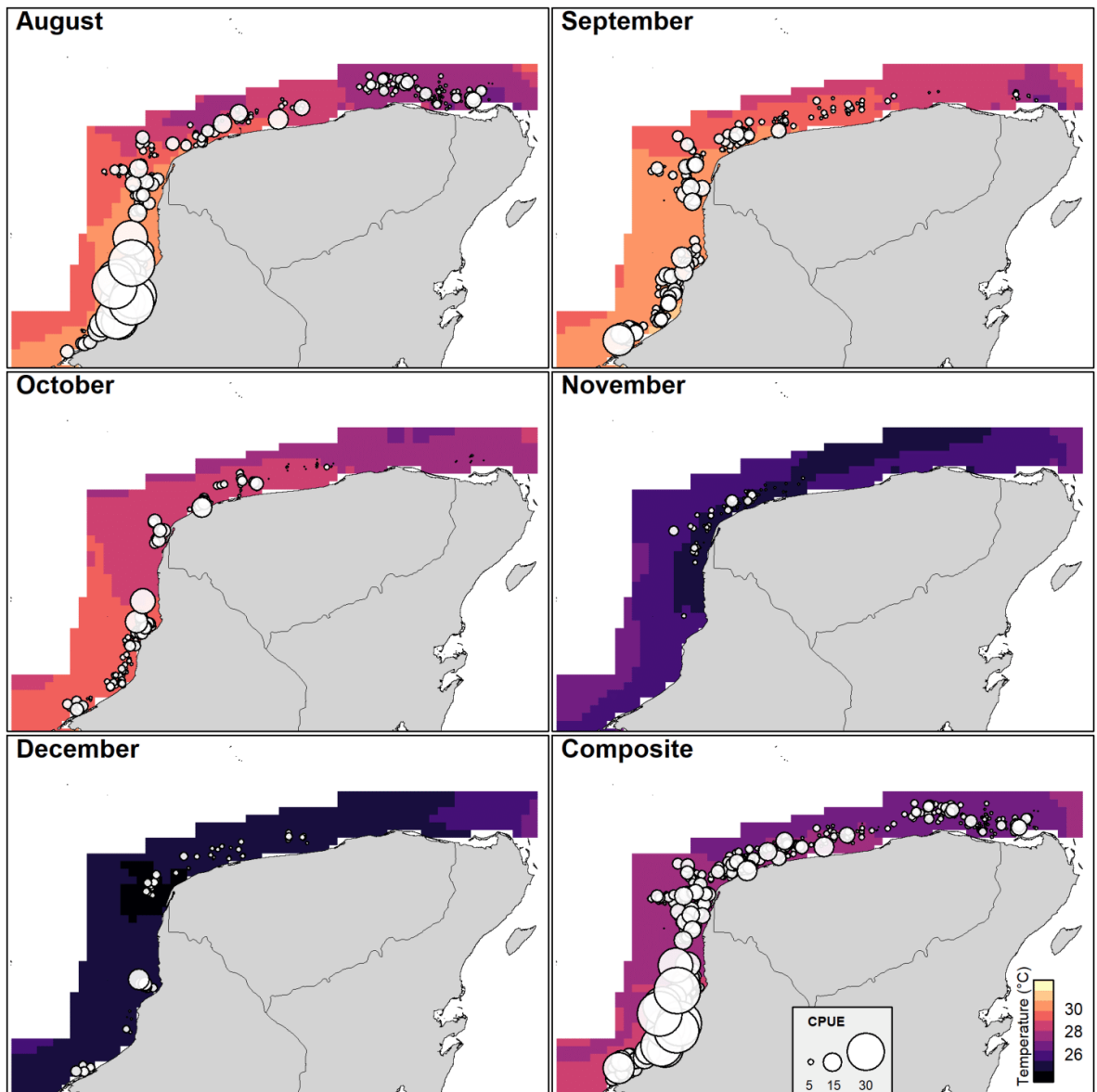


Fig. 7. Sea surface temperature of the Yucatan shelf for the fishing season and composite values with catch per unit effort (a proxy of abundance) overlapped. The environmental data were obtained from the GLORYS12V1 product from the Copernicus Marine Environment Monitoring Service. The resolution is $\sim 9 \text{ km}^2$ by pixel. The circles represent the catch per unit effort of the red octopus (*Octopus maya*). Salinity maps are added as Supplementary material 8. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

usually associated with colder waters than the red octopus (Guarneros-Narváez et al., 2020). In this sense, this species could be monitored with the DNC-abundance relationship since it may also be vulnerable to warming scenarios.

5. Conclusions

The DNC-abundance hypothesis may be a helpful tool to understand how environmental variables may control abundance patterns in marine organisms of commercial importance as it has been similarly seen in reef fishes around the world (Waldock et al., 2019). However, if this tool is

used in fisheries, environmental variables that can be easily interpreted should be used, especially for climate change scenarios. Moreover, the pixel size should have enough resolution to describe the DNC-abundance relationship more accurately. The results also suggest that at least for the red octopus, longer temporal environmental conditions may determine population numbers. Therefore, researchers are encouraged to test this hypothesis with more marine species. Finally, when interpreting the results, researchers should be aware that the abundance patterns came from a network of complex ecological and geographical processes (Doney et al., 2012), so arguments in favor and/or against the DNC-abundance relationship should be considered.

Declaration of Competing Interest

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

Acknowledgments

This study is the result of a Graduate Studies Doctoral degree thesis at Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México (UNAM); the authors are grateful to UNAM and to the Consejo Nacional de Ciencia y Tecnología (CONACYT) for the scholarship funding the development of this research and D.Fischer for English edition. All the data for the red octopus used in this study was obtained from the projects: “Patrones de movimiento y de distribución espacio temporal del pulpo *Octopus maya* en la plataforma continental de la península de Yucatán” (Grant number 154400), a project funded by CONACYT.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jembe.2021.151609>.

References

- Angeles-Gonzalez, L.E., Calva, R., Santos-Valencia, J., Avila-Poveda, O.H., Olivares, A., Diaz, F., Rosas, C., 2017. Temperature modulates spatio-temporal variability of the functional reproductive maturation of *Octopus maya* (Cephalopoda) on the shelf of the Yucatan peninsula, Mexico. *J. Molluscan Stud.* 83, 280–288. <https://doi.org/10.1093/mollus/eyx013>.
- Ángeles-González, L.E., Lima, F.D., Caamal-Monsreal, C., Díaz, F., Rosas, C., 2020. Exploring the effects of warming seas by using the optimal and pejus temperatures of the embryo of three Octopoda species in the Gulf of Mexico. *J. Therm. Biol.* 94. <https://doi.org/10.1016/j.jtherbio.2020.102753>.
- Ángeles-González, L.E., Martínez-Meyer, E., Yañez-Arenas, C., Velázquez-Abunader, I., López-Rocha, J.A., Torrejón-Magallanes, J., Rosas, C., 2021. Climate change effect on *Octopus maya* (Voss and Solís-Ramírez, 1966) suitability and distribution in the Yucatan peninsula, Gulf of Mexico: a correlative and mechanistic approach. *Estuar. Coast. Shelf. Sci.* <https://doi.org/10.1016/j.ecss.2021.107502>.
- Arreguín-Sánchez, F., 2019. Climate change and the rise of the octopus fishery in the Campeche Bank, México. *Reg. Stud. Mar. Sci.* 32. <https://doi.org/10.1016/j.rsm.2019.100852>.
- Arreguín-Sánchez, F., Chávez, E.A., 1995. How marine shelf fisheries are depending of mangrove ecosystems: The Campeche Bank, Mexico, an example. In: Yáñez-Arancibia, A., Lara-Domínguez, A. (Eds.), *Valoración Económica de Los Manglares*. Universidad Autónoma de Campeche.
- Arreguín-Sánchez, F., Albañez-Lucero, M.O., Del Monte-Luna, P., Zetina-Rejón, M.J., 2019. Fishery resource management challenges facing climate change. In: Ibáñez, A. (Ed.), *Mexican Aquatic Environments*. Springer, Cham, pp. 181–194. <https://doi.org/10.1007/978-3-030-11126-7>.
- Avendaño, O., Velázquez-Abunader, I., Fernández-Jardón, C., Ángeles-González, L.E., Hernández-Flores, A., Guerra, Á., 2019. Biomass and distribution of the red octopus (*Octopus maya*) in the north-east of the Campeche Bank. *J. Mar. Biol. Assoc. United Kingdom* 99, 1317–1323. <https://doi.org/10.1017/S0025315419000419>.
- Avendaño, O., Roura, Á., Cedillo-Robles, C.E., González, Á.F., Rodríguez-Canul, R., Velázquez-Abunader, I., Guerra, Á., 2020. *Octopus americanus*: a cryptic species of the *O. vulgaris* species complex redescribed from the Caribbean. *Aquat. Ecol.* 54, 909–925. <https://doi.org/10.1007/s10452-020-09778-6>.
- Biggs, D.C., McDermott, J.J., 1973. Variation in temperature-salinity tolerance between two estuarine populations of *Pagurus longicarpus* Say (Crustacea: Anomura). *Biol. Bull.* 145, 91–102. <https://doi.org/10.2307/1540350>.
- Birch, L.C., 1953. Experimental background to the study of the distribution and abundance of insects: I. the influence of temperature, moisture and food on the innate capacity for increase of three grain beetles. *Ecology* 34, 698–711. <https://doi.org/10.2307/1931333>.
- Blaszowski, C., Moreira, G.S., 1986. Combined effects of temperature and salinity on the survival and duration of larval stages of *Pagurus criniticornis* (Dana) (Crustacea, Paguridae). *J. Exp. Mar. Biol. Ecol.* 103, 77–86. [https://doi.org/10.1016/0022-0981\(86\)90133-4](https://doi.org/10.1016/0022-0981(86)90133-4).
- Brown, J.H., 1984. On the relationship between abundance and distribution of species. *Am. Nat.* 124, 255–279. <https://doi.org/10.2307/2461494>.
- Brown, S.D., Bert, T.M., Tweedale, W.A., Torres, J.J., Lindberg, W.J., 1992. The effects of temperature and salinity on survival and development of early life stage Florida stone crabs *Menippe mercenaria* (Say). *J. Exp. Mar. Biol. Ecol.* 157, 115–136. [https://doi.org/10.1016/0022-0981\(92\)90078-O](https://doi.org/10.1016/0022-0981(92)90078-O).
- Cade, B.S., Noon, B.R., 2003. A gentle introduction to quantile regression for ecologists. *Front. Ecol. Environ.* 1, 412–420. [https://doi.org/10.1890/1540-9295\(2003\)001\[0412:AGITQR\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2003)001[0412:AGITQR]2.0.CO;2).
- Carr, M.H., Neigel, J.E., Estes, J.A., Andelman, S., Warner, R.R., Largier, J.L., 2003. Comparing marine and terrestrial ecosystems : implications for the Design of Coastal Marine Reserves. *Ecol. Appl.* 13, 90–107. [https://doi.org/10.1890/1051-0761\(2003\)013\[0090:CMATEI\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2003)013[0090:CMATEI]2.0.CO;2).
- Criales, M.M., Zink, L.C., Browder, J.A., Jackson, T.L., 2011. The effect of acclimation salinity and age on the salinity tolerance of pink shrimp postlarvae. *J. Exp. Mar. Biol. Ecol.* 409, 283–289. <https://doi.org/10.1016/j.jembe.2011.09.007>.
- Czitrom, S.P.R., Ruiz, F., Alatorre, M.A., Padilla, A.R., 1986. Preliminary study of a front in the bay of Campeche, Mexico. *Elsevier Oceanogr. Ser.* 42, 301–311. [https://doi.org/10.1016/S0422-9894\(08\)71051-1](https://doi.org/10.1016/S0422-9894(08)71051-1).
- Dallas, T., Decker, R.R., Hastings, A., 2017. Species are not most abundant in the Centre of their geographic range or climatic niche. *Ecol. Lett.* 20, 1526–1533. <https://doi.org/10.1111/ele.12860>.
- Dallas, T.A., Santini, L., 2020. The influence of stochasticity, landscape structure and species traits on abundant-Centre relationships. *Ecography* 43, 1341–1351. <https://doi.org/10.1111/ecog.05164>.
- Diario Oficial de la Federación, 2014. ACUERDO por el que se da a conocer el Plan de Manejo Pesquero de pulpo (*O. maya* y *O. vulgaris*) del Golfo de México y Mar Caribe.
- Doney, S.C., Ruckelshaus, M., Emmett Duffy, J., Barry, J.P., Chan, F., English, C.A., Galindo, H.M., Grebmeier, J.M., Hollowed, A.B., Knowlton, N., Polovina, J., Rabalais, N.N., Sydeman, W.J., Talley, L.D., 2012. Climate change impacts on marine ecosystems. *Annu. Rev. Mar. Sci.* 4, 11–37. <https://doi.org/10.1146/annurev-marine-041911-111611>.
- Enriquez, C., Mariño-Tapia, L.J., Herrera-Silveira, J.A., 2010. Dispersion in the Yucatan coastal zone: implications for red tide events. *Cont. Shelf Res.* 30, 127–137. <https://doi.org/10.1016/j.csr.2009.10.005>.
- Enriquez, C., Mariño-Tapia, L., Jeronimo, G., Capurro-Filigrasso, L., 2013. Thermohaline processes in a tropical coastal zone. *Cont. Shelf Res.* 69, 101–109. <https://doi.org/10.1016/j.csr.2013.08.018>.
- Enriquez, C.E., Mariño-Tapia, L., 2014. Mechanisms driving a coastal dynamic upwelling. In: *Proceedings of the 17th Physics of Estuaries and Coastal Seas (PECS) Conference, Porto de Galinhas, Pernambuco, Brazil, 19–24 October 2014*.
- Escalante, T., Martínez-Meyer, E., 2013. Ecological niche modeling and wildlife management units (UMAS): an application to deer in Campeche, México. *Trop. Subtrop. Agroecosystems* 16, 183–191.
- Fernandes, J.A., Cheung, W.W.L., Jennings, S., Butenschön, M., De Mora, L., Frölicher, T. L., Barange, M., Grant, A., 2013. Modelling the effects of climate change on the distribution and production of marine fishes: accounting for trophic interactions in a dynamic bioclimate envelope model. *Glob. Chang. Biol.* 19, 2596–2607. <https://doi.org/10.1111/gcb.12231>.
- Gamboa-Álvarez, M.Á., López-Rocha, J.A., Poot-López, G.R., 2015. Spatial analysis of the abundance and Catchability of the red Octopus *Octopus maya* (Voss and Solís-Ramírez, 1966) on the continental shelf of the Yucatan peninsula, Mexico. *J. Shellfish Res.* 34, 481–492. <https://doi.org/10.2983/035.034.0232>.
- Guarneros-Narváez, P.V., Velázquez-Abunader, I., Avendaño, O., López-Rocha, J.A., 2020. Superposición espacial de los pulpos *Octopus vulgaris* tipo II y *Octopus maya* al noreste del banco de Campeche. In: Pérez-Morales, A., Aké-Castillo, J.A., Poot-Delgado, C.A. (Eds.), *Investigaciones Marinas En El Golfo de México y Mar Caribe Mexicano*. Universidad de Colima, Colima, México, pp. 242–259.
- Haefner, P.A., 1969. Temperature and salinity tolerance of the sand shrimp, *Crangon septemspinosa* Say. *Physiol. Zool.* 42, 388–397. <https://doi.org/10.1086/physzool.42.4.30155510>.
- Holt, R.D., 2009. Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. *Proc. Natl. Acad. Sci. U. S. A.* 106, 19659–19665. <https://doi.org/10.1073/pnas.0905137106>.
- Hooper, H.L., Connon, R., Callaghan, A., Fryer, G., Yarwood-Buchanan, S., Biggs, J., Maund, S.J., Hutchinson, T.H., Sibby, R.M., 2008. The ecological niche of *Daphnia magna* characterized using population growth rate. *Ecology* 89, 1015–1022. <https://doi.org/10.1890/07-0559.1>.
- Hutchinson, G.E., 1957. Concluding remarks. *Cold Spring Harb. Symp. Quant. Biol.* 22, 415–427.
- Jiménez-Valverde, A., 2012. Relationship between local population density and environmental suitability estimated from occurrence data. *Front. Biogeogr.* 3, 59–61. <https://doi.org/10.21425/f5fbg12408>.
- Juárez, O.E., Galindo-Sánchez, C.E., Díaz, F., Re, D., Sánchez-García, A.M., Caamal-Monsreal, C., Rosas, C., 2015. Is temperature conditioning *Octopus maya* fitness? *J. Exp. Mar. Biol. Ecol.* 467, 71–76. <https://doi.org/10.1016/j.jembe.2015.02.020>.
- Knout, J.H., 2018. Appropriate application of information from biodiversity databases is critical when investigating species distributions and diversity: a comment on Dallas et al. *Ecology Letters* 21 (7), 1119–1120. <https://doi.org/10.1111/ele.12959>.
- Koenker, R., 2019. *quantreg: Quantile Regression*.
- Lima, F., Ángeles-González, L., Leite, T., Lima, S., 2020. Global climate changes over time shape the environmental niche distribution of *Octopus insularis* in the Atlantic Ocean. *Mar. Ecol. Prog. Ser.* 652, 111–121. <https://doi.org/10.3354/meps13486>.
- Maguire Jr., B., 1973. Niche response structure and the analytical potentials of its relationship to the habitat. *The American Naturalist* 107, 213–246. <https://doi.org/10.1086/282827>.
- Markaida, U., Méndez-Loeza, I., Rosales-Raya, M.L., 2016. Seasonal and spatial trends of Mayan octopus, *Octopus maya*, population dynamics from Campeche, Mexico. *J. Mar. Biol. Assoc. United Kingdom* 97, 1663–1673. <https://doi.org/10.1017/S0025315416001132>.
- Martin, G.A., Yanez-Arenas, C., Roberts, B.J., Chen, C., Plowright, R.K., Webb, R.J., Skerratt, L.F., 2016. Climatic suitability influences species specific abundance

- patterns of Australian flying foxes and risk of Hendra virus spillover. *One Heal.* 2, 115–121. <https://doi.org/10.1016/j.onehlt.2016.07.004>.
- Martínez-Gutiérrez, P.G., Martínez-Meyer, E., Palomares, F., Fernández, N., 2018. Niche centrality and human influence predict rangewide variation in population abundance of a widespread mammal: the collared peccary (*Pecari tajacu*). *Divers. Distrib.* 24, 103–115. <https://doi.org/10.1111/ddi.12662>.
- Martínez-Meyer, E., Díaz-Porras, D., Peterson, A.T., Yáñez-Arenas, C., 2013. Ecological niche structure and rangewide abundance patterns of species. *Biol. Lett.* 9 <https://doi.org/10.1098/rsbl.2012.0637>.
- Monreal-Gómez, M., Salas-de León, D., Velasco-Mendoza, H., 2004. Hidrodinámica del Golfo de México. In: Caso, M., Pisanty, I., Ezcurra, E. (Eds.), *Diagnóstico Ambiental Del Golfo de México*. I. Instituto Nacional de Ecología (INE-SEMARNAT), Mexico, DF, pp. 47–67.
- Osorio-Olvera, L., Soberón, J., Falconi, M., 2019. On population abundance and niche structure. *Ecography.* 42, 1415–1425. <https://doi.org/10.1111/ecog.04442>.
- Osorio-Olvera, L., Lira-Noriega, A., Soberón, J., Peterson, A.T., Falconi, M., Contreras-Díaz, R.G., Martínez-Meyer, E., Barve, V., Barve, N., 2020a. Ntbox: an R package with graphical user interface for modeling and evaluating multidimensional ecological niches. *Methods Ecol. Evol.* 11, 1199–1206. <https://doi.org/10.1111/2041-210X.13452>.
- Osorio-Olvera, L., Yáñez-Arenas, C., Martínez-Meyer, E., Peterson, A.T., 2020b. Relationships between population densities and niche-centroid distances in north American birds. *Ecol. Lett.* 23, 555–564. <https://doi.org/10.1111/ele.13453>.
- Osorio-Olvera, L.A., Falconi, M., Soberón, J., 2016. Sobre la relación entre idoneidad del hábitat y la abundancia poblacional bajo diferentes escenarios de dispersión. *Rev. Mex. Biodivers.* 87, 1080–1088. <https://doi.org/10.1016/j.rmb.2016.07.001>.
- Pascual, C., Mascaró, M., Rodríguez-Canul, R., Gallardo, P., Sánchez, A.A., Rosas, C., Cruz-López, H., 2019. Sea surface temperature modulates physiological and immunological condition of *Octopus maya*. *Front. Physiol.* 10, 1–11. <https://doi.org/10.3389/fphys.2019.00739>.
- Peterson, T.A., Soberón, J., Pearson, R.G., Anderson, R.P., Martínez-Meyer, E., Nakamura, M., Araújo, M.B., 2011. *Ecological Niches and Geographic Distributions*. Choice Reviews Online. Princeton University Press.
- Phleger, F.B., Ayala-Castañares, A., 1971. Processes and history of Terminos lagoon, Mexico. *Am. Assoc. Pet. Geol. Bull.* 55, 2130–2140. <https://doi.org/10.1306/819a3e26-16c5-11d7-8645000102c1865d>.
- Qiao, H., Peterson, A.T., Campbell, L.P., Soberón, J., Ji, L., Escobar, L.E., 2016. NicheA: creating virtual species and ecological niches in multivariate environmental scenarios. *Ecography.* 39, 805–813. <https://doi.org/10.1111/ecog.01961>.
- R Core Team, 2020. *R: A Language and Environment for Statistical Computing*.
- Robinson, L.M., Elith, J., Hobday, A.J., Pearson, R.G., Kendall, B.E., Possingham, H.P., Richardson, A.J., 2011. Pushing the limits in marine species distribution modelling: lessons from the land present challenges and opportunities. *Glob. Ecol. Biogeogr.* 20, 789–802. <https://doi.org/10.1111/j.1466-8238.2010.00636.x>.
- Rosas, C., Gallardo, P., Mascaró, M., Caamal-Monsreal, C., Pascual, C., 2014. *Octopus maya*. *Cephalopod Culture*. Springer, pp. 383–396.
- Rothlisberg, P.C., 1979. Combined effects of temperature and salinity on the survival and growth of the larvae of *Pandalus jordani* (Decapoda: Pandalidae). *Mar. Biol.* 54, 125–134. <https://doi.org/10.1007/BF00386591>.
- Sanchez-García, A., Rodríguez-Fuentes, G., Díaz, F., Galindo-Sánchez, C.E., Ortega, K., Mascaró, M., López, E., Caamal-Monsreal, C., Juárez, O., Noreña-Barroso, E., Re, D., Rosas, C., 2017. Thermal sensitivity of *O. maya* embryos as a tool for monitoring the effects of environmental warming in the southern of Gulf of Mexico. *Ecol. Indic.* 72, 574–585. <https://doi.org/10.1016/j.ecolind.2016.08.043>.
- Santini, L., Pironon, S., Maiorano, L., Thuiller, W., 2019. Addressing common pitfalls does not provide more support to geographical and ecological abundant-Centre hypotheses. *Ecography.* 42, 696–705. <https://doi.org/10.1111/ecog.04027>.
- Sbrocco, E.J., Barber, P.H., 2013. MARSPEC: Ocean climate layers for marine spatial ecology. *Ecology* 94 (4), 979. <https://doi.org/10.1890/12-1358.1>.
- Soberón, J., Nakamura, M., 2009. Niches and distributional areas: concepts, methods, and assumptions. *Anal. Chim. Acta* 106, 19644–19650. <https://doi.org/10.1073/pnas.0901637106>.
- Soberón, J., Peterson, A.T., 2004. Biodiversity informatics: managing and applying primary biodiversity data. *Philos. Trans. R. Soc. B Biol. Sci.* 359, 689–698. <https://doi.org/10.1098/rstb.2003.1439>.
- Soberón, J., Peterson, A.T., 2020. What is the shape of the fundamental Grinnellian niche? *Theor. Ecol.* 13, 105–115. <https://doi.org/10.1007/s12080-019-0432-5>.
- Soberón, J., Peterson, T.A., 2005. Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodivers. Inform.* 2, 1–10. <https://doi.org/10.17161/bi.v2i0.4>.
- Soberón, J., Peterson, A.T., Osorio-Olvera, L., 2018. A comment on "species are not most abundant in the Centre of their geographic range or climatic niche". *Rethink. Ecol.* 3, 13–18. <https://doi.org/10.3897/rethinkingecology.3.24827>.
- Tórres, N.M., De Marco, P., Santos, T., Silveira, L., de Almeida Jácomo, A.T., Diniz-Filho, J.A.F., 2012. Can species distribution modelling provide estimates of population densities? A case study with jaguars in the Neotropics. *Diversity and Distribution.* <https://doi.org/10.1111/j.1472-4642.2012.00892.x>.
- Tremblay, N., Mascaró, M., Díaz, F., Caamal-Monsreal, C., Pascual, C., Rosas, C., 2017. Sensibilidad a las oscilaciones térmicas de las especies de importancia ecológica y pesquera de la Península de Yucatán ante escenarios de calentamiento global. In: Garza-Pérez, J., Ize-Lema, I.A. (Eds.), *Caracterización Multidisciplinaria de La Zona Costera de Sisal, Yucatán, México*, pp. 185–198.
- Ureña-Aranda, C.A., Rojas-Soto, O., Martínez-Meyer, E., Yáñez-Arenas, C., Ramírez, R.L., De Los Monteros, A.E., 2015. Using range-wide abundance modeling to identify key conservation areas for the micro-endemic bolson tortoise (*Gopherus flavomarginatus*). *PLoS One* 10. <https://doi.org/10.1371/journal.pone.0131452>.
- Van Aelst, S., Rousseeuw, P., 2009. Minimum volume ellipsoid. *Wiley Interdiscip. Rev. Comput. Stat.* 1, 71–82. <https://doi.org/10.1002/wics.19>.
- VanDerWal, J., Shoo, L.P., Johnson, C.N., Williams, S.E., 2009. Abundance and the environmental niche: environmental suitability estimated from niche models predicts the upper limit of local abundance. *The American Naturalist* 174 (2), 282–291. <https://doi.org/10.1086/600087>.
- Voss, G.L., Solís-Ramírez, M., 1966. *Octopus maya*, a new species from the bay of Campeche, Mexico. *Bull. Mar. Sci.* 16, 615–625.
- Waldock, C., Stuart-Smith, R.D., Edgar, G.J., Bird, T.J., Bates, A.E., 2019. The shape of abundance distributions across temperature gradients in reef fishes. *Ecol. Lett.* 22, 685–696. <https://doi.org/10.1111/ele.13222>.
- Yáñez-Arenas, C., Martínez-Meyer, E., Mandujano, S., Rojas-Soto, O., 2012. Modelling geographic patterns of population density of the white-tailed deer in Central Mexico by implementing ecological niche theory. *Oikos* 121, 2081–2089. <https://doi.org/10.1111/j.1600-0706.2012.20350.x>.
- Yáñez-Arenas, C., Mandujano, S., Martínez-Meyer, E., 2014b. Predicting the density and abundance of white-tailed deer based on ecological niche theory. *Deer Spec. Gr. IUCN Newsl.* 26, 20–30.
- Yáñez-Arenas, C., Martín, G., Osorio-Olvera, L., Escobar-Luján, J., Castaño-Quintero, S., Chiappa-Carrara, X., Martínez-Meyer, E., 2020. The abundant niche-centroid hypothesis: key points about unfilled niches and the potential use of Supraspecific modeling units. *Biodivers. Inform.* 15, 92–102.
- Yáñez-Arenas, Carlos, Guevara, R., Martínez-Meyer, E., Mandujano, S., Lobo, J.M., 2014a. Predicting species' abundances from occurrence data: effects of sample size and bias. *Ecol. Model.* 294, 36–41. <https://doi.org/10.1016/j.ecolmodel.2014.09.014>.
- Zarco-Perelló, S., Mascaró, M., Garza-Pérez, R., Simoes, N., 2013. Topography and coral community of the sisal reefs, Campeche Bank, Yucatán, México. *Hidrobiológica* 23, 28–41.

Capítulo tres - Fitness reflects landings trends of the red octopus, *Octopus maya* (Voss & Solís, 1966), in the Yucatan Peninsula

Estado: A someter

Luis Enrique Ángeles-González^{a,b,c,d}, Enrique Martínez-Meyer^e, Carlos Rosas^{c,d}

^a Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Av. Ciudad Universitaria 3000, 04510, Coyoacán, Ciudad de México, México

^b Laboratorio de Ecología Geográfica. Unidad de Conservación de la Biodiversidad, Parque Científico y Tecnológico de Yucatán, Unidad Académica Sisal, Facultad de Ciencias, Universidad Nacional Autónoma de México, Carretera Sierra Papacal Km 5, Mérida, Yucatán, México

^c Laboratorio Nacional de Resiliencia Costera, Facultad de Ciencias, Universidad Nacional Autónoma de México, 97356, Puerto de Abrigo, Sisal, Yucatán, México

^d Laboratorio de Ecofisiología Aplicada, Unidad Multidisciplinaria de Docencia e Investigación, Facultad de Ciencias, Universidad Nacional Autónoma de México, 97356, Puerto de Abrigo, Sisal, Yucatán, México

^e Instituto de Biología, Universidad Nacional Autónoma de México, Circuito Zona Deportiva Ciudad Universitaria, 04510, Ciudad de México, México

*Corresponding author: crv@ciencias.unam.mx

Abstract

Studies of the fishing yields of the red octopuses (*Octopus maya*) indicated that it was fully exploited by the year 1980s, at landings of ~8000 t in the Yucatan Peninsula. Nevertheless, from the mid-1980s onwards, the fishery nearly doubled. As for 2018, the landings reached about ~32000 t; thus, the increase in catches contradicts the notion that this species was fully exploited. It has been argued that, based on fishery trends, temperature increase, and predators' fishing, the octopus stock is increasing and would increase in the future even in climate change scenarios. Based on the ideas above, we argue that the current increase in the fishing yield occurred due to an increase in temperature that in turn, has increased the red octopus fitness. Therefore, if

thresholds of temperature are surpassed, we could expect a decrease in octopus landings. In this sense, we tested these ideas using physiological studies of survivability of red octopus juveniles as a proxy of fitness and the fishing effort (number of boats with permission to fish red octopus) as they influence the catches. Our results show that as for the period 1993-2008, the increase of red octopus' landings can be linked to the increase of fitness. Therefore, warming seas have been favorable for the moment. However, if the species' fitness is reduced under climate change scenarios, this could be reflected in a decrease in the total landings of the region.

1. Introduction

The octopus's exploitation in the Yucatan peninsula mainly focuses on the red octopus (*Octopus maya*). The red octopus is an endemic benthic species that inhabits the Yucatan continental shelf's shallow waters at depths of ~ 32 fathoms. Its distribution ranges from the waters adjacent to Isla del Carmen in Campeche to Holbox, Quintana Roo (Gamboa-Álvarez et al., 2015) (Figure 1). This species represents the seventh most important fishery in Mexico by volume and the fourth most important by economic output (CONAPESCA, 2018; DOF, 2018).

Previous studies of the fishing yields of the red octopuses indicated that it was fully exploited by the year 1980s (Solís-Ramírez and Arreguín-Sánchez, 1984; Arreguín-Sánchez et al., 1987) at landings of ~8000 t. Nevertheless, from the mid-1980s onwards, the fishery nearly doubled. As for 2018, the landings of red octopus reached about ~30000 t (CONAPESCA, 2018; DOF, 2018; Arreguín-Sánchez, 2019); thus, the increase in catches contradicts the idea that this fishing resource was fully exploited (Arreguín-Sánchez, 2019).

One important environmental variable that controls populations fitness is the temperature since they regulate the organisms' physiology (Frederich and Pörtner, 2000; Pörtner and Farrell, 2008; Angilletta, 2009; Pörtner et al., 2017); such effects on

the physiology makes them essential to account in the management in fishery resources (Pörtner and Peck, 2010). Indeed the effects of climate change on the region seem to influence marine species. For example, it has been hypothesized that the decrease in the fishery stocks and/or sightings of the *Farfantepenaeus duorarum*; *Epinephelus morio*, and *Eretmochelys imbricata* can be accounted on harmful climate conditions by climate change (Arreguín-Sánchez, 2009, 2012; del Monte-Luna et al., 2012; Arreguín-Sánchez et al., 2015). In this sense, the fitness of species is highly dependent on climate variability. Thus, if the species' fitness increases or decreases, it would be logical to expect that the abundance and, therefore, the catches and sighting would change. Such ideas correspond to the distance to the niche centroid-abundance hypothesis.

In that hypothesis, Maguire, (1973) stated that different regions of the niche correspond to different carrying intrinsic growth rates (r) of populations. This hypothesis expresses that the highest abundance, growth, and reproduction should occur in the niche's center, that is, the fundamental niche. The niche's center would correspond to a combination of environmental variables where the species' fitness is greater. As the population gets farther away from it, the fitness of populations would decrease. Validation of this hypothesis has shown overall a medium to good performance explaining the abundance of species (Martínez-Meyer et al., 2013; Yañez-Arenas et al., 2014; Ureña-Aranda et al., 2015; Waldock et al., 2019; Osorio-Olvera et al., 2020). Therefore, we propose that the increase of the red octopus' fishing yield reported could be associated with the species' niche, particularly temperature.

Physiological study of the red octopus (actual measurements of the fundamental niche - Soberón and Peterson, 2005; Peterson et al., 2011; Peterson et al., 2015) has shown that optimal temperatures occur between 20-26 °C in embryos (Caamal-Monsreal et al., 2016), 17-33 ° C in juveniles (Noyola et al., 2013), and 21-27 ° C in adults (Juárez et al., 2015, 2016; López-Galindo et al., 2019). Due to differences in thermal preferences during the ontogenic development, the red octopus could migrate toward

favorable environmental conditions if the warming ocean trends continue (Angeles-Gonzalez et al., 2017). On the other hand, Arreguín-Sánchez, (2019) argues that; based on fishery trends, temperature, and predators' decreases, the octopus stock would increase.

Based on the ideas above, we argue that the increase in the fishing yield of red octopus occurred derived from temperature increases. Therefore, if thresholds of the temperature are surpassed (i.e. $> 27\text{ }^{\circ}\text{C}$), we could expect a decrease in catches. In this sense, we tested these ideas using physiological studies as a proxy of fitness and the number of active fishers as they can influence the catches, something that Arreguín-Sánchez, (2019) didn't account for (Maunder and Punt, 2013; Pauly et al., 2013).

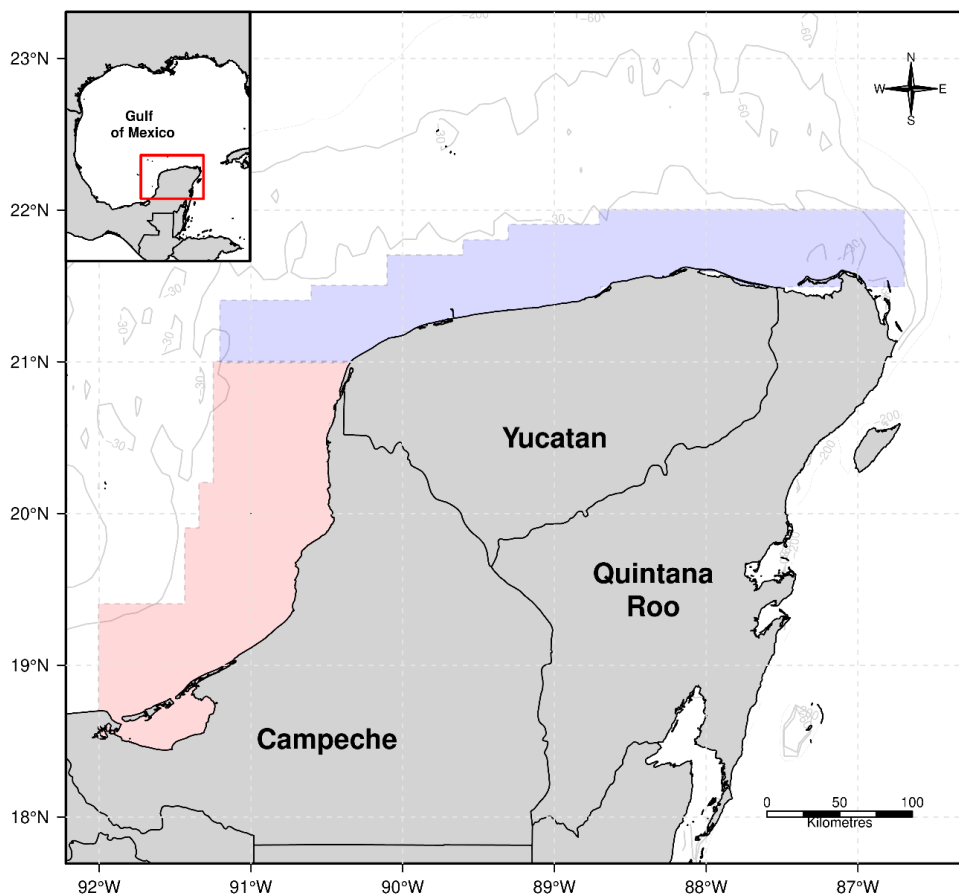


Figure 1. Yucatan Peninsula. Red polygon represents the fishing areas of Campeche, while blue ones from Yucatan are considered in this work. The polygons used here are

based on the fishing region of the red octopus (*Octopus maya*) reported by Gamboa-Álvarez et al., (2015).

2. Material and methods

2.1 Catch and fishing effort data

We reviewed official sources of red octopus landings from the Small-scale fleet for Campeche and Yucatan since most fishing production occurs in those states (DOF, 2018) (Table 1 – Figure 2). For some years, the catches of red octopus and common octopus (*Octopus americanus* - Avendaño et al., 2020) were recorded together; however, after the year 1998, the data has been separated by species. Nevertheless, since most of the red octopus catches occur near the coastal region while the *O. americanus* is targeted by the semi-industrial fleet far from the coast (Galindo-Cortez et al., 2014), we considered catches before 1998 as red octopus. In addition, the fishing effort (number of vessels dedicated to octopus fishing) for Campeche and Yucatan data were obtained from the Diario Oficial de la Federación, (DOF 2014) with data available from 1993 to 2008. Since we only used catch data from 1993 to 2008 to test our hypothesis, we considered only the fishing effort for that period in our analysis (Figure 2).

Table 1. Time series of catches of Campeche and Yucatán and data on the population growth rate of the red octopus (*Octopus maya*).

Time series	Period	Resolution	Source
Red octopus catches from the states of Campeche and Yucatán	1964-2015	Annual	SAGARPA (2015)
Red octopus catches from the states of Campeche and Yucatán	1999-2014	Monthly (August-December)	SAGARPA, Yucatán; by: CRIP Yucalpeten
Captures and income of species landed in Sisal, Yucatán	2006-2014	Annual	SAGARPA, Yucatan; by: CRIPA Yucalpeten

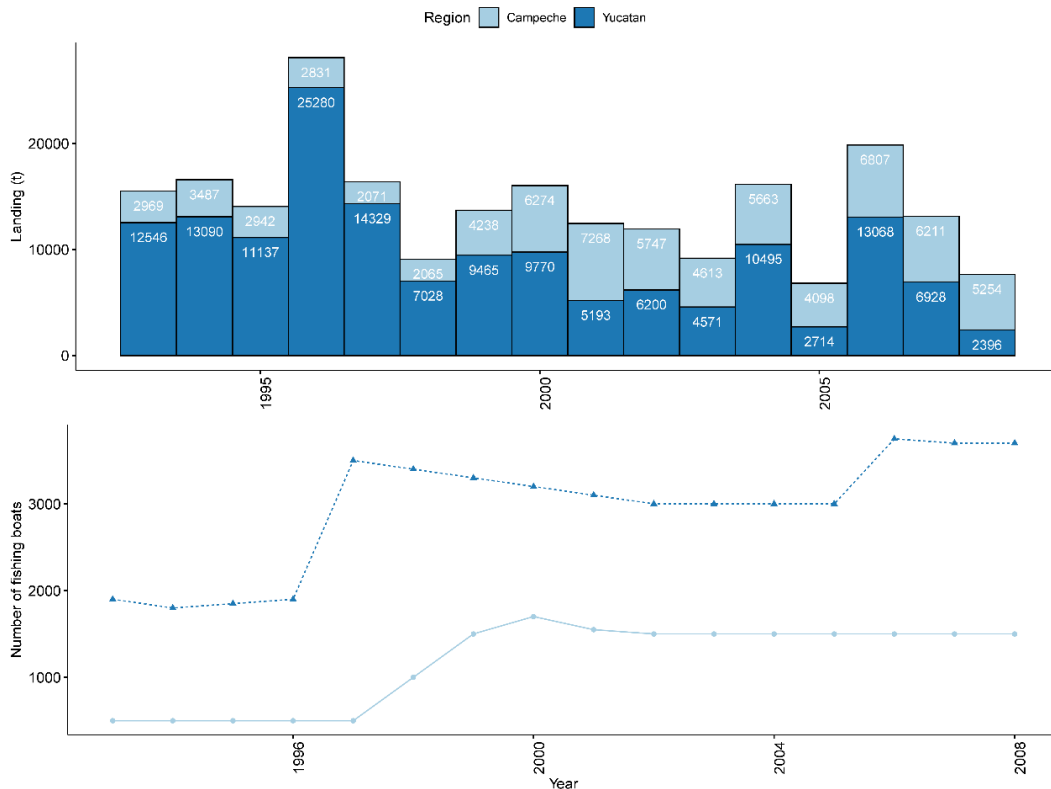


Figure 2. Total landings in tonne (top) and fishing effort by the number of fishing boats of red octopuses for the state of Campeche and Yucatan.

2.2 Physiological data of red octopus

The relationship between temperature ($^{\circ}\text{C}$) and mean red octopus fitness for juveniles was calculated using the methodology of Paschke et al., (2018). For that purpose, juveniles of red octopus obtained from embryos incubated at 24°C were acclimated at different temperatures in a range from 13 to 33°C . The temperature was used to induct a standardizable low (LMR) and high metabolic rate (HMR) as proxies of standard and maximum metabolic rate. Thermal metabolic scope (TMS) was calculated as $\text{HMR} - \text{LMR}$. This scope represents the surplus proportion of the energy flux (Paschke et al., 2018) and was associated with fitness since it reflects survivability (Figure 3).

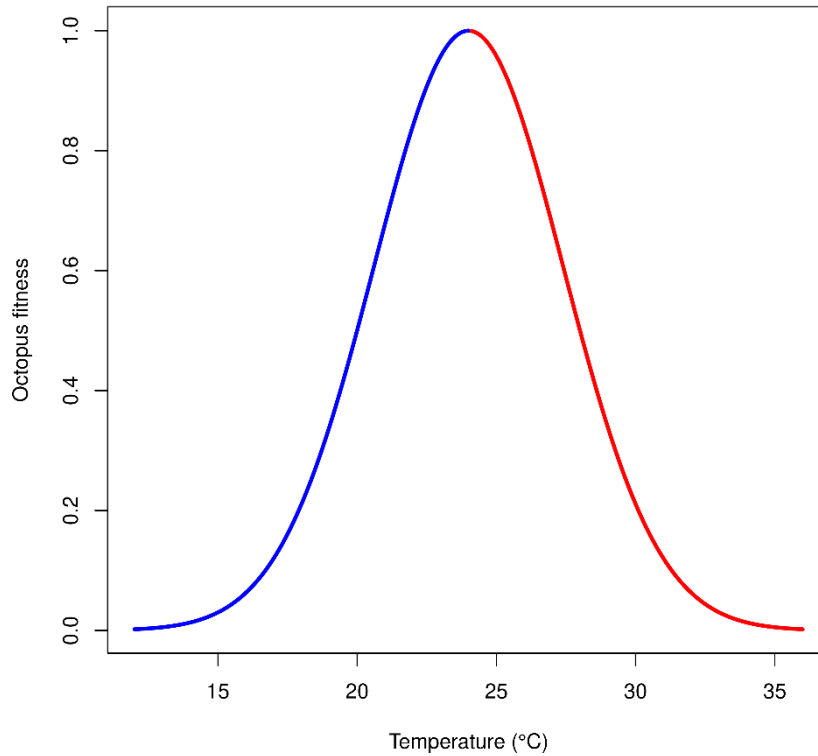


Figure 3. Gaussian distribution showing the temperatures that maximize and diminish the fitness on fertility on females of the red octopus (Juárez et al., 2015).

2.3 Environmental layers

We downloaded daily (365 days) data of bottom temperature (°C) from the GLORYS12V1 product from the Copernicus Marine Environment Monitoring Service (<https://resources.marine.copernicus.eu/>) from the year 1993-2008 at a resolution of 9 km². The layers were cropped according to the polygons of figure 1; one for Campeche and one for Yucatan. From these daily data, a yearly average (1993-2008) was calculated for both regions.

2.4 Modeling process

A generalized additive model (GAM) was used to model the relationship between temperature (°C) and red octopus' fitness. We used this approach since it can fit

nonlinear responses. The model assumed a Gaussian error distribution and identity link. The GAMs models were created using the library "mgcv" (Wood, 2017); we set a value of "k" (degrees of smoothness) of 15 to fit the data. Once the model was created, it was projected to the yearly average layer of bottom temperature from 1993 to 2008 for Campeche and Yucatan (see above), obtaining a fitness map for each year. We calculated a mean average of fitness for each layer and state. Later we create a database with the catch and fitness data for year and state. Finally, with this database, another GAM model was applied to set a k value of 3 to avoid overfitting. We used Campeche and Yucatan's total landings as a response variable and fitness and fishing effort as predictors variables. The GAMs were built using the "mgcv" library (Wood 2017) from the R software.

3. Results

From 1993 to 2008, the fitness of the red octopus has been relatively steady (Figure X) in Campeche and Yucatan, although a peak existed in 1996. However, the GAM model showed that the main effect of the number of boats was not significant ($P > 0.05$). In contrast, the main effect of fitness and fitness interaction with the fishing effort was statistically significant ($P = 0.01$). In this sense, as the fitness increases, the total landing of red octopus increases (figure 4); conversely, as the fitness decreases, the octopus's landings decrease. The GAM model explained 42.9% of the variance with an R^2 of 0.363.

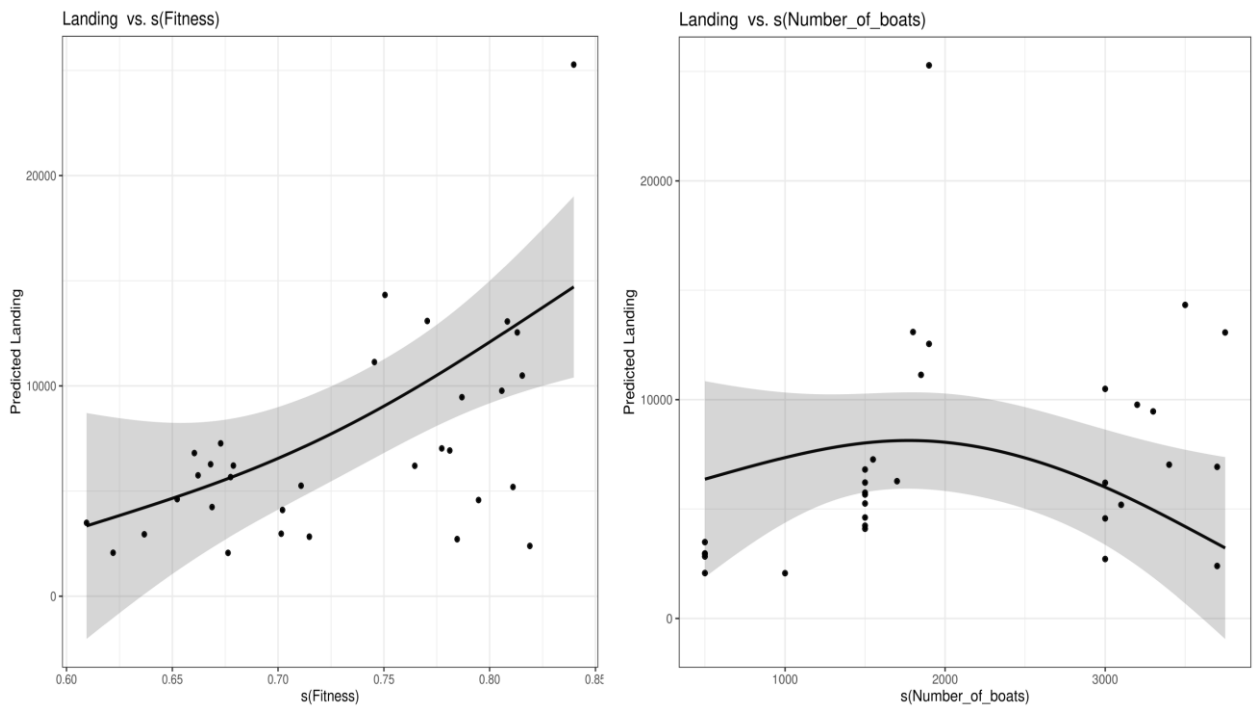


Figure 4. Visualization of the two main factors, fitness and fishing effort in the landing of red octopus (*Octopus maya*).

4. Discussion

The warming occurring in the Yucatan Peninsula seems to be increasing the fitness of the red octopus (Figure 4). Such a trend would explain why the catches have been currently increasing (Salas et al., 2006; CONAPESCA, 2018; Arreguín-Sánchez, 2019). These new conditions are not necessarily favorable only for survivability but also for the spawning rates, growth, survivability, and physiological and immunological conditions (Juárez et al., 2015, 2016; Caamal-Monsreal et al., 2016; López-Galindo et al., 2019; Pascual et al., 2019). Therefore, according to our results, we propose that warming trends may allow an increase in the species' overall fitness at least in the short term.

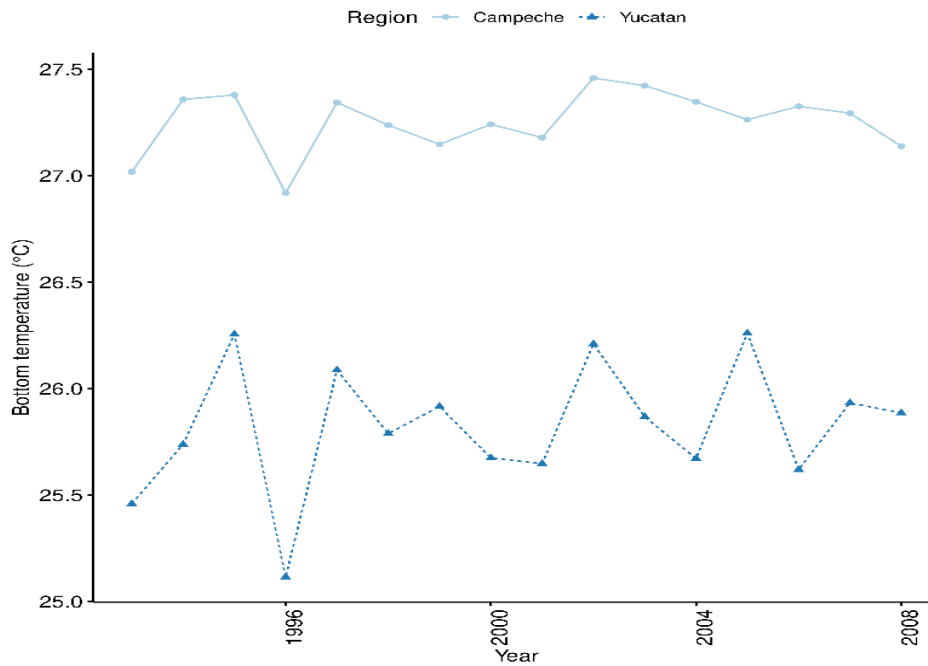


Figure 5. Mean bottom temperature for Campeche and Yucatan during the period 1993 to 2008.

Overall, it has been noticed a global proliferation of cephalopods catches (Doubleday et al., 2016). Indeed, studies demonstrate that cephalopod populations are highly responsive to environmental change, with ocean warming and the lack of predators being the main driver of the observed increase (Arreguín-Sánchez, 2019). In addition, it is thought that elevated temperatures accelerate the life cycles of cephalopods, increasing the abundance (Caddy and Rodhouse, 1998; Rodhouse et al., 2014; Arreguín-Sánchez, 2019). This pattern would be true only if the optimal temperatures are not exceeded and there is enough food to sustain the populations (Angeles-Gonzalez et al., 2017; Caddy and Rodhouse, 1998).

The points above mentioned are pretty essential to consider because the Carta Nacional Pesquera in Mexico; an instrument that provides precise and up-to-date information on where, when, and how much fishing is allowed, assumes that climate change is favorable for the red octopus (DOF, 2018). Therefore, based on our results, we agree with Arreguín-Sánchez, (2019) that environmental conditions are optimal for red octopuses for now. However, if the warming process continues, the stocks of red octopuses could fall.

We need to determine the temperature threshold that the red octopus' fitness could tolerate if proper monitoring of the fishing resource will be made. Multiple laboratory (Juárez et al., 2015; Caamal-Monsreal et al., 2016; Sanchez-García et al., 2017; Roubedakis et al., 2018; López-Galindo et al., 2019) and field samplings studies (Pascual et al., 2019) have determined a temperature threshold of about 30 °C. Based on this, it has been suggested that populations of the red octopus could migrate eastward where the upwellings could keep the temperatures lower (Merino, 1997; Monreal-Gómez et al., 2004; Juárez et al., 2013; Enriquez and Mariño-Tapia, 2014). If this is the case, then in a climatic warming scenario, populations could be concentrated in the upwelling zone in Yucatan (Angeles-Gonzalez et al., 2017) (Figure 6). In turn, this would significantly reduce the fishing yields on the state of Campeche.

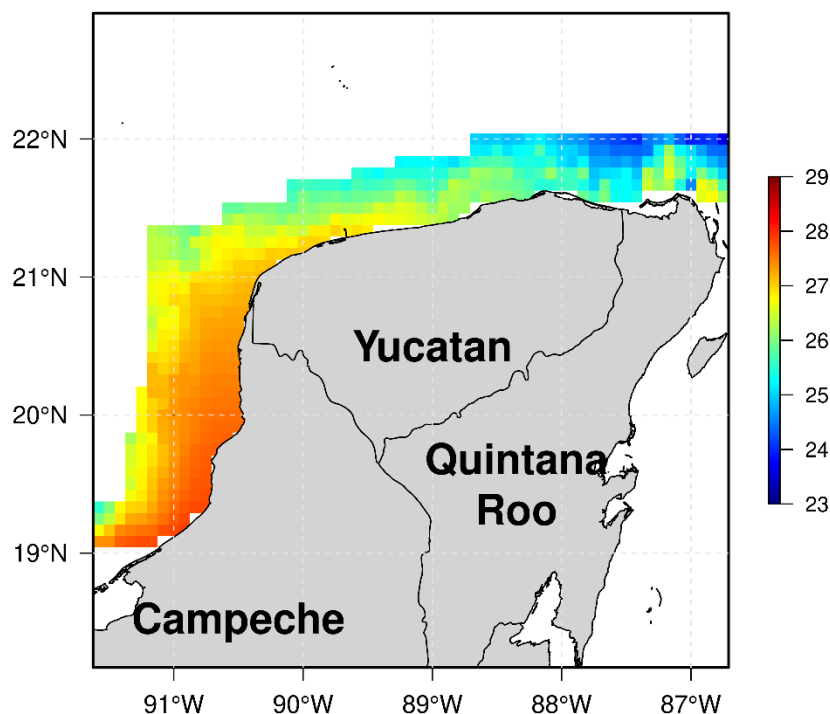


Figure 6. Mean bottom temperature for the Yucatan peninsula for the period 1993-2008. An upwelling influences northern region of the Yucatan Peninsula. The data was obtained from the GLORYS12V1 product from the Copernicus Marine Environment Monitoring Service (<https://resources.marine.copernicus.eu/>) at a resolution of 9 km².

From this work, we propose interesting hypotheses. For instance, we expect an increase in the fishing yields for the following years; however, the fisheries' landings would fall when the fitness threshold is exceeded. Particularly this would be noticed first in Campeche than in Yucatan. In turn, changes in populations' distribution could be used to indicate the effects of climate change since we are expecting a migration of octopuses eastward. In fact, if populations migrate to Yucatan, landings could momentarily increase in the region (Angeles-Gonzalez et al., 2017). Finally, using physiological data as a proxy to measure the "healthiness" of the catches is an exciting development of this work. As far as we know, no other study has related direct measurements of fitness and catches. Thus, this work could help create a "bridge" between the fishery biologists and ecophysiologicals, where experimental data could validate and predict catches reports.

5. References

- Angeles-Gonzalez, L. E., Calva, R., Santos-Valencia, J., Avila-Poveda, O. H., Olivares, A., Díaz, F., and Rosas, C. (2017). Temperature modulates spatio-temporal variability of the functional reproductive maturation of *Octopus maya* (Cephalopoda) on the shelf of the Yucatan Peninsula, Mexico. *Journal of Molluscan Studies*, 83(3), 280–288. <https://doi.org/10.1093/mollus/eyx013>
- Angilletta, M. J. (2009). *Thermal Adaptation A Theoretical and Empirical Synthesis* (M. J. Angilletta (ed.)). Oxford University Press.
- Arreguín-Sánchez, F. (2009). Cambio climático y el colapso de la pesquería de camarón rosado (*Farfantepenaeus duorarum*) de la Sonda de Campeche. In E. Rivera-Arriaga, I. Azuz-Adeath, G. Villalobos-Zapata, and L. Alpuche-Gual (Eds.), *Cambio Climático en México, un Enfoque Costero-Marino* (pp. 399–410). Universidad Autónoma de Campeche.
- Arreguín-Sánchez, F. (2012). The Dynamics Linking Biological Hierarchies, Fish Stocks and Ecosystems: Implications for Fisheries Management. In F. Jordan and S. Jørgensen (Eds.), *Models of Ecological Hierarchy: From Molecules to the Ecosphere* (pp. 501–516). Elsevier B.V.
- Arreguín-Sánchez, F. (2019). Climate change and the rise of the octopus fishery in the Campeche Bank, México. *Regional Studies in Marine Science*, 32, 100852. <https://doi.org/10.1016/j.rsma.2019.100852>
- Arreguín-Sánchez, F., del Monte-Luna, P., and Zetina-Rejón, M. J. (2015). Efectos del cambio climático en ecosistemas acuáticos y el reto para el manejo de pesquerías: el camarón rosado del sur del Golfo de México. *Fisheries*, 40(1), 15–19. <https://doi.org/10.1080/03632415.2015.988075>

- Arreguín-Sánchez, F., Seijo-Gutiérrez, J. ., Fuentes-Castellanos, D., and Solís-Ramírez, M. . (1987). *Estado del conocimiento de los recursos pesqueros de la plataforma continental de Yucatán y región adyacente*.
- Avendaño, O., Roura, Á., Cedillo-Robles, C. E., González, Á. F., Rodríguez-Canul, R., Velázquez-Abunader, I., and Guerra, Á. (2020). *Octopus americanus*: a cryptic species of the *O. vulgaris* species complex redescribed from the Caribbean. *Aquatic Ecology*, *54*, 909–925. <https://doi.org/10.1007/s10452-020-09778-6>
- Caamal-Monsreal, C., Uriarte, I., Farias, A., Díaz, F., Sánchez, A., Re, D., and Rosas, C. (2016). Effects of temperature on embryo development and metabolism of *O. maya*. *Aquaculture*, *451*, 156–162. <https://doi.org/10.1016/j.aquaculture.2015.09.011>
- Caddy, J. F., and Rodhouse, P. G. (1998). Cephalopod and groundfish landings: Evidence for ecological change in global fisheries? *Reviews in Fish Biology and Fisheries*, *8*(4), 431–444. <https://doi.org/10.1023/A:1008807129366>
- CONAPESCA. (2018). *Anuario Estadístico de Acuicultura y Pesca 2018*. <https://www.gob.mx/conapesca/documentos/anuario-estadistico-de-acuicultura-y-pesca>
- del Monte-Luna, P., Guzmán-Hernández, V., Cuevas, E. A., Arreguín-Sánchez, F., and Lluch-Belda, D. (2012). Effect of North Atlantic climate variability on hawksbill turtles in the Southern Gulf of Mexico. *Journal of Experimental Marine Biology and Ecology*, *412*, 103–109. <https://doi.org/10.1016/j.jembe.2011.11.005>
- DOF. (2014). *ACUERDO por el que se da a conocer el Plan de Manejo Pesquero de pulpo (*O. maya* y *O. vulgaris*) del Golfo de México y Mar Caribe*. http://dof.gob.mx/nota_detalle_popup.php?codigo=5338727
- DOF. (2018). *Carta Nacional Pesquera*. http://www.dof.gob.mx/nota_detalle.php?codigo=5525712andfecha=11/06/2018andprint=true
- Enriquez, C. E., and Mariño-Tapia, I. (2014). Mechanisms Driving a Coastal Dynamic Upwelling. *Proceedings of the 17th Physics of Estuaries and Coastal Seas (PECS) Conference, Porto de Galinhas, Pernambuco, Brazil, 19–24 October 2014*.
- Frederich, M., and Pörtner, H. O. (2000). Oxygen limitation of thermal tolerance defined by cardiac and ventilatory performance in spider crab, *Maja squinado*. *American Journal of Physiology - Regulatory Integrative and Comparative Physiology*, *279*(5), 1531–1538. <https://doi.org/10.1152/ajpregu.2000.279.5.r1531>
- Gamboa-Álvarez, M. Á., López-Rocha, J. A., and Poot-López, G. R. (2015). Spatial Analysis of the Abundance and Catchability of the Red Octopus *Octopus maya* (Voss and Solís-Ramírez, 1966) on the Continental Shelf of the Yucatan Peninsula, Mexico. *Journal of Shellfish Research*, *34*(2), 481–492. <https://doi.org/10.2983/035.034.0232>
- Juárez, O. E., Galindo-Sánchez, C. E., Díaz, F., Re, D., Sánchez-García, A. M., Camaal-Monsreal, C., and Rosas, C. (2015). Is temperature conditioning *Octopus maya* fitness? *Journal of Experimental Marine Biology and Ecology*, *467*, 71–76. <https://doi.org/10.1016/j.jembe.2015.02.020>
- Juárez, O. E., Hau, V., Caamal-Monsreal, C., Galindo-Sánchez, C. E., Díaz, F., Re, D., and Rosas, C. (2016). Effect of maternal temperature stress before spawning over the energetic balance of *Octopus maya* juveniles exposed to a gradual temperature change. *Journal of Experimental Marine Biology and Ecology*, *474*, 39–45. <https://doi.org/10.1016/j.jembe.2015.10.002>

- Juárez, O. E., Rosas, C., Arena, L., Enríquez, L., Camarena, F., McKeown, N., and Shaw, P. W. (2013). Characterization of microsatellite loci developed for the Mexican four-eyed octopus *Octopus maya*. *Conservation Genetic Resources*, 5(3), 803–805. <https://doi.org/10.1007/s12686-013-9912-x>
- López-Galindo, L., Galindo-Sánchez, C., Olivares, A., Avila-Poveda, O. H., Díaz, F., Juárez, O. E., Lafarga, F., Pantoja-Pérez, J., Caamal-Monsreal, C., and Rosas, C. (2019). Reproductive performance of *Octopus maya* males conditioned by thermal stress. *Ecological Indicators*, 96, 437–447. <https://doi.org/10.1016/j.ecolind.2018.09.036>
- Maguire, B. J. (1973). Niche Response Structure and the Analytical Potentials of Its Relationship to the Habitat. *The American Naturalist*, 107(954), 213–246. <https://doi.org/10.1086/282827>
- Martínez-Meyer, E., Díaz-Porras, D., Peterson, A. T., and Yáñez-Arenas, C. (2013). Ecological niche structure and rangewide abundance patterns of species. *Biology Letters*, 9(1). <https://doi.org/10.1098/rsbl.2012.0637>
- Maunder, M. N., and Punt, A. E. (2013). A review of integrated analysis in fisheries stock assessment. *Fisheries Research*, 142, 61–74. <https://doi.org/10.1016/j.fishres.2012.07.025>
- Merino, M. (1997). Upwelling on the Yucatan Shelf : hydrographic evidence. *Journal of Marine Systems*, 13(1–4), 101–121.
- Monreal-Gómez, M. ., Salas-de León, D. ., and Velasco-Mendoza, H. (2004). Hidrodinámica del Golfo de México. In M. Caso, I. Pisanty, and E. Ezcurra (Eds.), *Diagnóstico Ambiental del Golfo de México vol. I* (pp. 47–67). Instituto Nacional de Ecología (INE-SEMARNAT).
- Noyola, J., Caamal-Monsreal, C., Díaz, F., Re, D., Sánchez, A., and Rosas, C. (2013). Thermopreference, tolerance and metabolic rate of early stages juvenile *Octopus maya* acclimated to different temperatures. *Journal of Thermal Biology*, 38(1), 14–19. <https://doi.org/10.1016/j.jtherbio.2012.09.001>
- Osorio-Olvera, L., Yáñez-Arenas, C., Martínez-Meyer, E., and Peterson, A. T. (2020). Relationships between population densities and niche-centroid distances in North American birds. *Ecology Letters*, 23(3), 555–564. <https://doi.org/10.1111/ele.13453>
- Paschke, K., Agüero, J., Gebauer, P., Díaz, F., Mascaró, M., López-Ripoll, E., Re, D., Caamal-Monsreal, C., Tremblay, N., Pörtner, H. O., and Rosas, C. (2018). Comparison of aerobic scope for metabolic activity in aquatic ectotherms with temperature related metabolic stimulation: A novel approach for aerobic power budget. *Frontiers in Physiology*, 9(OCT), 1–15. <https://doi.org/10.3389/fphys.2018.01438>
- Pascual, C., Mascaró, M., Rodríguez-Canul, R., Gallardo, P., Sánchez, A. A., Rosas, C., and Cruz-López, H. (2019). Sea surface temperature modulates physiological and immunological condition of *Octopus maya*. *Frontiers in Physiology*, 10(JUN), 1–11. <https://doi.org/10.3389/fphys.2019.00739>
- Pauly, D., Hillborn, R., and Branch, T. (2013). Does catch reflect abundance? *Nature*, 494, 303–306. <https://doi.org/10.1038/494303a>
- Peterson, A. T., Papeş, M., and Soberón, J. (2015). Mechanistic and correlative models of ecological niches. *European Journal of Ecology*, 1(2), 28–38. <https://doi.org/10.1515/eje-2015-0014>
- Peterson, T. A., Soberón, J., Pearson, R. G., Anderson, R. P., Martínez-Meyer, E.,

- Nakamura, M., and Araújo, M. B. (2011). Ecological niches and geographic distributions. In *Choice Reviews Online*. Princeton University Press.
- Pörtner, H.-O., Bock, C., and Mark, F. C. (2017). Oxygen- and capacity-limited thermal tolerance: bridging ecology and physiology. *The Journal of Experimental Biology*, 220(15), 2685 LP – 2696. <https://doi.org/10.1242/jeb.134585>
- Pörtner, H. O., and Farrell, A. P. (2008). Physiology and Climate Change. *Science*, 322(5902), 690–692. <https://doi.org/10.1126/science.1163156>
- Pörtner, H. O., and Peck, M. A. (2010). Climate change effects on fishes and fisheries: Towards a cause-and-effect understanding. *Journal of Fish Biology*, 77(8), 1745–1779. <https://doi.org/10.1111/j.1095-8649.2010.02783.x>
- Rodhouse, P. G. K., Pierce, G. J., Nichols, O. C., Sauer, W. H. H., Arkhipkin, A. I., Laptikhovskiy, V. V., Lipiński, M. R., Ramos, J. E., Gras, M., Kidokoro, H., Sadayasu, K., Pereira, J., Lefkaditou, E., Pita, C., Gasalla, M., Haimovici, M., Sakai, M., and Downey, N. (2014). Environmental effects on cephalopod population dynamics: Implications for management of fisheries. In *Advances in Marine Biology* (Vol. 67). <https://doi.org/10.1016/B978-0-12-800287-2.00002-0>
- Roumbedakis, K., Mascaró, M., Martins, M. L., Gallardo, P., Rosas, C., and Pascual, C. (2018). Health status of post-spawning *Octopus maya* (Cephalopoda:Octopodidae) females from Yucatan Peninsula, Mexico. *Hydrobiologia*, 808(1), 23–34. <https://doi.org/10.1007/s10750-017-3340-y>
- Salas, S., Mexicano-Cintora, G., and Cabrera, M. A. (2006). ¿Hacia dónde van las pesquerías en Yucatán? *Tendencias, Retos y Perspectivas*. CINVESTAV.
- Sanchez-García, A., Rodríguez-Fuentes, G., Díaz, F., Galindo-Sánchez, C. E., Ortega, K., Mascaró, M., López, E., Caamal-Monsreal, C., Juárez, O., Noreña-Barroso, E., Re, D., and Rosas, C. (2017). Thermal sensitivity of *O. maya* embryos as a tool for monitoring the effects of environmental warming in the Southern of Gulf of Mexico. *Ecological Indicators*, 72, 574–585. <https://doi.org/10.1016/j.ecolind.2016.08.043>
- Soberón, J., and Peterson, T. A. (2005). Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodiversity Informatics*, 2, 1–10. <https://doi.org/10.17161/bi.v2i0.4>
- Solís-Ramírez, M., and Arreguín-Sánchez, F. (1984). Analysis of (*Octopus maya*) fishery in the Campeche Bank. *Mem. IX MEXUS Gulf Annual Meeting*, 31–38.
- Ureña-Aranda, C. A., Rojas-Soto, O., Martínez-Meyer, E., Yáñez-Arenas, C., Ramírez, R. L., and De Los Monteros, A. E. (2015). Using range-wide abundance modeling to identify key conservation areas for the micro-endemic Bolson tortoise (*Gopherus flavomarginatus*). *PLoS ONE*, 10(6), 1–14. <https://doi.org/10.1371/journal.pone.0131452>
- Waldock, C., Stuart-Smith, R. D., Edgar, G. J., Bird, T. J., and Bates, A. E. (2019). The shape of abundance distributions across temperature gradients in reef fishes. *Ecology Letters*, 22(4), 685–696. <https://doi.org/10.1111/ele.13222>
- Wood, S. N. (2017). *Generalized Additive Models: An introduction with R* (Chapman and Hall (ed.); Second edi. CRC Press.
- Yáñez-Arenas, C., Mandujano, S., and Martínez-Meyer, E. (2014). Predicting the density and abundance of white-tailed deer based on ecological niche theory. *Deer Specialist Group IUCN Newsletter*, 26(June), 20–30.

Capítulo cuatro - Exploring the effects of warming seas by using optimal and pejus temperatures of the embryo of three Octopoda species in the Gulf of Mexico

Sometido a: *Journal of Thermal Biology*

Estado: Aceptado



Contents lists available at ScienceDirect

Journal of Thermal Biology

journal homepage: <http://www.elsevier.com/locate/jtherbio>

Exploring the effects of warming seas by using the optimal and pejus temperatures of the embryo of three Octopoda species in the Gulf of Mexico

Luis Enrique Ángeles-González^{a,b,c,d}, Françoise D. Lima^e, Claudia Caamal-Monsreal^c, Fernando Díaz^f, Carlos Rosas^{c,d,*}

^a Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Av. Ciudad Universitaria 3000, Coyoacán, Ciudad de México, 04510, Mexico

^b Laboratorio de Ecología Geográfica. Unidad de Conservación de la Biodiversidad, UMDI-Sisal, Facultad de Ciencias, Universidad Nacional Autónoma de México (UNAM), Yucatán, Mexico

^c Universidad Nacional Autónoma de México, Unidad Multidisciplinaria de Docencia e Investigación, Facultad de Ciencias, Laboratorio de Ecofisiología Aplicada, Puerto de Abrigo Sisal, Yucatán, 97356, Mexico

^d Laboratorio Nacional de Resiliencia Costera (CONACYT-Fac. de Ciencias, UNAM), Puerto de Abrigo, 97356 Sisal, Yucatán, Mexico

^e Laboratory of Systematics and Evolutionary Ichthyology, Department of Botany and Zoology, Federal University of Rio Grande do Norte, 59078-900, Natal-RN, Brazil

^f Laboratorio de Ecofisiología de Organismos Acuáticos, Departamento de Biotecnología Marina, Centro de Investigación Científica y de Educación Superior de Ensenada (CICESE), Ensenada, Baja California, Mexico

ARTICLE INFO

Keywords:

Thermal preferences
Thermal optimum
Pejus temperature
Octopus maya
Octopus insularis
Gulf of Mexico

ABSTRACT

Using data related to thermal optimal and pejus of the embryos of *Octopus americanus* from Brazil and *O. insularis* and *O. maya* from Mexico, this study aimed to project the potential distribution areas in the Gulf of Mexico and predict distribution shifts under different Representative Concentration Pathway scenarios (RCP 6 and 8.5) for the years 2050 and 2100. The different thermal tolerances elicited different responses to current and future scenarios. In this sense, *O. insularis* and *O. maya* thermal niches stretch from the Caribbean to Florida. Nevertheless, *O. insularis* may inhabit warmer areas than *O. maya*. Surprisingly, no area was considered thermally habitable for *O. americanus*, which could have been associated with the use of data of populations thermally adapted to temperate conditions south of Brazil. According to models, a warming scenario would cause a restriction of the available thermal niche of *O. maya*, while *O. insularis* could expand under RCP 6 scenarios. This restriction was more substantial in the RCP 8.5 scenario. Nevertheless, under the RCP 8.5 scenario, the temperature in 2100 may negatively affect even *O. insularis*, the species most thermal tolerant. If our results are accurate, the fishing yield of *O. insularis* will increase in the future, replacing the heavily exploited *O. maya* in the coasts of the southern Gulf of Mexico. Regarding *O. americanus*, no inference might be made until thermal tolerances of locally adapted populations can be studied.

1. Introduction

Cephalopods are essential organisms in the World Ocean involved in a wide range of trophic positions (Judkins et al., 2009), which represent a group of a high production/biomass ratio (Boyle, 2002). However, cephalopod fisheries contributed only from ~2 to ~5% of the global landings from 1960 to 2014 when compared to marine fishes (Arkhipkin et al., 2020). Nonetheless, their importance has been steadily increasing despite their different life histories. The above has been associated with increase in temperature, fishing effort (Doubleday et al., 2016), and overfishing of predators and competitors (Caddy and Rodhouse, 1998).

For the Gulf of Mexico and the Caribbean, numerous cephalopod species have been reported. For instance, a checklist for this region by Judkins et al. (2010) reported 116 cephalopod species within 27 families. Specifically, the Octopodidae family is very diverse with ~19 species for the Gulf of Mexico and the Caribbean (Judkins et al., 2010). However, few members of this family are commercially exploited. Species, such as *Amphioctopus burryi*, *Macrotritopus defilippi*, *Octopus joubini* are not associated with any fishery.

Conversely, three important commercially-exploited octopus species live in the shallow waters of different thermal environments in the Gulf of Mexico and Caribbean: *O. americanus* (Avendaño et al., 2020a)

* Corresponding author. Universidad Nacional Autónoma de México, Unidad Multidisciplinaria de Docencia e Investigación, Facultad de Ciencias, Laboratorio de Ecofisiología Aplicada, Puerto de Abrigo Sisal, Yucatán, 97356, Mexico.

E-mail address: crv@ciencias.unam.mx (C. Rosas).

<https://doi.org/10.1016/j.jtherbio.2020.102753>

Received 20 May 2020; Received in revised form 10 September 2020; Accepted 5 October 2020

Available online 8 October 2020

0306-4565/© 2020 Elsevier Ltd. All rights reserved.

previously known as *O. vulgaris* type II (Avendaño et al., 2020b), *O. insularis* (González-Gómez et al., 2018), and *O. maya* (Gamboa-Álvarez et al., 2015). These three species represent almost 100% of the exploited octopuses in Mexican waters of the Atlantic with around 20 000 t/year (DOF, 2014).

Octopus americanus is broadly distributed in the American continent from Mar del Plata, Argentina, Brazil through the Caribbean Sea, the Gulf of Mexico to the coast of Virginia from temperate to warm environments (Avendaño et al., 2020b). *Octopus insularis* is a species of wide tropical distribution in the Atlantic Ocean (Lima et al., 2017). It has been recently recorded in the Veracruz Reef System in the Gulf of Mexico (Flores-Valle et al., 2018) where sea temperature is similar to the tropical areas of Brazil where it was described (22–30 °C) (Leite et al., 2008).

Octopus maya is a coastal species that inhabits shallow waters adjacent to the continental shelf of the Yucatan Peninsula (states of Campeche, Yucatan, and Quintana Roo, Mexico). This species is often associated with areas covered by seagrass (*Thalassia testudinum*), coral fragments, and empty gastropod shells (Voss and Solís-Ramírez, 1966). Recent studies of *O. maya* had demonstrated that growth and reproduction were favored by the presence of summer upwelling that maintained the bottom of one part of the continental shelf temperature below 27 °C, just in front of the state of Yucatán (Fig. 1). Conversely, warmer waters are found in the Campeche Bank (~27 °C) where mature adults are found seasonally in winter, which supports the hypothesis that temperatures below 27 °C appear to be favorable for functional reproductive maturation (Ángeles-González et al., 2017; Juárez et al., 2016).

Despite these species have similar habitat requirements, such as occurrences in rocky reefs, coexistence in the Gulf of Mexico could not

be possible mainly because they prefer different thermal zones. However, increase in seawater temperature could influence species distribution dynamics causing population expansion, retraction, or displacement along their occurrence area (Perry et al., 2005). Since temperature is considered an important regulator in species well-being and fitness (Pörtner and Farrell, 2008) at a population level, the animals might migrate searching for a thermal optimum. Recently, studies have demonstrated that *O. maya* adult population is overlapping with *O. americanus* in waters at a depth greater than 30 m where temperatures of 25 °C or lower were recorded during surveys (Avendaño et al., 2019, 2020a). Although *O. maya* is now found in an area that was previously considered exclusively of *O. americanus* for many years, it is still not known if *O. maya* population has always been there and misidentified (Lima et al., 2017) or is the result of the adult population moving and searching for lower temperatures for reproduction (Ángeles-González et al., 2017).

Thermal preferences are linked with the processes of uptake, transport, and supply of oxygen. According to Fry and Hart (1948), the difference between the standard and maximum metabolic rates allows calculating the species aerobic scope (AS). Thus, temperature that causes a maximum AS will indicate an optimal energy production. The thermal optimum allows species to increase performance and fitness, maximizing their responses in processes, such as growth and reproduction (Pörtner and Farrell, 2008). Ideally, in the wild, species would be found in the zones that maximize their fitness, which does not always occur because the processes that control population are also related to biological interactions or accessibility to optimal zones (Soberón and Peterson, 2005).

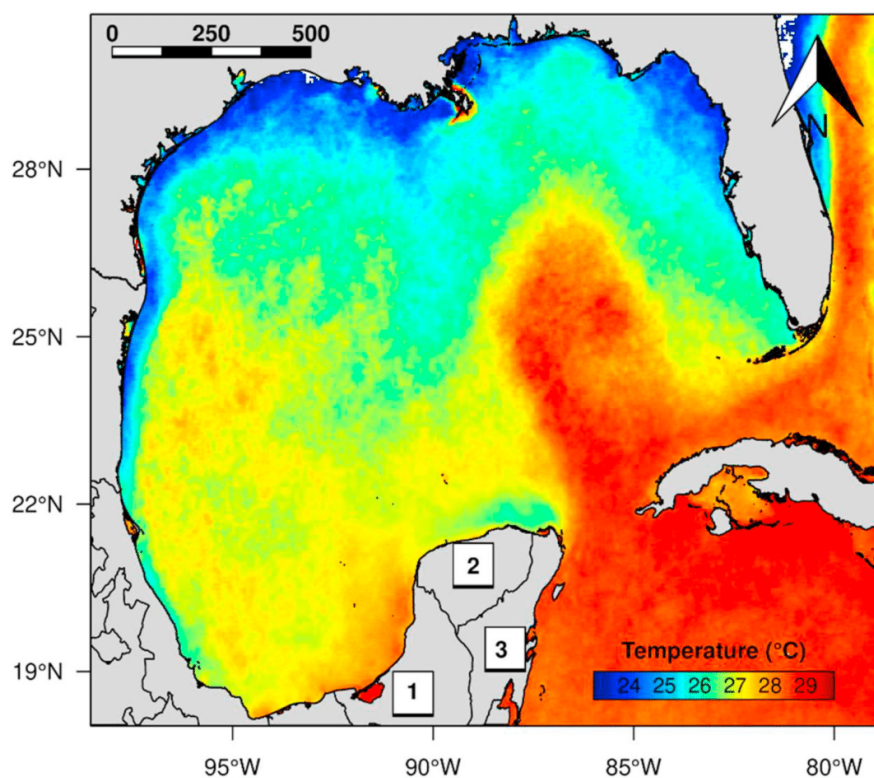


Fig. 1. The average daytime sea-surface temperature in the Gulf of Mexico during the year 2019. Numbers indicate the states that conform to the Yucatan Peninsula; (1) Campeche, (2) Yucatan, (3) Quintana Roo. The upwelling effect upwelling can be observed in front of the state of Yucatan. Data were obtained from the sensor MODIS-Aqua.

The species may also be found in non-optimal but tolerable areas, called the “Pejus” zone, where the AS decrease. Regardless of this stress, species populations can be found in this zone, but their performance is reduced. If thermal stress continues and aerobic capacity is exhausted, anaerobic metabolism and the antioxidant system can be activated to eliminate free radical excess and supply cellular energy demands. This process is known as critical temperature. It is the last resort of an organism (Frederich and Pörtner, 2000) before “denaturation” temperatures when tolerance becomes increasingly passive and time-limited (Pörtner and Farrell, 2008).

In marine environments, temperature may have increased up to 4 °C by 2100, which might promote severe consequences in the physiological, behavioral, and demographic patterns of aquatic organisms (Bijma et al., 2013; Hoegh-Guldberg and Bruno, 2010). Particular, in the Gulf of Mexico and Caribbean Sea, temperature increments have been predicted around 0.01 - 0.02 °C year⁻¹ (Glenn et al., 2015), suggesting increases in the area of the Yucatan Peninsula around 1 °C every 50 years. If the North Atlantic current slows down as it has been predicted, it may be anticipated that a reduction on Yucatán upwelling will be observed with consequences in the distribution area of those octopus species. Taking into consideration that a key phase of species survival is embryonic growth (Caamal-Monsreal et al., 2016) and spawning areas are linked with adult octopus thermal tolerances (Juárez et al., 2015, 2016; López-Galindo et al., 2019), this study used published and unpublished data to identify the optimum and pejus of *O. maya*, *O. insularis* and *O. americanus*. With this data, the potential distribution areas were projected based on the thermal niche of these octopus species in the Gulf of Mexico to predict the shifts or distribution expansion under different future global warming scenarios. This study was based on the idea that predicting the potential consequences of increasing sea temperature for marine organisms is essential to promote species conservation strategies and sustainable development plans for these critical fishery resources. Considering that *O. insularis* is a widely distributed species living in environments under different temperature levels, it could take advantage of future climate change and expand its distribution boundaries. In the Gulf of Mexico, warming could promote shifts on *O. maya* distribution towards deeper waters or higher latitudes where it should compete for space and food with *O. americanus* or be competitively excluded by *O. insularis* that is tolerant to warm environments (Lenz et al., 2015; Lima et al., 2014). Currently, the effect of a warming scenario for *O. americanus* distribution is difficult to hypothesize because of the (i) lack of laboratory data evaluating the thermal tolerance of the Gulf of Mexico population and (ii) scarce data of the wild population. Therefore, this study used embryo thermal sensitivity data obtained from southern Brazil, in the area of the city of Florianópolis, capital of the state of Santa Catarina.

2. Material and methods

2.1. Selection of thermal optimal and thermal pejus

To describe octopus species distribution in the Gulf of Mexico, the thermal optimum and pejus for *O. maya* (Tremblay et al., 2017; Caamal-Monsreal et al., 2016), *O. insularis* and *O. americanus* embryos (unpublished results) were obtained from experiments done in the aquaculture facilities of Universidad Nacional Autónoma de México (UNAM) in the Faculty of Sciences at Sisal, Yucatan, Mexico for *O. maya* and *O. insularis* and for *O. americanus*, in the facilities of the Universidade Federal de Santa Catarina in Brazil.

Although marine species change their thermal preferences along with their ontogenetic development, embryos and spawning adults have comparable thermal preferences (Pörtner and Farrell, 2008; Tremblay et al., 2017). For that reason, this study used published and unpublished data of the embryos of those species to estimate their potential species distribution. The described thermal optimum and pejus were obtained for each guide and recommendations of the European Union (EU)

Directive 2010/63/EU for animal experiments. This project was approved by the Committee of the Faculty of Chemistry at UNAM, Sisal. Permit Number Oficio/FQ/CICUAL/099/15.

2.1.1. *Octopus maya* data

Octopus embryos were obtained from aquaculture facilities where juveniles are frequently produced from captive broodstock. Four temperatures (18, 22, 26, and 30 °C) were considered to assess incubation temperature effects on morphological characteristics and growth, as well as on hatchling performance measured as survival after 10 days of fasting. The results of that study indicated that optimum temperatures for embryo development were in the ranges from 22 to 26 °C. A reduction of hatchling performance, survival, and morphological anomalies were recorded in embryos incubated at 30 °C, indicating that this temperature could be in the pejus range of this octopus species (Caamal-Monsreal et al., 2016).

To corroborate those conditions, embryos were later exposed to a thermal ramp from 24 to 30 °C with increments of 1 °C every five days, evaluating the respiratory metabolism and antioxidant defense mechanisms (Sanchez-García et al., 2017). The results indicated that embryos experienced changes in the antioxidant defense mechanisms above 27 °C and were not able to recover. These results suggest that pejus of *O. maya* embryos is from 27 to 30 °C, of which 30 °C is close to an extreme thermal condition where hatching and survival are too low (less than 5%). A similar response was observed in spawners when exposed to 30 °C (Juárez et al., 2015, 2016). For projections, this study chose a low pejus range of 12 °C, an optimum from 22 to 27 °C and a high pejus of 30 °C (Fig. 2A).

2.1.2. *Octopus insularis* data

Octopus embryos were obtained from adults captured in the Veracruz Reef System (Flores-Valle et al., 2018) and transferred by plane to the aquaculture facilities of Sisal, Yucatan, Mexico. These adults were adapted to laboratory conditions for 10 d. Later, females were placed in a spawning area where seawater was maintained at 24 °C (Rosas et al., 2014). The effects of incubation temperature on hatchling performance of *O. insularis* embryos artificially incubated were evaluated at two thermal conditions. One group was maintained at 24 °C and the other one was exposed to a thermal ramp from 24 to 31 °C changing 1 °C every other day (Sanchez-García et al., unpublished data). As in *O. maya* embryos, those of *O. insularis* were also evaluated based on changes in hatchling performance, morphological characteristics, and growth.

Embryo oxygen consumption was estimated every change of temperature to verify when a switch between optimum and pejus could be identified. The results indicated that optimum temperatures for embryo development were in a wide thermal range from 24 to 29 °C. Although a reduction of hatchling performance was not observed, morphological anomalies were recorded in embryos incubated at 30 °C, indicating that 30 °C could be the beginning of the pejus range of this octopus species up to 33 °C. For the projections of this study, a low pejus range of 18 with an optimum from 24 to 29 °C and a high pejus of 33 °C were used (Fig. 2A).

2.1.3. *Octopus americanus* data

Octopus embryos were obtained from adults captured in the coastal zone of the Coral Island close to the city of Florianópolis, Brazil. Once captured, animals were transferred by land to the mariculture facilities of Florianópolis. Once there, adults were individually acclimated to laboratory conditions for 30 days until spawning. During that time, animals were maintained at 21 °C.

To assess the effects of incubation temperature on hatchling performance of *O. americanus* embryos, they were artificially incubated and evaluated at two thermal conditions. One group was maintained at 18 °C constant, and the other one was exposed to a thermal ramp from 18 to 24 °C changing 1 °C every five days (Guzella et al., unpublished data). As in the other species, embryo changes in morphological characteristics, growth, and hatchling performance were evaluated. In this species, the

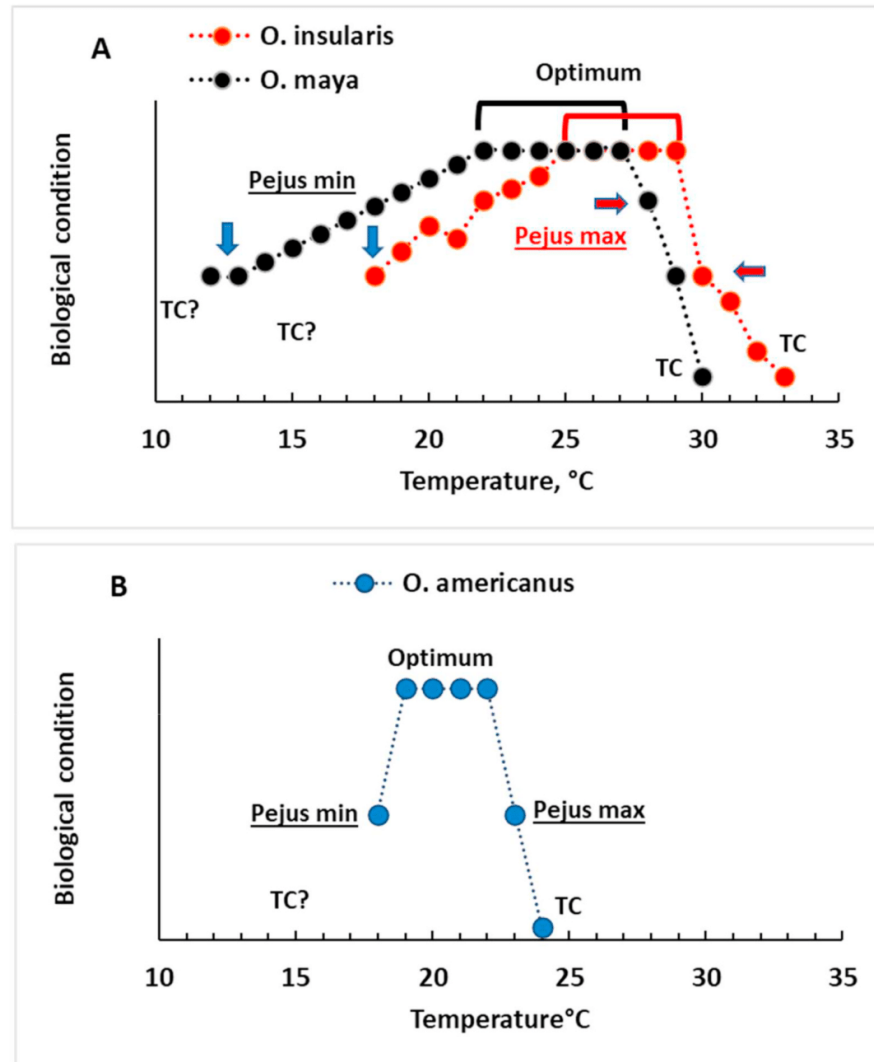


Fig. 2. Thermal ranges used to predict the potential consequences of increasing sea temperature to spawners and embryos of *Octopus insularis*, *O. maya* and *O. americanus* inhabiting the American Atlantic Ocean. Data of *O. maya* from Caamal-Monsreal et al. (2016), Sánchez-García et al. (2017), and Juárez et al. (2015). Data of *O. insularis* from Sánchez-García et al. (unpublished data). Data of *O. americanus* from Guzella et al., (unpublished data).

antioxidant defense mechanisms during embryo development were also assessed. The results indicated that optimum temperatures for embryo development were in the range from 19 to 22 °C. A reduction of hatchling performance, survival, and morphological anomalies were recorded in embryos incubated at 23 °C, indicating that this temperature could be in the pejus range of this octopus species. At the same time, 24 °C was identified as a critical temperature (Fig. 2B).

2.2. Environmental layers

World environmental layers of maximum and minimum benthonic temperatures (°C) were downloaded from Bio-Oracle (Assis et al., 2018) at a resolution of 5 arcmins (9.2×9.2 km, approximately). The maximum and minimum temperatures were chosen over mean temperature because of the relationship that exists among niche breadth and species distribution range (Slatyer et al., 2013).

Given that focal cells include a range of depth values in the process of downscaling in Bio-Oracle, different bathymetrical choices are available: maximum, average, and minimum depth (see Assis et al., 2018 for details). The minimum depth layer was chosen since these octopus species are restricted to shallow benthic areas (Leite et al., 2009, 2008; Batista and Leite, 2016; Avendaño et al., 2019, 2020a).

The downloaded environmental layers were for current (values obtained from a weighting process from 2000 to 2014) and future (2050 and 2100) scenarios based on the Representative Concentration Pathways (RCP) 6 and RCP 8.5 scenarios (Fig. 4 and Fig. 5). The RCP 6 scenario is considered as a medium-based scenario where emissions peak approximately 2080 and then decline while RCP 8.5 is a high emission scenario rising through the 21st century and beyond for some amount of time (van Vuuren et al., 2011; IPCC, 2014).

The environmental layers were cropped according to the ecoregions proposed by Spalding et al. (2007) that make up the Gulf of Mexico.

These ecoregions cover an area of the Caribbean (Fig. 3). According to Spalding et al. (2007), ecoregions can be defined as areas of homogeneous species composition. Each one has also characteristics determined by upwelling, nutrient inputs, temperature, bathymetric complexity, and many more. This study chose those ecoregions since they represent areas where these octopuses are fished and could potentially disperse in a warming scenario. Moreover, since *O. maya* has been recorded up to maximum depths of ~60 m (Avendaño et al., 2019) and *O. insularis* at ~30 m (Batista and Leite, 2016), the optimal and pejus temperatures were projected to depths up to 100 m.

2.3. Projections for present and future scenarios

Binarized maps of optimal and pejus temperatures were projected for the different scenarios selected. Literature recommending the values that should be used to binarize suitability or probability maps is vast (Jiménez-Valverde and Lobo, 2007; Liu et al., 2005, 2013). Despite those recommendations, a different approach was considered, that is, using pejus temperature as an end of the thermal available areas for octopus species following the ideas of Frederick and Pörtner (2000). Presence-absence for both species were produced, emphasizing that if at any time a pixel, either minimum or maximum temperature was outside the pejus tolerance of the octopuses, it was considered as absence.

These maps were superimposed to view the overlapping areas of thermal availability of the octopus species. Finally, the proportion of thermal available distribution (km²) was calculated for current and future scenarios. The number of pixels (presences had a value of 1 and absences of 0) was added and multiplied by the area of the pixel (~9.2 × 9.2 km). This process was done using the programming language R (R

Core Team, 2020) with the help of “raster” (Hijmans, 2020), “mapdata” (Becker et al., 2018) and “prettyMapr” (Dunnington, 2017) libraries. The results obtained were graphed in a stacked barplot with “ggpubr” (Kassambara, 2020). Environmental layers and a code are added as supplementary material for the replication in the creation of raster files.

3. Results

Surprisingly, using the experimentally obtained data of embryos from Brazil, no area was considered thermally habitable for *O. americanus* in the Gulf of México where current temperatures have been higher than the optimum range experimentally obtained in southern Brazil. Therefore, the results have been focused on *O. insularis* and *O. maya*. The projection of binarized maps showed that both species currently shared a wide area of thermal niche. However, optimal areas are very restricted for *O. insularis* and *O. maya*, which are mainly composed of pejus areas. These species thermal niche stretches from the Caribbean to Florida. Nevertheless, *O. insularis* may inhabit more tolerant warmer regions that are found in southern Belize, El Salvador, the state of Campeche in Mexico, and southern Florida.

The scenario RCP 6 for 2050 shows a contraction in the available thermal niche of *O. maya* while *O. insularis* seems to be favored by thermal changes. Due to thermal stress, *O. maya* could take refuge in greater depths although this pattern only becomes stronger in 2100. This pattern is stronger in RCP 8.5 scenario, especially in 2100 when even *O. insularis* finds unsuitable areas in the Caribbean in southern Belize and parts of El Salvador, Campeche in Mexico, and Florida due to temperatures >33 °C (Fig. 6). In fact, under this catastrophic scenario, both species lose favorable thermal areas. Losses or gains in km² of

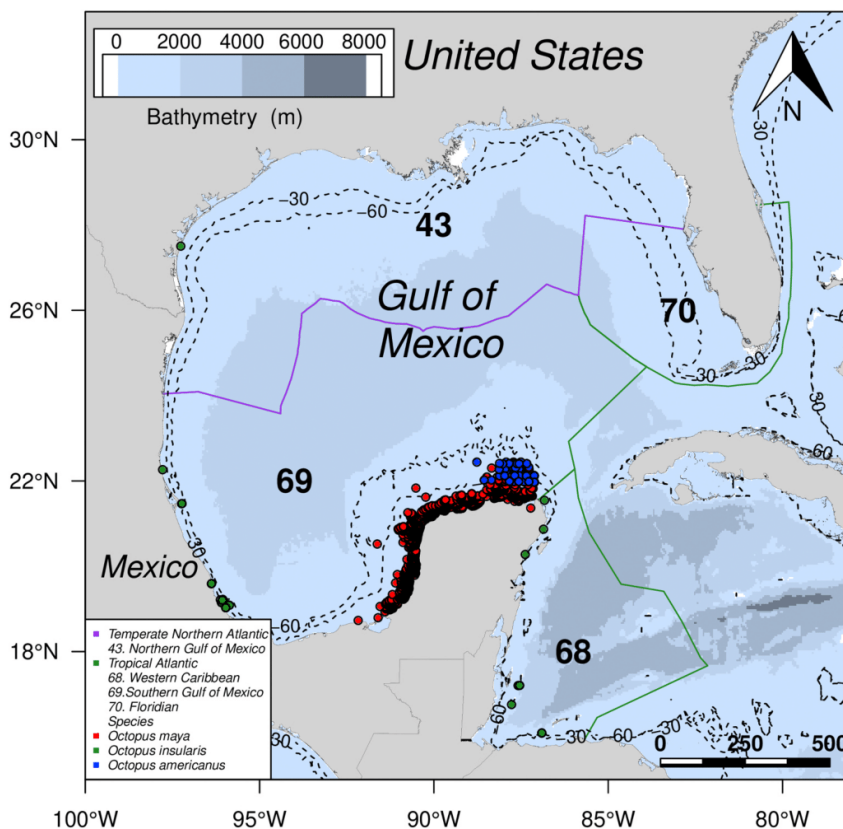


Fig. 3. Study area. The realms and ecoregions of the Gulf of Mexico and part of the Caribbean were proposed by Spalding et al. (2007). Purple line outlines the Temperate Northern Atlantic realm, which is composed by ecoregion 43. The green line outlines the Tropical Atlantic, which is formed by the ecoregions 68, 69, and 70. *Octopus maya* occurrences are shown in red color and come from a bibliographic review by Ángeles-González et al. (2020), while *O. insularis* occurrences are in blue color and were obtained from the Ocean Biodiversity Information System and Global Biodiversity Information Facility. Occurrences of *O. americanus* derived from the work from Avendaño et al., 2020a.

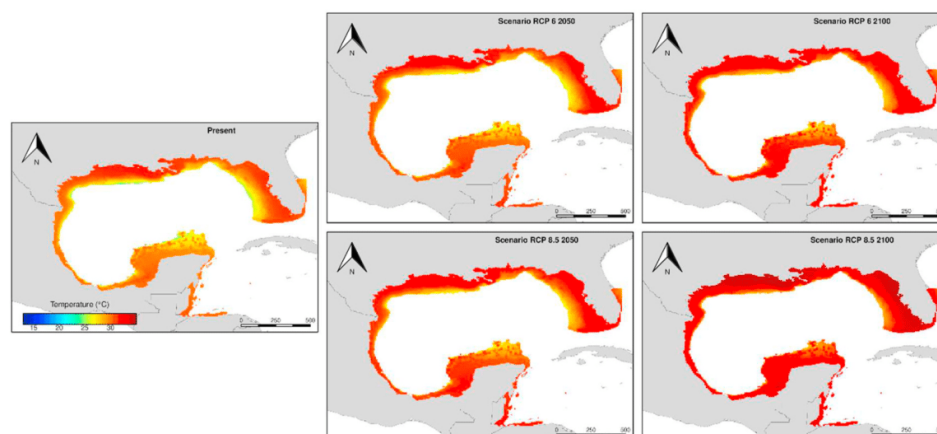


Fig. 4. Values of maximum temperature (°C) by pixel for present and future scenarios representative concentration pathway (RCP) 6 and RCP 8.5 in the ecoregions of the Gulf of Mexico and part of the Caribbean Sea for 2050 and 2100.

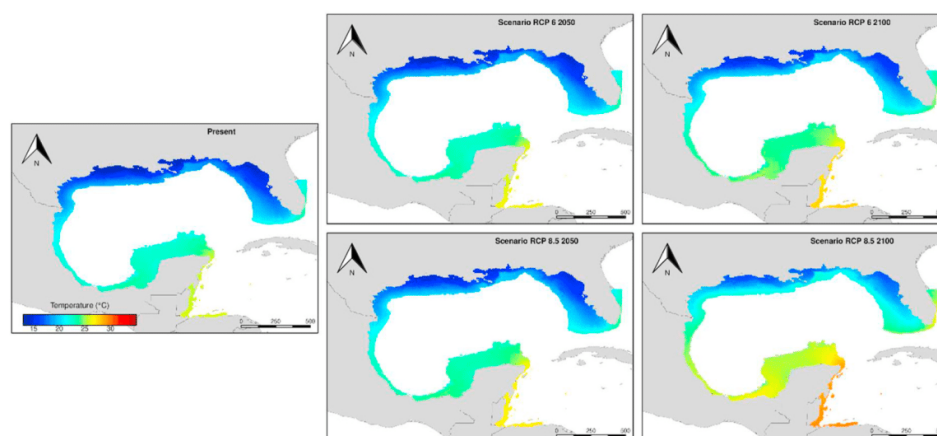


Fig. 5. Values of minimum temperature (°C) by pixel for present and future scenarios Representative Concentration Pathway (RCP) 6 and RCP 8.5 for the years 2050 and 2100 in the ecoregions of the Gulf of Mexico and part of the Caribbean Sea.

thermal zones can be seen more clearly in Fig. 7.

4. Discussion

Evidence has demonstrated the displacement of marine organisms to higher latitudes or deeper waters due to warming (Poloczanska et al., 2016). The results obtained for *O. maya* and *O. insularis* agree with the tendencies described above. According to field and laboratory data, *O. maya* (Noyola et al., 2013; Juárez et al., 2015, 2016; López-Galindo et al., 2019; Pascual et al., 2019) has an affinity for colder temperatures compared to *O. insularis* (Lenz et al., 2015; Lima et al., 2014).

For instance, during 2006–2015 a temperature increase of 2 °C affected *O. maya* landings in the western region of the Yucatan Peninsula negatively, leading to the hypothesis that octopus migration to the eastern region (Ángeles-González et al., 2017) occurred in search of seasonal upwelling (Enriquez et al., 2013). Moreover, specimens collected in warmer waters (28–30 °C) reflected metabolic stress while those captured at lower temperatures were in better physiological conditions, e.g. larger size organisms, high hemocyanin concentrations, and low phenoloxidase system activity. These results indicated that animals living in cold environments were healthier and immunologically

well-prepared than others living in warm waters (Pascual et al., 2019). Similarly, laboratory studies have described that temperatures above 27 °C may inhibit the reproductive performance of adult, embryo development and juvenile growth (Caamal-Monsreal et al., 2016; Juárez et al., 2015, 2016; Sanchez-García et al., 2017), which explained in part why juveniles and adults living in warm waters of the Yucatán Peninsula migrated to waters where upwelling favored temperatures lower than 26 °C (Ángeles-González et al., 2017).

Literature regarding thermal thresholds in *O. insularis* is less numerous since it is a recently described species (Leite et al., 2008). However, this species has been reported at estuarine areas and tidepools where significant temperature variation can occur as a consequence of high evaporation or local river discharge, which is found around a broad span of temperatures (22 °C–32 °C) (Leite et al., 2009, 2016).

The lack of suitable areas for *O. americanus* observed in this study could have been related to differences between the Yucatan Peninsula ecosystem and the Florianópolis populations. Florianópolis populations are part of the Temperate South America realm, while the occurrences reported by Avendaño et al. (2019) are in the Tropical Atlantic realm (Spalding et al., 2007). In this regard, realms are characterized by high levels of endemism driven in part by temperature and isolation

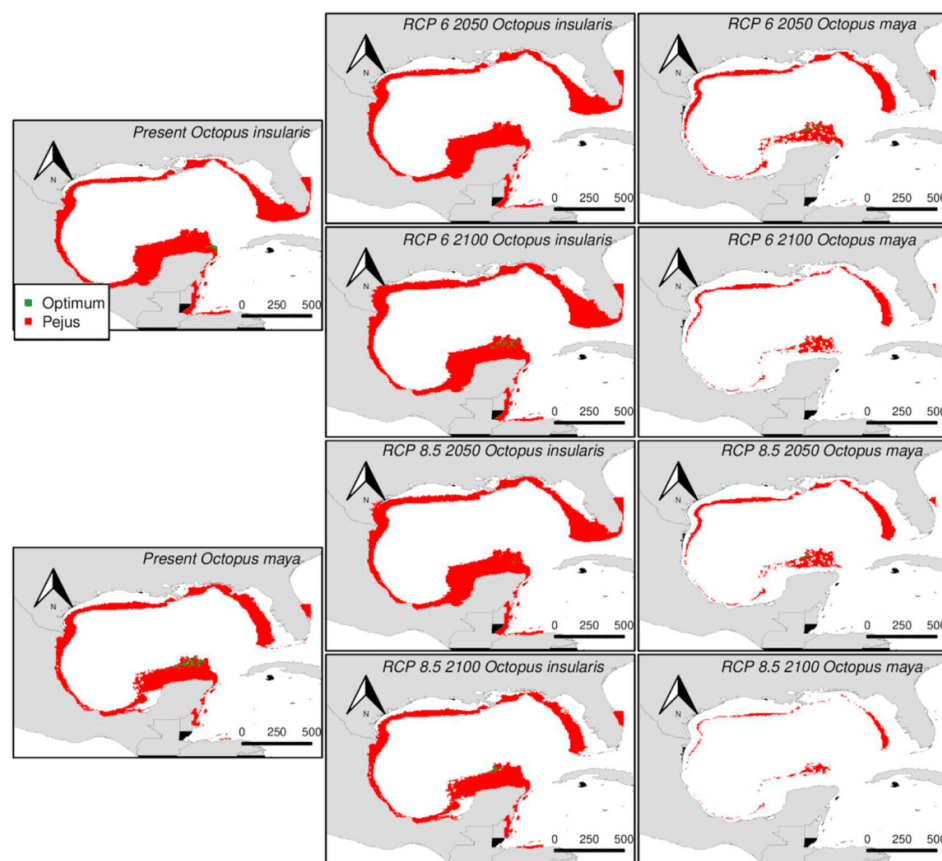


Fig. 6. Binary maps showing occurrence/absence of *Octopus maya* and *O. insularis* for present conditions and two future projections (2050 and 2100) for the Representative Concentration Pathway (RCP) 6 and RCP 8.5 scenarios in the ecoregions of the Gulf of Mexico and part of the Caribbean Sea.

(Spalding et al., 2007). Such isolation under different thermal regimes would generate evolving phenotypes (Angilletta, 2009; Angilletta et al., 2002) with higher fitness in their native environment. This factor could mean that an estimation obtained from a single located population could not be useful to infer the behavior of faraway populations because of local adaptation processes (Ángeles-González et al., 2020).

Warming will cause a contraction in suitable thermal areas of *O. maya* if compared to *O. insularis*. This tendency was observed for both RCP scenarios. Nonetheless, the loss of available suitable thermal areas was more substantial in the RCP 8.5 scenario. Under the RCP 8.5 scenario, by 2100 sea temperature may be too warm even for *O. insularis*. Besides, changes in temperature could bring alterations in the balance of mortality, growth, and reproduction rates (Pörtner and Peck, 2010).

Projections overestimated the known distribution for both species. For example, to our knowledge, no reliable reports of *O. maya* exist in the Mexican State of Veracruz or the United States. In this regard, the mechanistic approaches allow us to measure the fundamental niche (Soberón and Peterson, 2005) and set of environmental variables that permit a species to exist, thus, akin to optimum and pejus temperatures. Even so, most species occupy a realized niche, a subset of the fundamental niche caused by the presence of negatively interacting species (Soberón and Peterson, 2005). Although mechanistic approaches allow us to measure the fundamental niche, overextension of distribution occurred because these methods do not consider the limiting process already mentioned above (Kearney and Porter, 2009).

Furthermore, other environmental variables that could be acting

synergistically with temperature were neglected. In this case, not using salinity for predictions could stand out as an essential variable that potentially restricts *O. maya* to the Yucatan Peninsula. Possibly, *O. maya* distribution could have been confined due to the discharge of the Grijalva-Usumacinta rivers (Located at the North-West Gulf of Mexico coast), which modified salinity, substrate, and generated discharge of organic matter (Rabalais, 2004). Conversely, *O. insularis*, is a highly tolerant organism to salinity, characteristic that could allow this species to pass through the Grijalva-Usumacinta river influence zone to colonize the benthic ecosystem of the Yucatán Peninsula (Leite et al., 2009; Lima et al., 2017).

Regarding the availability of thermally habitable areas in the Caribbean for *O. maya*, this study considered that interspecific competition does not allow them to establish viable populations. In the Caribbean, mesocosm studies showed that *O. briareus* outcompeted the lobster *Panulirus argus* limiting local accessibility of lobsters to shelters and reduced lobster abundance (Butler and Lear, 2009). Nevertheless, it is unknown if similar processes are playing a role in distribution restriction to *O. maya* in the Caribbean reef zone, but it may be a viable hypothesis. Dispersion is also an essential factor, *O. maya* cannot disperse along sea currents due to the lack of paralarvae. Paralarvae is the planktonic stage of cephalopods that lack true metamorphosis (Young and Harman, 1988). This lack of planktonic stage does not allow *O. maya* to overcome environmental barriers, and suitable areas cannot be explored. In contrast, *O. tetricus* has recorded a range extension in Southern Australia (Edgar and Stuart-Smith, 2014) associated with the

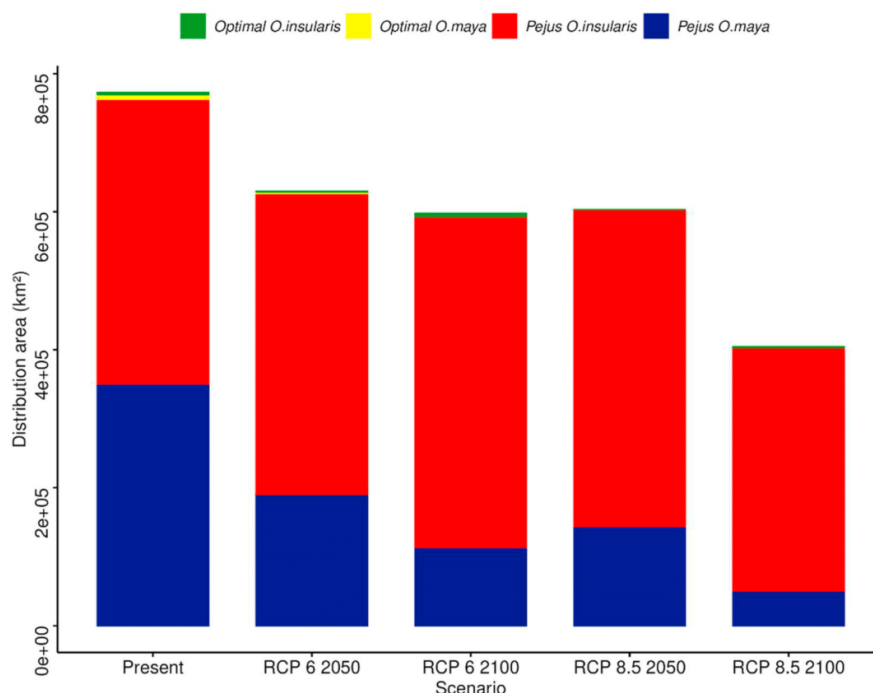


Fig. 7. Distribution of optimal and pejus thermal areas for *Octopus maya* and *O. insularis* for present conditions and two future projections (2050 and 2100) for the Representative Concentration Pathway (RCP) 6 and RCP 8.5 scenarios.

dispersal capacity of their paralarvae and strengthening of the East Australian Current (Ramos et al., 2018, 2014). In this sense, meroplanktonic cephalopods (unlike *O. maya*) could disperse faster (Villanueva et al., 2016) under warming scenarios, which implies that populations from lower latitudes of the Caribbean could migrate poleward if connectivity enables them to establish viable populations (Ramos et al., 2018).

Octopus insularis is a recently described species; for that reason, this study could not validate whether the projected distribution was overestimated. Until now, no peer-reviewed study has reported occurrences of *O. insularis* for the Gulf of Mexico coast of the United States. Further studies should confirm if this species is colonizing those zones, might have been misidentified, or simply, not present yet. Nevertheless, the coral reefs of the Caribbean area seem to be an ideal place since they prefer rock-bottom habitats (Leite et al., 2016). To our knowledge, occurrences of *O. insularis* have not been observed in the Yucatan coast; perhaps, this species is actively avoiding the cold waters caused by seasonal upwelling (Enriquez et al., 2013) or outcompeted although their physiology could allow them to inhabit this region.

It is essential to highlight the low availability of optimal areas for both species, even in the present, which does not mean that species never find areas that maximize their AS. However, it could be an indicator that species are continually migrating looking for thermally favorable regions (Pierce et al., 2008). In fact, recent results demonstrated that a fraction of the *O. maya* population occurred from 30 to 60 m deep where temperatures, independently of upwelling, are usually around 22–24 °C all the year (Avendaño et al., 2019). If that range of temperatures favors *O. maya* reproduction (Ángeles-González et al., 2017) this fraction of population could be contributing to their recruitment explaining the continuous migration of this species in the Yucatan Peninsula.

The predicted spread of *O. insularis* in the Gulf of Mexico could jeopardize even more *O. maya* if the life cycle of both species is

considered. For instance, these species share preferred habitats with similar diets; additionally, *O. insularis* is a highly fertile species producing ~85 000 eggs (Lenz et al., 2015) while *O. maya* produces only 1000–2000 eggs (Tercero et al., 2015). Probably, the main problem regarding the vulnerability of *O. maya* is its lack of ability to move to newly suitable areas, thus being more vulnerable to stochastic disturbances (Sunday et al., 2015). Therefore, due to thermal stress, overlapping diets, and refuges, their lower fertility and inability to disperse from warming waters, *O. insularis* could out compete *O. maya*.

Finally, it is important to point out the effects that future scenarios would bring to fishers who depend on these resources. In the Yucatan Peninsula, *O. maya* is currently the most important fishing resource due to its productivity, economic value, and international demand (Cabrera et al., 2012), contributing >60% of the fishing production in the region (Velázquez-Abunader et al., 2013). Human populations that traditionally depended on this resource could suffer substantial economic losses. However, if warming scenarios are unavoidable, the fishing effort could be redirected to *O. insularis*. Indeed, this species is heavily fished in Brazil (Leite et al., 2009; Lima et al., 2017) with several hundred tons of catches each year (Braga et al., 2007).

4.1. Data caveats

Although our results are useful to describe possible future patterns on octopus distribution, considerations must be taken into account. Projections show the movement of species to high depths; nevertheless, it is still unknown if shelters or prey availability could sustain migrating populations. Moreover, climate change will affect several attributes of an ecosystem, such as food webs (Pörtner and Peck, 2010), phenology (Poloczanska et al., 2016, 2013) or even habitats (Martínez-Arroyo et al., 2011). The measurement of those attributes was out of the scope of this study.

The most critical shortage of this study was related to the use of

octopus embryo data only although it was justified considering that reproduction is a key phase of the species life cycle and adults will spawn and care for the embryos during embryo development. In consequence, the thermal environment where reproduction and embryo development occur was considered also as the key factor to evaluate changes in species distribution. These procedures were based on the idea of indicating the widths of thermal preference shifts within life stages (Pörtner and Farrell, 2008) with lower tolerances than expected in earlier stages and spawning adults (Pörtner, 2010; Pörtner and Farrell, 2008). Despite taking this into consideration, it is interesting to notice that *O. insularis* was favored under specific future scenarios. Moreover, it is necessary to redirect effort in characterizing the thermal tolerance of *O. americanus* adapted locally to the Gulf of Mexico. Only then could predictions be made about the impact of climate change on this octopus species.

Remarkably, the coasts of Campeche, Mexico, an area characterized by *O. maya* fishing was not predicted as favorable. Nevertheless, a pulse of recruitment exists in this coast (Gamboa-Álvarez et al., 2015); thus, fisheries exploited might be juveniles who have a higher thermal tolerance than adults (Noyola et al., 2013) and embryos (Caamal-Monsreal et al., 2016). Adults, and potentially embryos could be more common when the water temperature is lower (Ángeles-González et al., 2017). With the problems mentioned above, variation in thermal tolerance should be considered throughout ontogeny when the objective is to describe the effect of the climate change scenarios (Klockmann et al., 2017).

5. Conclusions

Higher thermal tolerance of *O. insularis* could increase their fishing yield, especially in the RCP 6 scenario, replacing the heavily exploited *O. maya* in the coasts of the Yucatan Peninsula. If a population could establish in the northern Gulf of Mexico, it would also be exploited, but uncertainty still exists. Nevertheless, under the most catastrophic scenario (RCP 8.5 during the year 2100), both resources will experience a reduction in their distribution. The information obtained and derived from this study should be considered by fishery managers for better monitoring of marine resources.

Author statement

Luis Enrique Ángeles-González. Research ideas and aim of the study. Preparation, creation of the work, specifically writing the initial draft.

Françoise D. Lima. Research ideas and aim of the study.

Claudia Caamal-Monsreal. She performed physiological experiments. Provision of study materials, reagents, materials, laboratory and animals.

Fernando Díaz. He performed physiological experiments. Provision of study materials, reagents, materials, laboratory and animals.

Carlos Rosas. Preparation and presentation of the published work.

Management and coordination responsibility for the research activity planning and execution. Acquisition of the financial support for the project leading to this publication.

Disclosure of potential conflicts of interest

No potential conflicts of interest were disclosed.

Acknowledgments

This study is the result of a Graduate Studies doctoral degree thesis at Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México (UNAM); the authors are grateful to UNAM and to the Consejo Nacional de Ciencia y Tecnología (CONACYT) for the scholarship funding the development of this research. This study was partially financed by the Universidad Nacional Autónoma de México (UNAM) through its Programa de Apoyo a Proyectos de Investigación e

Innovación Tecnológica [CR IN 204019] and Consejo Nacional de Ciencia y Tecnología (CONACYT) infrastructure 294028, 61503 grant to CR. Thanks are given to CONACYT scholarship no. 264554 awarded to FD for a national sabbatical stay; to Diana Fischer for editorial services in English.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jtherbio.2020.102753>.

References

- Ángeles-González, L.E., Calva, R., Santos-Valencia, J., Avila-Poveda, O.H., Olivares, A., Diaz, F., Rosas, C., 2017. Temperature modulates spatio-temporal variability of the functional reproductive maturation of *Octopus maya* (Cephalopoda) on the shelf of the Yucatan Peninsula, Mexico. *J. Molluscan Stud.* 83, 280–288. <https://doi.org/10.1093/mollus/eyx013>.
- Ángeles-González, L.E., Martínez-Meyer, E., Yañez-Arenas, C., Velázquez-Abunader, I., García-Rueda, A., Díaz, F., Tremblay, N., Flores-Rivero, M.A., Gebauer, P., Rosas, C., 2020. Using realized thermal niche to validate thermal preferences from laboratory studies. How do they stand? *Ecol. Indic.* 118, 106741. <https://doi.org/10.1016/j.ecolind.2020.106741>.
- Angilletta, M.J., 2009. *Thermal Adaptation A Theoretical and Empirical Synthesis*. Oxford University Press, Oxford.
- Angilletta, M.J., Niewiarowski, P., Navas, C.A., 2002. The evolution of thermal physiology in ectotherms. *J. Therm. Biol.* 27, 249–268.
- Arkipkin, A.I., Hendrickson, L.C., Payá, I., Pierce, G.J., Roa-Ureta, R.H., Robin, J.-P., Winter, A., 2020. Stock assessment and management of cephalopods: advances and challenges for short-lived fishery resources. *ICES J. Mar. Sci.* <https://doi.org/10.1093/icesjms/fsaa038>.
- Assis, J., Tyberghin, L., Bosch, S., Verbruggen, H., Serrão, E.A., De Clerck, O., 2018. Bio-ORACLE v2.0: extending marine data layers for bioclimatic modelling. *Global Ecol. Biogeogr.* 27, 277–284. <https://doi.org/10.1111/geb.12693>.
- Avendaño, O., Hernández-Flores, A., Velázquez-Abunader, I., Fernández-Jardón, C., Cuevas-Jimenez, A., Guerra, A., 2020a. Potential biomass and distribution of octopus in the eastern part of the Campeche bank (Yucatán, Mexico). *Sci. Mar.* 84, 133–142. <https://doi.org/10.3989/scimar.05007.01A>.
- Avendaño, O., Roura, Á., Cedillo-Robles, C.E., González, Á.F., Rodríguez-Canul, R., Velázquez-Abunader, I., Guerra, A., 2020b. *Octopus americanus*: a cryptic species of the *O. vulgaris* species complex redescribed from the Caribbean. *Aquat. Ecol.* 6 <https://doi.org/10.1007/s10452-020-09778-6>.
- Avendaño, O., Velázquez-Abunader, I., Fernández-Jardón, C., Ángeles-González, L.E., Hernández-Flores, A., Guerra, Á., 2019. Biomass and distribution of the red octopus (*Octopus maya*) in the north-east of the Campeche Bank. *J. Mar. Biol. Assoc. U. K.* 1–7 <https://doi.org/10.1017/S0025315419000419>.
- Batista, A.T., Leite, T.S., 2016. *Octopus insularis* (Cephalopoda: Octopodidae) on the tropical coast of Brazil: where it lives and what it eats. *Braz. J. Oceanogr.* 64, 353–364. <https://doi.org/10.1590/S1679-87592016123406404>.
- Becker, R.A., Wilks, A.R., Brownrigg, R., 2018. *Mapdata: Extra Map Databases*.
- Bijma, J., Pörtner, H.O., Yesson, C., Rogers, A.D., 2013. Climate change and the oceans - what does the future hold? *Mar. Pollut. Bull.* 74, 495–505. <https://doi.org/10.1016/j.marpolbul.2013.07.022>.
- Boyle, P., 2002. Cephalopod biomass and production: an introduction to the symposium. *Bull. Mar. Sci.* 71, 13–16.
- Braga, M.S., Marinho, R., Batista, B., Rocha, E., 2007. Histórico e descrição da pesca do polvo, *Octopus cf. vulgaris*, com potes, no estado do Ceará. *Arq. Ciências do Mar* 40, 5–13. <https://doi.org/10.32360/acmar.v40i2.6105>.
- Butler, M.J. IV, Lear, J.A., 2009. Habitat-based intraguild predation by Caribbean reef octopus *Octopus briareus* on juvenile Caribbean spiny lobster *Panulirus argus*. *Mar. Ecol. Prog. Ser.* 386, 115–122. <https://doi.org/10.3354/meps08071>.
- Caamal-Monsreal, C., Uriarte, I., Farias, A., Díaz, F., Sánchez, A., Re, D., Rosas, C., 2016. Effects of temperature on embryo development and metabolism of *O. maya*. *Aquaculture* 451, 156–162. <https://doi.org/10.1016/j.aquaculture.2015.09.011>.
- Cabrera, M.A., Ramos-Miranda, J., Salas, S., Sosa-López, A., 2012. Análisis de la Estructura Poblacional del Pulpo Rojo (*Octopus maya*) en la Península de Yucatán, México. *Proceedings of the Gulf and Caribbean Fisheries Institute*, pp. 480–485.
- Caddy, J.F., Rodhouse, P.G., 1998. Cephalopod and groundfish landings: evidence for ecological change in global fisheries? *Rev. Fish Biol. Fish.* 8, 431–444. <https://doi.org/10.1023/A:1008807129366>.
- DOF, 2014. ACUERDO por el que se da a conocer el Plan de Manejo Pesquero de pulpo (*O. maya* y *O. vulgaris*) del Golfo de México y Mar Caribe. *Diario Oficial de la Federación*.
- Doubleday, Z.A., Prowse, T.A.A., Arkipkin, A., Pierce, G.J., Semmens, J., Steer, M., Leporati, S.C., Lourenço, S., Quetglas, A., Sauer, W., Gillanders, B.M., 2016. Global proliferation of cephalopods. *Curr. Biol.* 26, R406–R407. <https://doi.org/10.1016/j.cub.2016.04.002>.
- Dunnington, D., 2017. *Prettymapr: Scale Bar, North Arrow, and Pretty Margins in R*.
- Edgar, G.J., Stuart-Smith, R.D., 2014. Systematic global assessment of reef fish communities by the Reef Life Survey program. *Sci. Data* 1, 140007. <https://doi.org/10.1038/sdata.2014.7>.

- Enriquez, C., Mariño-Tapia, I., Jeronimo, G., Capurro-Filigrasso, L., 2013. Thermohaline processes in a tropical coastal zone. *Continental Shelf Res.* 69, 101–109. <https://doi.org/10.1016/j.csr.2013.08.018>.
- Flores-Valle, A., Pliego-Cárdenas, R., Jiménez-Badillo, L., Arredondo-Figueroa, J.L., Barriga-Sosa, I.D.L.A., 2018. First Record of *Octopus insularis* Leite and Haimovici, 2008 in the Octopus Fishery of a Marine Protected Area in the Gulf of Mexico. *J. Shellfish Res.* 37, 221–227. <https://doi.org/10.2983/035.037.0120>.
- Frederich, M., Pörtner, H.O., 2000. Oxygen limitation of thermal tolerance defined by cardiac and ventilatory performance in spider crab, *Maja squinado*. *Am. J. Physiol. Regul. Integr. Comp. Physiol.* 279, 1531–1538. <https://doi.org/10.1152/ajpregu.2000.279.5.r1531>.
- Fry, F.E., Hart, J., 1948. The relation of temperature to oxygen consumption in the goldfish. *Biol. Bull.* 94, 66–77. <https://doi.org/10.2307/1538211>.
- Gamboja-Álvarez, M.Á., López-Rocha, J.A., Poot-López, G.R., 2015. Spatial analysis of the abundance and catchability of the red Octopus *Octopus maya* (Voss and Solís-Ramírez, 1966) on the continental shelf of the Yucatan Peninsula, Mexico. *J. Shellfish Res.* 34, 481–492. <https://doi.org/10.2983/035.034.0232>.
- Glenn, E., Comarazamy, D., González, J.E., Smith, T., 2015. Detection of recent regional sea surface temperature warming in the Caribbean and surrounding region. *Geophys. Res. Lett.* 42, 6785–6792. <https://doi.org/10.1002/2015GL065002>.
- González-Gómez, R., De Los Angeles Barriga-Sosa, I., Pliego-Cárdenas, R., Jiménez-Badillo, L., Markaida, U., Meiners-Mandujano, C., Morillo-Velarde, P.S., 2018. An integrative taxonomic approach reveals *Octopus insularis* as the dominant species in the Veracruz Reef System (southwestern Gulf of Mexico). *PeerJ* 1–30. <https://doi.org/10.7717/peerj.6015>.
- Hijmans, R.J., 2020. Raster: geographic data analysis and modeling. R Package Raster Version 3, pp. 3–13.
- Hoegh-Guldberg, O., Bruno, J.F., 2010. The Impact of Climate Change on the World's Marine Ecosystems. *Science* 328, 1523–1528. <https://doi.org/10.1126/science.1189930>.
- IPCC, 2014. Climate Change 2014: Synthesis Report of the IPCC Fifth Assessment Report (AR5).
- Jiménez-Valverde, A., Lobo, J.M., 2007. Threshold criteria for conversion of probability of species presence to either-or presence-absence. *Acta Oecol.* 31, 361–369. <https://doi.org/10.1016/j.actao.2007.02.001>.
- Juárez, O.E., Galindo-Sánchez, C.E., Díaz, F., Re, D., Sánchez-García, A.M., Caamal-Monsreal, C., Rosas, C., 2015. Is temperature conditioning *Octopus maya* fitness? *J. Exp. Mar. Biol. Ecol.* 467, 71–76. <https://doi.org/10.1016/j.jembe.2015.02.020>.
- Juárez, O.E., Hau, V., Caamal-Monsreal, C., Galindo-Sánchez, C.E., Díaz, F., Re, D., Rosas, C., 2016. Effect of maternal temperature stress before spawning over the energetic balance of *Octopus maya* juveniles exposed to a gradual temperature change. *J. Exp. Mar. Biol. Ecol.* 474, 39–45. <https://doi.org/10.1016/j.jembe.2015.10.002>.
- Judkins, H.L., Vecchione, M., Roper, C.F., 2009. Cephalopoda (Mollusca) of the Gulf of Mexico. In: Felder, D.L., Camp, D.K. (Eds.), *Gulf of Mexico Origin, Waters, and Biota: Biodiversity*. Texas A&M University Press, pp. 701–709.
- Judkins, H.L., Vecchione, M., Roper, C.F.E., Torres, J., 2010. Cephalopod species richness in the wider Caribbean region. *ICES J. Mar. Sci.* 67, 1392–1400. <https://doi.org/10.1093/icesjms/fsq092>.
- Kassambara, A., 2020. Ggpubr: "ggplot 2". Based Publication Ready Plots.
- Kearney, M., Porter, W., 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecol. Lett.* 12, 334–350. <https://doi.org/10.1111/j.1461-0248.2008.01277.x>.
- Klockmann, M., Günter, F., Fischer, K., 2017. Heat resistance throughout ontogeny: body size constrains thermal tolerance. *Global Change Biol.* 23, 686–696. <https://doi.org/10.1111/gcb.13407>.
- Leite, T.S., Batista, A.T., Lima, F.D., Barbosa, J.C., Mather, J., 2016. Geographic variability of *Octopus insularis* diet: from oceanic island to continental populations. *Aquat. Biol.* 25, 17–27. <https://doi.org/10.3354/ab00655>.
- Leite, T.S., Haimovici, M., Mather, J., Oliveira, J.E.L., 2009. Habitat, distribution, and abundance of the commercial octopus (*Octopus insularis*) in a tropical oceanic island, Brazil: information for management of an artisanal fishery inside a marine protected area. *Fish. Res.* 98, 85–91. <https://doi.org/10.1016/j.fishres.2009.04.001>.
- Leite, T.S., Haimovici, M., Molina, W., Warnke, K., 2008. Morphological and genetic description of *Octopus insularis*, a new cryptic species in the *Octopus vulgaris* complex (Cephalopoda: Octopodidae) from the tropical southwestern Atlantic. *J. Molluscan Stud.* 74, 63–74. <https://doi.org/10.1093/mollus/eym050>.
- Lenz, T.M., Elias, N.H., Leite, T.S., Vidal, E.A.G., 2015. First description of the eggs and paralarvae of the tropical Octopus, *Octopus insularis*, under culture conditions. *Am. Malacol. Bull.* 33, 101–109. <https://doi.org/10.4003/006.033.0115>.
- Lima, F.D., Berbel-Filho, W.M., Leite, T.S., Rosas, C., Lima, S.M.Q., 2017. Occurrence of *Octopus insularis* leite and Haimovici, 2008 in the tropical Northwestern atlantic and implications of species misidentification to octopus fisheries management. *Mar. Biodivers.* <https://doi.org/10.1007/s12526-017-0638-y>.
- Lima, F.D., Leite, T.S., Haimovici, M., Lins, J.E., 2014. Gonadal development and reproductive strategies of the tropical octopus (*Octopus insularis*) in northeast Brazil. *Hydrobiologia* 725, 7–21. <https://doi.org/10.1007/s10750-013-1718-z>.
- Liu, C., Berry, P.M., Dawson, T.P., Pearson, R.G., 2005. Selecting thresholds of occurrence in the prediction of species distributions. *Ecography* 28, 385–393. <https://doi.org/10.1111/j.0906-7590.2005.03957.x>.
- Liu, C., White, M., Newell, G., 2013. Selecting thresholds for the prediction of species occurrence with presence-only data. *J. Biogeogr.* 40, 778–789. <https://doi.org/10.1111/jbi.12058>.
- López-Galindo, L., Galindo-Sánchez, C., Olivares, A., Avila-Poveda, O.H., Díaz, F., Juárez, O.E., Lafarga, F., Pantoja-Pérez, J., Caamal-Monsreal, C., Rosas, C., 2019. Reproductive performance of *Octopus maya* males conditioned by thermal stress. *Ecol. Indic.* 96, 437–447. <https://doi.org/10.1016/j.ecolind.2018.09.036>.
- Martínez-Arroyo, A., Manzanilla-Naim, S., Zavala-Hidalgo, J., 2011. Vulnerability to climate change of marine and coastal fisheries in México. *Atmósfera* 24, 103–123.
- Noyola, J., Mascaró, M., Caamal-Monsreal, C., Noreña-Barroso, E., Díaz, F., Re, D., Sánchez, A., Rosas, C., 2013. Effect of temperature on energetic balance and fatty acid composition of early juveniles of *Octopus maya*. *J. Exp. Mar. Biol. Ecol.* 445, 156–165. <https://doi.org/10.1016/j.jembe.2013.04.008>.
- Pascual, C., Mascaró, M., Rodríguez-Canul, R., Gallardo, P., Sánchez, A.A., Rosas, C., Cruz-López, H., 2019. Sea surface temperature modulates physiological and immunological condition of *Octopus maya*. *Front. Physiol.* 10, 1–11. <https://doi.org/10.3389/fphys.2019.00739>.
- Perry, A.L., Low, P.J., Ellis, J.R., Reynolds, J.D., 2005. Ecology: climate change and distribution shifts in marine fishes. *Science* 308, 1912–1915. <https://doi.org/10.1126/science.1111322>.
- Pierce, G.J., Valavanis, V.D., Guerra, A., Jereb, P., Orsi-Rellini, L., Bellido, J.M., Katara, I., Piatkowski, U., Pereira, J., Balguerías, E., Sobrino, I., Lefkaditou, E., Wang, J., Santurtun, M., Boyle, P.R., Hastie, L.C., MacLeod, C.D., Smith, J.M., Viana, M., González, A.F., Zuur, A.F., 2008. A review of cephalopod-environment interactions in European Seas. *Hydrobiologia* 612, 49–70. <https://doi.org/10.1007/s10750-008-9489-7>.
- Poloczanska, E.S., Brown, C.J., Sydeman, W.J., Kiessling, W., Schoeman, D.S., Moore, P.J., Brander, K., Bruno, J.F., Buckley, L.B., Burrows, M.T., Duarte, C.M., Halpern, B.S., Holding, J., Kappel, C.V., O'Connor, M.I., Pandolfi, J.M., Parmesan, C., Schwing, F., Thompson, S.A., Richardson, A.J., 2013. Global imprint of climate change on marine life. *Nat. Clim. Change* 3, 919–925. <https://doi.org/10.1038/nclimate1958>.
- Poloczanska, E.S., Burrows, M.T., Brown, C.J., García Molinos, J., Halpern, B.S., Hoegh-Guldberg, O., Kappel, C.V., Moore, P.J., Richardson, A.J., Schoeman, D.S., Sydeman, W.J., 2016. Responses of marine organisms to climate change across oceans. *Front. Mar. Sci.* 3, 1–21. <https://doi.org/10.3389/fmars.2016.00062>.
- Pörtner, H.-O., 2010. Oxygen- and capacity-limitation of thermal tolerance: a matrix for integrating climate-related stressor effects in marine ecosystems. *J. Exp. Biol.* 213, 881–893. <https://doi.org/10.1242/jeb.037523>.
- Pörtner, H.-O., Farrell, A.P., 2008. Physiology and Climate Change 322, 690–692. <https://doi.org/10.1126/science.1163156>.
- Pörtner, H.-O., Peck, M.A., 2010. Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. *J. Fish. Biol.* 77, 1745–1779. <https://doi.org/10.1111/j.1095-8649.2010.02783.x>.
- R Core Team, 2020. R: A Language and Environment for Statistical Computing.
- Rabalais, N.N., 2004. Hypoxia en el Golfo de México. *Diagnóstico Ambiental Del Golfo de México*. México, DF, pp. 773–788.
- Ramos, J.E., Pecl, G.T., Moltschanivskiy, N.A., Semmens, J.M., Souza, C.A., Strugnell, J.M., 2018. Population genetic signatures of a climate change driven marine range extension. *Sci. Rep.* 8, 1–12. <https://doi.org/10.1038/s41598-018-27351-y>.
- Ramos, J.E., Pecl, G.T., Moltschanivskiy, N.A., Strugnell, J.M., León, R.L., Semmens, J.M., 2014. Body size, growth and life span: implications for the polewards range shift of *Octopus tetricus* in South-Eastern Australia. *PLoS One* 9, 1–9. <https://doi.org/10.1371/journal.pone.0103480>.
- Rosas, C., Gallardo, P., Mascaró, M., Caamal-Monsreal, C., Pascual, C., 2014. *Octopus maya*. *Cephalop. Cult.* 2, 383–396. https://doi.org/10.1007/978-94-017-8648-5_20.
- Sánchez-García, A., Rodríguez-Fuentes, G., Díaz, F., Galindo-Sánchez, C.E., Ortega, K., Mascaró, M., López, E., Caamal-Monsreal, C., Juárez, O., Noreña-Barroso, E., Re, D., Rosas, C., 2017. Thermal sensitivity of *O. maya* embryos as a tool for monitoring the effects of environmental warming in the Southern of Gulf of Mexico. *Ecol. Indic.* 72, 574–585. <https://doi.org/10.1016/j.ecolind.2016.08.043>.
- Slatyer, R.A., Hirst, M., Sexton, J.P., 2013. Niche breadth predicts geographical range size: a general ecological pattern. *Ecol. Lett.* 16, 1104–1114. <https://doi.org/10.1111/ele.12140>.
- Soberón, J., Peterson, T.A., 2005. Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodivers. Inf.* 2, 1–10. <https://doi.org/10.17161/bi.v2i0.4>.
- Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdaña, Z.A., Finlayson, M., Halpern, B.S., Jorge, M.A., Lombana, A., Lourie, S.A., Martin, K.D., McManus, E., Molnar, J., Recchia, C., Robertson, J., 2007. Marine Ecoregions of the World: a bioregionalization of coastal and shelf areas. *Bioscience* 57, 573. <https://doi.org/10.1641/B570707>.
- Sunday, J.M., Pecl, G.T., Frusher, S., Hobday, A.J., Hill, N., Holbrook, N.J., Edgar, G.J., Stuart-Smith, R., Barrett, N., Wernberg, T., Watson, R.A., Smale, D.A., Fulton, E.A., Slawinski, D., Feng, M., Radford, B.T., Thompson, P.A., Bates, A.E., 2015. Species traits and climate velocity explain geographic range shifts in an ocean-warming hotspot. *Ecol. Lett.* 18, 944–953. <https://doi.org/10.1111/ele.12474>.
- Tercero, J.F., Rosas, C., Mascaró, M., Poot, G., Domingues, P., Noreña, E., Caamal-Monsreal, C., Pascual, C., Estefanel, J., Gallardo, P., 2015. Effects of parental diets supplemented with different lipid sources on *Octopus maya* embryo and hatching quality. *Aquaculture* 448, 234–242. <https://doi.org/10.1016/j.aquaculture.2015.05.023>.
- Tremblay, N., Mascaró, M., Díaz, F., Caamal-Monsreal, C., Pascual, C., Rosas, C., 2017. Sensibilidad a las oscilaciones térmicas de las especies de importancia ecológica y pesquera de la Península de Yucatán ante escenarios de calentamiento global. *Caracterización Multidisciplinaria de La Zona Costera de Sisal, Yucatán*. Yucatán, México, p. 200.
- van Vuuren, D.P., Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K., Hurtt, G.C., Kram, T., Krey, V., Lamarque, J.F., Masui, T., Meinshausen, M., Nakicenovic, N., Smith, S.J., Rose, S.K., 2011. The representative concentration

- pathways: an overview. *Climatic Change* 109, 5–31. <https://doi.org/10.1007/s10584-011-0148-z>.
- Velázquez—Abunader, I., Salas, S., Cabrera, M.A., 2013. Differential catchability by zone, Fleet, and size: the case of the red Octopus (*Octopus maya*) and common Octopus (*Octopus vulgaris*) fishery in Yucatan, Mexico. *J. Shellfish Res.* 32, 845–854. <https://doi.org/10.2983/035.032.0328>.
- Villanueva, R., Vidal, E.A.G., Fernández-Álvarez, F.Á., Nabhitabhata, J., 2016. Early mode of life and hatchling size in cephalopod molluscs: influence on the species distributional ranges. *PLoS One* 11, e0165334.
- Voss, G.L., Solís-Ramírez, M., 1966. *Octopus maya*, a new species from the Bay of Campeche, Mexico. *Bull. Mar. Sci.* 16, 615–625.
- Young, R.E., Harman, R.F., 1988. ‘Larva’, ‘Paralarva’ and ‘Subadult’ in cephalopod terminology. *Malacologia* 29, 201–207.

**Capítulo cinco - Climate change effect
on *Octopus maya* (Voss and Solís-
Ramírez, 1966) distribution in the
Yucatan Peninsula, Gulf of Mexico: A
correlative and mechanistic approach**
Sometido a: *Estuarine, Coastal and Shelf
Science*

Estado: Aceptado



ELSEVIER

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

Climate change effect on *Octopus maya* (Voss and Solís-Ramírez, 1966) suitability and distribution in the Yucatan Peninsula, Gulf of Mexico: A correlative and mechanistic approach

Luis Enrique Ángeles-González^{a,b,c,d}, Enrique Martínez-Meyer^e, Carlos Yañez-Arenas^b, Iván Velázquez-Abunader^f, Jorge A. López-Rocha^g, Josymar Torrejón-Magallanes^h, Carlos Rosas^{c,d,*}

^a Posgrado en Ciencias Del Mar y Limnología, Universidad Nacional Autónoma de México, Av. Ciudad Universitaria 3000, 04510, Coyoacán, Ciudad de México, México

^b Laboratorio de Ecología Geográfica, Unidad de Conservación de La Biodiversidad, Parque Científico y Tecnológico de Yucatán, Unidad Académica Sisal, Facultad de Ciencias, Universidad Nacional Autónoma de México, Carretera Sierra Papacal Km 5, Mérida, Yucatán, México

^c Laboratorio Nacional de Resiliencia Costera, Facultad de Ciencias, Universidad Nacional Autónoma de México, 97356, Puerto de Abrigo, Sisal, Yucatán, México

^d Laboratorio de Ecofisiología Aplicada, Unidad Multidisciplinaria de Docencia e Investigación, Facultad de Ciencias, Universidad Nacional Autónoma de México, 97356, Puerto de Abrigo, Sisal, Yucatán, México

^e Instituto de Biología, Universidad Nacional Autónoma de México, Circuito Zona Deportiva Ciudad Universitaria, 04510, Ciudad de México, México

^f Laboratorio de Pesquerías, Centro de Investigación y de Estudios Avanzados Del IPN (CINVESTAV-IPN) Unidad Mérida, Carretera Antigua a Progreso Km. 6, Cordemex, C.P. 97310, Mérida, Yucatán, México

^g Laboratorio de Análisis Espacial de Zonas Costeras, Unidad Multidisciplinaria de Docencia e Investigación, Facultad de Ciencias, Universidad Nacional Autónoma de México, 97356, Puerto de Abrigo, Sisal, Yucatán, México

^h Instituto Politécnico Nacional, Centro Interdisciplinario de Ciencias Marinas, 23090, La Paz, Baja California Sur, México

ARTICLE INFO

Keywords:

Ecological niche models
Physiology
Climate change
Thermal tolerance
Fisheries

ABSTRACT

Fisheries play critical roles in food supply and income for human communities worldwide. Unfortunately, the fishery distribution have been changing due to anthropogenic climate change (CC). In this sense, this study analyses were directed to predict the suitability and distribution of red octopus (*Octopus maya*), an endemic and commercially important species of the Yucatan Peninsula (YP) in Mexico under different CC scenarios. For this purpose, a correlative (CNM) and mechanistic (MNM) niche models based on temperature and salinity and on metabolic scope, respectively, were projected to different Representative Concentration Pathway (RCP) scenarios (2.6, 4.5, 6, 8.5) for the 2040–2050 and 2090–2100 periods. The CNM results suggest that red octopus suitability and potential distribution (PD) could be slightly reduced for the RCP 2.6 scenario. Whereas, RCP 4.5 shows higher suitabilities at the northern region of the YP, which is characterized by a seasonal upwelling which could act as climate refugia. In contrast, a significant suitability and PD reduction occurs during 2090–2100 for the RCP 6 and 8.5 scenarios. On the other hand, MNM indicates the red octopus could retain most of its PD except for the most catastrophic scenario, finding climate refugia north of the YP and deeper waters. Overall, the CNM is more pessimistic than MNM regarding forecasts. Differences between outputs could be based on the MNM using a single variable as proxy to a multivariate niche and the statistical weight of surface environmental variables in the CNM compared to MNM, which considered only bottom temperature data. In addition, coastal data may be overrepresented, which may bias the CNM. Regardless of the differences in the results, both approaches usually predicted suitability reduction in all RCP scenarios showing that temperatures of ~ 30 °C are detrimental for the red octopus. Assuming that a relationship between abundance and the niche suitability exists, landings in the region will be reduced and less accessible for small-scale fisheries, which is especially important since Mexican regulations assume this species will benefit from CC.

* Corresponding author. Laboratorio Nacional de Resiliencia Costera, Facultad de Ciencias, Universidad Nacional Autónoma de México, 97356, Puerto de Abrigo, Sisal, Yucatán, México.

E-mail address: crv@ciencias.unam.mx (C. Rosas).

<https://doi.org/10.1016/j.ecss.2021.107502>

Received 8 February 2021; Received in revised form 30 June 2021; Accepted 7 July 2021

Available online 12 July 2021

0272-7714/© 2021 Elsevier Ltd. All rights reserved.

1. Introduction

Fisheries play critical roles in food supply security, livelihoods, and income generation for human communities worldwide. During 2017, fisheries generated USD 152 billion in exports, providing an income for ~40 million people and indirectly supporting over 200 million people (FAO, 2018). In Mexico, catches have reported ~2 million t, representing an income of ~1% of gross domestic product (GDP) (<http://www.fao.org/fi/oldsite/FCP/es/MEX/profile.htm>). Given its little contribution to the GDP, fishery importance could be considered secondary to other economic activities. Nevertheless, fishery provides income for at least ~300 000 fishers. Particularly, the Gulf of Mexico (GM) and the Caribbean region contribute to 15% of the fisheries landings in Mexico (CONAPESCA, 2018).

Marine communities are complex networks linked by their biological interactions and environmental factors. However, alterations in environmental variables, such as temperature, salinity, and oxygen have occurred worldwide due to anthropological climate change (CC). In turn, such alteration has provoked shifts in marine communities on account of species physiological intolerance (Doney et al., 2012). Thus, changes in marine community distribution threaten food security, livelihoods, and human community income (FAO, 2018). Indeed, the modeled scenarios highlight latitudinal changes, predicting an increase from 30–70% of potential catches in high-latitude regions and a reduction of up to 40% in the tropics (Cheung et al., 2010).

Correlative niche models (CNMs) are valuable tools to assess such potential changes in distribution. The CNM objective is to characterize the fundamental niche, a multivariate environmental space that defines species physiological limits (Hutchinson, 1957) using georeferenced occurrences and environmental layers linked through algorithms (Martinez-Meyer, 2005). The wide abundance of spatial environmental data and species occurrence makes CNMs more feasible than mechanistic niche models (MNM), which use physiological data. However, these models are biased by the assumption that occurrences are in equilibrium with their environment, which would not always be the case due to dispersal limitations, biotic interactions, or sample biases (Peterson et al., 2011; Soberón and Peterson, 2005). Nevertheless, few studies in marine realms have used CNMs to predict future impacts of climate change and species invasion and have been focused mainly on conservation planning (Robinson et al., 2011). Particularly, models in the GM have focused on spatio-temporal description of fishing resources (e.g. Avendaño et al., 2020, 2019; Gamboa-Álvarez et al., 2015; López-Rocha and Arreguín-Sánchez, 2013) with few studies related to CC (Lima et al., 2020; Martínez-Arroyo et al., 2011; Muhling et al., 2011).

In contrast to CNMs, the use of MNMs has been proposed as a more suitable approach to predict CC impact on species. Indeed, direct physiological measurements may be preferable since they characterize the species fundamental niche (Kearney and Porter, 2004; Kearney et al., 2010; Peterson et al., 2015). Thus, to locally predict changes of marine species in the GM, thermal tolerance has been determined in the Multidisciplinary Research and Education Unit of the Faculty of Sciences at Sisal-UNAM (Universidad Nacional Autónoma de México), Yucatán, México (Noyola et al., 2015; Tremblay et al., 2017).

Particularly, significant focus has been placed on the red octopus, *Octopus maya* (Voss and Solís-Ramírez, 1966) (Caamal-Monsreal et al., 2016; Juárez et al., 2015, 2016, 2015; López-Galindo et al., 2019; Sanchez-García et al., 2017), an endemic species of the Yucatan Peninsula (YP), which represents one of the most important fisheries in Mexico by volume and economic output (Diario Oficial de la Federación, 2018). Product of those studies, Ángeles-González et al. (2020a) used physiological data to predict CC impact on red octopus embryos. Nonetheless, similarly to CNMs, the use of MNM also has drawbacks. For example, the use of locally adapted populations may be incurred and lacks consideration of biotic interactions or dispersal process. Moreover, due to experiment complexity, efforts tend to be directed only to a few

environmental variables (Peterson et al., 2015).

Currently, a global increase in cephalopod catches linked to rising temperatures and predator overfishing has been noted in fishing yields (Doubleday et al., 2016), and specifically for the red octopus since 1990 (Arreguín-Sánchez, 2019); thus the notion exists that red octopus may benefit under the CC (Arreguín-Sánchez, 2019; Diario Oficial de la Federación, 2018). Possibly at the moment, the increase in temperature may be favorable for cephalopods. However, if the optimal environmental conditions are exceeded, the species fitness may decrease. Thus, other authors have proposed that under CC scenarios, the red octopus might migrate to thermally favorable areas (Sanchez-García et al., 2017; Tremblay et al., 2017) north of the YP, an area characterized by seasonal upwelling (Enriquez et al., 2013; Enriquez and Mariño-Tapia, 2014; Monreal-Gómez et al., 2004). Those proposals are based on the consideration that temperatures below 30 °C are favorable for the red octopus fitness (Caamal-Monsreal et al., 2016; Juárez et al., 2015, 2016, 2015; López-Galindo et al., 2019; Pascual et al., 2019).

The CNMs and MNMs are helpful tools to test such hypotheses. However, as shown above, both CNMs and MNMs have strengths and weaknesses. Nevertheless, a comparison between both outputs could provide certainty to predictions if the results agree (Kearney and Porter, 2009; Peterson et al., 2015). Conversely, if differences are found, the next step would be to inquire about the reasons for those differences (Strasburg et al., 2007; Webber et al., 2011). In this sense, this study was meant to complement the predictions made by the physiological studies performed in Sisal-UNAM to help decision-makers establish adaptation plans to CC. Based on the measurement of the fundamental thermal niche of the red octopus, this study hypothesizes that CC will negatively affect the red octopus populations. This situation greatly contrasts with the idea that the red octopus may increase its fitness under warming scenarios (Arreguín-Sánchez, 2019; Diario Oficial de la Federación, 2018).

2. Material and methods

2.1. Study area

The YP western region has a strong seasonality with surface temperatures ranging from 24 to 30 °C; while the northern region has temperatures from 23 to 29 °C in the Nortes (northern winds) and Rainy seasons, respectively (Ángeles-González et al., 2017). Lower temperatures of the YP northern region occur due to the Yucatan Current, which generates seasonal upwelling during spring and summer (Enriquez et al., 2013; Enriquez and Mariño-Tapia, 2014; Monreal-Gómez et al., 2004) lowering the temperature. Regarding salinity, studies indicated that values from 36.25 to 36.75 PSU are found in the northern region of the YP in summer (Enriquez et al., 2013). However, in the western region near the Sabancuy port, a haline front exists due to the discharge by various rivers (Czitrom et al., 1986), reducing salinity to values of ~30 PSU (Phleger and Ayala-Castanares, 1971). This is particularly notable in the Terminos Lagoon (Fig. 1).

2.2. Correlative niche model

Fig. 2 shows the complete workflow of the CNM. Subsequent sections explain the processes in detail.

2.2.1. Occurrence records

Occurrence records of red octopus were obtained from a literature review by Ángeles-González et al. (2020b), which consisted of 62 references that recorded 1621 occurrences along its distribution area from 1966 to 2020. However, on average, most of the occurrences were obtained during the 2012–2013 period (Gamboa-Álvarez et al., 2015). Since sampling bias can lead to an environmental over-representation of higher sampling regions (Boria et al., 2014), only one occurrence by pixel was considered, leaving a total of 94 occurrences. Subsequently,

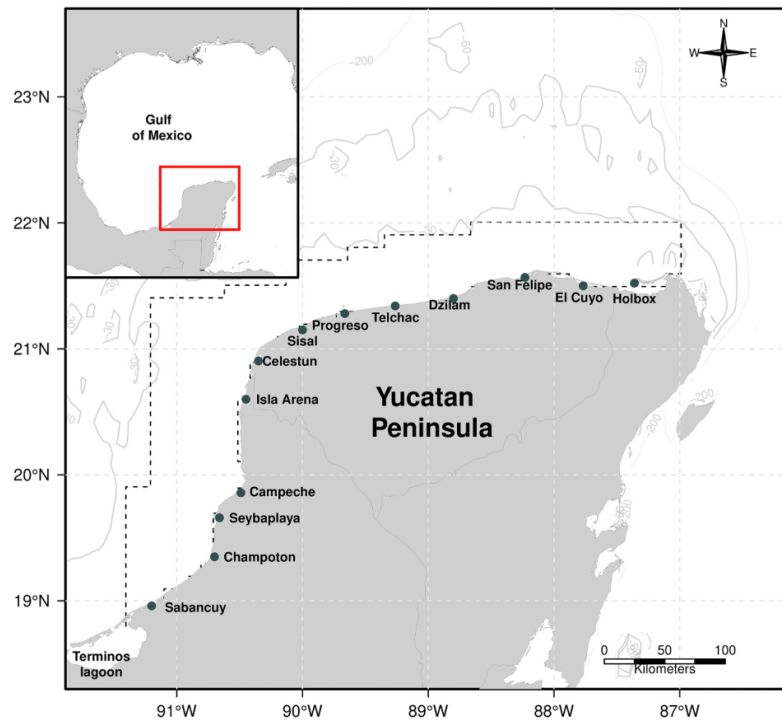


Fig. 1. Study area on the Yucatan Peninsula continental shelf, showing the ports where coastal fleet samplings were performed. The polygon represents the area where the red octopus (*Octopus maya*) is typically fished (Gamboa-Álvarez et al., 2015). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

75% of occurrences were randomly extracted for training, while 25% of the remaining data were used for testing (Supplementary material S1). In addition, a joint dataset (100% of occurrences) was used to evaluate model complexity (see below).

2.2.2. Environmental layers for the correlative niche model

Environmental layers for maximum and minimum temperature ($^{\circ}\text{C}$) and salinity (PSU) were downloaded from Bio-ORACLE (Assis et al., 2017) for benthonic and surface environments for current (2000–2014 period) and Representative Concentration Pathways (RCP) 2.6, 4.5, 6, and 8.5 (2040–2050 and 2090–2100 period) scenarios (Table 1) at a resolution of $\sim 9 \text{ km}^2$. In the RCP 2.6 scenario, carbon dioxide (CO_2) emission will have declined by 2020 and gone to zero by 2100. The RCP 4.5 scenario is an intermediate one, where emissions will have peaked by around 2040, eventually declining. The RCP 6 scenario consists of a scenario in which CO_2 emissions will have peaked by 2080; then, they will gradually decline. Finally, the RCP 8.5 scenario represents an exponential growth of greenhouse gases (IPCC, 2014).

All scenarios were chosen since some researchers consider that more catastrophic scenarios may occur (Schwalm et al., 2020a, 2020b, 2020b), while others do not agree (Hausfather and Peters, 2020) or point out the need for a broader range of global scenarios (Pedersen et al., 2020). In reality, this is a hotly debated topic that has not been settled yet.

Environmental layers were cropped according to an accessibility hypothesis (M) for the red octopus; this M region represents the calibration area delimitation and the ideal area for model calibration and testing (Barve et al., 2011). For such endeavor, this study used the marine ecoregions developed by Spalding et al. (2007) and the package “ENMGadgets” using the function “CropRaster” (Barve and Barve, 2013) of R 4.0.0 software (R Core Team, 2020). Additionally, since no red

octopus occurrence has been found beyond depths of $\sim 50 \text{ m}$ (Avenidaño et al., 2019), calibration was performed at depths of $\sim 50 \text{ m}$ since no reliable information was available about the possibility that red octopuses inhabit greater depths. Later, variables that summarized the environmental information of occurrences were filtered using the variance inflation factor (VIF) with the R package “usdm” using the “vifstep” function (Naimi et al., 2014). The VIF is the ratio of a full model variance, divided by a model variance with one term alone. Values above 10 indicate that a variable might have a collinearity problem (Kutner et al., 2004); if this threshold was surpassed, the environmental layer was deleted.

2.2.3. Calibration and selection of the best performing correlative niche model

CNMs were generated using the Maxent algorithm (Phillips et al., 2006). Maxent uses the maximum entropy to correlate occurrence records with environmental variables to estimate suitability. Candidate models were generated, consisting of different combinations of regularization multipliers (RM - 0.5, 1, 1.5, 2, 2.5, 3, 3.5, 4) and features (Linear - L, Linear-Quadratic - LQ, Linear-Quadratic-Product - LQP) using the R package “kuenm” (Cobos et al., 2019b). Model selection was based on statistical significance, predictive ability, and complexity - in that order of priority.

A total of 24 candidate models were generated using the training dataset. The performance of the models was evaluated with the test dataset considering first the statistical significance ($P < 0.05$) with the partial Receiver Operating Characteristic (pROC), an analysis derived from the classical ROC. Graphically, the x-axis represents the suitable proportion of M, while the y-axis evaluates an acceptable level of omission error (see Peterson et al., 2008 - $E = 5\%$ in this study). Candidate models without statistical significance were eliminated. The

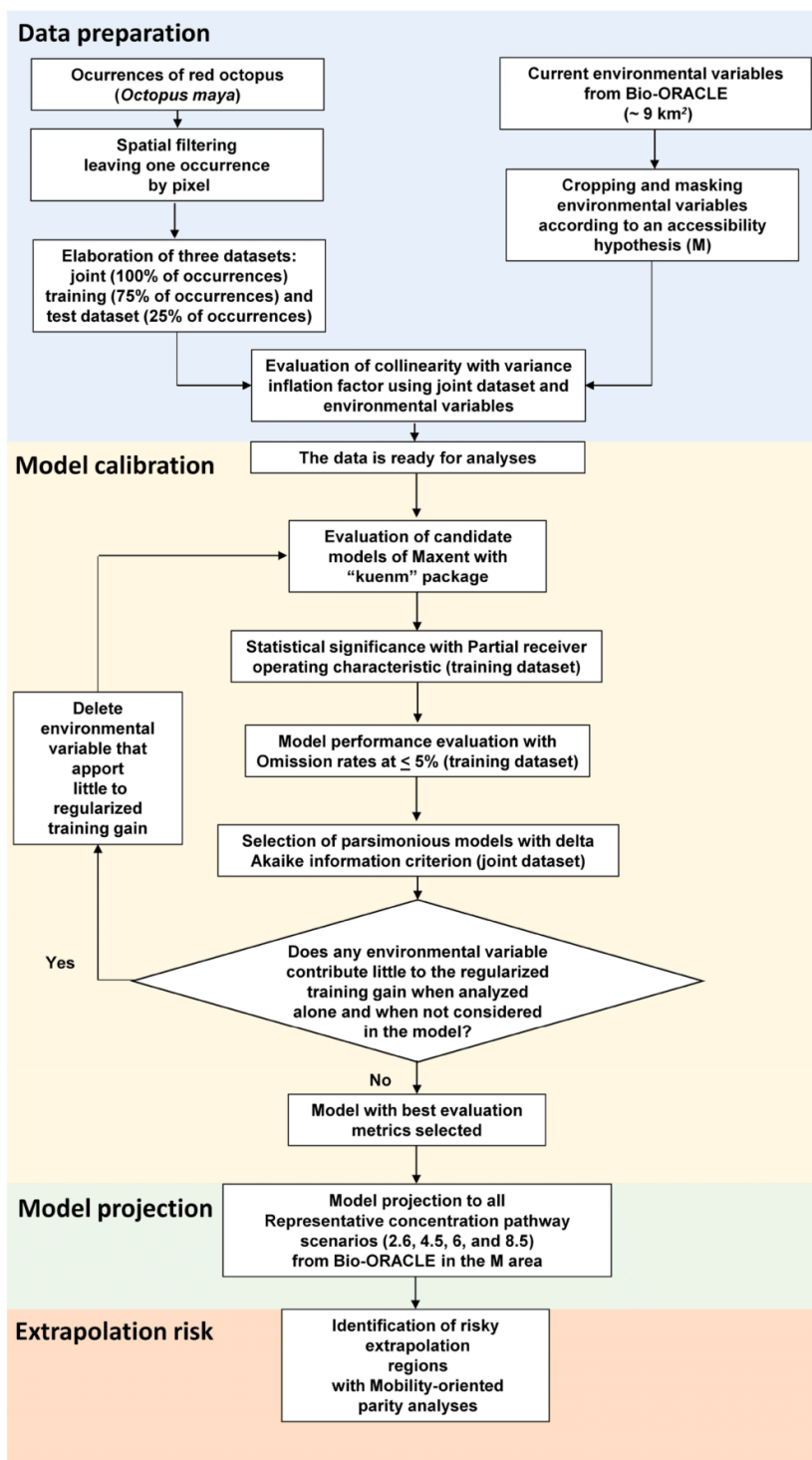


Fig. 2. Flow chart of the full procedure for correlative niche models.

Table 1

Environmental variables were used to model the correlative niche model. Abbreviations were used on the online repository GitHub (<https://github.com/ejosymart/octopusNiche>) and results. The asterisk (*) indicates environmental layers remaining after the calibration process. For more details about the environmental layer see Assis et al., (2017).

Environmental layer	Units	Abbreviation
Maximum surface temperature	°C	Sur_tem_max*
Minimum surface temperature	°C	Sur_tem_min
Maximum surface salinity	PSU	Sur_sal_max*
Minimum surface salinity	PSU	Sur_sal_min*
Maximum benthic temperature at minimum depth	°C	Min_tem_max
Minimum benthic temperature at minimum depth	°C	Min_tem_min
Maximum benthic salinity at minimum depth	PSU	Min_sal_max
Minimum benthic salinity at minimum depth	PSU	Min_sal_min

remaining models were chosen according to an omission rate at 5% (OR_5). Values above that threshold typically indicate model overfitting (see Peterson et al., 2008). Next, with the joint dataset, the model complexity evaluation was done via delta Akaike Information criterion ($\Delta AICc$), a metric that reflects the model goodness-of-fit and complexity (Warren and Seifert, 2011). Models with a value of $\Delta AICc \leq 2$ were the last remaining in the filtering process, where the model with the lowest value was chosen.

Finally, using the jackknife test built-in Maxent, an estimation of the most important variables was done. For example, if an environmental variable had a low regularized training gain (how much better the Maxent distribution fits the presence data than a uniform distribution) when analyzed alone and in conjunction with other variables, it was eliminated, and the calibration process was repeated (Fig. 2).

2.2.4. Correlative niche model projections to current and future scenarios

The selected CNM was projected onto current and future climate RCP 2.6, 4.5, 6, and 8.5 scenarios (2040–2050 and 2090–2100 periods) at depths of ~50 m to obtain suitability maps. Maxent allowed to easily choose three different types of model response: extrapolation, extrapolation with clamping, and truncation. An extrapolation response was used where response curves in non-analogous conditions (environmental conditions differ to the calibration regions) followed trends calculated in the calibration region (Cobos et al., 2019b; Owens et al., 2013).

2.2.5. Extrapolation risk analysis

The model interpretation outside the calibration range can be perilous; for instance, a positive linear relationship between environmental variables and suitability could indefinitely increase in a future scenario regardless of ecological viability. Therefore, the mobility-oriented parity metric analysis was used to detect non-analogous regions. This analysis calculates a multivariate environmental distance between calibration and transference region based on a user-specified proportion. A value of 5% was chosen for this study. This calculation allows quantifying environmental similarity between calibration and transfer (projection) regions and highlights regions in geographic space where extrapolation occurs, that is, non-analogous conditions (Owens et al., 2013).

2.3. Mechanistic niche model

2.3.1. Physiological data

The relationship between temperature (°C) and mean red octopus fitness for juveniles was obtained from Ripoll et al., (unpublished data) and calculated using the method of Paschke et al. (2018). For that purpose, juveniles of red octopus obtained from embryos incubated at 24 °C (Rosas et al., 2014) were acclimated to laboratory conditions at different temperatures in a range from 13 to 33 °C. Briefly, once animals were acclimated for 30 days, low and high metabolic rate were measured following the method of Paschke et al. (2018) where the

temperature was used to induct a standardizable low (LMR) and high metabolic rate (HMR), as proxies of standard and maximum metabolic rate used in athletic fishes (Chabot et al., 2016). Thermal metabolic scope (TMS; Paschke et al., 2018) was calculated as: $HMR - LMR$, also considered a proxy of aerobic scope (Leeuwis et al., 2019; Rodríguez-Fuentes et al., 2017) (Fig. 3). This scope represents the surplus proportion of the energy flux left after basal maintenance costs of an organism are met (Paschke et al., 2018). In optimal temperatures, energy production is maximized, increasing fitness of the species (survival in this work); in addition, the species also has “pejus” temperatures, where although fitness is reduced, it is still positive, so they represent the limit range of species distribution (Frederich and Pörtner, 2000).

2.3.2. Model fit of physiological data

A generalized additive model (GAM) approach was used to model the relationship between temperature (°C) and red octopus fitness. This approach was selected since it fit nonlinear responses for a wide range of statistical distributions. The model assumes a Gaussian error distribution and identity link:

$$g(\eta) = \beta_0 + s(\text{Bottom temperature}, k)$$

where β_0 is the intercept, η is an estimate of fitness of the red octopus and g is the link function between η and additive predictors ($\eta = \mu$); $s(X)$ denotes a tensor spline smoother function of the covariate X , and k is the degree of smoothness. A high value of k (15) was set to adjust the model to the physiological data. The GAMs were built using the “mgcv” library (Wood, 2017) from the R software.

2.3.3. Environmental layer for the mechanistic niche model

Mean benthic temperature at minimum depth was downloaded from Bio-ORACLE (Assis et al., 2017) for current (2000–2014) and RCP 2.6, 4.5, 6, and 8.5 (2040–2050 and 2090–2100) scenarios at a resolution of ~9 km². As in the CNM dataset, layers were cropped according to an M (Barve et al., 2011) using the ecoregions proposed by Spalding et al. (2007) with the library ENMGadgets (Barve and Barve, 2013).

2.3.4. Mechanistic niche model projections to current and future scenarios

The MNM were projected onto current and future climate RCP 2.6, 4.5, 6, and 8.5 scenarios (2050–2100) to obtain suitability maps. The projections of all the scenarios were done down to ~50 m in depth, following the procedure of CNMs. Since this model represents an actual measurement of the fundamental thermal niche (Kearney et al., 2010; Peterson et al., 2015), there was no need to calculate any extrapolation risk.

2.4. Potential red octopus distribution

Potential distribution (PD - presence-absence maps) were made from the environmental suitability maps of the CNM selected and the MNM. For the CNM, the PD was obtained from suitability maps using the fifth percentile training presence method, a threshold value that leaves out 5% of occurrence records with the lowest suitability values (Peterson et al., 2008). This threshold was used to prevent the consideration of occurrences from sink populations, taxonomic misidentifications, or wrongly georeferenced occurrences (Peterson et al., 2008) while generating PD maps. In the case of the MNMs, values above 0 were considered presence because they represent the pejus range – temperatures that delimit the range of maximum performance and scope for activity which defines the geographic distribution limits (Frederich and Pörtner, 2000). Maps obtained from both procedures were overlapped for each RCP scenario and compared.

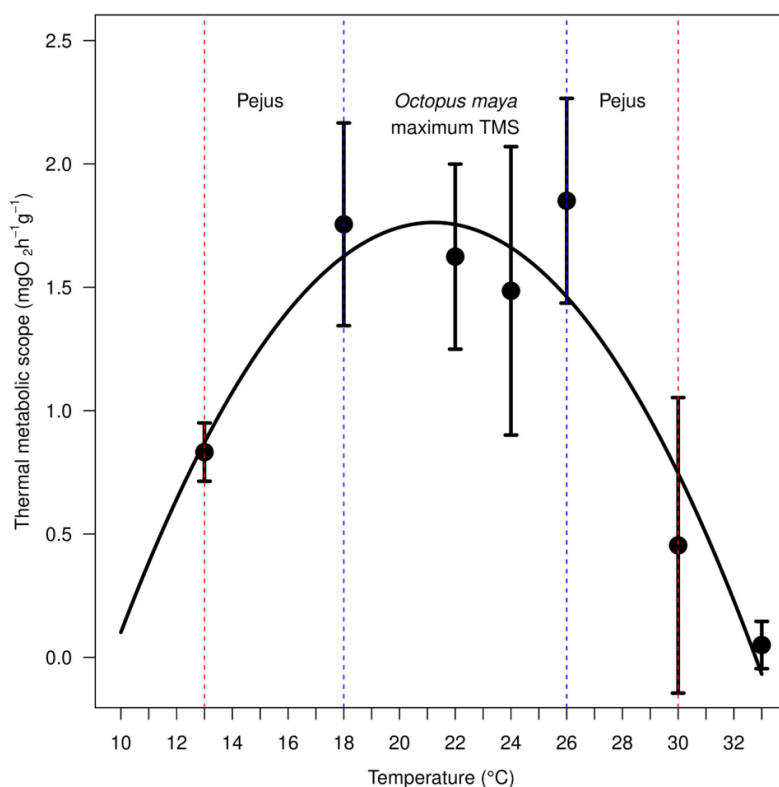


Fig. 3. Thermal metabolic scope (TMS) of the red octopus (*Octopus maya*) juveniles obtained following the method of Paschke et al. (2018). Data from Ripoll et al. (unpublished data). Red dashed lines indicate extreme pejus temperature where the life of the animals is compromised. Blue dashes indicate the limits of the maximum TMS where the maximum physiological performance of octopus is expected. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

3. Results

3.1. Correlative niche model results

3.1.1. Characteristics of the selected correlative niche model

A configuration of 'L' features with RM of 0.5 was selected as the best model. The procedure showed that the model had statistical significance with a pROC of $P < 0.05$ and a performance value of $OR_5 = 0.04$. Furthermore, variables selected with the Jackknife test were Sur_tem_max, Sur_sal_max, and Sur_sal_min. Overall the variable that contributes the most to the training gain of the model is Sur_tem_max. According to the model in this study, detrimental environments are found at surface temperatures of ~ 30 °C. Similarly, despite the uncertainty, surface salinities values below 30 PSU might harm the red octopus, however, it was not possible to characterize the upper salinity tolerances (Fig. 4).

3.1.2. Correlative niche model on landscape and future scenarios

The results suggest that suitable areas of red octopus are restricted mainly to the YP in Mexico. In the western YP, suitability decreased nearby the Sabancuy port (Fig. 5). The Maxent results showed that higher suitable areas occurred north of the YP. Under CC, by 2040–2050 suitability will have decreased in the western YP area and to a lesser extent in the north for most scenarios. Nevertheless, the RCP 2.6 scenario showed the possibility for the red octopus to have regained and maintained its current suitability by 2090–2100. Under the RCP 4.5 scenario, suitability will be higher on the northern coast of the YP by the 2040–2050 and 2090–2100 periods. However, stronger environmental pressures will have significantly reduced the overall suitability of red octopus by 2090–2100 in the RCP 6 and 8.5 scenarios (Fig. 5).

3.1.3. Regions of non-analogous conditions for future scenarios

Analogous conditions were detected north of the YP in all scenarios for the year 2050. However, by the year 2100, most of the YP will have shown non-analogous conditions during the RCP 4.5, 6, and 8.5. In contrast, the RCP 2.6 scenario showed analogous conditions in the western and northeast regions of the YP (Supplementary material S2).

3.2. Mechanistic niche model results

3.2.1. Mechanistic niche model on landscape and future scenarios

The MNMs showed suitable regions in the western region of the GM, the Yucatan shelf, and the Caribbean mainly at greater depths. Nevertheless, the lowest suitabilities were predicted in the Caribbean region and the western region of the Yucatan shelf. Therefore, suitabilities on those regions will have been the most negatively affected under warming scenarios, particularly the RCP 6 and RCP 8.5 scenarios by the 2090–2100 period. Regarding the coastal region of the Yucatan shelf where the species is fished, the northern region seems more suitable and acts as a "refuge" under warming scenarios. However, higher suitabilities will have been found away from the coast at deeper waters if warming intensifies (RCP 8.5, 2090–2100 period - Fig. 6).

3.2.2. Potential distribution of red octopus according to correlative and mechanistic niche models for current and future scenarios

The presence-absence outputs for CNM (threshold value of 0.14) show PD on the shores of the Yucatan shelf and in the western region of the GM. For the CNM, a contraction in PD exists toward the coast area for most scenarios. However, under RCP 2.6, 4.5, the red octopus will have retained most of its current PD and even recovering most of it (RCP 2.6 period 2090–2100), which was not the case for RCP 6 and 8.5 at 2090–2100 scenarios since a significant reduction in PD is predicted. On

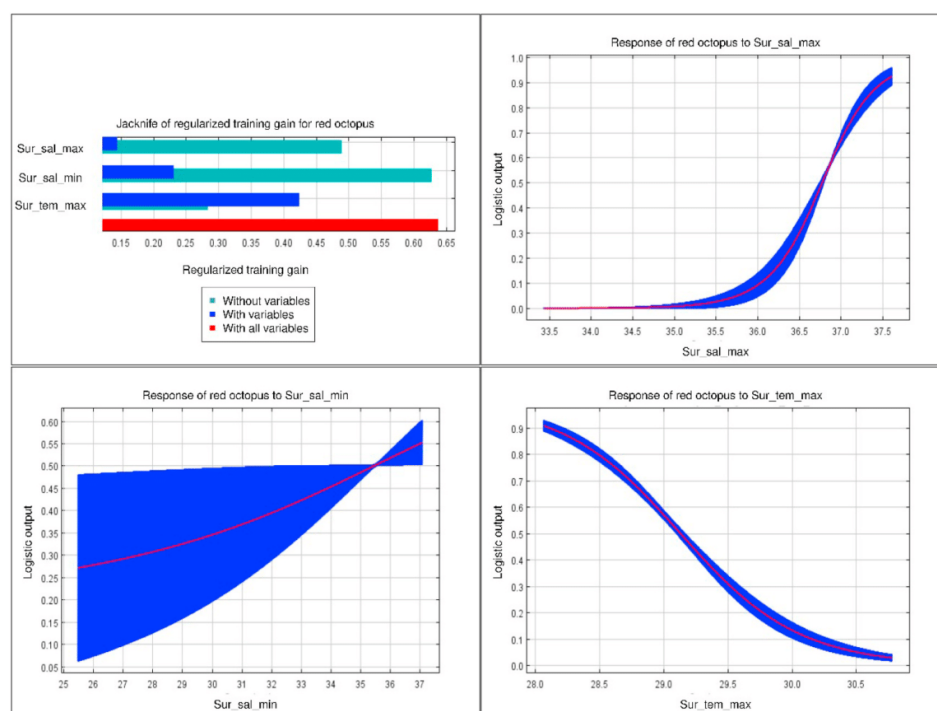


Fig. 4. Jackknife test of variable importance for training data for the red octopus (*Octopus maya*). Additionally, logistics curves show the response of the red octopus to the maximum surface salinity (Sur_sal_max), minimum surface salinity (Sur_sal_min), and maximum surface temperature (Sur_tem_max) according to the predictions of Maxent prediction. The curves show how the logistics prediction of suitability varied while keeping all other environmental variables at their average sample value. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

the other hand, binary maps obtained from MNM predict as PD regions the whole calibration area. According to the binary output obtained from MNM, the red octopus will have retained its PD for most scenarios except at the RCP 8.5 scenario in 2090–2100, where the western and the Mexican Caribbean regions surpass the threshold of thermal tolerance. Lastly, PD areas obtained from the MNM were noted to be more stable than those obtained from CNM (Fig. 7).

4. Discussion

4.1. Current suitability and potential distribution of the red octopus

The CNM showed statistical significance and good performance. According to the jackknife test, the Sur_tem_max contribute more to the regularized training of the model. The importance of predicted temperature is not surprising because it influences the metabolism and physiology in ectothermic animals due to its effects on oxygen uptake (Pörtner et al., 2017; Pörtner, 2012; Pörtner and Farrell, 2008). Although octopus species are usually associated with bottom environments, the Sur_tem_max contributed more to the model, which could be explained because the red octopus was usually found nearby the coast. In addition, data calculated from satellite measurement may be more reliable than the interpolation process of bottom temperatures from oceanographic models like the ones used in the environmental layers of Bio-ORACLE (Assis et al., 2017). For the most part, predictions of suitability and PD are consistent with the known distribution of the red octopus (Ángeles-González et al., 2020b; Gamboa-Álvarez et al., 2015). However, it was noted that it could potentially inhabit the western region of the GM (Fig. 7).

In contrast, the MNM predicted suitable and PD regions far from

where the red octopus is reported. That the MNM predicted a wider PD is not surprising (Gutiérrez-Ruelas et al., 2019). For instance, the CNM indirectly includes biotic interactions in their calculations, while physiological data do not account for such information (Soberón and Peterson, 2005). Perhaps negative interactions, (competitors or predators) prevent species expansion (Gutiérrez-Ruelas et al., 2019; Soberón and Peterson, 2005) which could be the case of the red octopus, particularly to deeper waters where other octopus species inhabit (Avendaño et al., 2020). Also, it is possible that the red octopus occurrences used for the CNM may have been biased to the coast – a phenomenon that could be generalized for marine species due to the greater ease of being fished out or observed; thus, the niche characterization would be only partial.

In addition, using a single variable as a proxy to a multivariate niche in a MNM may expand their suitability and PD since other limiting variables were not considered (Soberón and Arroyo-Peña, 2017), for example, salinity. Indeed, although both CNM and MNM found PD regions in western GM, no reliable source of occurrence has been reported in that area. Unfortunately, no salinity tolerance data exist for this species. However, successful cultures occur at >32 PSU (Rosas et al., 2014), with lower values being detrimental for the red octopus, according to our model (Fig. 4). Thus, the distribution could be restricted due to the sharp decrease in salinity (<30 PSU) nearby the Terminos Lagoon (Phleger and Ayala-Castañares, 1971). Moreover, the Grijalva-Usumacinta rivers (further west than Sabancuy) modify salinity, substrate, and organic matter (Rabalais, 2004), which could affect octopus populations negatively (Sobrinho et al., 2002), probably restricting, even more, the red octopus distribution.

Therefore, the over predictions by the MNM in comparison to CNM suggest that salinity acts as an environmental barrier. Similarly, in the Mexican Caribbean region, no well-founded occurrence of red octopus

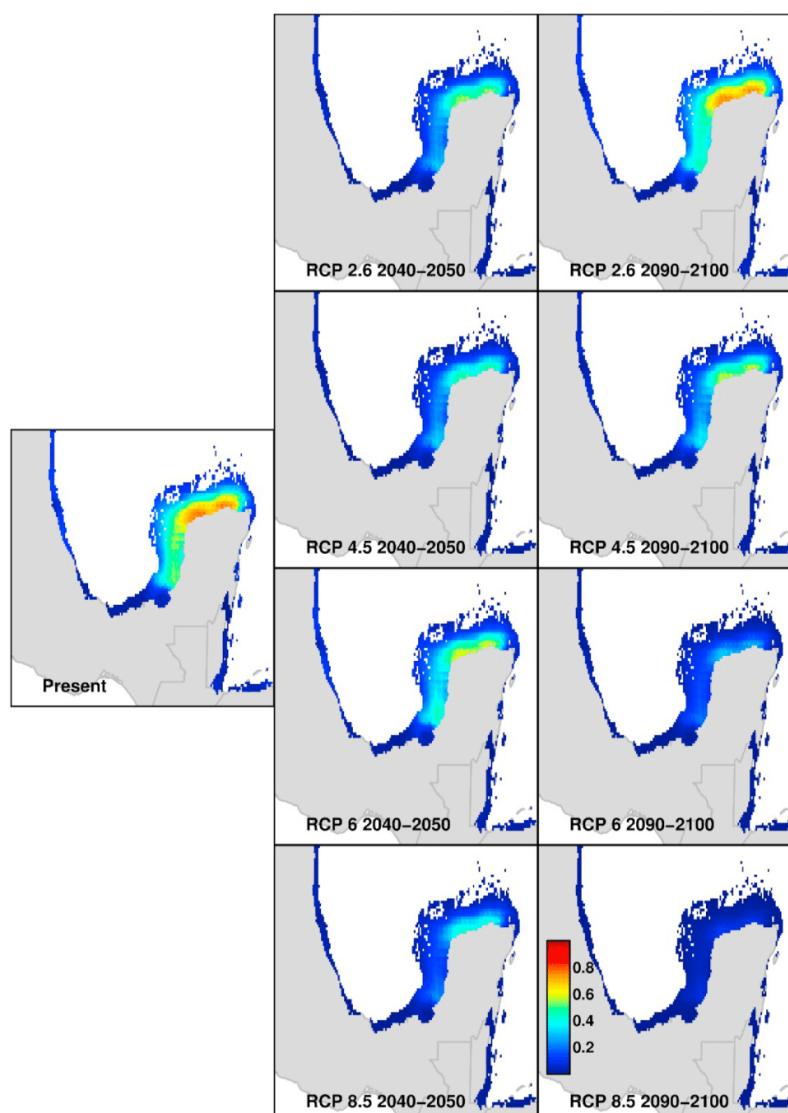


Fig. 5. Suitability outputs of correlative niche models for the present (2000–2014) and the Representative Concentration Pathways scenarios (2.6, 4.5 6, and 8.5) for 2040–2050 and 2090–2100 for the red octopus (*Octopus maya*). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

exists; this region is characterized by mean temperatures even higher than in the western region of the YP. Perhaps, although the red octopus could tolerate the temperatures of that region according to physiological data (Ángeles-González et al., 2020a) and the MNM, it may not inhabit it since ectothermic species tend to have a “safety thermal buffer” (Angilletta, 2009).

Finally, both the CNM and MNM showed high suitability in the northern fishing region of the YP— a region characterized by upwellings that keep temperatures $\sim 27^\circ\text{C}$ (Enriquez et al., 2013; Ruiz-Castillo et al., 2016; Zavala-Hidalgo et al., 2006). The conditions of that region have been hypothesized to optimize octopus fitness. For instance, laboratory studies have shown that below 27°C , reproduction success and embryonic development increase (Caamal-Monsreal et al., 2016; Juárez et al., 2015, 2016), and growth rate in juveniles is optimum (Noyola et al.,

2013). Whereas temperatures of $\sim 30^\circ\text{C}$, fitness and performance decrease when thermal stress begins to express itself in the octopus (Caamal-Monsreal et al., 2016; Juárez et al., 2015, 2016, 2015; López-Galindo et al., 2019; Pascual et al., 2019).

4.2. Future potential distribution of the red octopus

As environmental alterations continue to affect species performance, distribution changes may occur to find favorable temperatures (Poloczanska et al., 2013, 2016). In this sense, suitability and PD suggest a negative impact on red octopus due to the negative relationship with temperature, indicating potential metabolic stress for the red octopus in the future. In this sense, the vulnerability of the red octopus to the CC can be easily explained due to their restricted distribution

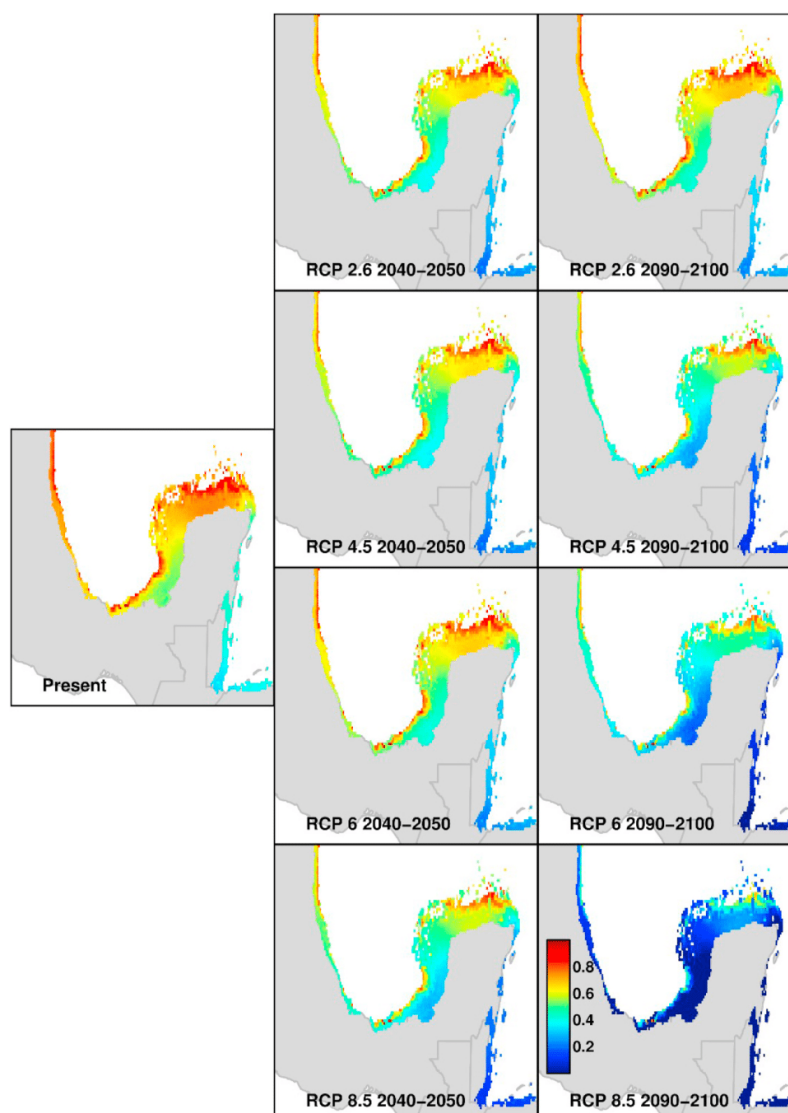


Fig. 6. Suitability outputs of mechanistic niche models for the present (2000–2014) and the Representative Concentration Pathways scenarios (2.6, 4.5 6, and 8.5) for 2040–2050 and 2090–2100 for the red octopus (*Octopus maya*). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

(Ángeles-González et al., 2020b; Gamboa-Álvarez et al., 2015), low dispersal capabilities (lack of planktonic stage - Rosas et al., 2014), and cold tolerance affinities (Caamal-Monsreal et al., 2016; Juárez et al., 2015, 2016, 2015; Noyola et al., 2013).

Indeed, this study noted that the red octopus populations in the YP western region are particularly vulnerable to warming scenarios, especially under the RCP 8.5 scenarios where the CNM and MNM suggest that the thermal window threshold will have been overcome by the 2090–2100 period. Nevertheless, the MNM also suggests that deeper waters can potentially act as thermal refugia under the RCP 8.5 scenarios. However, not all CNMs scenarios are catastrophic. For example, the most favorable scenario, RCP 2.6, showed that the red octopus might retain most of its distribution with little change, whereas the RCP 4.5 scenario showed a slighter reduction in suitability and PD in the western

region. At the same time, higher suitabilities of the red octopus could occur at the north of the YP for most scenarios, as hypothesized by Angeles-Gonzalez et al. (2017). Therefore, this would indicate that landings in the YP's northern coast could be more stable than in the western region.

Regardless of the differences in the results, both approaches usually predicted a reduction in suitability in all RCP scenarios. It is worth pointing out that even if the species retains its PD -as the MNM suggests- overall suitability is reduced. Therefore, assuming that a relationship between abundance and the niche exists (e.g., Martínez-Meyer et al., 2013; Osorio-Olvera et al., 2020; Yañez-Arenas et al., 2012), landings in the region will be reduced. In addition, if MNM predictions are accurate, it would also suggest that red octopus could take refuge in deeper waters. Therefore, the resource would be less accessible for small-scale

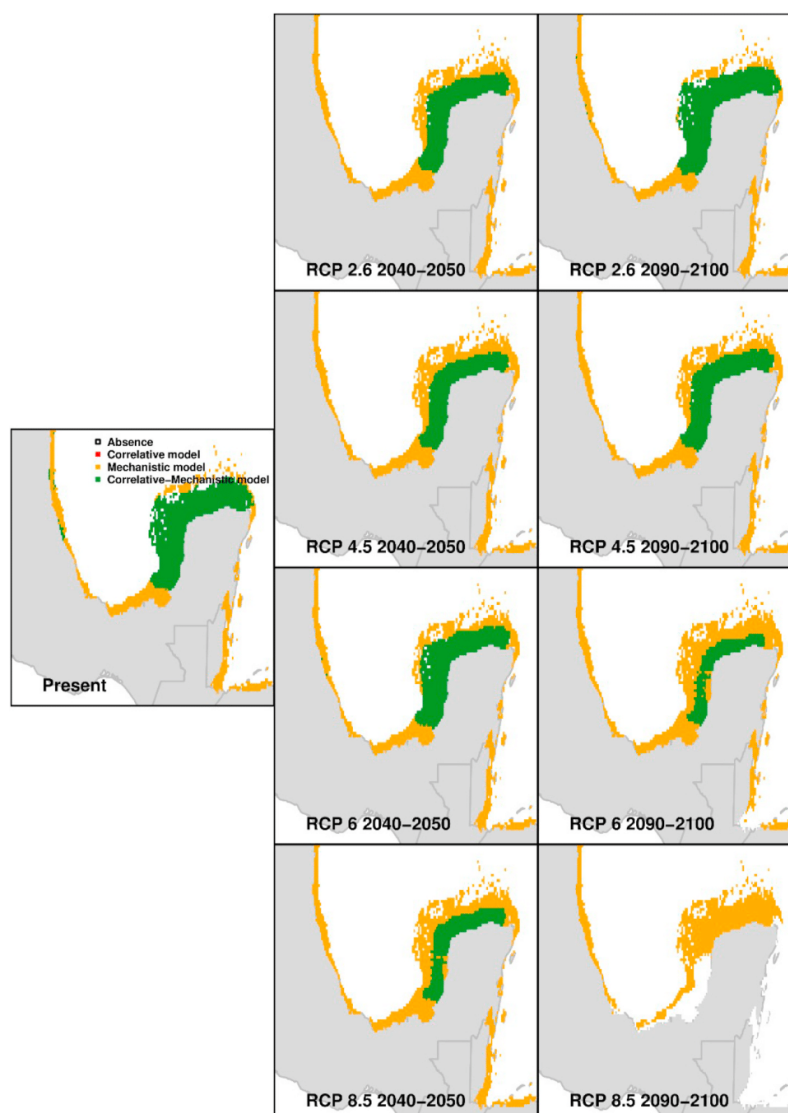


Fig. 7. Binary outputs of correlative niche model and mechanistic niche model for the present (2000–2014) and the Representative Concentration Pathways scenarios (2.6, 4.5, 6, and 8.5) for 2040–2050 and 2090–2100 for the red octopus (*Octopus maya*). Note that the mechanistic niche models completely overlap the correlative niche models. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

fisheries, and it would be exploited mainly by the medium-scale fisheries.

4.3. Caveats

Predicting accurately how the communities will behave is difficult since they are complex networks of ecological processes. For instance, the CC is expected to affect several of the ecosystem attributes, including food webs (Pörtner and Peck, 2010; Noyola et al., 2015), phenology (Poloczanska et al. 2013; 2016), and habitats (Martínez-Arroyo et al., 2011). However, the analyses of such effects are usually out of the scope of niche models. Moreover, both CNM and the MNM models accounted mainly for effects of thermal stress. Nonetheless, evidence indicates that vulnerability of ectotherms to temperature generally increased when

they were exposed to additional stressors, such as reduced oxygen, CO₂, and ocean acidification (Deutsch et al., 2015; Pörtner et al., 2005; Pörtner and Peck, 2010).

An inherent uncertainty is also possible in the CNM procedures where algorithm and parameter settings selection can create different outputs predicted (Cobos et al., 2019a; Peterson et al., 2018). Moreover, for the MNM, this study used only the data of juveniles that tend to have higher thermal tolerance than adults or embryos (Tremblay et al., 2017), so the impact of CC might be more substantial if all life stages of the red octopus are considered. Several authors suggest that MNMs should also incorporate morphology, behavior, and demography in their calculation (Kearney and Porter, 2009; Peterson et al., 2015). Future work could associate laboratory data of the complete life cycle of the red octopus with demographic processes to evaluate the impact of CC on the entire

ontogenetic development of the species. Additionally, the projections of models to different circulation global models may further reduce the uncertainty (Cobos et al., 2019a; Peterson et al., 2018) instead of one environmental source as it was done in this work. Finally, assessing if octopuses could potentially adapt to CC or the effect of biotic interaction was not part of the scope of this study. Nonetheless, the possibility should be weighed.

5. Conclusions

The models developed in this study seemed to be helpful tools for inferring climate change impact direction. Although the results differed, both correlative and mechanistic niche model predicted an overall reduction in suitability. Thus, considering the scenarios, an eastward or more profound water migration could occur (Ángeles-González et al., 2017) at least for the bulk of the red octopus population available to the small-scale fisheries. The fact that the species could move from places that have been historically accessible indicates the need to develop contingency plans for this fishing resource. This is especially important since Mexican regulations assume that this species will benefit from climate change (Diario Oficial de la Federación, 2018), which is not supported by the results in this study. Finally, all the codes and input data to replicate this study are provided in the following GitHub link: <https://github.com/ejosymart/octopusNiche>.

Declaration of competing interest

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

No conflict of interest existed in the development of this work.

Acknowledgments

This study is the result of a doctoral degree thesis performed in Graduate Studies in Ciencias del Mar y Limnología, UNAM and to the Consejo Nacional de Ciencia y Tecnología (CONACYT, Mexico) for the scholarship to develop graduate studies. The authors are also grateful to Diana Fischer for English edition. This study was partially financed by PAPIIT program-UNAM to CR (IN204019) and CONACYT Project No. 61503 to CR.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecss.2021.107502>.

References

- Ángeles-González, L.E., Calva, R., Santos-Valencia, J., Avila-Poveda, O.H., Olivares, A., Díaz, F., Rosas, C., 2017. Temperature modulates spatio-temporal variability of the functional reproductive maturation of *Octopus maya* (Cephalopoda) on the shelf of the Yucatan Peninsula, Mexico. *J. Molluscan Stud.* 83, 280–288. <https://doi.org/10.1093/mollus/eyx013>.
- Ángeles-González, L.E., Lima, F.D., Caamal-Monsreal, C., Díaz, F., Rosas, C., 2020a. Exploring the effects of warming seas by using the optimal and pejus temperatures of the embryo of three Octopoda species in the Gulf of Mexico. *J. Therm. Biol.* 94. <https://doi.org/10.1016/j.jtherbio.2020.102753>.
- Ángeles-González, L.E., Martínez-Meyer, E., Yañez-Arenas, C., Velázquez-Abunader, I., García-Rueda, A., Díaz, F., Tremblay, N., Antonio Flores-Rivero, M., Gebauer, P., Rosas, C., 2020b. Using realized thermal niche to validate thermal preferences from laboratory studies. How do they stand? *Ecol. Indic.* 118. <https://doi.org/10.1016/j.ecolind.2020.106741>.
- Angilletta, M.J., 2009. *Thermal Adaptation A Theoretical and Empirical Synthesis*. Oxford University Press.
- Arreguín-Sánchez, F., 2019. Climate change and the rise of the octopus fishery in the Campeche Bank, México. *Reg. Stud. Mar. Sci.* 32, 100852. <https://doi.org/10.1016/j.rsm.2019.100852>.
- Assis, J., Tyberghein, L., Bosch, S., Verbruggen, H., Serrão, E.A., De Clerck, O., 2017. BioORACLE v2.0: extending marine data layers for bioclimatic modelling. *Global Ecol. Biogeogr.* 27, 277–284. <https://doi.org/10.1111/geb.12693>.
- Avendaño, O., Hernández-Flores, A., Velázquez-Abunader, I., Fernández-Jardón, C., Cuevas-Jimenez, A., Guerra, A., 2020. Potential biomass and distribution of octopus in the eastern part of the Campeche bank (Yucatán, Mexico). *Sci. Mar.* 84, 133–142. <https://doi.org/10.3989/scimar.05007.01A>.
- Avendaño, O., Velázquez-Abunader, I., Fernández-Jardón, C., Ángeles-González, L.E., Hernández-Flores, A., Guerra, A., 2019. Biomass and distribution of the red octopus (*Octopus maya*) in the north-east of the Campeche Bank. *J. Mar. Biol. Assoc. U. K.* 1317–1323. <https://doi.org/10.1017/S0025315419000419>.
- Barve, N., Barve, V., 2013. ENMGadgets: Tools for Pre and Post Processing in ENM Workflows.
- Barve, N., Barve, V., Jiménez-Valverde, A., Lira-Noriega, A., Maher, S.P., Peterson, A.T., Soberón, J., Villalobos, F., 2011. The crucial role of the accessible area in ecological niche modeling and species distribution modeling. *Ecol. Model.* 222, 1810–1819. <https://doi.org/10.1016/j.ecolmodel.2011.02.011>.
- Boria, R.A., Olson, L.E., Goodman, S.M., Anderson, R.P., 2014. Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. *Ecol. Model.* 275, 73–77. <https://doi.org/10.1016/j.ecolmodel.2013.12.012>.
- Caamal-Monsreal, C., Uriarte, I., Fariás, A., Díaz, F., Sánchez, A., Re, D., Rosas, C., 2016. Effects of temperature on embryo development and metabolism of *O. maya*. *Aquaculture* 451, 156–162. <https://doi.org/10.1016/j.aquaculture.2015.09.011>.
- Chabot, D., Steffensen, J., Farrell, A., 2016. The determination of standard metabolic rate in fishes. *J. Fish. Biol.* 88, 81–121.
- Cheung, W.W.L., Lam, V.W.Y., Sarmiento, J.L., Kearney, K., Watson, R., Zeller, D., Pauly, D., 2010. Large-scale redistribution of maximum fisheries catch potential in the global ocean under climate change. *Global Change Biol.* 16, 24–35. <https://doi.org/10.1111/j.1365-2486.2009.01995.x>.
- Cobos, M.E., Osorio-Olvera, L., Peterson, A.T., 2019a. Assessment and representation of variability in ecological niche model predictions. *bioRxiv*. <https://doi.org/10.1101/603100>.
- Cobos, M.E., Peterson, A.T., Barve, N., Osorio-Olvera, L., 2019b. kuenm: an R package for detailed development of ecological niche models using Maxent. *PeerJ* 7, e6281. <https://doi.org/10.7717/peerj.6281>.
- CONAPESCA, 2018. *Anuario Estadístico de Acuicultura y Pesca 2018*. Comisión Nacional de Acuicultura y Pesca, Secretaría de Agricultura, Ganadería, Desarrollo Rural, Pesca y Alimentación, México.
- Czitrom, S.R.R., Ruiz, F., Alatorre, M.A., Padilla, A.R., 1986. Preliminary study of a front in the Bay of Campeche, Mexico. *Elsevier Oceanogr. Ser.* 42, 301–311. [https://doi.org/10.1016/S0422-9894\(08\)71051-1](https://doi.org/10.1016/S0422-9894(08)71051-1).
- Deutsch, C., Ferrel, A., Seibel, B., Portner, H.O., Huey, R.B., 2015. Climate change tightens a metabolic constraint on marine habitats. *Science* 348, 1132–1135. <https://doi.org/10.1126/science.1261605>.
- Diario Oficial de la Federación, 2018. *Carta Nacional Pesquera*.
- Doney, S.C., Ruckelshaus, M., Emmett Duffy, J., Barry, J.P., Chan, F., English, C.A., Galindo, H.M., Grebmeier, J.M., Hollowed, A.B., Knowlton, N., Polovina, J., Rabalais, N.N., Sydeman, W.J., Talley, L.D., 2012. Climate change impacts on marine ecosystems. *Ann. Rev. Mar. Sci.* 4, 11–37. <https://doi.org/10.1146/annurev-marine-041911-111611>.
- Doubleday, Z.A., Prowse, T.A.A., Arkhipkin, A., Pierce, G.J., Semmens, J., Steer, M., Leporati, S.C., Lourenço, S., Quetglas, A., Sauer, W., Gillanders, B.M., 2016. Global proliferation of cephalopods. *Curr. Biol.* 26, R406–R407. <https://doi.org/10.1016/j.cub.2016.04.002>.
- Enriquez, C., Mariño-Tapia, I., Jeronimo, G., Capurro-Filigrasso, L., 2013. Thermohaline processes in a tropical coastal zone. *Contin. Shelf Res.* 69, 101–109. <https://doi.org/10.1016/j.csr.2013.08.018>.
- Enriquez, C.E., Mariño-Tapia, I., 2014. Mechanisms driving a coastal dynamic upwelling. In: *Proceedings of the 17th Physics of Estuaries and Coastal Seas (PECS) Conference, Porto de Galinhas, Pernambuco, Brazil, 19–24 October 2014*.
- FAO, 2018. *Brief the State of World Fisheries and Aquaculture*.
- Frederich, M., Pörtner, H.O., 2000. Oxygen limitation of thermal tolerance defined by cardiac and ventilatory performance in spider crab, *Maja squinado*. *Am. J. Physiol. Regul. Integr. Comp. Physiol.* 279, 1531–1538. <https://doi.org/10.1152/ajpregu.2000.279.5.r1531>.
- Gamboa-Álvarez, M.Á., López-Rocha, J.A., Poot-López, G.R., 2015. Spatial analysis of the abundance and catchability of the red Octopus *Octopus maya* (voss and solis-ramírez, 1966) on the continental shelf of the yucatan Peninsula, Mexico. *J. Shellfish Res.* 34, 481–492. <https://doi.org/10.2983/035.034.0232>.
- Gutiérrez-Ruelas, J.S., Jiménez, L., Quiroz-Reyes, A.P., Sotelo-Pedroza, S.C., Jorge, S., 2019. On some problems of estimating fundamental niche from physiological data. *bioRxiv*, 716688. <https://doi.org/10.1101/716688>.
- Hausfather, Z., Peters, G.P., 2020. RCP8.5 is a problematic scenario for near-term emissions. *Proc. Natl. Acad. Sci. U. S. A.* 117, 27791–27792. <https://doi.org/10.1073/pnas.2017241117>.
- Hutchinson, G.E., 1957. Concluding remarks. *Cold Spring Harbor Symp. Quant. Biol.* 22, 415–427.
- IPCC, 2014. *Summary for Policymakers, Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. <https://doi.org/10.1017/CBO9781107415324>.
- Juárez, O.E., Galindo-Sánchez, C.E., Díaz, F., Re, D., Sánchez-García, A.M., Caamal-Monsreal, C., Rosas, C., 2015. Is temperature conditioning *Octopus maya* fitness? *J. Exp. Mar. Biol. Ecol.* 467, 71–76. <https://doi.org/10.1016/j.jembe.2015.02.020>.
- Juárez, O.E., Hau, V., Caamal-Monsreal, C., Galindo-Sánchez, C.E., Díaz, F., Re, D., Rosas, C., 2016. Effect of maternal temperature stress before spawning over the energetic balance of *Octopus maya* juveniles exposed to a gradual temperature change. *J. Exp. Mar. Biol. Ecol.* 474, 39–45. <https://doi.org/10.1016/j.jembe.2015.10.002>.

- Kearney, M., Porter, W., 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecol. Lett.* 12, 334–350. <https://doi.org/10.1111/j.1461-0248.2008.01277.x>.
- Kearney, M., Porter, W.P., 2004. Mapping the fundamental niche: physiology, climate, and the distribution of a nocturnal lizard. *Ecology* 85, 3119–3131.
- Kearney, M.R., Wintle, B.A., Porter, W.P., 2010. Correlative and mechanistic models of species distribution provide congruent forecasts under climate change. *Conserv. Lett.* 3, 203–213. <https://doi.org/10.1111/j.1755-263X.2010.00097.x>.
- Kutner, M., Nachtsheim, C., Neter, J., 2004. In: *Applied Linear Regression Models*, fourth ed. McGraw-Hill Irwin.
- Leeuwis, R., N. G.W., Sandrelli, R., Zanuzzo, F., Gamperl, A., 2019. The environmental tolerances and metabolic physiology of sablefish (*Anoplopoma fimbria*). *Comp. Biochem. Physiol. Part A Mol. Integr. Physiol.* 231, 140–148.
- Lima, F., Ángeles-González, L., Leite, T., Lima, S., 2020. Global climate changes over time shape the environmental niche distribution of *Octopus insularis* in the Atlantic Ocean. *Mar. Ecol. Prog. Ser.* 652, 111–121. <https://doi.org/10.3354/meps13486>.
- López-Galindo, L., Galindo-Sánchez, C., Olivares, A., Avila-Poveda, O.H., Díaz, F., Juárez, O.E., Lafarga, F., Pantoja-Pérez, J., Caamal-Monsreal, C., Rosas, C., 2019. Reproductive performance of *Octopus maya* males conditioned by thermal stress. *Ecol. Indic.* 96, 437–447. <https://doi.org/10.1016/j.ecolind.2018.09.036>.
- López-Rocha, J.A., Arreguín-Sánchez, F., 2013. Spatial dynamics of the red grouper *Epinephelus morio* (pisces: serranidae) on the campeche bank, Gulf of Mexico. *Sci. Mar.* 77, 313–322. <https://doi.org/10.3989/scimar.03565.13B>.
- Martínez-Arroyo, A., Manzanilla-Naim, S., Zavala-Hidalgo, J., 2011. Vulnerability to climate change of marine and coastal fisheries in México. *Atmósfera* 24, 103–123.
- Martínez-Meyer, E., 2005. Climate change and biodiversity: some considerations in forecasting shifts in species' potential distributions. *Biodivers. Inf.* 2, 42–55. <https://doi.org/10.17161/bi.v2i0.8>.
- Martínez-Meyer, E., Díaz-Porras, D., Peterson, A.T., Yáñez-Arenas, C., 2013. Ecological niche structure and rangewide abundance patterns of species. *Biol. Lett.* 9 <https://doi.org/10.1098/rsbl.2012.0637>.
- Monreal-Gómez, M., Salas-de León, D., Velasco-Mendoza, H., 2004. Hidrodinámica del Golfo de México. In: *Caso, M., Pisanty, I., Ezcurra, E. (Eds.), Diagnóstico Ambiental Del Golfo de México, Vol. I. Instituto Nacional de Ecología (INE-SEMARNAT), México, D.F., pp. 47–67*.
- Muhling, B.A., Lee, S.-K., Lamkin, J.T., Liu, Y., 2011. Predicting the effects of climate change on bluefin tuna (*Thunnus thynnus*) spawning habitat in the Gulf of Mexico. *ICES J. Mar. Sci.* 68, 1051–1062. <https://doi.org/10.1093/icesjms/fsr008>.
- Naimi, B., Hamm, N.A.S., Groen, T.A., Skidmore, A.K., Toxopeus, A.G., 2014. Where is positional uncertainty a problem for species distribution modelling? *Ecography* 37, 191–203. <https://doi.org/10.1111/j.1600-0587.2013.00205.x>.
- Noyola, J., Mascaró, M., Caamal-Monsreal, C., Noreña-Barroso, E., Díaz, F., Re, D., Sánchez, A., Rosas, C., 2013. Effect of temperature on energetic balance and fatty acid composition of early juveniles of *Octopus maya*. *J. Exp. Mar. Biol. Ecol.* 445, 156–165. <https://doi.org/10.1016/j.jembe.2013.04.008>.
- Noyola, J., Mascaró, M., Díaz, F., Denisse Re, A., Sánchez-Zamora, A., Caamal-Monsreal, C., Rosas, C., 2015. Thermal biology of prey (*Melongena corona bispinosa*, *Strombus pugilis*, *Uca lineata* and *Libinia dubia*) and predators (*Ocyropsis chrysurus*, *Centropomus undecimalis*) of *Octopus maya* from the Yucatan Peninsula. *J. Therm. Biol.* 53, 151–161. <https://doi.org/10.1016/j.jtherbio.2015.11.001>.
- Osoerio-Olvera, L., Yáñez-Arenas, C., Martínez-Meyer, E., Peterson, A.T., 2020. Relationships between population densities and niche-centroid distances in North American birds. *Ecol. Lett.* 23, 555–564. <https://doi.org/10.1111/ele.13453>.
- Owens, H.L., Campbell, L.P., Dornak, L.L., Saube, E.E., Barve, N., Soberón, J., Ingenloff, K., Lira-Noriega, A., Hensz, C.M., Myers, C.E., Peterson, A.T., 2013. Constraints on interpretation of ecological niche models by limited environmental ranges on calibration areas. *Ecol. Model.* 263, 10–18. <https://doi.org/10.1016/j.ecolmodel.2013.04.011>.
- Paschke, K., Agüero, J., Gebauer, P., Díaz, F., Mascaró, M., López-Ripoll, E., Re, D., Caamal-Monsreal, C., Tremblay, N., Pörtner, H.O., Rosas, C., 2018. Comparison of aerobic scope for metabolic activity in aquatic ectotherms with temperature related metabolic stimulation: a novel approach for aerobic power budget. *Front. Physiol.* 9 <https://doi.org/10.3389/fphys.2018.01438>.
- Pascual, C., Mascaró, M., Rodríguez-Canul, R., Gallardo, P., Sánchez, A.A., Rosas, C., Cruz-López, H., 2019. Sea surface temperature modulates physiological and immunological condition of *Octopus maya*. *Front. Physiol.* 10, 1–11. <https://doi.org/10.3389/fphys.2019.00739>.
- Pedersen, J.S.T., van Vuuren, D.P., Aparicio, B.A., Swart, R., Gupta, J., Santos, F.D., 2020. Variability in historical emissions trends suggests a need for a wide range of global scenarios and regional analyses. *Commun. Earth Environ.* 1, 1–7. <https://doi.org/10.1038/s43247-020-00045-y>.
- Peterson, A.T., Cobos, M.E., Jiménez-García, D., 2018. Major challenges for correlative ecological niche model projections to future climate conditions. *Ann. N. Y. Acad. Sci.* 1429, 66–77. <https://doi.org/10.1111/nyas.13873>.
- Peterson, A.T., Papeš, M., Soberón, J., 2015. Mechanistic and correlative models of ecological niches. *Eur. J. Ecol.* 1, 28–38. <https://doi.org/10.1515/eje-2015-0014>.
- Peterson, A.T., Papeš, M., Soberón, J., 2008. Rethinking receiver operating characteristic analysis applications in ecological niche modeling. *Ecol. Model.* 213, 63–72. <https://doi.org/10.1016/j.ecolmodel.2007.11.008>.
- Peterson, T.A., Soberón, J., Pearson, R.G., Anderson, R.P., Martínez-Meyer, E., Nakamura, M., Araújo, M.B., 2011. *Ecological Niches and Geographic Distributions*, Choice Reviews Online. Princeton University Press.
- Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. *Int. J. Global Environ. Issues* 190, 231–259. <https://doi.org/10.1016/j.ecolmodel.2005.03.026>.
- Phleger, F.B., Ayala-Castañares, A., 1971. Processes and history of Terminos Lagoon, Mexico. *Am. Assoc. Petrol. Geol. Bull.* 55, 2130–2140. <https://doi.org/10.1306/819a3e26-16c5-11d7-8645000102c1865d>.
- Pörtner, H.-O., Bock, C., Mark, F.C., 2017. Oxygen- & capacity-limited thermal tolerance: bridging ecology & physiology. *J. Exp. Biol.* 220, 2685–2696. <https://doi.org/10.1242/jeb.134585>.
- Poloczanska, E.S., Brown, C.J., Sydeman, W.J., Kiessling, W., Schoeman, D.S., Moore, P. J., Brander, K., Bruno, J.F., Buckley, L.B., Burrows, M.T., Duarte, C.M., Halpern, B.S., Holding, J., Kappel, C.V., O'Connor, M.I., Pandolfi, J.M., Parmesan, C., Schwing, F., Thompson, S.A., Richardson, A.J., 2013. Global imprint of climate change on marine life. *Nat. Climate Chang.* 3, 919–925. <https://doi.org/10.1038/nclimate1958>.
- Poloczanska, E.S., Burrows, M.T., Brown, C.J., García Molinos, J., Halpern, B.S., Hoegh-Guldberg, O., Kappel, C., Moore, P.J., Richardson, A.J., Schoeman, D.S., Sydeman, W.J., 2016. Responses of Marine Organisms to Climate Change across Oceans. *Front. Mar. Sci.* 3 <https://doi.org/10.3389/fmars.2016.00062>.
- Pörtner, H., 2012. Integrating climate-related stressor effects on marine organisms: unifying principles linking molecule to ecosystem-level changes. *Mar. Ecol. Prog. Ser.* 470, 273–290. <https://doi.org/10.3354/meps10123>.
- Pörtner, H.O., Farrell, A.P., 2008. Physiology and climate change. *Science* 322, 690–692. <https://doi.org/10.1126/science.1163156>.
- Pörtner, H.O., Langenbuch, M., Michaelidis, B., 2005. Synergistic effects of temperature extremes, hypoxia, and increases in CO₂ on marine animals: from Earth history to global change. *J. Geophys. Res.* 110, C09S10. <https://doi.org/10.1029/2004JC002561>.
- Pörtner, H.O., Peck, M.A., 2010. Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. *J. Fish. Biol.* 77, 1745–1779. <https://doi.org/10.1111/j.1095-8649.2010.02783.x>.
- R Core Team, 2020. *R: A Language and Environment for Statistical Computing*.
- Rabalais, N.N., 2004. Hypoxia en el Golfo de México. In: *Diagnóstico Ambiental Del Golfo de México*. México, DF, pp. 773–788.
- Robinson, L.M., Elith, J., Hobday, A.J., Pearson, R.G., Kendall, B.E., Possingham, H.P., Richardson, A.J., 2011. Pushing the limits in marine species distribution modelling: lessons from the land present challenges and opportunities. *Global Ecol. Biogeogr.* 20, 789–802. <https://doi.org/10.1111/j.1466-8238.2010.00636.x>.
- Rodríguez-Fuentes, G., Murúa-Castillo, M., Díaz, F., Rosas, C., Caamal-Monsreal, C., Sánchez, A., Paschke, K., Pascual, C., 2017. Ecophysiological biomarkers defining the thermal biology of the Caribbean lobster *Panulirus argus*. *Ecol. Indic.* 78, 192–204. <https://doi.org/10.1016/j.ecolind.2017.03.011>.
- Rosas, C., Gallardo, P., Mascaró, M., Caamal-Monsreal, C., Pascual, C., 2014. *Octopus maya*. In: Iglesias, J., Fuentes, L., Villanueva, R. (Eds.), *Cephalopod Culture*. Springer, pp. 383–396. https://doi.org/10.1007/978-94-017-8648-5_20.
- Ruiz-Castillo, E., Gomez-Valdes, J., Scheinbaum, J., Rioja-Nieto, R., 2016. Wind-driven coastal upwelling and westward circulation in the Yucatan shelf. *Contin. Shelf Res.* 118, 63–76. <https://doi.org/10.1016/j.csr.2016.02.010>.
- Sánchez-García, A., Rodríguez-Fuentes, G., Díaz, F., Galindo-Sánchez, C.E., Ortega, K., Mascaró, M., López, E., Caamal-Monsreal, C., Juárez, O., Noreña-Barroso, E., Re, D., Rosas, C., 2017. Thermal sensitivity of *O. maya* embryos as a tool for monitoring the effects of environmental warming in the Southern of Gulf of Mexico. *Ecol. Indic.* 72, 574–585. <https://doi.org/10.1016/j.ecolind.2016.08.043>.
- Schwalm, C.R., Glendon, S., Duffy, P.B., 2020a. RCP8.5 tracks cumulative CO₂ emissions. *Proc. Natl. Acad. Sci. U. S. A.* 117, 19656–19657. <https://doi.org/10.1073/PNAS.2007117117>.
- Schwalm, C.R., Glendon, S., Duffy, P.B., 2020b. Reply to Hausfather and Peters: RCP8.5 is neither problematic nor misleading. *Proc. Natl. Acad. Sci. U. S. A.* 117, 27793–27794. <https://doi.org/10.1073/pnas.2018008117>.
- Soberón, J., Arroyo-Peña, B., 2017. Are fundamental niches larger than the realized? Testing a 50-year-old prediction by Hutchinson. *PLoS One* 12 (4), 1–14. <https://doi.org/10.1371/journal.pone.0175138>.
- Soberón, J., Peterson, T.A., 2005. Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodivers. Inf.* 2, 1–10. <https://doi.org/10.17161/bi.v2i0.4>.
- Sobrinho, I., Silva, L., Bellido, J.M., Ramos, F., 2002. Rainfall, river discharges and sea temperature as factors affecting abundance of two coastal benthic cephalopod species in the Gulf of Cádiz (SW Spain). *Bull. Mar. Sci.* 71, 851–865.
- Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdaña, Z.A., Finlayson, M., Halpern, B.S., Jorge, M.A., Lombana, A., Lourie, S.A., Martin, K.D., McManus, E., Molnar, J., Recchia, C., Robertson, J., 2007. Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. *Bioscience* 57, 573. <https://doi.org/10.1641/B570707>.
- Strasburg, J.L., Kearney, M., Moritz, C., Templeton, A.R., 2007. Combining phylogeography with distribution modeling: multiple Pleistocene range expansions in a parthenogenetic gecko from the Australian arid zone. *PLoS One* 2. <https://doi.org/10.1371/journal.pone.0000760>.
- Tremblay, N., Mascaró, M., Díaz, F., Caamal-Monsreal, C., Pascual, C., Rosas, C., 2017. Sensibilidad a las oscilaciones térmicas de las especies de importancia ecológica y pesquera de la Península de Yucatán ante escenarios de calentamiento global. In: Garza-Pérez, J., Ize-Lema, I.A. (Eds.), *Caracterización Multidisciplinaria de La Zona Costera de Sisal, Yucatán*. Yucatán, México, pp. 185–198.
- Voss, G.L., Solís-Ramírez, M., 1966. *Octopus maya*, a new species from the Bay of Campeche, Mexico. *Bull. Mar. Sci.* 16, 615–625.
- Warren, D.L., Seifert, S.N., 2011. Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. *Ecol. Appl.* 21, 325–342. <https://doi.org/10.1890/1018-0117.1>.
- Webber, B.L., Yates, C.J., Le Maître, D.C., Scott, J.K., Kriticos, D.J., Ota, N., McNeill, A., Le Roux, J.J., Midgley, G.F., 2011. Modelling horses for novel climate courses: insights from projecting potential distributions of native and alien Australian acacias

- with correlative and mechanistic models. *Divers. Distrib.* 17, 978–1000. <https://doi.org/10.1111/j.1472-4642.2011.00811.x>.
- Wood N., S, 2017. *Generalized Additive Models: An Introduction with R*, 2nd Ed. CRC Press.
- Yañez-Arenas, C., Martínez-Meyer, E., Mandujano, S., Rojas-Soto, O., 2012. Modelling geographic patterns of population density of the white-tailed deer in central Mexico by implementing ecological niche theory. *Oikos* 121, 2081–2089. <https://doi.org/10.1111/j.1600-0706.2012.20350.x>.
- Zavala-Hidalgo, J., Gallegos-García, A., Martínez-López, B., Morey, S.L., O'Brien, J.J., 2006. Seasonal upwelling on the western and southern shelves of the Gulf of Mexico. *Ocean Dynam.* 56, 333–338. <https://doi.org/10.1007/s10236-006-0072-3>.

Capítulo seis - Discusión y conclusiones

6.1 Discusión

Durante la realización de este trabajo, se demostró que la caracterización del nicho ecológico (*sensu* Grinnell) puede ser utilizado como una herramienta útil para el manejo de recursos pesqueros, dado que la relación de centralidad del nicho con la abundancia describe los patrones espacio-temporales de captura de *Octopus maya* (Periodo 2012) (capítulo dos). A través del análisis de las tendencias históricas de captura (1993-2008), los resultados sugieren un incremento a corto plazo en los desembarcos de *O. maya* en la Península de Yucatán (capítulo tres), sin embargo, si se rebasa un umbral de tolerancia fisiológica (temperatura >30 °C) los volúmenes de captura disminuirán. Adicionalmente los resultados obtenidos a partir de los datos fisiológicos, los MC y MM señalan reducciones en la adecuación y distribución de *O. maya* y *O. insularis* en escenarios de CC (capítulo cuatro y cinco) particularmente en los escenarios de calentamiento más fuerte.

La relación obtenida entre la captura por unidad de esfuerzo (CPUE) y su posición con respecto al nicho es consistente con las hipótesis ecológicas derivadas de Maguire, (1973). Maguire (1973) describe el nicho como un elipsoide (con base en estudios fisiológicos – ej. Birch, 1953; Haefner, 1969; Biggs y McDermott, 1973; Blaszkowski y Moreira, 1986; Hooper et al., 2008), estableciendo que diferentes regiones de la estructura del nicho corresponden a diferentes tasas de crecimiento intrínseco (r) de las poblaciones.

De lo anterior, se desarrolló la idea de distancia al centroide del nicho (DCN) como una medición que se relaciona con atributos de la adecuación, como lo es la abundancia. Esta propuesta estipula que en el centro del nicho (en el espacio ambiental) existen las condiciones ambientales óptimas para las poblaciones y, por ende, la adecuación máxima, y conforme se aleja de éste la adecuación y la abundancia disminuyen progresivamente (Escalante y Martínez-Meyer, 2013; Yañez-Arenas et al., 2014; Ureña-Aranda et al., 2015; Martin et al., 2016; Martínez-Gutiérrez et al., 2018; Osorio-Olvera et al., 2020). Con base en los resultados de este trabajo se corroboró que esta

relación existe en *O. maya*. Así también, aportando posibles nuevos paradigmas a estudiar.

Por ejemplo, es interesante notar que en el presente estudio se estableció que los datos de temperatura (2002-2010) y salinidad (1955-2006) obtenidos para intervalos temporales de varios años tuvieron una mayor correlación con las CPUE de *O. maya* que los datos correspondientes a una escala temporal de mayor resolución (mensual). Esto probablemente debido a que los datos de temperatura y salinidad provenientes de periodos largos están mejor correlacionados con las agregaciones periódicas y recurrentes en la región occidental de la Península de Yucatán (Arreguín-Sánchez, 2000; Gamboa-Álvarez et al., 2015; Arreguín-Sánchez, 2019; Arreguín-Sánchez et al., 2019), lo que produce una “fidelidad estacional” fácilmente reconocible a partir de las variaciones de la CPUE, tal estacionalidad se reflejaría en el reclutamiento (Muñiz et al., 2021). Esta fidelidad estacional de la abundancia contrasta con las variaciones mensuales de las capturas, las cuales aparecen como tendencias incompletas de la CPUE.

Este tipo de relación podría ser el caso particular de una especie bentónica con una capacidad de dispersión baja como *O. maya*. Sin embargo, posible la asociación entre las fechas de presencia y los datos ambientales en especies de alta movilidad (ej., especies nectónicas) pueda ser diferente (Ingenloff y Peterson, 2021; Torrejon-Magallanes et al., 2021), particularmente considerando que los organismos marinos pueden responder rápidamente a los cambios ambientales (Pinsky et al., 2013), lo que se reflejaría en una relación más estrecha entre los cambios mensuales de condiciones ambientales y la captura.

Otro factor importante es la relación entre la heterogeneidad ambiental y la distribución de la población de *O. maya* en la plataforma de Yucatán. Se ha observado que los juveniles tienden a agregarse en temperaturas mayores de 25 °C en la región occidental durante agosto a octubre en la plataforma yucateca (Gamboa-Álvarez et al., 2015), donde existen florecimientos de productividad primaria (Arreguín-Sánchez y

Chávez, 1995; Arreguín-Sánchez, 2019; Arreguín-Sánchez et al., 2019), un predictor no considerado en este estudio. Aunque no existe un estudio ecológico detallado que considere los florecimientos de productividad primaria, se ha especulado que este favorece la madurez de los pulpos por vía del enriquecimiento de las redes tróficas asociadas con la abundancia de nutrientes (Arreguín-Sánchez, 2000, 2019; Arreguín-Sánchez et al., 2019).

En contraste, durante noviembre y diciembre, los vientos procedentes del norte provocan que el ambiente costero se homogenice, por lo que los adultos, con preferencias por temperaturas más bajas (24 °C), presentan abundancias mayores en la plataforma de Yucatán, particularmente en zonas cercanas a la costa donde las hembras adultas desovan (Angeles-Gonzalez et al., 2017). Bajo tales circunstancias, la relación DCN-abundancia disminuye, indicando que es altamente sensible a la heterogeneidad ambiental (Figura 6).

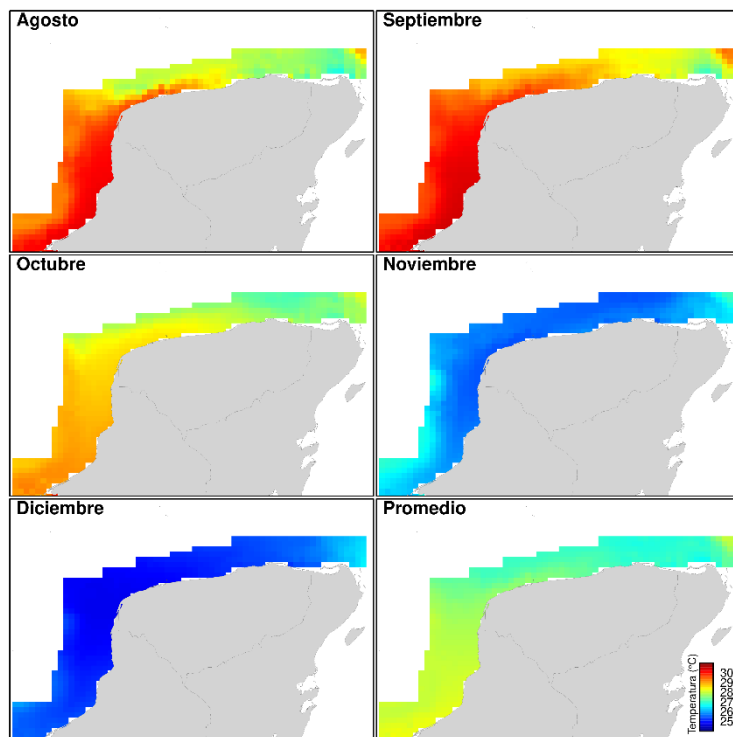


Figura 6. La temperatura de la superficie del mar de la plataforma de Yucatán para la temporada de pesca de pulpo. Los datos ambientales se obtuvieron del producto GLORYS12V1 del Servicio de Monitoreo del Medio Marino de Copernicus (<https://www.copernicus.eu/>). La resolución es de ~ 9 km² por píxel.

Dado que las preferencias en condiciones ambientales cambian durante el ciclo de vida (Carr et al., 2003; Pörtner y Farrell, 2008; Robinson et al., 2011; Tremblay et al., 2017), los cambios ontogénicos deben tener un efecto en la relación DCN-abundancia. En la teoría del nicho desarrollada parte de la idea de Maguire, (1973) se ha sugerido que el nicho en realidad es una estructura que cambia en función de la ontogenia de las especies modificando las tasas de crecimiento, los hábitos alimenticios y la condición reproductiva (Pörtner y Farrell, 2008; Soberón y Peterson, 2020) (Figura 7).

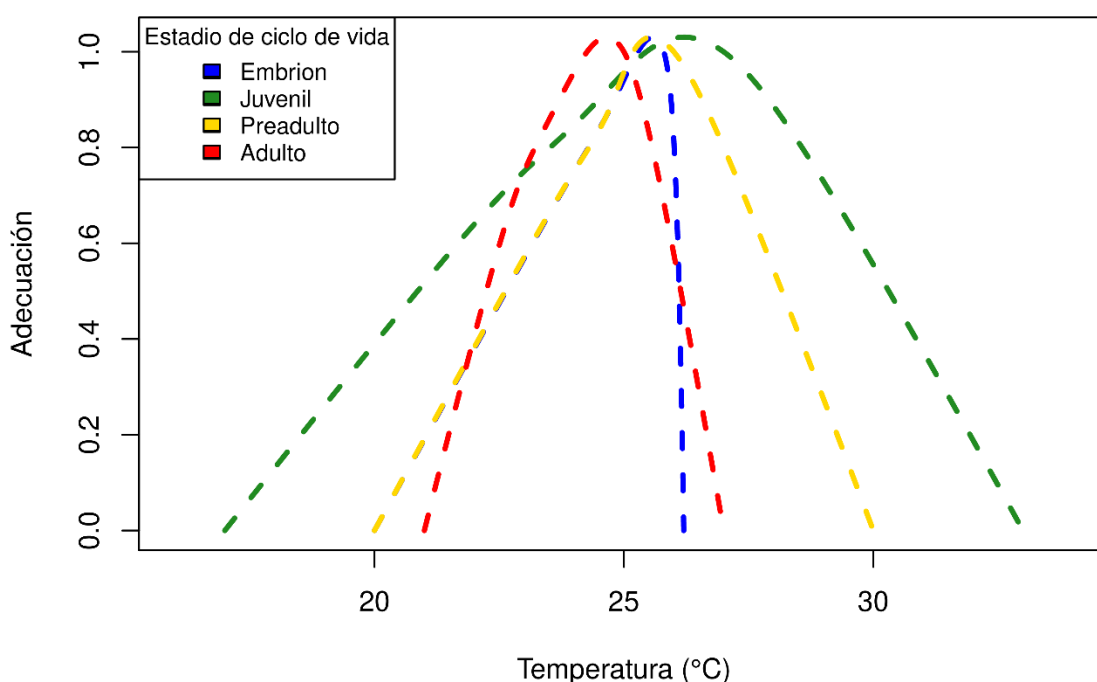


Figura 7. Ventana térmica de *Octopus maya* a lo largo de su ciclo de vida. Los embriones (Caamal-Monsreal et al., 2016), juveniles, preadultos (Noyola, Caamal-Monsreal, et al., 2013; Noyola, Mascaró, et al., 2013) y adultos (Juárez et al., 2015, 2016) fueron aclimatados a temperaturas de 18, 22, 26, 30 °C. En los embriones las curvas de respuesta indican en las temperaturas en las que estos se desarrollan en un tiempo menor al que sobreviviría una hembra durante el cuidado parental. En los juveniles los intervalos indican las temperaturas preferidas. En los pre adultos y adultos corresponden a las temperaturas en la que los organismos desovan. Estos rangos de tolerancia térmica pueden interactuar con otras variables como oxígeno disuelto, CO₂ o productividad primaria modificando las preferencias térmicas (Pörtner et al., 2005; Angilletta, 2009), aunque actualmente se desconoce el efecto de estas variables en *O. maya*. La figura se encuentra basada en el trabajo de Tremblay et al., (2017).

Los datos de embriones de *O. maya* proporcionan evidencia de la importancia en estos cambios ontogénicos y en la estacionalidad al delimitar distribuciones. En Campeche las temperaturas máximas superan el umbral térmico de embriones de *O. maya* (28 °C); sin embargo, el evento reproductivo es muy estacional ocurriendo principalmente en invierno (Markaida et al., 2016; Angeles-Gonzalez et al., 2017) cuando las temperaturas más bajas (< 25 °C) permiten desoves y eclosiones exitosos (Juárez et al., 2015; Caamal-Monsreal et al., 2016). Lo anterior muestra que especies de ciclos de vida anual, como el *O. maya*, tienen nichos no convexos, particularmente en ambientes estacionales (Soberón y Peterson, 2020), por lo que, para el caso particular de los embriones, considerar la estacionalidad podría ser útil para delimitar distribuciones dinámicas (Ingenloff, 2017; Ingenloff y Peterson, 2021).

Los efectos en la plasticidad fenotípica de los organismos (Angilletta, 2009; Semsar-kazerouni y Verberk, 2018) y en la alimentación (Angilletta, 2009; Semsar-kazerouni et al., 2020) no suelen ser considerados en los modelos de nicho (Soberón y Nakamura, 2009; Peterson et al., 2011), probablemente debido a la dificultad de obtener información confiable sobre todo de las poblaciones silvestres, por lo que abre la oportunidad a desarrollar trabajos futuros que exploren la forma en la que el nicho es modulado por estos elementos.

Los cambios de condiciones ambientales se reflejan no solo en la distribución espacio-temporal de las especies, sino también en los registros de capturas comerciales (Simpson et al., 2011; Cheung et al., 2013; Doubleday et al., 2016). Con base en los resultados obtenidos, es posible proponer que el aumento en el rendimiento de la pesca de *O. maya* reportado (Salas et al., 2006; DOF, 2014, 2018; Arreguín-Sánchez, 2019) se debe a un incremento en la adecuación de la especie como resultado al aumento de la temperatura. En estudios realizados en otras especies de cefalópodos se ha observado un fenómeno similar (Doubleday et al., 2016; Lopes et al., 2021). Por ejemplo, en series de tiempo de *O. insularis* en Brasil, las capturas incrementaron a medida que aumentó la temperatura superficial del mar, reportándose mayores

descargas a 28 °C (Lopes et al., 2021), lo cual corresponde a sus preferencias fisiológicas. Considerando que *O. insularis* tiene una adecuación óptima a temperaturas más altas (~28 °C) que *O. maya* (~24 °C en adultos y embriones), esta especie se verá menos afectada por el CC. Incluso podría desplazar al *O. maya* alcanzando abundancias que le permitan convertirse en una pesquería potencial (Lima et al., 2020). No obstante, si los umbrales del NF son superados, el rendimiento pesquero disminuirá (Cheung et al., 2013; Doubleday et al., 2016).

Los efectos que el CC tendrá en los recursos pesqueros siempre estarán sujetos a un nivel de incertidumbre intrínseca debido a las metodologías asociadas a la selección de modelos o a su parametrización (Peterson et al., 2015, 2018; Qiao et al., 2015; Cobos et al., 2019). Con la finalidad de mitigar el margen de incertidumbre en los resultados obtenidos de los MC y MM, estos fueron integrados en el capítulo cinco del presente estudio (Kearney y Porter, 2009; Kearney et al., 2010; Kumar et al., 2014; Peterson et al., 2015; Meineri et al., 2015).

En ese sentido, los datos fisiológicos utilizados en los MM y MC indican que el CC provocará una contracción en las condiciones favorables de *O. maya* en el Golfo de México, lo que se verá reflejado en un cambio de distribución potencial. Dado que en el presente estudio se asume que existe una relación entre la abundancia y el nicho (Osorio-Olvera et al., 2016; Osorio-Olvera et al., 2020), los resultados sugieren que los desembarques en la región de *O. maya* disminuirán dado que este pulpo se podría refugiar en aguas más profundas. No obstante, las corrientes frías procedentes de la surgencia estacional en la región norte de la plataforma continental adyacente a Yucatán permiten suponer que mientras esa surgencia permanezca, la zona norte tenderá a ser térmicamente más favorable indicando que las capturas podrían ser más estables en esa región (Angeles-Gonzalez et al., 2017).

El hecho de que la especie pudiera migrar de lugares que ha sido históricamente accesible indica la necesidad de desarrollar planes de manejo que permitan la reorganización de la pesca en escenarios futuros teniendo en cuenta los posibles

cambios de abundancia. Esto es especialmente importante ya que estudios previos (Arreguín-Sánchez, 2019; Arreguín-Sánchez et al., 2019) y regulaciones mexicanas (DOF, 2014) suponen que los pulpos, y en particular el *O. maya*, se beneficiará con el CC, lo cual, acorde a esta y otras investigaciones (Noyola, Mascaró, et al., 2013; Juárez et al., 2015, 2016; Caamal-Monsreal et al., 2016; López-Galindo et al., 2019; Pascual et al., 2019), no podría ocurrir.

Desafortunadamente, con los datos fisiológicos de *O. americanus* no fue posible realizar inferencias en su distribución. Esto podría estar relacionado con diferencias entre el ecosistema de la Península de Yucatán y las poblaciones de Florianópolis, Brasil (región de donde provienen los datos). Las poblaciones de Florianópolis pertenecen a regiones templadas de América del Sur (Spalding et al., 2007), mientras que las presencias registradas por Avendaño et al. (2019) se encuentran en el Atlántico Tropical (Spalding et al., 2007). Tal aislamiento bajo diferentes regímenes térmicos generaría fenotipos con mayor adecuación en su entorno nativo (Angilletta et al., 2002; Angilletta, 2009).

Se destaca que los resultados en la relación DCN-abundancia y los MC y MM difieren en la delimitación de la región geográfica más favorable en la Península de Yucatán. La diferencia en estos resultados probablemente depende del sesgo asociado a la calibración de los modelos. En la relación DCN-abundancia, se modeló un proceso de reclutamiento ocasionado por un incremento en la productividad, en tanto que en el MC, el proceso de filtrado (una presencia por pixel) redujo este efecto de reclutamiento, caracterizando principalmente un nicho “térmico” que corresponde con los resultados del MM. Aceptando la conjetura de que estos análisis son representaciones de la adecuación de la especie, algunas preguntas podrían ser planteadas: (1) ¿Cuáles son las dimensiones (variables) del NF que se relacionan fuertemente con la adecuación? (2) ¿Qué proceso ecológico intentamos representar (un proceso de reclutamiento, reproducción o supervivencia)? Está claro que

dependerá del objetivo de la investigación y es un elemento a considerar durante el desarrollo de los análisis, particularmente para monitorear un recurso pesquero.

A pesar de que el enfoque integrativo para la evaluación y monitoreo de recursos pesquero es prometedor, trabajos posteriores podrían dilucidar más a fondo algunas de las incógnitas observadas durante este estudio. Por ejemplo, aunque los cambios en la composición pesquera están asociados a procesos como el calentamiento global (Simpson et al., 2011; Cheung et al., 2013; Doubleday et al., 2016), no existen otras comparaciones directas entre el estado fisiológico de las poblaciones y las capturas históricas. Si efectivamente las relaciones descritas en el presente trabajo son encontradas para otras especies, el marco teórico aquí propuesto podría ser una herramienta poderosa de monitoreo para recursos pesqueros.

Finalmente, es necesario desarrollar modelos que nos permitan evaluar el ciclo de vida completo de las especies y vincularlo a las variables ambientales (Klockmann et al., 2017). Por ejemplo, existe un fuerte cambio en las ventanas térmicas en *O. maya* durante su desarrollo ontogénico (Tremblay et al., 2017); la utilización de matrices que consideren preferencias térmicas a lo largo del nicho ontogénico podrían ser una metodología que resuelva esta problemática (Osorio-Olvera et al., 2016), especialmente porque permitiría un monitoreo dinámico de recursos (al considerar la estacionalidad) o separar la modelación por estadio de vida y procesos ecológicos, estimando los nichos de las especies con mayor detalle.

6.2 Conclusiones

Este trabajo buscó evaluar la capacidad de la teoría del nicho ecológico como herramienta para el manejo pesquero, particularmente con el interés de comprender el efecto potencial del CC en las pesquerías de pulpo del sur del Golfo de México, una zona identificada como vulnerable. Las conclusiones de esta tesis son las siguientes:

- Existe una correlación negativa entre la CPUE y la DCN, lo que sugiere que la modelación de la estructura interna del nicho ecológico puede ser utilizada como una herramienta de monitoreo en las capturas.
- Los resultados muestran que el incremento histórico de capturas de *O. maya* reportado en los anuarios estadísticos se ha debido al aumento en su adecuación en su región de pesca, como consecuencia del aumento de la temperatura del mar. Lo anterior sugiere que, una vez que se supere un umbral de tolerancia, las capturas podrían disminuir.
- Para la especie *O. maya*, los datos fisiológicos de embriones muestran que el CC tendrá un impacto negativo en las poblaciones de la Península de Yucatán. El pulpo *O. insularis*, al ser una especie adaptada a mayores temperaturas, es más tolerante a los escenarios de CC; sin embargo, si el calentamiento rebasa su límite de tolerancia térmica (~33 °C) esta especie también se vería afectada negativamente.
- Los MC y MM indicaron una disminución de la adecuación en la Península de Yucatán para *O. maya*. Adicionalmente los modelos mecanísticos sugieren la posibilidad de que el *O. maya* se refugie en aguas más profundas.

6.3 Literatura citada

- Angeles-Gonzalez, L. E., Calva, R., Santos-Valencia, J., Avila-Poveda, O. H., Olivares, A., Diaz, F., y Rosas, C. (2017). Temperature modulates spatio-temporal variability of the functional reproductive maturation of *Octopus maya* (Cephalopoda) on the shelf of the Yucatan Peninsula, Mexico. *Journal of Molluscan Studies*, 83(3), 280–288. <https://doi.org/10.1093/mollus/eyx013>
- Angilletta, M. J. (2009). *Thermal Adaptation A Theoretical and Empirical Synthesis* (M. J. Angilletta (ed.)). Oxford University Press.
- Angilletta, M. J., Niewiarowski, P., y Navas, C. A. (2002). The Evolution of Thermal Physiology in Ectotherms. *Journal of Thermal Biology*, 27, 249–268.
- Arreguín-Sánchez, F. (2000). Octopus-red grouper interaction in the exploited ecosystem of the northern continental shelf of Yucatan, Mexico. *Ecological Modelling*, 129, 119–129. [https://doi.org/10.1016/S0304-3800\(00\)00218-0](https://doi.org/10.1016/S0304-3800(00)00218-0)
- Arreguín-Sánchez, F. (2019). Climate change and the rise of the octopus fishery in the Campeche Bank, México. *Regional Studies in Marine Science*, 32.

<https://doi.org/10.1016/j.rsma.2019.100852>

- Arreguín-Sánchez, F., Albaladejo-Lucero, M. O., Del Monte-Luna, P., y Zetina-Rejón, M. J. (2019). Fishery Resource Management Challenges Facing Climate Change. In A. Ibáñez (Ed.), *Mexican Aquatic Environments* (1st ed., pp. 181–194). Springer, Cham. <https://doi.org/10.1007/978-3-030-11126-7>
- Arreguín-Sánchez, F., y Chávez, E. A. (1995). How marine shelf fisheries are depending of mangrove ecosystems: the Campeche Bank, Mexico, an example. In A. Yáñez-Arancibia y A. Lara-Domínguez (Eds.), *Valoración económica de los manglares*. Universidad Autónoma de Campeche.
- Avendaño, O., Velázquez–Abunader, I., Fernández–Jardón, C., Ángeles–González, L. E., Hernández-Flores, A., y Guerra, Á. (2019). Biomass and distribution of the red octopus (*Octopus maya*) in the north-east of the Campeche Bank. *Journal of the Marine Biological Association of the United Kingdom*, 99(6), 1317–1323. <https://doi.org/10.1017/S0025315419000419>
- Biggs, D. C., y McDermott, J. J. (1973). Variation in Temperature-Salinity Tolerance Between Two Estuarine Populations of *Pagurus Longicarpus* Say (Crustacea: Anomura). *The Biological Bulletin*, 145(1), 91–102. <https://doi.org/10.2307/1540350>
- Birch, L. C. (1953). Experimental Background to the Study of the Distribution and Abundance of Insects: I. The Influence of Temperature, Moisture and Food on the Innate Capacity for Increase of Three Grain Beetles. *Ecology*, 34(4), 698–711. <https://doi.org/10.2307/1931333>
- Blaszkowski, C., y Moreira, G. S. (1986). Combined effects of temperature and salinity on the survival and duration of larval stages of *Pagurus criniticornis* (Dana) (Crustacea, Paguridae). *Journal of Experimental Marine Biology and Ecology*, 103, 77–86. [https://doi.org/10.1016/0022-0981\(86\)90133-4](https://doi.org/10.1016/0022-0981(86)90133-4)
- Caamal-Monsreal, C., Uriarte, I., Farias, A., Díaz, F., Sánchez, A., Re, D., y Rosas, C. (2016). Effects of temperature on embryo development and metabolism of *O. maya*. *Aquaculture*, 451, 156–162. <https://doi.org/10.1016/j.aquaculture.2015.09.011>
- Carr, M. H., Neigel, J. E., Estes, J. A., Andelman, S., Warner, R. R., y Largier, J. L. (2003). Comparing Marine and Terrestrial Ecosystems: Implications for the Design of Coastal Marine Reserves. *Ecological Applications*, 13(1), 90–107. [https://doi.org/10.1890/1051-0761\(2003\)013\[0090:CMATEI\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2003)013[0090:CMATEI]2.0.CO;2)
- Cheung, W. W. L., Watson, R., y Pauly, D. (2013). Signature of ocean warming in global fisheries catch. *Nature*, 497(7449), 365–368. <https://doi.org/10.1038/nature12156>
- Cobos, M. E., Osorio-Olvera, L., y Peterson, A. T. (2019). Assessment and representation of variability in ecological niche model predictions. *BioRxiv*, April. <https://doi.org/10.1101/603100>
- DOF. (2014). *ACUERDO por el que se da a conocer el Plan de Manejo Pesquero de pulpo (O. maya y O. vulgaris) del Golfo de México y Mar Caribe*. http://dof.gob.mx/nota_detalle_popup.php?codigo=5338727
- DOF. (2018). *Carta Nacional Pesquera*. http://www.dof.gob.mx/nota_detalle.php?codigo=5525712yfecha=11/06/2018yprintr=true
- Doubleday, Z. A., Prowse, T. A. A., Arkhipkin, A., Pierce, G. J., Semmens, J., Steer, M., Leporati, S. C., Lourenço, S., Quetglas, A., Sauer, W., y Gillanders, B. M.

- (2016). Global proliferation of cephalopods. *Current Biology*, 26(10), R406–R407. <https://doi.org/10.1016/j.cub.2016.04.002>
- Escalante, T., y Martínez-Meyer, E. (2013). Ecological Niche Modeling and Wildlife Management Units (UMAS): An Application to Deer in Campeche, México. *Tropical and Subtropical Agroecosystems*, 16, 183–191.
- Gamboa-Álvarez, M. Á., López-Rocha, J. A., y Poot-López, G. R. (2015). Spatial Analysis of the Abundance and Catchability of the Red Octopus *Octopus maya* (Voss and Solís-Ramírez, 1966) on the Continental Shelf of the Yucatan Peninsula, Mexico. *Journal of Shellfish Research*, 34(2), 481–492. <https://doi.org/10.2983/035.034.0232>
- Haefner, P. A. (1969). Temperature and salinity tolerance of the sand shrimp, *Crangon septemspinosa* Say. *Physiological Zoology*, 42(4), 388–397. <https://doi.org/https://doi.org/10.1086/physzool.42.4.30155510>
- Hooper, H. L., Connon, R., Callaghan, A., Fryer, G., Yarwood-Buchanan, S., Biggs, J., Maund, S. J., Hutchinson, T. H., y Sibly, R. M. (2008). The ecological niche of *Daphnia magna* characterized using population growth rate. *Ecology*, 89(4), 1015–1022. <https://doi.org/10.1890/07-0559.1>
- Ingenloff, K. (2017). Biologically informed ecological niche models for an example pelagic, highly mobile species. *European Journal of Ecology*, 3(1), 55–75. <https://doi.org/10.1515/eje-2017-0006>
- Ingenloff, K., y Peterson, A. T. (2021). Incorporating time into the traditional correlational distributional modelling framework: A proof-of-concept using the Wood Thrush *Hylocichla mustelina*. *Methods in Ecology and Evolution*, 12(2), 311–321. <https://doi.org/10.1111/2041-210X.13523>
- Juárez, O. E., Galindo-Sánchez, C. E., Díaz, F., Re, D., Sánchez-García, A. M., Camaal-Monsreal, C., y Rosas, C. (2015). Is temperature conditioning *Octopus maya* fitness? *Journal of Experimental Marine Biology and Ecology*, 467, 71–76. <https://doi.org/10.1016/j.jembe.2015.02.020>
- Juárez, O. E., Hau, V., Caamal-Monsreal, C., Galindo-Sánchez, C. E., Díaz, F., Re, D., y Rosas, C. (2016). Effect of maternal temperature stress before spawning over the energetic balance of *Octopus maya* juveniles exposed to a gradual temperature change. *Journal of Experimental Marine Biology and Ecology*, 474, 39–45. <https://doi.org/10.1016/j.jembe.2015.10.002>
- Kearney, M., y Porter, W. (2009). Mechanistic niche modelling: Combining physiological and spatial data to predict species' ranges. *Ecology Letters*, 12(4), 334–350. <https://doi.org/10.1111/j.1461-0248.2008.01277.x>
- Kearney, M. R., Wintle, B. A., y Porter, W. P. (2010). Correlative and mechanistic models of species distribution provide congruent forecasts under climate change. *Conservation Letters*, 3(3), 203–213. <https://doi.org/10.1111/j.1755-263X.2010.00097.x>
- Klockmann, M., Günter, F., y Fischer, K. (2017). Heat resistance throughout ontogeny: body size constrains thermal tolerance. *Global Change Biology*, 23(2), 686–696. <https://doi.org/10.1111/gcb.13407>
- Kumar, S., Neven, L. G., y Yee, W. L. (2014). Evaluating correlative and mechanistic niche models for assessing the risk of pest establishment. *Ecosphere*, 5(7). <https://doi.org/10.1890/ES14-00050.1>
- Lima, F., Ángeles-González, L., Leite, T., y Lima, S. (2020). Global climate changes over time shape the environmental niche distribution of *Octopus insularis* in the

- Atlantic Ocean. *Marine Ecology Progress Series*, 652, 111–121. <https://doi.org/10.3354/meps13486>
- Lopes, P. F. M., Andrade, L. C. A., Pennino, M. G., y Leite, T. S. (2021). The inter-annual fishing variability in *Octopus insularis* (Leite y Haimovici 2008) as a result of oceanographic factors. *Fisheries Oceanography*, 30(5), 515–526. <https://doi.org/10.1111/fog.12534>
- López-Galindo, L., Galindo-Sánchez, C., Olivares, A., Avila-Poveda, O. H., Díaz, F., Juárez, O. E., Lafarga, F., Pantoja-Pérez, J., Caamal-Monsreal, C., y Rosas, C. (2019). Reproductive performance of *Octopus maya* males conditioned by thermal stress. *Ecological Indicators*, 96, 437–447. <https://doi.org/10.1016/j.ecolind.2018.09.036>
- Maguire, B. J. (1973). Niche Response Structure and the Analytical Potentials of Its Relationship to the Habitat. *The American Naturalist*, 107(954), 213–246. <https://doi.org/10.1086/282827>
- Markaida, U., Méndez-Loeza, I., y Rosales-Raya, M. L. (2016). Seasonal and spatial trends of Mayan octopus, *Octopus maya*, population dynamics from Campeche, Mexico. *Journal of the Marine Biological Association of the United Kingdom*, 97(8), 1663–1673. <https://doi.org/10.1017/S0025315416001132>
- Martin, G. A., Yanez-Arenas, C., Roberts, B. J., Chen, C., Plowright, R. K., Webb, R. J., y Skerratt, L. F. (2016). Climatic suitability influences species specific abundance patterns of Australian flying foxes and risk of Hendra virus spillover. *One Health*, 2, 115–121. <https://doi.org/10.1016/j.onehlt.2016.07.004>
- Martínez-Gutiérrez, P. G., Martínez-Meyer, E., Palomares, F., y Fernández, N. (2018). Niche centrality and human influence predict rangewide variation in population abundance of a widespread mammal: The collared peccary (*Pecari tajacu*). *Diversity and Distributions*, 24(1), 103–115. <https://doi.org/10.1111/ddi.12662>
- Meineri, E., Deville, A. S., Grémillet, D., Gauthier-Clerc, M., y Béchet, A. (2015). Combining correlative and mechanistic habitat suitability models to improve ecological compensation. *Biological Reviews*, 90(1), 314–329. <https://doi.org/10.1111/brv.12111>
- Muñiz, C., McQuaid, C. D., & Weidberg, N. (2021). Seasonality of primary productivity affects coastal species more than its magnitude. *Science of the Total Environment*, 757, 143740. <https://doi.org/10.1016/j.scitotenv.2020.143740>
- Noyola, J., Caamal-Monsreal, C., Díaz, F., Re, D., Sánchez, A., y Rosas, C. (2013). Thermopreference, tolerance and metabolic rate of early stages juvenile *Octopus maya* acclimated to different temperatures. *Journal of Thermal Biology*, 38(1), 14–19. <https://doi.org/10.1016/j.jtherbio.2012.09.001>
- Noyola, J., Mascaró, M., Caamal-Monsreal, C., Noreña-Barroso, E., Díaz, F., Re, D., Sánchez, A., y Rosas, C. (2013). Effect of temperature on energetic balance and fatty acid composition of early juveniles of *Octopus maya*. *Journal of Experimental Marine Biology and Ecology*, 445, 156–165. <https://doi.org/10.1016/j.jembe.2013.04.008>
- Osorio-Olvera, L. A., Falconi, M., y Soberón, J. (2016). Sobre la relación entre idoneidad del hábitat y la abundancia poblacional bajo diferentes escenarios de dispersión. *Revista Mexicana de Biodiversidad*, 87(3), 1080–1088. <https://doi.org/10.1016/j.rmb.2016.07.001>
- Osorio-Olvera, L., Yañez-Arenas, C., Martínez-Meyer, E., y Peterson, A. T. (2020). Relationships between population densities and niche-centroid distances in North American birds. *Ecology Letters*, 23(3), 555–564.

<https://doi.org/10.1111/ele.13453>

- Pascual, C., Mascaro, M., Rodríguez-Canul, R., Gallardo, P., Sánchez, A. A., Rosas, C., y Cruz-López, H. (2019). Sea surface temperature modulates physiological and immunological condition of octopus maya. *Frontiers in Physiology*, 10(JUN), 1–11. <https://doi.org/10.3389/fphys.2019.00739>
- Peterson, A. T., Cobos, M. E., y Jiménez-García, D. (2018). Major challenges for correlational ecological niche model projections to future climate conditions. *Annals of the New York Academy of Sciences*, 1429(1), 66–77. <https://doi.org/10.1111/nyas.13873>
- Peterson, A. T., Papeş, M., y Soberón, J. (2015). Mechanistic and correlative models of ecological niches. *European Journal of Ecology*, 1(2), 28–38. <https://doi.org/10.1515/eje-2015-0014>
- Peterson, T. A., Soberón, J., Pearson, R. G., Anderson, R. P., Martínez-Meyer, E., Nakamura, M., y Araújo, M. B. (2011). Ecological niches and geographic distributions. In *Choice Reviews Online*. Princeton University Press.
- Pinsky, M. L., Worm, B., Fogarty, M. J., Sarmiento, J. L., y Levin, S. A. (2013). Marine Taxa Track Local Climate Velocities. *Science*, 341, 1239–1242.
- Pörtner, H. O., y Farrell, A. P. (2008). Physiology and Climate Change. *Science*, 322(5902), 690–692. <https://doi.org/10.1126/science.1163156>
- Pörtner, H. O., Langenbuch, M., y Michaelidis, B. (2005). Synergistic effects of temperature extremes, hypoxia, and increases in CO₂ on marine animals: From Earth history to global change. *Journal of Geophysical Research*, 110(C9), C09S10. <https://doi.org/10.1029/2004JC002561>
- Qiao, H., Soberón, J., y Peterson, A. T. (2015). No silver bullets in correlative ecological niche modelling: Insights from testing among many potential algorithms for niche estimation. *Methods in Ecology and Evolution*, 6(10), 1126–1136. <https://doi.org/10.1111/2041-210X.12397>
- Robinson, L. M., Elith, J., Hobday, A. J., Pearson, R. G., Kendall, B. E., Possingham, H. P., y Richardson, A. J. (2011). Pushing the limits in marine species distribution modelling: Lessons from the land present challenges and opportunities. *Global Ecology and Biogeography*, 20(6), 789–802. <https://doi.org/10.1111/j.1466-8238.2010.00636.x>
- Salas, S., Mexicano-Cintora, G., y Cabrera, M. A. (2006). *¿Hacia dónde van las pesquerías en Yucatán? Tendencias, Retos y Perspectivas*. CINVESTAV.
- Semsar-kazerouni, M., Boerrigter, J. G. J., y Verberk, W. C. E. P. (2020). Changes in heat stress tolerance in a freshwater amphipod following starvation: The role of oxygen availability, metabolic rate, heat shock proteins and energy reserves. *Comparative Biochemistry and Physiology -Part A: Molecular and Integrative Physiology*, 245(April), 110697. <https://doi.org/10.1016/j.cbpa.2020.110697>
- Semsar-kazerouni, M., y Verberk, W. C. E. P. (2018). It's about time: Linkages between heat tolerance, thermal acclimation and metabolic rate at different temporal scales in the freshwater amphipod *Gammarus fossarum* Koch, 1836. *Journal of Thermal Biology*, 75(May), 31–37. <https://doi.org/10.1016/j.jtherbio.2018.04.016>
- Simpson, S. D., Jennings, S., Johnson, M. P., Blanchard, J. L., Schön, P. J., Sims, D. W., y Genner, M. J. (2011). Continental shelf-wide response of a fish assemblage to rapid warming of the sea. *Current Biology*, 21(18), 1565–1570. <https://doi.org/10.1016/j.cub.2011.08.016>

- Soberón, J., y Arroyo-Peña, B. (2017). Are fundamental niches larger than the realized? Testing a 50-year-old prediction by Hutchinson. *PLoS ONE*, 12(4), 1–14. <https://doi.org/10.1371/journal.pone.0175138>
- Soberón, J., y Nakamura, M. (2009). Niches and distributional areas: Concepts, methods, and assumptions. *Analytica Chimica Acta*, 106, 19644–19650. <https://doi.org/10.1073/pnas.0901637106>
- Soberón, J., y Peterson, A. T. (2020). What is the shape of the fundamental Grinnellian niche? *Theoretical Ecology*, 13(1), 105–115. <https://doi.org/10.1007/s12080-019-0432-5>
- Soberón, J., y Peterson, T. A. (2005). Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodiversity Informatics*, 2, 1–10. <https://doi.org/10.17161/bi.v2i0.4>
- Spalding, M. D., Fox, H. E., Allen, G. R., Davidson, N., Ferdaña, Z. A., Finlayson, M., Halpern, B. S., Jorge, M. A., Lombana, A., Lourie, S. A., Martin, K. D., McManus, E., Molnar, J., Recchia, C., y Robertson, J. (2007). Marine Ecoregions of the World: A Bioregionalization of Coastal and Shelf Areas. *BioScience*, 57(7), 573. <https://doi.org/10.1641/B570707>
- Torrejón-Magallanes, J., Ángeles-González, L. E., Csirke, J., Bouchon, M., Morales-Bojórquez, E., & Arreguín-Sánchez, F. (2021). Modeling the Pacific chub mackerel (*Scomber japonicus*) ecological niche and future scenarios in the northern Peruvian Current System. *Progress in Oceanography*, August, 102672. <https://doi.org/10.1016/j.pocean.2021.102672>
- Tremblay, N., Mascaró, M., Díaz, F., Caamal-Monsreal, C., Pascual, C., y Rosas, C. (2017). Sensibilidad a las oscilaciones térmicas de las especies de importancia ecológica y pesquera de la Península de Yucatán ante escenarios de calentamiento global. In J. . Garza-Pérez y I. A. . Ize-Lema (Eds.), *Caracterización Multidisciplinaria de la Zona Costera de Sisal, Yucatán* (pp. 185–198).
- Ureña-Aranda, C. A., Rojas-Soto, O., Martínez-Meyer, E., Yáñez-Arenas, C., Ramírez, R. L., y De Los Monteros, A. E. (2015). Using range-wide abundance modeling to identify key conservation areas for the micro-endemic Bolson tortoise (*Gopherus flavomarginatus*). *PLoS ONE*, 10(6). <https://doi.org/10.1371/journal.pone.0131452>
- Yáñez-Arenas, C., Mandujano, S., y Martínez-Meyer, E. (2014). Predicting the density and abundance of white-tailed deer based on ecological niche theory. *Deer Specialist Group IUCN Newsletter*, 26, 20–30.